Monocular depth cues which are hypothesized to be operative in the Ponzo illusion and in size constancy are acquired through experience (*6*). If this is so, differential experience with such cues should influence magnitudes of the illusion (*7*). The Guam students were of the same age and educational level as the Pennsylvania subjects, but they had spent their entire lives on the island of Guam where the terrain is markedly different from that of central Pennsylvania. There are no railroads on the island, vistas on land are short due to hilly terrain covered by tropical plant growth, and such individuals do not normally view the kind of environments typified by the photographs used in this study. The Guamanians do not show the effects of context provided by the photographic stimuli that the Pennsylvania students do (Fig. 2). The illusory effect for the geometric figure and the two photographs is essentially the same, the function tending to resemble, at a significantly higher level ($F = 15.6$, d.f. $= 1$ for 42 subjects, $P < .01$), the data from Pennsylvania subjects viewing inverted stimuli. The data from island subjects are also different from that of the Pennsylvania subjects viewing upright stimuli ($F = 4.4$, d.f. $= 1$ for 42 subjects, $P < .05$).

The Ponzo illusion is apparently one manifestation of the general process by which observers compensate for the diminished retinal image size of more distant objects. In actual viewing conditions, size is signaled by a number of cues in addition to stereopsis which may include perspective as well as other monocular cues such as the position of the object in the visual field. Thus, it seems that the more cues available, the larger the magnitude of the overestimation or illusion. With the classic or geometric Ponzo figure, an illusion of 10 percent, which is only a fraction of the real-life effect, is observed in support of the hypothesis that the two-dimensional illusion is a special case representing the operation of only one of the many cues available in three-dimensional space. The influence of familiarity is illustrated by rotation of the figures which essentially eliminates the effectiveness of the additional cues provided by the full-tone photographs, but it has only a slight effect on the abstract geometric figure (*8*). The role of previous experience as a factor in determining the utilization of these cues is emphasized by their reduced influence among a group of subjects reared in a different physical setting. Finally, the study of complex cues and cross-cultural effects as factors in the perspective illusion is facilitated by the use of photographs. Such stimuli are more sensitive to manipulation of those variables of experience upon which the illusion is assumed to be based.

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References and Notes

1. R. Tausch, *Psychol. Forsch.* **24**, 299 (1954); E. V. Holst, *Studium Gen.* **10**, 231 (1957); R. L. Gregory, *Eye and Brain* (World Univ. Library, New York, 1966), p. 145.
2. The photographs were taken with a 90-mm lens on film (5.7 by 7.0 cm) enlarged six times and viewed at a distance of 61 cm. In the real scene, the board was 182.9 by 10.2 cm and located 18.29 m from the subject. The length of the variable boards ranged from 61 to 152.4 cm in increments of 10.2 cm, were 5.1 cm wide, and located 914.1 cm from the subject.
3. The instructions given in the natural setting in effect required the subjects to judge which board subtended the larger visual angle, that is, retinal instructions. The subjects who viewed photographs of the scene (Fig. 1, B and C) and the line figures (Fig. 1, A and D) were asked to indicate verbally which actual line in the photograph or drawing was larger. These instructions were thus equivalent to the visual angle instructions for the natural setting condition.
4. V. R. Carlson, *J. Exp. Psychol.* **63**, 68 (1962).
5. W. James, *The Principles of Psychology* (Dover, New York, 1950), vol. 2, p. 264.
6. H. P. Zeigler and H. Leibowitz, *Amer. J. Psychol.* **70**, 106 (1957); H. Leibowitz and J. Judisch, *ibid.* **80**, 105 (1967).
7. M. H. Segall, D. T. Campbell, M. J. Herskovits, *Science* **139**, 769 (1963); *The Influence of Culture on Visual Perception* (Bobbs-Merrill, Indianapolis, 1966).
8. For the abstract figure (Fig. 1A), the absence of significant differences as a function of orientation and culture suggest that variables of experience are not the only determinants of the illusory effect for this particular stimulus.
9. Supported by NIH grant MH08061 and by the Council for Intersocietal Studies of Northwestern University.

