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Postural Congruence in a Captive Group of Tonkean Macaques (*Macaca tonkeana*)

by

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Abstract

Postural congruence occurs when two or more individuals adopt similar body postures at the same point in time in the context of social interaction. The small number of existing studies on this topic have been limited to human subjects alone. The purpose of this research project is to establish quantitatively for the first time whether or not postural congruence occurs in a nonhuman primate species and to test factors including sex, age, rank, posture, and behaviour in order to evaluate several hypotheses about the expression and function of posture sharing. Observations of the social and postural behaviour of 26 Tonkean macaques (*Macaca tonkeana*) living in semi-liberty conditions at the Strasbourg Primate Centre were made over a four month period and postural congruence was observed. Sex, age and rank influenced the frequency and duration of posture sharing episodes. Posture and behaviour both affected the amount of time spent in postural congruence.

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1. An Introduction to the Study of Postural Congruence in a Captive Group of Tonkean Macaques

Introduction

Body posture is a basic component of nonverbal communication which has been widely studied across several fields of research. One specific phenomenon called postural congruence, has been well documented, although I have located only eleven quantitative tests of the phenomenon to date. Until the present study which involves nonhuman primates, all such studies have been carried out on human subjects exclusively. Postural congruence (also known as posture sharing or postural echo) is part of a larger complex observed in behaviour matching studies. These, along with studies in movement synchrony, make up a research area called interpersonal co-ordination, which is concerned with the co-ordinated aspects of everyday life. While movement synchrony studies look at the temporal aspects, or timing of movement during an interaction, behaviour matching studies examine the similarity in physical appearances at a single point in time (Bernieri 1988). Despite the small number of studies on posture sharing, it remains one of the best examples of behaviour matching in the literature.

Due to the relatively small number of original research studies into the phenomenon of postural congruence (Scheflen 1964; Charny 1966; LaFrance & Broadbent 1976; LaFrance 1979; Trout & Rosenfeld 1980; Beattie & Beattie 1981; LaFrance & Ickes 1981; Maxwell & Pringle 1981; Maurer & Tindall 1983; Maxwell &

Cook 1985; Bernieri 1988), a review will be made of each study. Additionally, literature discussing posture sharing and its possible functions (Scheflen 1972; Davis 1973; Kendon 1977; Morris 1977; Smith 1977; LaFrance 1982; Beattie 1983; Bavelas, Black, Lemery & Mullett 1986; Ellis & Beattie 1986) will be examined. Other relevant research studies on interaction rhythms (Kendon 1970; Bull & Brown 1977; McDowall 1978; Gatewood & Rosenwein 1981; Austin & Peery 1983; Isabella, Belsky & von Eye 1989; Bernieri, Davis, Rosenthal & Knee 1994, Slavoff 1997), on body posture (James 1932; Deutsch 1947, 1952; Hewes 1957; Ekman 1965; Ekman & Friesen 1967, 1968, 1969b, 1974; Mehrabian 1968a, 1968b, 1969; Mehrabian & Friar 1969) and on spatial behaviour (Chance 1956; Hall 1959, 1963, 1966, 1974; Rosenblum, Kaufman & Stynes 1964; Rondinelli & Klein 1976; Mori 1977; Hornshaw 1985; Lopez-Lujan, Ochoa, Mayagoitia & Mondragon-Ceballos 1989) will be summarised.

Relevant studies on positional behaviour (Prost 1965; Sade 1971, 1973; Rose 1974, 1976, 1977, 1978; Fleagle 1976, 1978; Mendel 1976; Mittermeier & Fleagle 1976; Hausfater 1977; Morbeck 1977; Mittermeier 1978; Cant 1986; Sugardjito & van Hooff 1986; Fontaine 1990; Hunt 1992; Bicca-Marques & Calegaro-Marques 1993; Curtis & Feistner 1994; Gebo & Chapman 1995), thermoregulation (Paterson 1982, 1986; Dahl, Bernstein & Williams 1982; Stelzner & Hausfater 1986; Stelzner 1988) and non-vocal communication (Miller, Murphy & Mirsky 1959; Hinde & Rowell 1962; van Hooff 1962, 1967; Chalmers 1968; Christopher & Gelini 1977; Wade 1977; Chevalier-Skolnikoff 1982; Pelaez 1982; Zeller 1981, 1985, 1986) in various

nonhuman primate species will be discussed and a review will be made of the limited literature on the study species, Tonkean macaques (*Macaca tonkeana*) (Fooden 1969, 1976; Thorington & Groves 1970; Groves 1976, 1980; Thierry 1984, 1985a, 1985b, 1986a, 1986b; Thierry & Herrenschmidt 1985; Takenaka, Hotta, Takenaka, Kwamoto, Suryobroto & Brotoisworo 1987; Desportes, Demaria & Thierry 1989; Thierry, Gautier & Peignot 1990; Wantabe, Matsumura, Wantabe & Hamada 1991; Wantabe, Lapasere & Tantu 1991; Suryobroto 1992; Supriatna, Froehlich, Erwin & Southwick 1992; Petit, Desportes & Thierry 1992; Thierry, Anderson, Demaria & Petit 1992; Petit & Thierry 1992, 1994a, 1994b; Masataka & Thierry 1993; Thierry, Anderson, Demaria, Desportes & Petit 1994). Finally, the present study of postural congruence in a captive group of Tonkean macaques will be introduced.

The History of Postural Congruence Studies

In 1964, A. E. Scheflen published a paper in which he describes how people who speak English, also "move in English". He suggests that the postural shifts which accompany spoken language serve to demarcate the components of the interaction, and that the total interaction can be viewed as a "program" which is culturally determined. In viewing eighteen films of psychotherapy sessions with different therapists and patients, Scheflen noticed that "members of a group often hold their heads and extremities in the same position," (Scheflen 1964). He coined the term "postural congruence" to describe this phenomenon. Scheflen distinguishes between direct postural congruence in which interactants are "carbon copies" of each other, and homologous postural congruence in which

interactants are "mirror images" of each other. This distinction was later found to be inconsequential by other researchers (Charny 1966; LaFrance & Broadbent 1976; LaFrance 1979).

Scheflen (1964) speculates that postural congruence is a manifestation of mutual identification which functions as an indicator of continuity in a relationship. He also suggests that it is tied to social status. According to Scheflen, peers are more likely to exhibit postural congruence than interactants of unequal status.

Results from the first attempt to quantitatively test for postural congruence were published in 1966 by E. J. Charny. A film of the interaction between a patient and her psychotherapist was examined for congruence and incongruence in body posture, and their verbal behaviour was correlated with their nonverbal behaviour according to structure and theme. Charny (1966) reports that the verbal conversations associated with postural congruence were "consistently positive, interpersonal, specific, and bound to the therapeutic situation," while the conversations associated with incongruence in posture were "self-oriented, negational, and nonspecific, and tended to be self-contradictory and nonreferenced," (Charny 1966). Charny suggests that nonverbal behaviours such as postural congruence function as an indicator of rapport or "relatedness" in the dyadic relationship, which can be manipulated by the therapist to enhance treatment.

It was a decade later when the next quantitative study of postural congruence was published (LaFrance & Broadbent 1976). This particular study examines the relationship between postural congruence and "self-report indications of rapport" in twelve college classrooms. Observations were made of the episodes of postural congruence between the instructor and his/her students, and these were correlated with student reports of rapport, based on questionnaires administered immediately following the class. The results show a significant positive relationship between postural congruence and perceptions of rapport, which appear to support Charny's (1966) speculations. One especially important aspect of this study is its recognition that environmental factors may inhibit or facilitate posture sharing.

In an attempt to improve on the methodology of previous studies on posture sharing, LaFrance (1979) conducted research similar to the 1976 study, this time employing the cross-lag panel technique (Kenny 1975), which takes into account the possible influence of a third unmeasured variable. Initially, fourteen different college classes were filmed, of which thirteen were available to be filmed five weeks later. Once again, observed episodes of posture sharing were correlated with student self-reports of rapport. These results, like the 1976 study, indicate a significant positive relationship between postural congruence and student perceptions of rapport. The cross-lag technique appears to have little influence on the outcome (LaFrance 1979). This study is significant for its attempt

to establish systematic research techniques, and for raising the issue of causation, although its own results on the latter are inconclusive.

Trout and Rosenfeld (1980) conducted an experiment to test the effects of postural lean and body congruence on the judgement of rapport. Six 40-second segments of simulated client-therapist interactions were videotaped in which postural lean and postural congruence were manipulated by the researchers. The segments were then viewed by 30 male and 30 female undergraduate students who were asked to rate the levels of rapport in each interaction. Both postural lean and body congruence were found to have a positive influence on judgements of psychotherapeutic rapport. The authors suggest that the level of rapport attributed to the interactions may be affected by the combination of postural lean and body congruence, for example "forward-leaning congruent postures communicate more rapport than upright or backward-leaning congruent postures," (Trout & Rosenfeld 1980).

During the 1960s and 1970s the studies on postural congruence involved relationships which were "characterized by relative longevity, a known structure, and mutual commitment," (LaFrance & Ickes 1981) such as psychotherapy sessions and the classroom situation, and did not address the possible influence of sex role typing. These factors are taken into account in the LaFrance & Ickes study (1981). Sixty male and sixty female undergraduate students were equally divided into "sex types" and "androgynous" categories based on scores from the Bem

Sex-Role Inventory (Bem 1974). Two subjects of varying category were left alone for five minutes in a waiting room to interact while they were videotaped. Immediately after the interaction, the subjects were asked to fill out a questionnaire designed to elicit their perceptions about their own and the other subject's behaviour. Results indicate that "sex-typed" females tended to exhibit more postural congruence than "sex-typed" males, but "androgynous" males showed more postural congruence than "androgynous" females (LaFrance & Ickes 1981). The researchers were surprised to find a significant negative correlation between postural congruence and self-report indications of rapport, and a positive correlation between posture sharing and anxiety. They suggest that in situations where subjects are strangers interacting under forced and strained conditions, interactants may demonstrate more posture sharing in an effort to establish rapport or influence the other's behaviour (LaFrance & Ickes 1981).

