Socialization processes in primates: Use of multivariate analyses. I: Application to social development of captive mangabeys

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Socialization processes in primates: Use of multivariate analyses. I: Application to social development of captive mangabeys

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Abstract

We hypothesized that, within a primate group, socialization processes are influenced by each group member behaving according to his own social network. Therefore socialization processes would differ in various social environments. In this study, we considered two main socialization processes, the acquisition of a social behavioral repertoire and the development of a network of social relationships, and consequently defined six comprehensive developmental parameters. We analyzed the variability of these parameters using a new multifactorial method, the Principal Components Analysis with Instrumental Variable, PCAIV, derived from the Principal Components Analysis and Multivariate Analyses of Variance. This technique allowed us to jointly represent the influence of the independent variables and the complex relationships between the six dependent variables. The study of the social ontogeny of eight infant mangabeys (Cercocebus albigena), reared in three different social environments, served as an illustration of the use of the new multivariate analysis. A 3-variable-model (age, social environment and sex) significantly explained the variability of the developmental parameters. The results confirmed the importance of social interactions in non-human primate infants' development. The application of multivariate methods to the study of individual social development looks promising for future research.

Keywords: Multivariate analysis; Socialization process; Social environment; Methodology; Non-human primate

1. Introduction

Within a social group of monkeys, there is a complex network of relationships between individuals (Hinde, 1975; Hinde and Stevenson-Hinde, 1976; Seyfarth et al., 1978). The social organization is partly a consequence of demographic structure parameters such as the size and the composition of the social groups (Rowell, 1972; Altmann and Altmann, 1979; Van Schaik and Van Hooff, 1983). Both

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social organization and demographic structure influence the emergence of behavioral differentiations resulting in different behavioral profiles more or less specific to age, sex and social status (Bernstein and Sharpe, 1966; Bernstein, 1971; Bramblett, 1973; Fedigan, 1976). As Mason (1963) demonstrated, a social environment is crucial for a primate individual to remain social and, possibly, to stay alive. From birth, primate infants become a source of attraction for other partners and very soon infants themselves are attracted by partners. Hence the social development of an individual is often considered as an interactive process, a developmental process through social interactions (e.g. Hinde, 1971; Lewis and Cherry, 1977; Poirier, 1977; Berman, 1982a). Consequently the diversity of social environments might yield differences in learning patterns which eventually result in a large variability in behavioral profiles of young through diverse socialization processes (Baldwin and Baldwin, 1979; Poirier, 1982).

Social behavioral development could actually be defined by two inter-dependent processes, namely the acquisition of a social repertoire and the construction of a social network. Therefore, in a given species, it can be hypothesized that large and complex groups would provide a young with greater chances to acquire a large behavioral repertoire rapidly, or, possibly, a larger one than that of a young in smaller and less diverse groups. However, an infant will acquire a greater and/or more complex repertoire only if he actually interacts with a large variety of partners having different behavioral profiles. The complexity of a repertoire refers to the variety and the recurrence of behaviors displayed by an individual during social interactions.

In this paper we ask the questions: (1) how does the availability of partners who differ in their behavioral expression, influence the social development of young?; and (2) how this influence could be documented and analyzed?

We tested these questions in a study on the social development of young captive grey-cheeked mangabeys reared in different social environments.

Using Altmann's approach to behavioral diversity (Altmann, 1965), we assess that a rich and complex individual repertoire would include most, if not all, of the previously defined behavioral units, and a high proportion of units would be observed with a comparable high frequency. Contrastingly, a rich, but simple repertoire, would include the same number of units as previously, but only a few units would be observed more frequently. The behavioral complexity could then be illustrated by the frequency distribution of behavioral patterns and by comprehensive parameters such as diversity or uncertainty indices, derived from Shannon's information theory (Altmann, 1965). The complexity of interaction patterns can be assessed in the same way: a complex network of interactions will be the consequence of a balanced level of interactions with all available partners. In contrast, a simple network will be assessed if an individual interacts most of the time with only one or a few of the available partners.