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Rhesus Monkeys: Mating Season Mobility of Adult Males

Abstract. *Groups of rhesus monkeys, heretofore described as closed social units, experience a seasonal exchange of a portion of the adult males. Male shifting corresponds with the season of mating, and results in copulation with females of newly joined groups. This pattern is socially disruptive, but provides opportunity for exchange of genetic material between groups of a region.*

A portion of the adult male rhesus monkeys (*Macaca mulatta*) in northern India change groups during the mating season. Macaque groups have previously been characterized as "closed," highly inbred social units, similar to those described for savannah baboons and certain other primate species (*1*). Although intergroup transfer of males is reported for the colony introduced on Santiago Island in 1938 (*2, 3*) the effects of the spatial limitations, high population density, and intergroup familiarity of Santiago Island on group dynamics are not known.

Male shifts were studied for five groups residing on the grounds of the Forest Research Institute near the city of Dehra Dun. These groups ranged in size from 8 to 40 monkeys when observations began (Table 1). The total area of frequent use for all groups equalled about 2.59 km^2. Most of the nearly 400 hours of observation were evenly distributed between September 1965 and May 1966. Visits to the area in the preceding 5 months were irregular.

Transfers varied in details, but in all instances the shifting male clearly altered his patterns of foraging, resting, and travel to conform to those of the group joined. In some of the transfers, initial contacts consisted of short visits, but once the above pattern was established, it persisted from day to day. The shortest observed transfer lasted for 25 consecutive days. Although the five groups in the study area came into frequent contact, there were no observed contacts by individual animals apart from those of the shifting males. Thus, the simplest criterion for transfer is the sighting of any individual male within the vicinity of a group other than his group of origin.

The recorded transfers were somewhat complex (Table 2), involving shifts of varying duration, and without apparent relationship to group size or age (excluding subadults) or rank of the participating males. Four of the five groups received at least one alien male and all groups experienced departures at some point during the observation period, but no more than a single male from any one group shifted permanently. The largest group in the area (II) had the same contingent of males at the end of the shifting period as when it began. A small group (III) was without a resident male for about

Table 1. Composition of groups of rhesus monkeys *Macaca mulatta* on the grounds of the Indian Forest Research Institute at Dehra Dun as of September 1965.

Group	Adult		Subadult males	Juveniles	Infants
	Males	Females*			
I	3	10	1	8	10
II	4	11	1	14	10
III	1	3	0	2	2
V	4	9	1	8	4
VI	1	4	0	3	2

* Include subadult females, all of which gave birth in the spring. The single adult male of Group III disappeared in late October.

6 weeks of the mating season. The three females of this group experienced estrus during this time and mated with three different males from other groups. In this instance, however, the copulating males did not foresake their group of origin, but mated during periods when whole groups came into contact. The pattern here is one of intergroup contact rather than male transfer.

Shifts at least 1 month long were seen for 4 of the original 12 fully adult males. Shifts of similar duration are reported to occur annually on Cayo Santiago for about one-third of the males above 3 years of age (*3*). In my study, none of the subadult males shifted.

Two factors indicate that intergroup exchange of males is related to reproduction. (i) The period of shifts corresponded to the season of copulations. Mating activity for the 1965–66 season began in mid-October, peaked in November, and became relatively infrequent by late January. Correspondingly, all male shifts occurred between 21 October and 24 January, excepting the return of one male to his original group in March. (ii) Males who changed groups completed copulations with females of the groups newly joined in all instances save one. The one male which joined two different groups copulated with females in both in addition to his group of origin.

Male shifting is accomplished only after a transition period during which groups show their intolerance of the intrusion. During this period the intruding male usually remains at a distance of some 100 m from the group periphery. From this distance he engages in an exchange of branch shaking and threats with resident males. On three occasions, however, shifting males approached the periphery and copulated with resident females during the early stages of transfer. Although subjected to harassment, these copulations were carried to completion. Actual fighting between males in such situations was observed only once, but the occurrence of a number of severe wounds in adults of both sexes during transition periods suggests it may have been more frequent.

In most transfers hostile responses toward aliens abated after 3 to 4 days of continuous contact. The one exception to this pattern involved a male who was invariably greeted with hostility for a 25-day period of continuous peripheral association. At this point the male shifted to the small all-female group (III) and remained as its leader to the end of the study.