Also in 1981, Beattie & Beattie published the results of their research conducted at a holiday beach in the south of France. For a period of two weeks, they collected data on postural congruence for ten male-male and ten male-female dyads. Female-female dyads are not taken into account in this study because females at this beach had a tendency to either pair off with males or visit in clusters. The authors report that male-female dyads exhibited episodes of postural congruence more frequently than the male-male dyads, however, the male-male dyads tended to maintain longer durations of posture sharing. Male-

male dyads also displayed a greater range of postures. This study is especially significant because it is the first one to examine postural congruence in a "naturalistic setting", it does not take into account verbal communication or self-reports, and it eliminates the problem of environmental interference by only observing dyads who are lying or sitting without a chair. It is also the first study to test the hypothesis that postural congruence arises from random coincidences in body posture and the authors determine that postural congruence is not a chance phenomenon. The researchers hypothesise that postural congruence may act as a "social signal of the bonds between individuals," (Beattie & Beattie 1981). Additionally, they find no evidence to support the Scheflen (1964) hypothesis that posture sharing acts as an indicator of similarity in roles, since male-female dyads exhibited a greater amount of posture sharing than male-male dyads (Beattie & Beattie 1981).

Maxwell & Pringle (1981) examine the correlation between postural congruence and feelings of positive affect and perceived similarity. They employ a regression technique to predict liking and similarity in a group of twenty-four young adults. Postural congruence was observed in dyadic interactions between the subjects, and later correlated with self-reports of liking and perceived similarity administered immediately after the interaction. A significant positive relationship was found between upper-body posture sharing and reports of liking and perceived similarity, and measures of postural congruence using the lower half of the body were not found to be useful (Maxwell & Pringle 1981). The regression

technique appears to have little influence upon the results of the research (Maxwell & Pringle 1981). Like the LaFrance study (1979), the importance of this project lies in its attempt to systematically measure postural congruence.

The relationship between postural congruence and a client's perception of counsellor empathy is examined in a study conducted by Maurer & Tindall (1983). Eighty adolescents (forty males and forty females) were asked to meet with a counsellor for a fifteen minute interview to discuss career planning. Students were randomly assigned to categories which determined the postural behaviour of the counsellor (to maintain or to avoid postural congruence with the subject). Immediately following the meeting, students were asked to fill out questionnaires regarding their perception of the counsellor's empathy towards them. The results indicate that students who met with counsellors that maintained postural congruence rated the counsellors as having significantly higher degrees of empathy than counsellors who avoided postural congruence (Maurer & Tindall 1983). The authors interpret their results as lending empirical support to the hypothesis that postural congruence is an indication of rapport (Scheflen 1964; Charny 1966), and suggest that this information may aid in the counselling process.

Maxwell & Cook (1985) conducted a study to examine the relationship of postural congruence and judgement of liking. In this research, however, both postural congruence and liking were manipulated by the researchers. Posture sharing was influenced by providing similar or dissimilar chairs to the subjects and

liking was manipulated by assigning the subjects to certain roles that dictated their attitude towards a potential roommate, in a role-playing scenario. Sixteen male-male and female-female dyads were observed. Levels of postural congruence were lower for dyads that had dissimilar chairs and for dyads in which one or both subjects were to play the role of disliking the other. The results indicate that postural congruence can be successfully manipulated both by furniture and judgements of liking in role playing scenarios (Maxwell & Cook 1985).

Finally, in the most recent posture sharing study (Bernieri 1988), both postural congruence and interactional synchrony are measured in nineteen teacher-student dyadic interactions. All subjects were high school juniors, where half were assigned to take the teaching role and half the student role in teaching and learning new words and definitions. Subjects who knew each other well were prevented from working together. Immediately following the interaction session, subjects were asked to provide self-reports on levels of perceived rapport. Videotapes were made and later examined for postural congruence and interactional synchrony. These were then correlated with the self-reports. Unexpectedly, movement synchrony was strongly positively correlated with rapport, while postural congruence was not. The researchers suggest that in situations where interactants are familiar with each other or involved in an ongoing relationship, there is a strong positive correlation between posture sharing and rapport, while in situations where interactants are strangers, there is not. They indicate that further research in this area may shed light on why it is that "we can

'hit it off' immediately with some people and never 'get it together' with others," (Bernieri 1988).

These studies on postural congruence, although limited in number, show a progression towards more systematic research methods and analysis techniques, and the inclusion of more variables which may influence the occurrence or expression of the phenomenon, such as environmental factors, sex roles, relative familiarity of the subjects, the setting structure, content of the verbal conversation, attitudes about liking and perceived similarity, and self-report indicators of feelings of rapport and empathy. In addition to these original research studies, much has been written about postural congruence by authors speculating on its possible function (Scheflen 1972; Davis 1973; Kendon 1977; Morris 1977; Smith 1977; LaFrance 1982; Beattie 1983; Bavelas, Black, Lemery & Mullett 1986; Ellis & Beattie 1986).

Scheflen's early work on nonverbal communication, including postural congruence, led him to suggest that there is an evolutionary scheme of communicative development (1972). In this scheme, nonhuman primates are capable only of limited communication in the contexts of territory maintenance, mating, mother-offspring interactions, and dominance-submission behaviours. Associated with the human-specific verbal ability, are the "complex" communicative behaviours, including postural congruence. Scheflen argues that the type of complex communicative behaviour, and the frequency with

which it occurs is largely dependent upon factors such as age, sex, and culture (1972). Because he believes that nonverbal communication, such as postural congruence, operates to facilitate verbal communication, he does not consider that these "complex" communications could occur independent of conversation.

This view, that postural congruence occurs in the context of verbal communication to express rapport and continuity of a relationship, is adopted by other authors in the 1970s who write about postural congruence, but do not conduct their own research into the phenomenon (Davis 1973; Kendon 1977; Morris 1977; Smith 1977). Reflecting on the scarcity of empirical studies of postural congruence, and the very small amount of elaboration on Scheflen's hypothesis (1964) by later researchers, LaFrance (1982) traces the history of motor mimicry studies, and finds that the idea that those who share body posture also share a viewpoint, has its roots in the late nineteenth century.

The Scheflen (1964) hypothesis that posture sharing is related to social status, is presented in popular psychology books (Davis 1973; Morris 1977) dealing with body language as the topic of interest in the 1970s. Morris (1977) even suggests that postural congruence can intentionally be adopted by dominants to relax subordinates, while subordinates can use it as a strategy to unnerve dominants.

There are other, less well-known speculations about the possible function of posture sharing. Some researchers hypothesise that it works as a "tie sign" to

indicate social or sexual bonding (Morris 1977; Beattie & Beattie 1981; Beattie 1983; Ellis & Beattie 1986). Others suggest that it may work not only to indicate rapport between individuals (Charny 1966), but also to aid in the establishment of rapport (LaFrance & Ickes; LaFrance 1982). Finally, it is proposed that postural congruence serves as an indicator that one individual "knows" and "cares" how the other "feels" (Bavelas, Black, Lemery & Mullett 1986). Clearly, there is no real consensus among the psychology professionals about the function of postural congruence. It appears likely, however, that there are multiple reasons why posture sharing occurs, which may be dependent upon the context in which it is expressed.

Relevant Psychology Literature

Closely related to postural congruence, is the phenomenon of interactional synchrony, which takes into account the timing of body movements, and not the congruence of those movements. The work of Adam Kendon (1970, 1977) greatly resembles the work on postural congruence by Scheflen (1964, 1965, 1972), after which it is modelled. Kendon also uses a hierarchical scheme to break verbal conversation up into levels and units, and he correlates motor synchrony with these units. The hypotheses derived from the studies by Scheflen (1964, 1965, 1972) and Kendon (1970, 1972) were empirically tested by Bull & Brown (1977), who found some evidence to support the notion that certain categories of speech are accompanied by postural "markers", but Scheflen's hypothesis that postural shifts work to maintain a culturally determined 'program' of behaviour was not supported.

Many studies have been conducted which examine the phenomenon of interactional synchrony. While most (Kendon 1970, 1977; Bull & Brown 1977; Gatewood & Rosenwein 1981; Austin & Peerly 1983; Bernieri 1988; Reznick & Rosenthal 1988; Isabella, Belsky & von Eye 1989; Bernieri, Davis, Rosenthal & Knee 1994) report that it occurs above the level of random chance, it came under intense scrutiny after McDowall (1978) published the results of his own study which led him to suggest that it occurs only by coincidence. The reliability of the methods of measuring and analysing interactional synchrony was questioned (McDowall 1977; Beattie 1983; Ellis & Beattie 1986) which may have in turn prompted the effort to improve methodology in studies of postural congruence.

The first study of interactional synchrony in a nonhuman primate species (*Cebus apella*) was reported recently (Slavoff 1997). The normal interactions of six capuchin monkeys were recorded on videotape, and a microanalysis of the movements was conducted "to assess body position changes, muscle movements, nonverbal gestures, and spatial proximity to the other members of the troop," (Slavoff 1997). The results indicate that interactional synchrony was found to occur in this troop of capuchins, and the researcher suggests that her findings lend support to the hypothesis that "coordinated interaction developed long before the emergence of signal systems," (Slavoff 1997). This study is especially significant because it establishes that interactional synchrony is not located exclusively in the context of human interaction and spoken conversation.

In the field of psychology, there is a considerable amount published on the topic of body posture and while most of it is outdated and/or irrelevant to the topic of postural congruence, there are some works worth mentioning. W.T. James (1932) published the first extensive study on the expression of body posture. He suggests that the orientation of the head and trunk convey "general" messages, while the limbs convey "specific" messages. Of particular importance is James' proposal that the "situation" or the environmental context may influence the postural behaviour as well as the attitude of the observer.

F. Deutsch (1947, 1952) contributes two especially important concepts to posture studies in psychology. Firstly, in positional behaviour, "voluntary and involuntary, conscious and unconscious motivations are always involved, " (Deutsch 1947). Research into postural congruence suggests that it is a phenomenon which occurs unconsciously (Beattie & Beattie 1981). Secondly, Deutsch recognises the need in postural studies for a predetermined catalogue of body positions, which he calls a "posturogram" (Deutsch 1952). Researchers of postural congruence have successfully employed this concept, and "posturograms" for each study have been very different, ranging from four distinct postures (Charny 1966) to twenty-three (Beattie & Beattie 1981).