Developmental studies most often present frequency-time plots for selected behaviors. However single-factor models of social development are not suitable to explain the complex and dynamic variables involved in social interactive processes (Poirier, 1982; Thoman et al., 1979; Dennenberg, 1979). Hinde and colleagues introduced the use of several indices to deal with the interactive character of social development (Hinde and White, 1974; Hinde and McGinnis, 1977). Only a few studies made use of multifactorial analysis (Deputte, 1986, Deputte, 1991; Deputte and Goy, 1991). In this paper a new kind of multifactorial analysis, Principal Components Analysis with Instrumental Variables (PCAIV) (Sabatier et al., 1989; Lebreton et al., 1991), is used to investigate the influence of social environment parameters on the acquisition of a social repertoire and the construction of a social
network during the development of captive grey-cheeked mangabey infants. This method has been chosen as results could be presented both in the tables of statistics and on graphs best suited to perceive all at once, in a single figure, the complex relationships of interrelated variables. To our knowledge this is one of the first attempts to apply these multivariate methods to primate social development: one of the main purposes of this paper is to demonstrate the application of this methodology and its potential for future studies.

2. Materials and methods

2.1. Subjects

This study is part of a 6-year study of social ontogeny conducted by one of us (B.L.D.) on 9 grey-cheeked mangabeys (*Cercocebus albigena albigena*; 5 females and 4 males), from their birth to various ages (not less than 6 months and up to 6 years). The subjects are born in social environments which differed in size and, especially, in the number of adult males and/or females. This study reports only on the first 18 months of 8 subjects. Compared to captive macaques, the fertility rate of mangabeys was rather low and birth could occur any time during the year (Deputte, 1991); the eight subjects were born over 5 years with a peak of 4 births during the next to last year of the study. Even though the sample size is small, it should be noted that the Paimpont colony of grey-cheeked mangabeys is, as far as we know, the largest in the world (see Deputte, 1991, Deputte, 1992).

2.2. Sampling procedures

Focal-animal sampling was used (Altmann, 1974). A total of 18,777 five-min-focal-animal samples (1,565 hours) were completed for the study reported here. During an observation session all of the individuals in a group were observed at least once. The per-month observation time was held more or less constant at a level of 38 h per month, on average, of focal animal sampling. Observation sessions lasted 2 h, on average, 5 days a week, and were randomly distributed between 08:00 hrs to 18:00 hrs to evenly cover a daily cycle.

2.3. Observational procedures and data computation

During a 5-min-focal-animal sample, all the behaviors given and received by the focal subject were hand-written while preserving the sequential aspects of the interactions. The recorded behaviors were predefined behaviors constituting a repertoire of 154 mutually exclusive behavioral units (Deputte, 1983, Deputte, 1986). This behavioral repertoire was large in order to cover the behavioral expression of individuals from birth to adulthood and to permit a fine-grain analysis of social ontogeny. The recorded behavioral units were considered as events (Altmann, 1974), hence long lasting units such as 'Grooms someone' were scored every 10 s when they were uninterrupted. Frequency per 5-min-focal sample were computed for each behavior. For a given dyad, for each month, the frequencies of each behavior were weighted in order to obtain frequencies per unit of sampling time. Processing of data yielded three ‘i-behaviors, j-partners’ matrices, [T], [B] and [V], per each month per each subject (85 month-subjects), the first one for all the behaviors, the second one for the behaviors other than visual.
behavior and the third one for visual behavior (Fig. 1). In these matrices the rows are the k behaviors, and the columns are the \( \ell \) partners. Whether they were focal animals or not, subjects were considered as ‘Initiators’ when they addressed behaviors to partners and as ‘Receivers’ when partners addressed
behaviors to them. Then two sets of three matrices were actually computed, one for the subject as Initiator, one for the subject as Receiver.

2.4. Analyzed variables

Six dependent, to-be-explained, variables are extracted from each month–subject matrix. The first three variables were intended to describe more specifically the acquisition of a social behavioral repertoire, while the last three specifically describe the development of a social network.

2.4.1. Size of the social repertoire

This measure is the number of different behavioral units observed, at least once, during a given month-subject (Fig. 1), reflecting the overall variety of an infant's behavioral expression, or the variety of the social stimulation received by an infant. It is identical to the ‘Y’ variable defined by Fagen and Goldman (1977) in the computation of ‘behavioral catalogue completeness’. The sizes of observed repertoires varied from 33–103 and from 47–118, respectively for infants as initiators or as receivers. These figures represented respectively 21–67% and 30–77% of the pre-defined behavioral repertoire.