In addition to the disruption directly provoked by the appearance of alien males, there is evidence of social instability within groups as a result of male departure. This was particularly clear in a multimale group (I) whose leader switched to a smaller, single male group (VI). In subsequent weeks the No. 2 male failed in virtually every attempt to police intragroup disputes, often being driven from the central part of the group by the combined attack of several females. It was not until the No. 1 position was filled by a male from another group that regulation of intragroup disputes was restored.

Koford (*3*) reports that male shifting in the Cayo Santiago colony bears no apparent relationship to age of adult males, or to the size, sex ratio, or identity of the different groups. Rank of shifting males is not discussed in his report, but my sample is diverse in this respect. Although the males who shifted permanently in this study copulated at a significantly higher frequency per observation hour (*4*) than males who did not shift, there is no certainty that opportunities for copulation were increased by shifting. The near similarity of adult sex ratios in all five groups (Table 1) meant that males had potentially equal access to receptive females, and such males, furthermore, generally mated with females in their group of origin before they joined other groups.

Regulation of the process of interchange of males is therefore complex in nature, but may be related primarily to the strength of a male's ties to his group. Longitudinal studies are required to verify this hypothesis, and data from Cayo Santiago have shown that a male's attachment to his group may be affected by presence or absence of his mother, the mother's rank, or by his success or failure in attaining a position of leadership (*3*, *5*). Contact between groups in my study occurred periodically, and provided an opportunity for males to become aware of receptive females in other groups. The consort association which is typical of mating pairs constitutes a temporary loosening of attachment, lasting for several hours and at a distance of up to 200 m in some cases. Consort patterns of this nature are not limited to males who otherwise maintain peripheral associations with the group, but often include high-ranking males as well. Eventual and final separation for some males may be an extension of the spatial relationships of consort behavior, particularly when other groups are in the immediate vicinity. Females do not participate in final separation, having strong ties to offspring and other relatives in their natal group (*6*).

Table 2. Record of group changes by adult male rhesus monkeys *Macaca mulatta* on the grounds of the Indian Forest Research Institute at Dehra Dun. Changes noted as permanent extended to the end of the study.

Male identity	Group joined	Date consummated	Duration of shift	Males in groups joined
No. 1, Group I	VI	10/21	Permanent	1
Single, Group VI	II	11/11	25 days	4
	III	12/6	Permanent	0
No. 3, Group V	I	11/18	Permanent	2
No. 4, Group II	I	12/2	102 days	3
Young male, unknown origin	III	1/24	Permanent	1

These observations show that opportunity for exchange of genetic material between all five groups of the region was present. An occurrence of this nature, based on observations from a single area, could be attributed to some unusual characteristic, such as high population density, were it not for evidence from other areas which indicates a pattern of widespread occurrence. In addition to the five groups considered in this report, I observed male shifts in a forest habitat 11 km away, with much lower population density. Neville (*7*) also reports the appearance of alien males during the mating season for groups in the Haldwani area, more than 150 km to the east. These observations, together with the persistence of this phenomenon on Cayo Santiago over several years, indicate that annual shifting of males between groups is basic to the species.

Composition of groups of rhesus monkeys is basically stable, and contacts with extragroup animals are antagonistic and unfriendly. Less than 4 percent of the total population in the study area changed groups, but this percentage is significant, for it constitutes fully one-third of the original adult males. It is doubtful if the transfer of adult females or immature individuals of either sex would be as costly in terms of social disruption. The theory that sexual attraction promotes group cohesiveness has been criticized on the basis that group composition is stable in those primate species which mate seasonally (*8*). In this species sexual attraction apparently extends across group boundaries, resulting in a limited redistribution of adult males.

An important consequence of intergroup transfer by adult males is the dissemination of genetic material among the groups of a region. The rhesus monkey has a vast geographical distribution, extending from eastern Afghanistan across much of the southern part of China (*9*). It is unlikely that populations from the extremes of this range would show only relatively minor phenotypic variation if groups were as impermeable to gene flow as is commonly believed. Furthermore, inbreeding is generally considered to reduce the evolutionary potential of a species through a reduction of genetic variation.