G. W. Hewes (1957) documents the variability in human postures based on sex and cultural differences and notes that many differences arise from environmental factors. He suggests that postural studies may shed light on both the biological and social evolution of humans. He views the evolution of postural

and motor habits as being attributable to a complex of factors such as anatomy, physiology, psychology, culture, environment and technology. A series of related articles on postural cues and communication (Ekman 1965; Ekman & Friesen 1967, 1968, 1969a, 1969b, 1974; Mehrabian 1968a, 1968b, 1969; Mehrabian & Friar 1969) have established an empirical relationship between head and body cues and attitude. These studies have largely paved the way for research into postural congruence and its link to emotional attitudes, such as judgements of liking.

Spatial Behaviour

The research summarised so far has dealt almost exclusively with human subjects. The study of spatial behaviour, or "proxemics" (Hall 1963) has involved examination of human as well as nonhuman behaviour. Hall (1959, 1963, 1966, 1974) suggests that individual populations, both human and animal, are controlled by physiological mechanisms that respond to density. He proposes the possibility that space is organised in such a way that it facilitates communication between individuals (Hall 1974). Like Hewes (1957), Hall notes that spatial differences between humans are often due to cultural norms.

Of particular importance are several research studies on spatial behaviour that have been conducted on nonhuman primate subjects, including howler monkeys (Carpenter 1942), spider monkeys (Carpenter 1942; Rondinelli & Klein 1976) rhesus macaques (Chance 1956), bonnet and long tailed macaques (Rosenblum, Kaufman & Stynes 1964), Japanese macaques (Mori 1977), lion-tailed

macaques (Hornshaw 1985), and stumptailed macaques (Lopez-Lujan, Ochoa, Mayagoitia & Mondragon-Ceballos 1989). Differences in spatial behaviour have been found to exist between species, between groups and between members of the same group (Hornshaw 1985). This is relevant to the study of postural congruence in monkeys because it establishes the significance of nonvocal communication in nonhuman primate interaction.

Primate Positional Behaviour

There is a growing body of literature involving the positional behaviour of nonhuman primates. Positional behaviour (Prost 1965) refers to both postural and locomotor patterns. Troubled by the disagreement among primatologists over definitions of primate locomotion, Prost (1965) introduced his classification of primate locomotor behaviour, which has since become the "definitional system" used by researchers interested in primate positional behaviour. Prost argues that locomotion and posture operate mutually exclusively of each other and details what can be described as locomotor and postural behaviour. He also takes into account environmental factors such as substrata, which influence positional behaviour.

Most research into primate positional behaviour emphasises physiology and habitat (Rose 1974, 1978; Mendel 1976; Morbeck 1977; Sugardjito & van Hooff 1986; Curtis & Feistner 1994; Gebo & Chapman 1995), evolutionary significance

(Mittermeier & Fleagle 1976; Fleagle 1976, 1978; Mittermeier 1978; Cant 1986; Fontaine 1990; Bicca-Marques & Calegaro-Marques 1993), and the implications for hominid evolution (Rose 1976; Fleagle 1976). Other studies on primate positional behaviour examine posture in the context of thermoregulation (Paterson 1982, 1986; Dahl, Bernstein & Williams 1982; Stelzner & Hausfater 1986; Stelzner 1988). While these studies do not take into account the communicative aspects of posture, they are relevant to the study of posture sharing in primates because they have established repertoires of positional behaviour for various primate species and have documented empirically the importance of environmental factors such as temperature and substrate use in the positional behaviour of primates.

Primate Communication

There are many books and articles devoted to the topic of primate communication, many dealing exclusively with vocal communication. However there have been a number of primatological studies conducted which examine aspects of nonverbal communication, and of these studies, a few are relevant to the research in postural congruence among primates.

One of the first studies on the use of posture and facial expression in communication found that rhesus macaques appropriately avoid fearful pictures of other macaques when all other "behavioural expression" is removed except posture and facial cues (Miller, Murphy & Mirsky 1959). In 1962, Hinde and Rowell published a paper dealing with posture and facial expression as communicative

devices among rhesus macaques. They identified specific postures and facial expressions which appeared to be associated with certain types of communication. Since that time, several studies on nonvocal communication in primates have emphasised facial expression (i.e. van Hooff 1962, 1967; Chalmers 1968; Christopher & Gelini 1977; Chevalier-Skolnikoff 1982; Zeller 1981, 1986), while body posture has largely been neglected.

Tail carriage was briefly thought to be a form of nonvocal communication in rhesus macaques (Sade 1971) and to be related to dominance rank and age in baboons (Hausfater 1977). Neither of these hypotheses could be supported with empirical evidence, and the concept of tail carriage as a communicative device was dismissed. Greeting movements among adult males were examined for patterns in a captive colony of baboons (Pelaez 1982). Results of this study indicate that hamadryas baboons demonstrated a broader repertoire of greeting movements than yellow baboons, leading the researcher to suggest that greeting movements are species-specific and related to their differing social systems. In a study involving rhesus macaques (Sade 1973), movements from a high to low physical position were correlated with "mood". Sade notes that "Darwin (1872) showed that moods which contrast markedly are accompanied by expressive behaviors which emphasize opposite or strongly contrasting characteristics," (Sade 1973). Sade identifies five distinctive moods based upon differing postures and movements observed in social displays.

From the perspective of the postural congruence research, two studies of primate communication are especially relevant. Rose (1977) examines the relationship of positional behaviour to maintenance and social activities in olive baboons and finds that positional behaviour directly contributes to both maintenance and social activities. He found by examining the distribution of positional behaviour over social activities, that animals of differing age, sex and social status exhibit particular patterns in postures and activities. Rose argues that positional, maintenance and social activities must evolve in order to maximise the chances of survival of "an individual within the group and of the group in time," (Rose 1977).

The second study of particular importance (Wade 1977) deals with "complementary" relationships between female rhesus macaques. Dyads of animals familiar and unfamiliar with each other are observed for "symmetric" (mutual) or "complementary" (non-mutual) behaviours. In nonhuman primates, normal and stable relationships are characterised by high levels of complementary behaviour, while relationships in change or conflict are characterised by high levels of symmetrical behaviour (Bateson 1972). Basic behaviours were recorded, but postural behaviour was not addressed in this study. The results indicate that dyads who were familiar with each other exhibited a higher degree of complementary behaviours while dyads of unfamiliar females showed higher degrees of symmetry, supporting the Bateson hypothesis (1972).

Wade suggests that this is due to established status relationships between the dyads of familiar females.

A Summary of the Literature Relevant to the Study of Posture Sharing

Review of the literature relevant to the study of postural congruence in nonhuman primates raises several interesting points. The study of postural congruence grew from the observations of one psychologist made in the 1960's. Scheflen is responsible for more than coining the term "postural congruence". His attitudes about communication may have in many ways shaped the study of posture sharing by later psychologists.

Scheflen's opinion that there is an evolutionary scheme of communicative development which links all "complex" communicative behaviours, like postural congruence, to verbal language, excludes the possibility that complex communication can occur independently of spoken conversation. Therefore the assumption is made that the potential for complex communication can only be found in human interaction. Scheflen's assumption that complex communicative behaviours such as postural congruence, are human specific has not directly been challenged, and all research into the phenomenon has exclusively involved human subjects. However, the Beattie and Beattie (1981) study is especially important because it is the only study to challenge the Scheflen hypothesis that postural congruence is linked to the verbal ability, suggesting that postural

congruence cannot be accounted for solely in terms related to linguistic communication.

Scheflen may have also influenced later researchers by choosing psychotherapy sessions as the environment in which he examined postural congruence. The Beattie and Beattie (1981) research is the only study that is situated in a naturalistic setting. All other research into the "natural" phenomenon of posture sharing has taken place in environments such as therapy sessions, classrooms, guidance situations, or other carefully constructed and controlled settings.

Much of the literature dealing with postural congruence is concerned with its function. There is a consensus among the researchers that it appears to function generally as a sign of "rapport". Beyond this, there are many details which are not agreed upon, including the relationship between posture sharing and emotions, postural congruence as an indicator of similarity in social status and social role, postural congruence working as a "tie sign", and postural congruence being used in an effort to establish rapport or influence the behaviour of another individual.

The scarcity of original research in the literature on postural congruence combined with the lack of consensus among researchers about the function, if not the expression of posture sharing, contribute to an environment where there is the

space and the need for further exploration. Old assumptions, largely left unchallenged need to be tested in order to gain more insight into the scope and role of posture sharing.

A Review of the Literature on Tonkean Macaques

Due to a rather long period of geological isolation, Sulawesi, Indonesia is home to many species of endemic flora and fauna (Groves 1976, 1980). Among the island's unique fauna, are several macaque taxa, which share many morphological and physiological traits and are thought to be derived from a single ancestral population (Fooden 1969; Takenaka et al 1987; Suryobroto 1992). Prior to a major revision in 1969, the monkeys were divided into two separate genera. The moor macaque (*M. maurus*) was the only monkey on Sulawesi to be allocated to the genus *Macaca*, while the others were placed into the genus *Cynopithecus* (e.g. *C. niger*).

This taxonomic classification was substantially altered by Jack Fooden in 1969, when he placed all the Sulawesi monkeys into the genus *Macaca*. Based on pelage colour and pattern, Fooden recognises seven distinct species including the crested macaque (*M. nigra*, formerly *C. niger* as the type species), Gorontalo macaque (*M. nigrescens*), Heck's macaque (*M. hecki*), Tonkean macaque (*M. tonkeana*), moor macaque (*M. maurus*), booted macaque (*M. ochreata*), and Muna-Buton macaque (*M. brunnescens*) (Fooden 1969). Another study (Groves & Thorington 1970) proposes to allocate all Sulawesi macaques to a single species,

M. nigra, since there is some evidence of intergradation among the macaques. Today, the Sulawesi macaques are classified as either seven species (Fooden 1969) or as four species (Groves 1980). Groves (1980) assigns full specific status to only four Sulawesi macaques and makes further distinctions at the subspecific level.

Tonkean macaques are large black monkeys who inhabit the central land mass and the eastern peninsula of Sulawesi. These are the areas of the island least accessible to and least populated by humans (Groves 1980). There have been observations of Tonkean hybridisation with neighbouring populations of Heck's macaques, booted macaques and moor macaques (Groves 1980; Watanabe, Lapasere & Tantu 1991; Watanabe, Matsumura, Watanabe & Hamada 1991; Supriatna, Froehlich, Erwin & Southwick 1992).