2.4.2. Total frequency of behaviors

This measure was an expression of the intensity of social interactions. It was the mean overall frequency of behaviors, given or received, per 5 min sample over a month. It is \( B \), the grand total of the \( B_{ij} \) cells of the \([B]\) matrix (Fig. 1). The visual behaviors were not taken into account. The total varied from 3.5–27.5 and to 6.1–22.2 behavioral occurrences per 5-min sample, respectively, for infants as initiators or as receivers.

2.4.3. Diversity of behaviors

This refers to social behavioral complexity, i.e. to the structure of the observed behavioral repertoire. It describes whether the behavioral expression, given or received by a young, is dominated by only a few, often recurring, behaviors (low diversity) or is balanced between a large number of behaviors (high diversity). It is a measure derived from ‘behavioral-abundance distribution’ computed as the Shannon index (Altmann, 1965; Fagen and Goldman, 1977).

\[
D_b = - \sum_{i=1}^{k} \left( \frac{T_i}{T} \right) \log \left( \frac{T_i}{T} \right)
\]

where \( k = 154; T_i \) and \( T \) are respectively the sum of the ith row and the grand total (Fig. 1). As \( \log \left( \frac{T_i}{T} \right) \) is negative the minus sign before the sum sign makes, by convention, the value of the diversity index positive.

2.4.4. Total frequency of looks

This variable showed the importance of social visual attention. It was the mean frequencies of all the visual behaviors given per sample, over a month. It is \( V \), the grand total of the \([V]\) matrix (Fig. 1). It varied from 2.6–14.3 and from 2.9–22.6 looks per 5-min sample, respectively for infants as initiators or as receivers.
2.4.5. Diversity of interactions

This refers to the complexity of interaction patterns. It describes how a subject interacts with its partners, irrespective of the nature of the behaviors displayed during these interactions. It shows whether a subject initiates interactions with or is contacted by very few partners very often (low diversity) or distributes evenly his interactions between, or is contacted evenly by, a large number of partners (high diversity).

\[
D_i = - \sum_{j=1}^{\ell} \left( B_{ij}/B_j \right) \left( \log(B_{ij}/B_j) \right)
\]

where \( B_j \) the total of the jth column and \( \ell \) varying from 3 to 8 depending on the group size (Fig. 1).

2.4.6. Diversity of attention

Similar to the diversity of interaction except that only social visual behaviors, e.g. looking at a partner, are taken into account (Fig. 1).

\[
D_a = - \sum_{j=1}^{\ell} \left( V_{ij}/V_j \right) \left( \log(V_{ij}/V_j) \right)
\]

Only relative diversity indices were used since these indices are independent from the number of items (behaviors or partners), hence providing comparative measures of diversity, between subjects who belong to different groups and/or display behavioral repertoires of different sizes (Cancela da Fonseca, 1969; Deputte, 1985):

\[
D_b = D_b^{*} 100/\log(k), D_i = D_i^{*} 100/\log(\ell) \quad \text{and} \quad D_a = D_a^{*} 100/\log(\ell)
\]

where \( \log(k) \) and \( \log(\ell) \) were the maximum diversities. Relative diversity indices were expressed as percentages.

We created two matrices \([y]_{np}\), of order \( n \) and \( p \), one for subjects as initiators, one for subjects as receivers. Let \( n \), the 85 month-subjects, be the number of rows of both matrices, and let \( p \), the six dependent variables, be the number of columns (Fig. 1).

2.5. Observational design and data analysis

We consider 4 independent variables that could explain the sources of variation of \([y]_{np}\): Social Environment, Age, Sex, Infant Individuality (Fig. 2). The observational design was set prior to the birth of the first subject. The reproductive parameters previously mentioned had made it impossible to balance the experimental observational design between Sex, Social Environment and Age variables (Fig. 2).

The independent variables are, for each of the \( n \) month-subjects, those corresponding to the underlying explanatory model (age, sex, social environment, individuality), and the related observational design.