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References and Notes

1. I. DeVore, in *Classification and Human Evolution*, S. L. Washburn, Ed. (Aldine, Chicago, 1963), p. 308.
2. C. Carpenter, *J. Comp. Psychol.* **33**, 122 (1942).
3. C. Koford, *Tulane Stud. Zool.* **13**, 5 (1966).
4. Mann-Whitney *U* test, two-tailed, $P < .02$.
5. C. Koford, *Science* **141**, 356 (1963).
6. D. Sade, *Amer. J. Phys. Anthropol.* **23**, 2 (1965).
7. M. Neville, *Primates* **9**, 20 (1968).
8. S. Washburn and I. DeVore, *Sci. Amer.* **204**, 70 (1961); J. Lancaster and R. Lee, in *Primate Behavior: Field Studies of Monkeys and Apes*, I. DeVore, Ed. (Holt, Rinehart and Winston, New York, 1965), p. 512; A. Jolly, *Lemur Behavior* (Univ. of Chicago Press, Chicago, 1966), p. 158.
9. J. Napier and P. Napier, *A Handbook of Living Primates* (Academic Press, New York, 1967), p. 404.
10. Supported by NIH grant FR-00169 to the National Center for Primate Biology. I thank L. Schmidt for providing the opportunity to participate in the India Primate Ecology Project and P. Jay-Dolhinow for assistance in planning and conducting the field study. T. Srivastava (president of the Forest Research Institute, Dehra Dun, India) granted permission to study the monkey population on the institute grounds.

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Hearing, Single-Unit Analysis, and Vocalizations in Songbirds

Abstract. *Auditory neurons in the avian cochlear nucleus are systematically arranged according to their best frequencies. The thresholds of single auditory neurons at their best frequencies match the thresholds of hearing obtained by behavioral methods for the same frequencies. The upper range of single-unit best frequencies shows distinct interspecific variation which is correlated with the differences in the range of vocal frequencies. Most songbirds do not seem to produce frequencies below 1 kilohertz but can hear them.*

Bird vocalizations have become popular examples of auditory communication in animals. One of the most important prerequisites for communication is discrimination of signals. So far we have not been able to answer even the most basic questions, such as: "Can birds use the entire frequency range of their vocalizations in signaling?" and "What is the sensitivity of the bird's ear, and how is it related to the distance-transmission of its vocal signals?" This report shows how single-unit techniques can provide some of the information essential for answering these questions.

Birds were anesthetized with urethan. The cerebellum was removed by suction so as to expose the floor of the fourth ventricle where the cochlear nuclei are visible. Tungsten microelectrodes were used to record single units in the cochlear nucleus. The electrode was placed on desired points in the nucleus under a Zeiss operating microscope with the aid of a head holder-electrode carrier assembly. Tone bursts 100 msec in duration were used as stimuli. The thresholds of auditory neurons were judged by the rate of discharge which was monitored both visually and acoustically (*1*). All experiments were conducted in a soundproof room.

Different auditory neurons, whether primary or secondary, respond to different ranges of frequencies. The frequency to which a fiber shows the lowest threshold is called the best frequency of that fiber. Systematic exploration of the cochlear nucleus shows orderly sequences of best frequencies, as expected from the pattern of termination of primary auditory fibers. High, intermediate, and low best frequencies correspond to fibers innervating, respectively, the basal, middle, and apical parts of the basilar membrane (*2*). This arrangement enables us to determine the range of best frequencies quickly and systematically. The range of best frequencies, especially at its highest limit, varies distinctly from species to species. The avian cochlear nucleus consists of two major subdivisions, nucleus magnocellularis and nucleus angularis. In all cases the highest best frequency encountered in the nucleus magnocellularis is about 2 khz lower than that found in the nucleus angularis (*3*).

Now let us investigate whether single-unit best frequencies are related to audible frequencies. In the cat the range of single-unit best frequencies and that of audible frequencies determined by behavioral methods are in excellent agreement. Interestingly, the lowest thresholds of single primary units at their best frequencies coincide with the audibility thresholds for the same frequencies (*4*).

The above correlation seems to hold also for songbirds, even when the thresholds of second-order neurons are used. Figure 1 presents a comparison of an audibility curve averaged for four birds (*5*) and the distribution of single-unit thresholds from one canary (*Serinus canarius*). The behavioral and the single-unit data are in good agreement except for the highest- and lowest-frequency regions. These differences can be easily explained by the fact that