No in-depth population survey has been published for Tonkean macaques, and information on wild groups is mainly limited to descriptions of sightings and informal tallies (Groves 1980; Watanabe, Lapasere & Tantu 1991; Watanabe, Matsumura, Watanabe & Hamada 1991), hybridisation on the border zones (Groves 1980; Watanabe Lapasere & Tantu 1991; Takanaka et al 1992; Supriatna, Froehlich, Erwin & Southwick 1992) and interactions with humans as pests, pets or a food resource (Groves 1980; Babo 1995).

Research concerning the behaviour of Tonkean macaques only began to emerge during the 1970s (Thierry 1985), and is based exclusively on captive and semi-free ranging populations. Like other macaque species, the group structure of Tonkean macaques is matrilineal, however the social behaviour of Tonkean macaques differs in many ways from the typical macaque model.

Much of the research on the genus *Macaca*, especially the early work, focuses on Japanese (*M. fuscata*) and rhesus (*M. mulatta*) macaques (Fedigan 1982; Fedigan & Asquith 1991; Thierry, Anderson, Demaria, Desportes & Petit 1994). Both species are characterised by weak tolerance for other individuals, high levels of aggression and submission, strong kin ties, and a rigid system of dominance rank (Thierry, Anderson, Demaria, Desportes & Petit 1994). This became the general model for macaque social behaviour. Later, increased attention to the behaviour of other macaque species such as bonnet macaques (*M. radiata*) (Rosenblum & Kaufman 1967; Sugiyama 1971), Barbary macaques (*M. sylvanus*) (Taub 1980), lion-tailed macaques (*M. silenus*) (Johnson 1985) and the Sulawesi macaques (Thierry 1984, 1985a, 1985b; Thierry, Gautier & Peignot 1990; Matsumura 1991; Petit & Thierry 1992, 1994a, 1994b) demonstrated that many variations in social behaviour exist across the genus.

Four main behavioural traits characteristic of Tonkean macaques have been identified, including a relaxed system of dominance rank and social tolerance, high levels of conciliation, open relations and group cohesion, and

manipulative abilities (Thierry, Anderson, Demaria, Desportes & Petit 1992, 1994). Unlike rhesus and Japanese macaques, the dominance relationships among Tonkean macaques cannot be measured by examining the outcome of agonistic interactions. In many cases, the aggressee counter-attacks or lipsmacks to the aggressor rather than submitting, and the interaction becomes bidirectional with no clear winner or loser (Thierry 1985a). Tonkean macaques show no ritualised signal of submission (Thierry, Anderson, Desportes, Demaria & Petit 1994). Additionally, spontaneous displacements and supplantations are poor indicators of dominance in Tonkean macaques as they occur only rarely (Thierry, Anderson, Demaria, Desportes & Petit 1994) and a study of social grooming among adult females (Thierry, Gautier & Peignot 1990) reveals that there is no correlation between dominance rank and amount of social grooming received or performed.

To measure dominance relations among Tonkean macaques, researchers increased "the rate of supplantation and unidirectional aggression" (Thierry, Anderson, Demaria, Desportes & Petit 1994) by conducting competition tests around a source of fruit juice and examined factors such as which individual initiated the aggressive interaction and which one screeched (Desportes, Demaria & Thierry 1989). A low gradient of dominance was found to exist among Tonkean macaques, however, dominance relationships appear to remain quite stable from year to year (Thierry 1985a, personal communication 1997; Thierry, Anderson, Desportes & Petit 1994).

Tonkean macaques have an unusually large repertoire of affiliative and reconciliatory behaviours by macaque standards (Thierry 1984, 1985a, 1986a, 1986b; Thierry, Gautier & Peignot 1990; Demaria & Thierry 1992; Petit & Thierry 1994a). High rates of lipsmacking, clasping, and peaceful intervention in conflicts by a third individual are characteristic of this species. Tonkean macaques form cohesive groups marked by frequent contact calls (Masataka & Thierry 1993), close proximity and coordinated movement, however they appear to be especially aggressive towards other macaque species (Thierry, Anderson, Desportes, Demaria & Petit 1994).

Tonkean macaques show high levels of social tolerance among group members, even among unrelated individuals (Thierry 1985a, 1986). Biting occurs infrequently while affinitive displays are common and interaction among Tonkean macaques can occur between any combination of group members, regardless of age and sex classes or kinship ties (Thierry 1984, 1985a, 1985b, 1986a). Tonkean mothers appear to be quite permissive with their infants, and alloparental care is common among both related and unrelated individuals (Thierry 1985b, personal communication 1996; Thierry & Herrenschmidt 1985).

Tonkean macaques show high levels of interest in object manipulation, which has been observed to occur in several contexts. The spontaneous and repeated use of plant stems to reach nasal mucus has been reported in an adult male Tonkean macaque (Bayart 1982) as well as an adult female (cf. Thierry 1991),

who modifies the stem before inserting it into her nostril. A comparative study of interest in novel objects carried out on rhesus, longtail and Tonkean macaques found that the duration of object manipulation was longer in Tonkean macaques than in other macaques, especially so in comparison with the rhesus monkeys (reported in Thierry, Anderson, Demaria, Desportes & Petit 1994). Further research on object manipulation found that two adolescent male members of a Tonkean group spontaneously learned to use a metal rod to obtain honey placed out of direct reach (Anderson 1985). Another study demonstrated that while Tonkean macaques do not show signs of self-recognition, they do have the ability to spontaneously use a mirror to facilitate searches for food items (Anderson 1986).

Present Study

The present study was designed to explore various hypotheses about the expression and function of postural congruence. The primary objective was to test quantitatively for the first time whether or not postural congruence occurs in a nonhuman primate species, thereby directly testing the assumption that the phenomenon is human specific (contra Scheflen 1972).

The secondary objective of this study was to test factors including age, sex, dominance rank, body posture and social behaviour for their influence on posture sharing in order to provide more data that can be used to evaluate the following hypotheses:

(1) Postural congruence is correlated with similarity in social status and social roles (Scheflen 1964).

(2) Postural congruence functions as a general indicator of "relatedness" (Charny 1966).

(3) Postural congruence acts as a signal of pair bonds (Beattie & Beattie 1981).

(4) Postural congruence is a mechanism by which one can establish rapport or influence another individual's behaviour (La France & Ickes 1981).

Finally, the third objective of this project was to add to the scant collection of original research into postural congruence, another study of the phenomenon in a naturalistic setting.

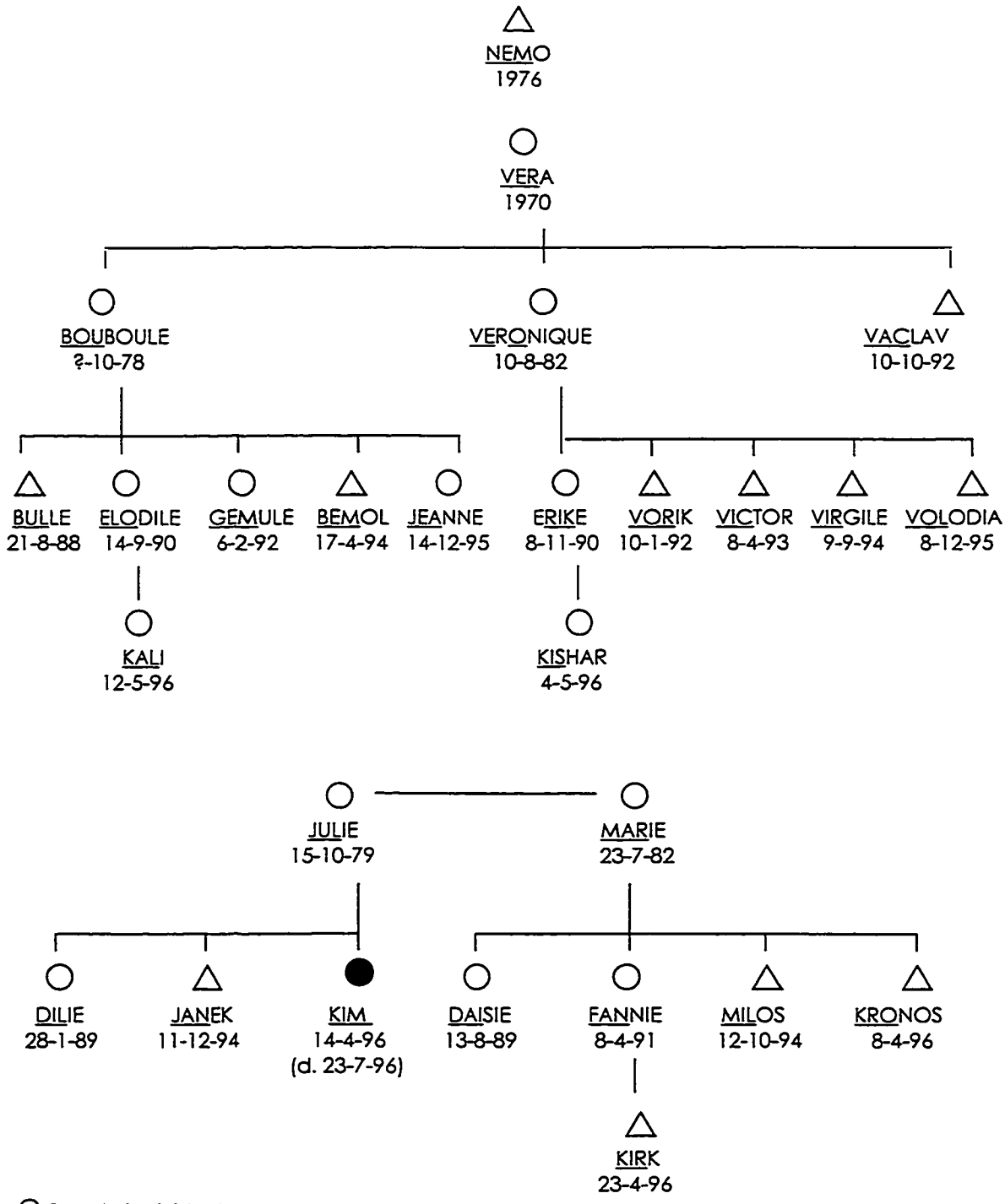
2. Materials and Methods

Study Site and Subjects

This study was conducted on one group of Tonkean macaques (*Macaca tonkeana*) housed at the Université Louis Pasteur Centre de Primatologie in Strasbourg, France. The monkeys were semi-free ranging within a wooded park of approximately one hectare surrounded by an electric fence. The group was composed of 26 individuals; two adult males, ten adult females, eight immature males, two immature females, two infant males and two infant females. Ages were calculated at the beginning of the study and individuals five years of age and older were classified as adults, individuals between six months and five years were classified as immatures, and individuals less than 6 months old were classified as infants. See Figure 2.1 for a diagram of the group composition indicating kin relationships, full names and name codes, sex, and ages when known.