We set an independent variable matrix, \([x]_{nu}\) (\( n = 85, u = 4 \)). Once the independent variables were transformed into 'Dummy variables', zeros or ones, they yield \( q \) new variables; Sex is represented with two variables \( M \) and \( F \); Infant Individuality with variables \#1 to \#8, Age with three 6-month periods, \( P1, P2, P3 \), and Social Environment with 3 modalities, I, II and III (Fig. 2); the Social
Environment I was characterized by a small size (3 to 4) including a mated adult pair and a juvenile male. The Social Environment II was characterized by an intermediate size (5 to 6), and included one adult male, 2 adult females and 2 juveniles. The Social Environment III was characterized by the largest size (6 to 8) including 2 adult males, 2 or more adult females and 0 to 4 juveniles. Let $[X]_{nq}$ be the new matrix, with $n = 85$ and $q = 16$.

Frequency scores and relative diversity indices of the matrix $[y]_{np}$ were transformed using the square root and the angular arcsine transformation respectively, in order to normalize their distributions and to linearize the relationships (Sokal and Rohlf, 1969). In addition, the 6 variables were standardized to balance their influence in the global analysis. Let $[Y]_{np}$ be the resultant matrix.

### 2.6. Choice of a technique for data analysis

The Multivariate Analysis of Variance (MANOVA) is an adequate technique to unravel, to measure and to assess statistically the proportion of variation of the dependent variables (matrix $[Y]$) which could be attributed to the considered independent variables (matrix $[X]$). These independent variables defined sub-sets of observations. The MANOVA technique is intended to decompose the Total variability into Between and Within (sub-sets) variabilities. Actually the MANOVA technique computes the SSCP matrices (Sum of Squares and Cross Products) such as $[S_{Total}] = [S_{Between}] + [S_{Within}]$. However, the MANOVA is a more algebraically than geometrically oriented technique and so does not provide graphs illustrating either the mutual relationships between the dependent variables or the effects of the independent variables on the dependent variables.

The Principal Component Analysis, PCA, is one of the techniques which would allow us to consider simultaneously several dependent variables, to analyze their correlations. When $[Y]$ is a
standardized matrix, the correlations are measured by the Total SSCP matrix, $S_{\text{Total}} = [Y][Y]^\top 1/n$, where $[Y]$ is the transposed matrix of $[Y]$. The PCA is based on geometrical principles. It determines, in multidimensional spaces, the best fitted representation of the variables (columns) and of the observations (rows). The variables are represented as vectors in the space, $\mathbb{R}^n$, defined by the $n$ observations and the observations as data points represented in the space, $\mathbb{R}^p$, defined by the $p$ variables. Therefore a PCA is a suitable technique to illustrate the complexity of data with both comprehensive graphs and tables of statistics. However, in the classical PCA technique, it is impossible to determine easily the influence of the independent variables related to the dependent variables. Hence we chose a new technique, the Principal Component Analysis with Instrumental Variables, PCAIV, first introduced by Rao (1964) and subsequently developed by several authors (Sabatier, 1987; Ter Braak, 1987; Sabatier et al., 1989; Lebreton et al., 1990; Lebreton et al., 1991). This technique combines the properties of the MANOVA and those of the PCA. Its general principle consists in computing the expected values of the matrix $[Y]$ in relation to the model. Geometrically speaking, this computation is equivalent to the projection of the vectors of the matrix $[Y]$ onto the subspace defined by $[X]$:

$$[\hat{Y}] = [X].[([X]'.[X])^{-1}.[X]'[Y]$$

where $[X]'$ is the transposed matrix of $[X]$.