Plate 2.1: A Juvenile Male Tonkean Macaque (*M. tonkeana*) at the Centre de Primatologie, Strasbourg, France in August 1996

Figure 2.1: Kin Diagram of the Tonkean Macaques at the Centre de Primatologie, Strasbourg, France, Summer and Fall 1996



In addition to food items obtained through foraging in the park, water and commercial monkey chow were available ad libitum and fresh fruits and vegetables were provided every Thursday afternoon to the group. The monkeys had free access to a heated indoor enclosure located inside the park.

Data Collection

Observations were generally conducted between 1200 and 1900 hours Monday through Friday and between 0800 and 1200 hours on Saturdays, over a period of four months, between July1 and October 31, 1996.

Observations stopped 30 minutes to one hour prior to the Thursday afternoon feedings and resumed 30 minutes to one hour after the fruit and vegetables had been distributed to the group.

Observation samples were 15 minutes in duration and rest periods of at least 5 minutes were taken between each sample in order to avoid observer fatigue. Each testing round included one 15 minute sample on each research subject, and an ad hoc selection order of observation was employed until the entire sample rotation was over. In total, 30 testing rounds were completed, and 7.5 hours of data were collected for each individual with the exception of two subjects (Fannie and Kirk) who were reincorporated into the group following medical treatment, during the 15th testing round. For these individuals, 16 testing

rounds were completed and 4 hours of observation were collected per animal. A total of 752 samples were collected, yielding 188 hours of raw data.

Data on social behaviours, body postures and episodes of postural congruence were recorded using a variant of the focal animal sampling technique (see Altmann, 1974) with pencil, paper and a stopwatch. This technique took into account the congruence or incongruence in body posture of the three animals ("nearest neighbours") in closest proximity to the focal animal within a radius of 3 metres. In order for a sample to begin, at least three individuals had to be within 3 metres of the focal animal. Samples were discarded if the focal animal was out of sight for three minutes or longer, and if there were no nearest neighbours within 3 metres for a total of three minutes or more during the sample. In the event that more than three animals were within 3 metres of the focal individual, the three subjects closest to the focal animal were observed. Because the three individuals always in closest proximity to the focal were observed, the identity of the nearest neighbours sometimes changed in the course of a sample if movement occurred among the nearest neighbours. Infants were not considered to be nearest neighbours unless they were moving independently of their mothers.

A "bullseye" plotting technique (see Figure 2.2) was employed alongside the focal animal sampling in order to record the body orientation of the focal subject and nearest neighbours as well as the proximity of the nearest neighbours to the focal individual. Records were made when changes in body orientation or

proximity to the focal subject occurred. This provided a visual record or map of the positions and body orientations of the nearest neighbours in relation to the focal animal and to each other.

Figure 2.2: Bullseye Plotting Diagram

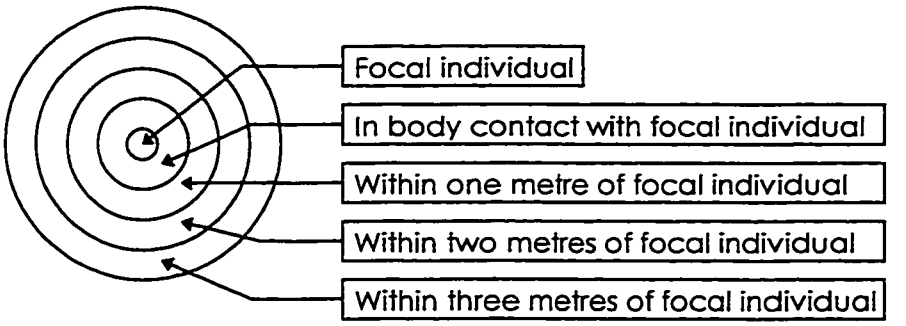


Fig. 2.2 shows the plotting technique used in data collection to record body orientation and proximity of focal subject and nearest neighbours

Social behaviour was recorded following a predetermined ethogram composed of 91 mutually exclusive behavioural categories. (See Appendix A for full ethogram.) Similarly, postural data were recorded following a predetermined catalogue of 73 body postures observed as regular components in the postural repertoire of Tonkean macaques. The basic features of the "posturogram" include sitting, standing, laying, movement and clinging postures. Variations are noted on arm positionings (tucked against body, extended beside body, reaching away from body, planted on substrate in front of body) leg positionings (tucked against body, extended away from body, angled upward against substrate, dangling downward from substrate), and head positionings (chin up or chin

tucked onto chest). The basic components were observed to occur with many combinations of the arm, leg and head positionings, leading to the construction of a large postural inventory. (See Appendix B for the full catalogue of body postures.)

No distinction was made between "mirror image" and "carbon copy" postural congruence in this study. Partial postural congruence, for example upper body postural congruence, was recorded as "incongruent", as only total body posture sharing was considered to be postural congruence for the purposes of this study.

Analysis and Statistical Tests

While the four infants were included in the data collection phase, they were not included in the analysis since they spent a large portion of their time clinging to their mothers and were therefore not moving independently. This severely restricted their postural repertoire and their potential for postural congruence with other group members. The analysis was conducted on the 22 group members who were 6 months or older at the beginning of the study period. A total of 646 samples, yielding 161.5 hours of data were analysed.

Due to the small sample size, a fine-grained analysis of age-sex classes was not appropriate, and it was necessary therefore to partition only at the broader levels of sex, age and rank. Because most female subjects were adults and most

male subjects were immatures, there is a large degree of overlap between sex and age categories in the analysis.

To determine whether the distribution of posture sharing episodes were random or nonrandom throughout the 15 minute samples, chi square goodness of fit tests were conducted on 10 samples for each focal individual. Samples were selected where at least one nearest neighbour was in proximity to the focal individual for the entire 900 seconds and an effort was made to test a variety of nearest neighbour individuals. The samples were divided into fifteen 60 second units and the chi square statistic was computed by comparing the actual distribution of posture sharing with a set of expected frequencies. A total of 220 chi square tests were conducted. The alpha level was set at .001. Basic descriptive (*Z* scores) and inferential (*t* tests, chi square) statistics were used to show the effect of sex, age and rank on postural congruence as well as the postures and behaviours most frequently associated with postural congruence. Postures were divided into four broad categories and behaviours into five broad categories to provide a general picture of how postural congruence is distributed among the postural and behavioural inventories.

3. Results

The General Distribution of Postural Congruence in the Study Group

A total of 4660 episodes of full body postural congruence were observed to occur among the subjects during this study. The number of posture sharing episodes ranged from 0 to 23 per 15 minute sample, with an overall average of 7.2 episodes per sample.

Table 3.1: A Breakdown of the 4660 Posture Sharing Episodes by Sex, Age and Rank Categories

Sex	Frequency (f)	Percentage (%)	Rate Per Sample
Female	3005	64.5	4.6
Male	1655	35.5	2.6
	N = 4660	100.00%	7.2
Age	**Frequency (f)**	**Percentage (%)**	**Rate Per Sample**
Adult	3011	64.6	4.7
Immature	1649	35.4	2.5
	N = 4660	100.00%	7.2
Rank	**Frequency (f)**	**Percentage (%)**	**Rate Per Sample**
High	2826	60.6	4.4
Low	1834	39.4	2.8
	N = 4660	100.00%	7.2

Of the 161.5 hours of observation, 92 hours 24 minutes and 49 seconds were spent in postural congruence with at least one nearest neighbour. Therefore, group members were engaged in posture sharing behaviour 57.2% of the overall observation time, however the percentage of time spent in postural congruence per 15 minute sample ranged from 0 to 100%. The duration of posture sharing episodes ranged from 1 to 900 seconds per 15 minute sample.

Table 3.2: A Breakdown of the Duration Spent in Postural Congruence by Sex, Age and Rank Categories

Sex	Mean Duration per Posture Sharing Bout	Percentage (%) of Total *PC Duration	Percentage (%) of Total Time by Sex
Female	97.7 seconds	64.3	68.7%
Male	87.8 seconds	35.7	44.0%
		100.0%	
Age	**Mean Duration per Posture Sharing Bout**	**Percentage (%) of Total *PC Duration**	**Percentage (%) of Total Time by Age**
Adult	97.6 seconds	64.2	68.6%
Immature	88.0 seconds	35.8	44.1%
		100.0%	
Rank	**Mean Duration per Posture Sharing Bout**	**Percentage (%) of Total *PC Duration**	**Percentage (%) of Total Time by Rank**
High	93.7 seconds	63.3	52.7%
Low	94.8 seconds	36.7	69.1%
		100.0%	

*PC = Postural Congruence

Timing in Postural Congruence

Posture sharing behaviour was indeed observed to occur in the study population. To determine if there was a temporal rhythm in the occurrence of postural congruence, 220 chi square goodness of fit tests were conducted, with an alpha level of $p<.001$ for significance. Table 3.3 displays the results from all 220 tests. The distribution of posture sharing was found to vary significantly from minute to minute across the 15 minute samples. In each case, the test statistic fell well into the critical region beginning at 36.123, with results ranging from 73.32 to 773.81. This indicates that postural congruence occurred in a nonrandom fashion in the study population, and that the observed pattern of posture sharing was unlikely to have occurred by random chance alone.

Table 3.3: Test Statistics (χ^2 obtained) from 220 Chi Square Goodness of Fit Tests

	1	2	3	4	5	6	7	8	9	10
NEM	538.59	511.52	446.80	614.44	439.34	479.60	288.21	490.79	494.90	375.47
BUL	226.98	461.62	529.01	562.80	624.62	343.40	112.70	301.36	494.00	540.91
VOR	180.23	555.24	633.90	362.62	737.83	373.37	538.95	460.56	425.43	480.50
VAC	482.19	715.62	659.74	452.91	559.72	639.68	559.47	673.19	539.46	423.95
VIC	271.63	571.64	572.74	638.87	542.28	569.11	575.52	477.51	334.72	453.51
VIR	653.45	670.06	521.47	437.61	597.61	246.29	292.10	453.11	773.81	408.22
VOL	472.96	593.04	686.85	336.00	589.56	695.75	524.78	545.83	438.65	667.99
BEM	153.11	536.80	474.29	606.56	674.75	429.70	560.76	518.99	444.70	485.75
MIL	346.98	521.45	525.88	498.92	531.05	181.52	686.85	497.98	612.46	684.28
JAN	418.08	613.89	645.97	670.36	214.60	547.69	355.94	572.19	481.75	758.30
VER	450.60	581.31	268.53	635.61	587.28	559.27	472.56	646.23	347.49	544.85
VEO	315.96	560.60	325.10	521.96	418.67	422.36	373.82	503.94	206.04	553.20
BOU	480.55	357.09	364.70	470.96	270.58	484.39	537.14	551.33	148.68	408.00
RIK	419.14	338.42	364.62	522.63	424.95	338.54	394.72	494.53	181.49	176.01
ELO	281.75	367.86	642.44	179.39	565.56	258.87	255.75	73.32	505.93	261.42
GEM	189.65	485.14	563.06	606.00	498.26	532.21	375.92	267.40	594.60	640.26
JEA	438.26	723.47	417.45	643.70	553.75	617.31	339.18	507.12	406.01	252.00
JUL	297.52	414.16	659.49	208.61	300.30	328.88	318.92	374.86	492.62	502.03
MAR	417.93	331.30	387.71	336.45	178.09	369.49	276.24	470.82	252.26	344.04
DIL	238.66	306.69	473.68	560.46	355.27	199.97	361.01	289.65	417.43	314.67
DAI	639.93	539.05	656.82	585.23	445.04	409.54	693.59	392.60	408.24	157.78
FAN	382.92	468.97	305.81	216.24	483.41	522.33	368.43	381.79	264.89	258.14

Table 3.3 displays the results of all 10 chi square tests conducted for each focal individual. All tests indicate that postural congruence occurred in the study population in a nonrandom fashion, and the observed pattern of posture sharing was unlikely to have occurred by random chance alone. See Fig. 2.1 for full names and codes of focal subjects.

In addition to the chi square goodness of fit tests, an all-data t-test was conducted to cover all of the non-selected cases, and to verify the results of the selected ones. The difference between all time spent in postural congruence by focal subjects and all time spent not in postural congruence was tested and found to be significant ($t = 16.49$, $df = 21$, $p < .001$).

The Effect of Sex on Posture Sharing

The influence of sex on the frequency and duration of postural congruence was examined in the data set. Of the total 4660 episodes of observed postural congruence, 3005 were attributed to female focal individuals, while 1655 were attributed to male focal subjects. Therefore, females accounted for 64.5% of all posture sharing episodes while males accounted for 35.5%. Female subjects showed a significant difference in frequency of posture sharing from the population as a whole ($z = 11.98$, $p<.01$), as did the male subjects ($z = -10$, $p <.01$). On average, females engaged in 4.6 episodes of postural congruence per 15 minute sample, while males engaged in 2.6 episodes per sample.

Plate 3.1 : Two Adult Females Engaging In Postural Congruence at the Strasbourg Primate Centre , August 1996.

Females were observed to spend 68.7% and males 44% of their overall time posture sharing with at least one other individual. Female subjects spent significantly more time engaging in postural congruence than the study group as a whole ($z = 11.98$, $p<.01$), while males spent significantly less ($z = -9.99$, $p<.01$). Male focal individuals not only spent less of their time posture sharing than females, but the average duration of their posture sharing episodes was shorter at 87.8 seconds, than for female subjects, who averaged 97.7 seconds per episode.

Figure 3.1: Frequency of Posture Sharing Episodes by Sex

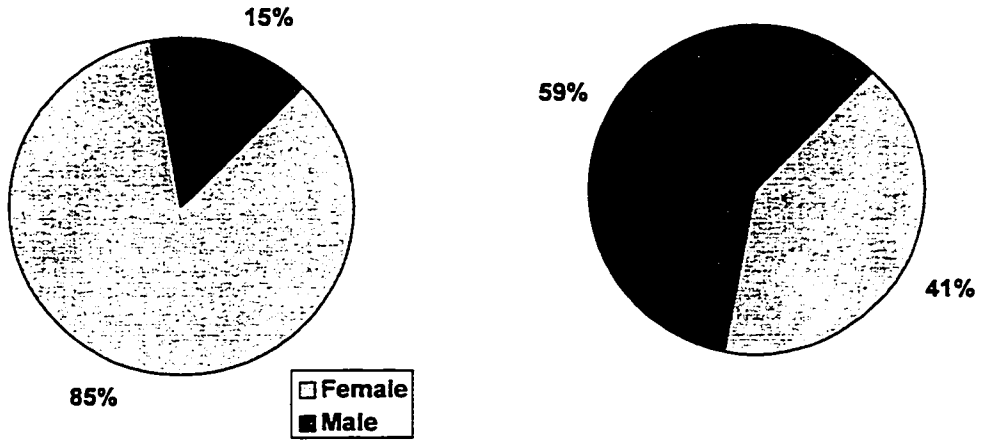


Fig. 3.1 shows that both female and male study subjects engaged more frequently in posture sharing behaviour with same-sex partners than they did with partners of the opposite sex.

The influence of sex on partner preference was also examined. Figure 3.1 shows that there was a bias in favour of same-sex posture sharing partners. Female focal subjects engaged in posture sharing behaviour with other females much more often than with males ($t = 11.15$, $df = 11$, $p<.01$) and male focal subjects engaged in postural congruence with other male partners more frequently than with female partners ($t = 9.01$, $df = 9$, $p<.01$). Additionally, female subjects engaged in significantly longer periods of postural congruence when their partner was also female ($t = 34.24$, $df = 11$, $p<.01$). While male subjects showed a slight increase in mean duration of postural congruence when their partner was also male (as indicated in Figure 3.2), the difference was not significant ($p = 0.08$).

Figure 3.2: Mean Duration of Posture Sharing Episodes by Sex

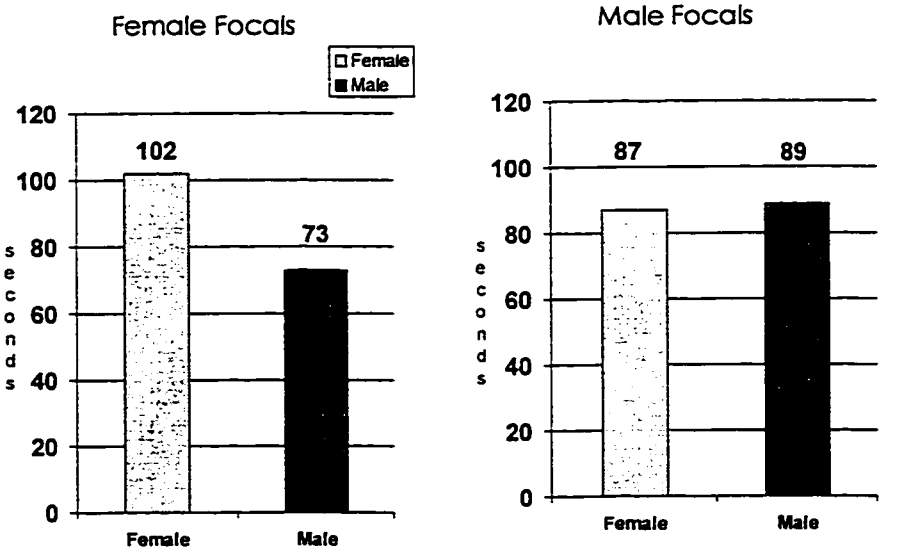


Fig. 3.2 shows that female focal subjects engaged in significantly longer episodes of posture sharing with other females than they did with males. Male focal individuals engaged in slightly longer episodes of postural congruence with other males than with females, but the difference was insignificant.

The Effect of Age on Posture Sharing

Age was examined for its influence on the frequency and duration of postural congruence. Adult focal individuals accounted for 64.6%, or 3011 of the 4660 total episodes of posture sharing, while immature individuals accounted for 35.4%, or 1649 episodes. Adults show a higher frequency of posture sharing behaviour than the whole group ($z = 11.99$, $p<.01$), and immature subjects show a lower frequency than the study group ($z = -10$, $p<.01$). The average number of posture sharing episodes per 15 minute sample period by an adult individual was 4.7 episodes, while the average for an immature individual was 2.5 episodes.

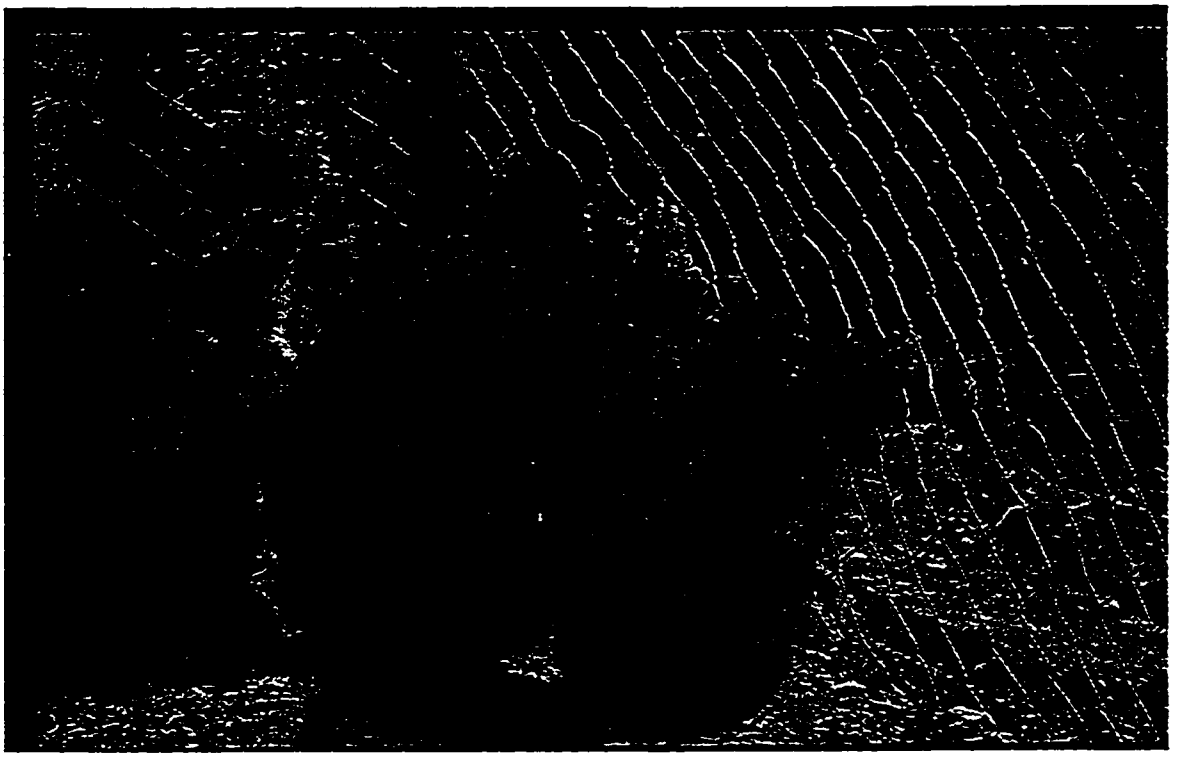


Plate 3.2 : Posture Sharing Between Two Males
An adult male and an immature male engage in posture sharing behaviour, August 1996