Consequently the matrix $[\hat{Y}]$ includes the means of the variables for each of the sub-sets of observations, i.e. the coordinates of the centers of gravity of the different sub-clusters of data points defined in $[X]$. Then the Between SSCP matrix, $S_{\text{Between}} = [\hat{Y}][\hat{Y}]^\top 1/n$, was computed. The subsequent non-standardized PCA, carried out on $S_{\text{Between}}$, is intended to maximize the Between variance (in contrast to the PCA technique which is carried out on $S_{\text{Total}}$). The graphical representation of the factorial planes yields a clear picture of the effects of the model variables on the observed data because the factorial axes maximize the dispersion of the centers of gravity. On the graphs, the variables are interpreted as vectors within a correlation circle (radius of 1). The length of a vector representing a variable which is well explained by the model, will be close to 1 and the end of the vector will be close to the circle limit. On the contrary a vector representing a variable which is only loosely explained by the model will have its end close to the center of the correlation circle. The correlations between the dependent variables are represented by the cosines of the angles formed by the corresponding vectors, as in classical PCA.

The relevance of the explanatory variables is globally measured by comparing the trace of the Between SSCP matrix $[S_{\text{Between}}]$ with that of the Total SSCP matrix $S_{\text{Total}}$. A multivariate Fisher’s F ($[S_{\text{Between}}]$ trace/$[S_{\text{Within}}]$ trace) can be computed and the value of this Multivariate F can be tested using a Monte Carlo technique (Ter Braak, 1992).

In our study, the underlying hypothesis is that the observed variables are influenced by additive effects of age, sex and social environment. These effects were assumed to be significantly greater than those due to individuality or to the uncontrolled residual variation. When the tested model is balanced, it is possible to determine, in a strictly additive way, the variation due to each of independent variables. Our experimental design is unfortunately too unbalanced (see above). Nevertheless we computed the adjusted sum of squares for each of the 3 explanatory variables: in this way each source of variation is underestimated, hence the sum of the explained variances by each of the variables is smaller than the total explained variance.
Table 1
Relative contribution of the independent variables, Social Environment, Age, Sex, and Individuality, to the overall variation (sum of squares) of the dependent variables of the socialization processes

| Sources of variation | Infants | | | | | | Receptors | | | | |
|----------------------|---------|---|---|---|---|---|---|---|---|---|---|---|
|                      | df      | SS | %  | F  | df | SS | %  | F  | df | SS | %  | F  |
| Soc. Envir. + Age + Sex | 5 | 2.17 | 36.2 | 8.95 *** | 1.99 | 33.2 | 7.85 *** |
| Soc. Envir. | 2 | 0.68 * | 11.3 | 6.93 | 1.12 * | 18.7 | 10.89 |
| Age | 2 | 0.81 * | 13.5 | 8.26 | 0.20 * | 3.3 | 2.02 |
| Sex | 1 | 0.02 * | 0.3 | 0.33 | 0.32 * | 5.3 | 6.40 |
| Individuality | 7 | 0.74 * | 12.3 | | 0.84 * | 14.0 | |
| Error | 72 | 3.09 | 51.5 | | 3.16 | 52.7 | |
| Total | 84 | 6.00 | 100.0 | | 6.00 | 100.0 | |

The significance of the Multivariate F is obtained after 1000 permutations (Monte-Carlo test). \( P < 0.001 = \cdots \).
+ Adjusted SS: each term is fit after all other terms in the model.

2.7. Software used in this study

The classical MANOVA was carried out with MINITAB Release 9 (1993), the PCAIV was carried out using BIOMECO (Lebreton et al., 1990) and the GLModel and the AnaComP procedures of GTABM (Quris, 1994), elementary computations on matrices with CALMAT (Quris, 1991) and the permutation tests with CANOCO (Ter Braak, 1991).

3. Results

3.1. Global analysis

Individuality has no special predictive power. It actually represents the background noise against which other explanatory variables should be tested.

The global 3-variable model significantly explained 36% and 33% of the variability of the data for infants as initiators and infants as receivers, respectively (Multivariate F = 6.93; \( P < 0.001 \) and Multivariate F = 7.85; \( P < 0.001 \), respectively; Table 1). When infants were initiators the significant sources of variation were age and social environment (13.5% and 11.3%, respectively; Table 1), whereas when infants were receivers it was the social environment and the infant's sex to a much lesser extent (18.7% and 5.3%, respectively; Table 1). The variables related to the socialization processes were therefore significantly influenced by maturation and experience and by parameters of the social environment.