Adult focal subjects spent 68.6% of their overall time in postural congruence with at least one nearest neighbour, while immature focal subjects spent 44.1% of their overall time posture sharing. In comparison with the whole population, adults spent more of their time engaging in postural congruence ($z = 11.98$, $p<.01$), and immatures spent significantly less ($z = -9.99$, $p<.01$). The mean duration of posture sharing episodes by adult individuals was longer, at 97.6 seconds than the mean duration by immature focals at 88 seconds per posture sharing episode.

Figure 3.3: Frequency of Posture Sharing Episodes by Age

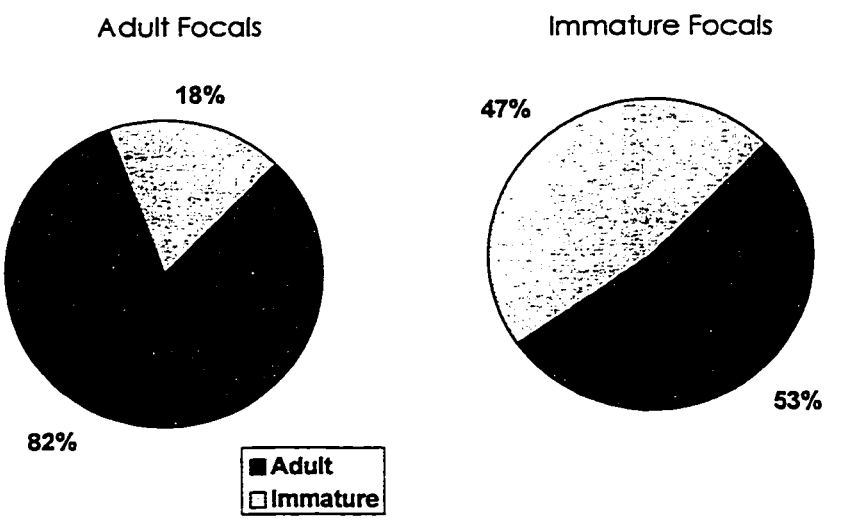


Fig. 3.3 shows that adult subjects engaged in postural congruence much more frequently with other adults, while immature focal subjects divided their posture sharing episodes more equally between adult and immature posture sharing partners.

The influence of age on partner preference was also tested in this study. Adults clearly preferred other adult group members to immature group members

as posture sharing partners ($t = 9.24$, $df = 11$, $p<.01$). Immature subjects spread their episodes of postural congruence more evenly between adults and immatures, showing a slight preference for adult posture sharing partners, but the difference was not significant ($p = 0.059$). As shown in Figure 3.4, adult focal subjects exhibited significantly longer episodes of posture sharing when their partners were other adults than when they were engaged in posture sharing with immature individuals ($t = 27.31$, $df = 11$, $p<.01$), and immatures also maintained longer periods of postural congruence with adults than with other immature individuals ($t = 18.08$, $df = 9$, $p<.01$).

Figure 3.4: Mean Duration of Posture Sharing Episodes by Age

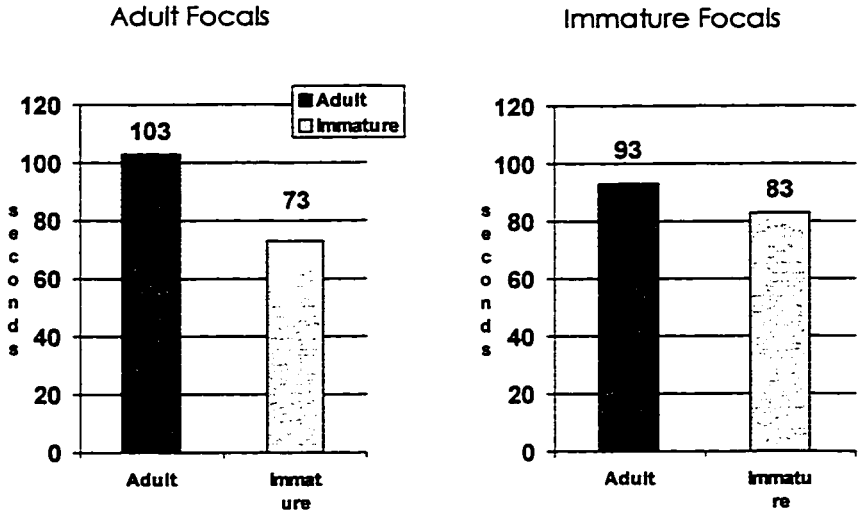


Fig. 3.4 shows that both adult and immature study subjects engaged in longer episodes of postural congruence when the posture sharing partners were adult individuals.

The Effect of Dominance Rank on Posture Sharing

Dominance rank, like sex and age, was examined for its influence on the frequency and duration of posture sharing episodes in the study population of Tonkean macaques. Of the total number of observed episodes of postural congruence in this study, 2826 were attributed to high ranking focal subjects, while 1834 were attributed to low ranking focal subjects. Therefore, high ranking subjects accounted for 60.6% of the group's posture sharing episodes, while low ranking subjects accounted for 39.4%. However, high ranking individuals had a lower mean frequency of postural congruence when compared with the entire study population ($z = -15$, $p<.01$). The average number of posture sharing episodes for the 15 high ranking individuals was 188.4 episodes per individual, ranging from 112 to 276. The 7 low ranking individuals had a higher mean frequency of postural congruence in comparison to the whole study group ($z = 6.99$, $p<.01$), averaging 262 episodes each, and ranging from 163 to 387.

While high ranking focal individuals may have accounted for a higher percentage of the total time spent in postural congruence, low ranking subjects spent more of their overall time in postural congruence with at least one other individual in comparison to the whole study group ($z = 6.98$, $p<.01$). High ranking subjects spent less time engaging in posture sharing behaviour than the population in general ($z = -14.98$, $p<.01$). Low ranking focals spent 69.1% of their time in postural congruence and high ranking focals spent 52.7% of their time posture sharing with at least one other individual. The mean duration of posture

sharing episodes by high ranking individuals averaged 93.7 seconds per episode, while low ranking individuals averaged 94.8 seconds per episode.

Figure 3.5: Frequency of Posture Sharing Episodes by Rank

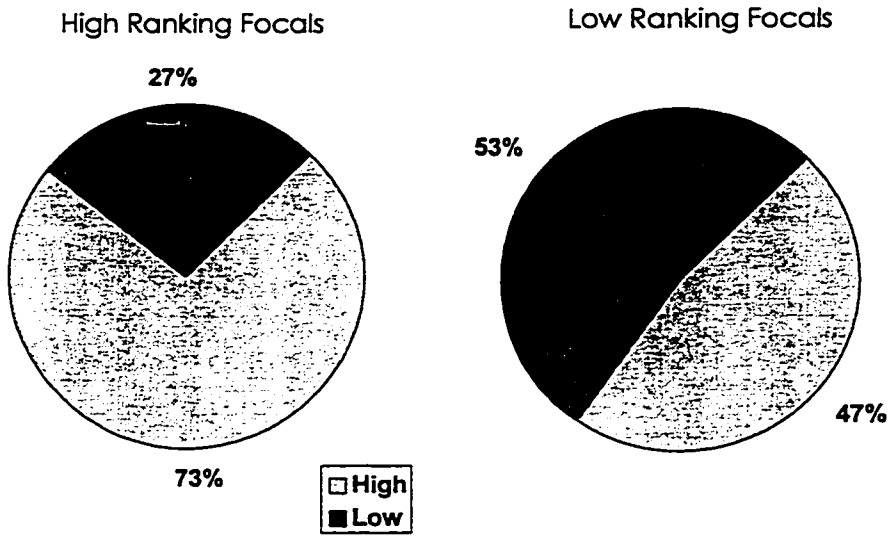


Fig. 3.5 shows that while high ranking focal subjects engaged in posture sharing much more frequently with other high ranking individuals, low ranking study subjects divided their posture sharing episodes more equally between high and low ranking partners.

Dominance rank also appears to have had an effect on partner preference. Figure 3.5 shows that there was a strong preference among high ranking focals to favour other high ranking individuals as posture sharing partners ($t = 18.91$, $df = 14$, $p<.01$). While low ranking subjects showed a slight preference for other low ranking individuals as posture sharing partners, the difference was not significant ($p = 0.127$). Dominance rank did not have a significant influence

on the mean duration of posture sharing episodes for high ranking individuals ($p = 0.606$) nor low ranking individuals ($p = 0.102$), as indicated in Figure 3.6.