3.2. Graphic interpretations

3.2.1. Infants as initiators

With the 3-variable model, 83.1% of the explained variability is accounted in the first two factors of the graphical representation (Fig. 3A). All but one (Frequency of Behaviors) dependent variables...
Fig. 3. (A) Graphical display of the results of the 3-variable Principle Components Analysis with Instrumental Variables (PCAIV): Infants as initiators. Representation of the projections on the plane of the first 2 factors of the PCAIV, of the 6 dependent variables and of the centers of gravity of the sub-clusters of data points featuring the individuals defined by the independent variables (these centers of gravity are represented by a Female or Male symbol preceded by a number in italics, referring to the age period). These centers of gravity belonging to the same social environment are enclosed in a colored ellipse (dark grey, light grey and white for Social Environments I, II and III, respectively). The dashed circle features the 'correlation circle' (radius = 1). Within this circle, the length of the vectors features how much a dependent variable is explained by the model. On each axis the percentage of the explained variation is indicated. The Age-arrow on the left of the figure indicates the influence of the Age variable which opposed the first 6 months (P1) to the following periods (P2 = 7–12 months, P3 = 13–18 months). (B) Graphical display of the results of the 3-variable Principle Components Analysis with Instrumental Variables (PCAIV): Infants as receivers (refer to legend for (A)). The two curved lines, ended with a Female or Male symbol in a box, enclosed all the centers of gravity featuring either males (top part) or females (bottom part).
were well represented in the plane, meaning that their variation were well explained by the model. Three dependent variables, Size of the Repertoire, Diversity of Interactions and Frequency of Looks, were highly positively correlated with each other (a high correlation is represented by an acute angle between the two variable-vectors; Fig. 3A). Observations (centers of gravity of the sets of points featuring the individuals) were scattered on the plane along two major directions which were the bisectors of the axes.

Age actually opposed the first period to the subsequent ones along the first bisector. Four dependent variables (Size of the Repertoire, Diversity of Interactions, Frequency of Looks and Diversity of Behaviors) were positively correlated with age, one, Diversity of Attention, was negatively correlated (Fig. 3A). The highest positive correlation was found between age and the size of the repertoire (Fig. 3A). The 3 Social Environments were discriminated along the second bisector (Fig. 3A). The Diversity of Behaviors was the most highly correlated with the Social Environment variable, being the greatest in the social milieu I (Fig. 3A).

3.2.2. Infants as receivers

With the 3-variable model, 81.4% of the explained variability is accounted in the first two factors of the analysis (Fig. 3B). There was a general lack of correlation between the dependent variables although the Frequency of Looks and the Diversity of Behaviors were negatively correlated (Fig. 3B). The Diversity of Attention and to a lesser extent the Frequency of Behaviors were not well represented in the plane, meaning that their variations were not influenced by the considered factors.

The Social Environment factor was highly correlated with the first, horizontal axis (Fig. 3B): the Social Environment I was opposed to the two others. The Age variable had no influence whereas the Sex variable was loosely correlated with the vertical axis (Fig. 3B). The social environment I was mainly correlated with a low Diversity of Interactions whereas the Sex was mainly correlated with the Size of the Repertoire, being greater when partners initiated interactions with the young females.

4. Discussion

When infants initiate interactions, age has the strongest effect; before six months, the nature of the infant-partners interactions is highly dependent on the infants' physical maturation. At 6 months, infants begin to develop their own social network and to differentiate their social behavior according to the partners they are interacting with. This differentiation leads to an increase in the richness of the social repertoire.

In addition the positive relation between a high level of visual awareness (Frequency of Looks) and an evenly distributed large amount of interactions (high Diversity of Interactions) suggests the importance of processing visual contextual information prior to and associated with interactions during social development. The lack of correlation between the behavioral diversity and the richness of an infant's repertoire suggests that an infant is able to display a large variety of behaviors even though he used only few behaviors at a high frequency (see Altmann, 1965; Deputte, 1986).

The Social Environment I mainly differs from the 2 other ones by a high behavioral diversity of the infants' repertoire. In this social milieu the two males extensively play together. This suggests that their play interactions involve, repeatedly, a large variety of behaviors and also, likely, many different types of play (no-contact, challenge, wrestle, scrimmage, chase, etc.).
Acquiring a behavioral repertoire and building-up a social network does not seem to be different in male and female infants.

When partners initiate interactions to infants, the social environment has the primary influence on the considered socializing processes whatever the infants' age. The Social Environment III is characterized by a high amount of visual attention given to the infant. This likely suggests that a high degree of social constraints imposed on some individuals prevents them to have access to the infant even though they are attracted by him. This high degree of social constraints in the largest groups is likely a consequence of the captive settings. The relative Diversity of Interactions opposed the Social Environments II and III to the Social Environment I. It was minimal in the latter and this was likely again, in this smallest social environment, a consequence of highly selective interactions between immature males who were attracted to each other to play (e.g. Goldfoot et al., 1984; Goy et al., 1988; Deputte and Goy, 1991 and Berman, 1982b, on either captive or free-ranging rhesus macaques, respectively). This high mutual attraction could have an additional influence on the small amount of different social behaviors that were displayed in comparison with groups including a larger number and a greater diversity of social partners.

Partners seem to treat female and male infants differentially. They provide a richer repertoire of social stimulations (size of repertoire) to female infants than to male infants and within a group more partners contact infant females than infant males (diversity of interactions). Partners could contact female infants to play like they do with male infants but they also involve female infants in a greater diversity of contact behaviors (e.g. grooming, posturo-tactile behaviors) than they do with male infants (Deputte, 1985, Deputte, 1986). In addition, previous studies have shown that when the whole social behavior is considered instead of some specific behaviors (e.g. mounting, play, grooming), the influence of sex is much weaker than that of the behavioral diversity of partners to which infants are exposed (Deputte and Goy, 1991). In a companion study completed on groups of macaque infant–mother pairs, with a completely balanced design between the different independent variables, the proportion of the variance explained by the variable Sex within the Social Environment-Age-Sex model was much greater than that tentatively found in this study for infants as initiators (rhesus: 11.0% vs mangabey: 0.33%) and about the same for infants as receivers (rhesus: 5.5% vs mangabey: 5.3%; Deputte et al., in prep).

Several studies have shown that detailed ways of describing partner's diversity were needed to provide precise pictures of group influences on infant social development: e.g. the number of infant partners (of one or both sexes) or of adult female partners could have a greater influence on infant socializing processes than the presence of several adult males (Berman, 1982b; Deputte, 1986).

The Social Environment variable actually includes several dimensions, such as the size of the groups, their demographic structure (mating structure and presence of a certain number of immatures), their social organization (social networks and nature of social relationships), the 'personal history' of each group member as well as their individual behavioral flexibility. Our 3 social environments vary in numbers of available partners for an infant, from 3 to 8, but also in the number of adults of both sexes. The Social Environment I refers to a Uni-Male/Uni-Female structure (following the Fedigan (1982)'s classification), the Social Environment II to a Uni-male/Multi-Female structure and the Social Environment III to a Multi-Male/Multi-Female structure. Considering the other variables which characterize a social group, it seems justified to refer to our Social Environment variable as a Social Complexity variable, with increasing level of complexity from Social Environment I to Social Environment III.
5. Conclusion

The influence of the social environment on infants’ social development is greater when interactions are initiated by social partners. Each level of complexity of the social environments has a specific effect on socialization processes, whatever the age of infants. The greatest variety of social stimulations seems to be found in a social milieu with a middle complexity. The influences of social environment illustrate the social constraints imposed on individuals attempting to contact infants: although a large multi-male/multi-female group potentially provides infants with a large diversity of social phenotypes, all this diversity would be available to infants only if the social organization of the group allows partners to evenly contact any infants. If it is not the case, infants would be exposed to a partner diversity not different from that of the less complex social environments.

The PCAIV technique is basically similar to a MANOVA. However, it additionally provides a graphical presentation of the results which is helpful to perceive the complex relationships of social variables involved in multidimensional processes such as socialization processes. This quantitative multifactorial analysis shows that social environments and age, and to a lesser extent sex, affect two fundamental socialization processes, the building-up of a social repertoire and the development of a social network of interactions.

The results of this study, obtained on an highly arboreal species, add to the generality of the social network concept that until now was mainly developed from macaque studies.

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