Figure 3.6: Mean Duration of Posture Sharing Episodes by Rank

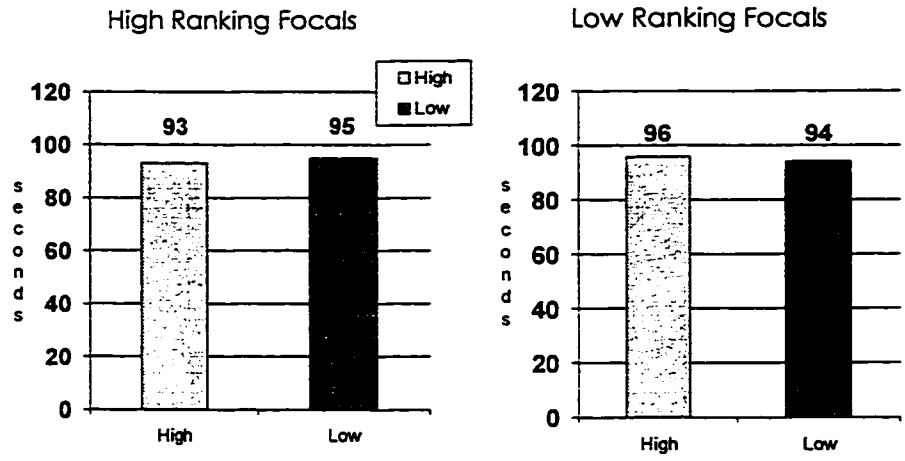


Fig. 3.6 shows that no significant difference in mean duration of postural congruence was observed to occur among high or low ranking study subjects.

Postural Congruence and Body Posture

The Tonkean macaques in the study group were observed to have a postural repertoire of 73 distinct postures. Male subjects were observed to use the entire postural repertoire, while female subjects were observed to use only 56 different postures. Immature subjects used 71 different postures, and adults used 56 throughout the total observation period. High ranking individuals showed a wider range of postures at 71, than low ranking individuals did at 60. Table 3.4

shows the distribution of all observed body postures across sex, age and rank categories.

Table 3.4: The Distribution of Postures Across Sex, Age and Rank Categories

Posture	Male	Female	Adult	Immature	High Rank	Low Rank
cs	★	★	★	★	★	★
os	★	★	★	★	★	★
hos	★	★	★	★	★	★
bl	★	★	★	★	★	★
ob	★	★	★	★	★	★
hob	★	★	★	★	★	★
cat	★	★	★	★	★	★
ocat	★	★	★	★	★	★
ccat	★	★	★	★	★	★
rcat	★	★	★	★	★	★
catex	★		★		★	
cex	★	★	★	★	★	★
chex	★	★	★	★	★	★
cvex	★	★	★	★	★	
oex	★	★	★	★	★	★
ohex	★	★	★	★	★	★
hoex	★	★	★	★	★	★
hohex	★	★	★	★	★	★
cch	★	★	★	★	★	★
och	★			★	★	
chch	★	★	★	★	★	★
hoch	★			★	★	★
hohch	★	★	★	★	★	★
ohch	★			★	★	
rea	★	★	★	★	★	★
hrea	★	★	★	★	★	★
reaex	★	★		★	★	
reahex	★	★	★	★	★	★
hreaex	★			★	★	★
hreahex	★	★	★	★	★	★
cv	★	★	★	★	★	★
ov	★	★	★	★	★	★
hov	★	★	★	★	★	★
chv	★	★	★	★	★	★
ohv	★	★	★	★	★	★
hohv	★	★	★	★	★	★
cvb	★	★		★	★	
ovb	★		★	★	★	
reav	★		★	★	★	★
reahv	★	★		★	★	★
hreav	★		★	★	★	★
hreahv	★	★	★	★	★	★
reach	★			★	★	

reahch	★			★	★	★
hreach	★			★	★	
hreahch	★			★		★
cvch	★			★	★	★
hovch	★			★	★	★
qs	★	★	★	★	★	★
tri	★	★	★	★	★	★
cr	★	★	★	★	★	★
bicon	★	★	★	★	★	★
lat	★	★	★	★	★	★
sup	★	★	★	★	★	★
spr	★	★	★	★	★	★
pc	★	★	★	★	★	★
cu	★	★	★	★	★	★
uex	★	★		★	★	
lex	★	★		★	★	
tw	★	★	★	★	★	★
r	★	★	★	★	★	★
w	★	★	★	★	★	★
clu	★	★	★	★	★	★
cld	★	★	★	★	★	★
qucl	★	★	★	★	★	★
tricl	★			★		★
ja	★	★	★		★	★
jd	★	★	★	★	★	★
sus	★	★	★	★	★	★
vcl	★	★		★	★	
sli	★		★	★	★	
ind	★		★	★	★	★
o/s	★	★	★	★	★	★
73	73	56	56	71	71	60

Table 3.4 shows the distribution of all observed body postures across sex, age and rank categories. See Appendix B for posture codes and definitions.

Postural congruence was observed to occur in only 37 of the 73 postures. Table 3.5 shows the breakdown of body postures into the four broad categories used in the analysis and the particular postures associated with postural congruence, including sitting, standing, laying and other.

Table 3.5: Body Posture and Postural Congruence by Broad Category:

★ Indicates posture is associated with postural congruence

SIT		STAND	LIE	OTHER
★ cs	★ rea	★ qs	★ lat	★ r
★ os	★ hrea	★ tri	★ sup	★ w
★ hos	reaex	★ cr	spr	★ clu
★ bl	reahex	★ bicon	pc	cld
ob	hreaex		cu	qucl
★ hob	hreahex		uex	tricl
★ cat	★ cv		lex	ja
★ ocat	★ ov		tw	jd
★ ccat	★ hov			★ sus
★ rcat	★ chv			★ vcl
catex	★ ohv			sli
★ cex	★ hohv			ind
chex	★ cvb			o/s
cvex	★ ovb			
★ oex	reav			
ohex	reahv			
hoex	hreav			
hohex	hreahv			
★ cch	reach			
★ och	reahch			
★ chch	hreach			
★ hoch	hreahch			
★ hohch	cvch			
ohch	hovch			
48		4	8	13

Table 3.5 shows the breakdown of body postures into the four broad categories and indicates the postures associated with postural congruence. See Appendix B for posture codes and definitions.

An examination of the distribution of the total seconds in postural congruence shows that the phenomenon occurred almost always in association with sitting postures (see Table 3.6). A chi square test for independence was conducted and it was confirmed that body posture does indeed have an effect on the amount of time spent in postural congruence ($\chi^2 = 81.99$, df = 12, $p<.001$).

Table 3.6: The Distribution of Seconds in Postural Congruence by Broad Postural Category

Category	# Posture Sharing Seconds	Percentage (%)
Sit	315389	94.8
Stand	9647	2.9
Lay	4657	1.4
Other	2996	0.9
	332689	100.0%

Postural Congruence and Behaviour

Over the course of the study, 91 behaviours were observed to occur among the Tonkean macaques, representing a complete ethogram list. (See Appendix A for full descriptions.) Sex did not appear to influence the range of behaviours displayed, as females engaged in 74 and males 75 of the total behavioural repertoire. A greater difference in behaviour was observed between adult and immature focal individuals. Adults engaged in 73 of the 91 behaviours, while immatures engaged in 81. A greater difference still was observed to occur between low and high ranking subjects. Low ranking subjects participated in only 68 different behaviours, while high ranking subjects participated in 86.

Table 3.7: The Distribution of Behaviours Across Sex, Age and Rank Categories:

Behaviours	Male	Female	Mature	Immature	High Rank	Low Rank
ag	★	★	★	★	★	★
ap	★	★	★	★	★	★
bou	★	★	★	★	★	
btd	★	★	★	★	★	★
ca	★			★	★	
cd		★	★		★	★
ch	★	★	★	★	★	★
clsp		★	★			★
cw	★	★	★	★	★	★
dg	★			★	★	★
dr	★	★	★	★	★	★
ds	★		★	★	★	
eb	★	★	★	★	★	★
ed	★			★	★	★
el	★			★	★	
fe	★	★	★	★	★	★
fi	★			★	★	★
fl		★	★			★
fo	★	★	★	★	★	★
fol	★	★	★	★		★
gr	★	★	★	★	★	★
grb	★	★	★	★	★	★
hh	★		★		★	
ind	★			★	★	★
ins	★		★	★	★	
lea	★	★	★	★	★	★
li	★	★	★	★	★	★
lo	★	★	★	★	★	★
lp	★	★	★	★	★	★
mag	★	★	★	★	★	★
man	★	★	★	★	★	★
map	★	★	★	★	★	★
mas	★		★	★	★	★
mbtd	★	★	★	★	★	★
mgr	★	★	★	★	★	★
mlp	★	★	★	★	★	★
mmap	★	★	★	★	★	★
mou	★	★	★	★	★	★
mt	★	★	★	★	★	★
nu	★	★	★	★	★	★
o/s	★	★	★	★	★	★
pl	★	★	★	★	★	★
plbi	★			★	★	
pos	★		★	★	★	
pr		★	★	★	★	★
rag	★	★	★	★	★	★
rap	★	★	★	★	★	★
rb	★	★	★	★	★	★
rbtd	★	★	★	★	★	★
rcd	★	★	★	★	★	★

rch	★			★	★	★
rclsp	★	★	★	★	★	★
rds	★	★	★	★	★	★
re	★	★	★	★	★	★
res		★	★		★	★
rgr	★	★	★	★	★	★
rgrb		★		★	★	
rh	★	★	★	★	★	★
rins		★	★		★	
rlea	★	★	★	★	★	★
rlp	★	★	★	★	★	★
rmap	★	★	★	★	★	★
rmou		★		★	★	
rmt	★	★	★	★	★	★
rpr	★	★	★	★	★	★
rres	★	★		★	★	
rsb	★	★	★	★	★	★
rtou	★	★	★	★	★	★
rvcl		★	★			★
sb	★	★	★	★	★	★
sc	★	★	★	★	★	★
scr	★	★	★	★	★	★
sgr	★	★	★	★	★	★
ss	★	★	★	★	★	★
sta	★	★	★	★	★	★
str		★		★	★	
stre	★	★	★	★	★	
tou	★	★	★	★	★	★
vcl	★	★		★	★	
vo	★	★	★	★	★	★
wr	★			★	★	★
yn	★		★	★	★	
btd-tou	★			★	★	
rag-lp		★	★		★	
rgr-gr	★	★	★	★	★	★
rgr-man		★		★	★	
rgr-mou		★		★	★	
rgr-sc	★	★	★	★	★	★
rgr-scr		★	★		★	
rgr-sgr	★	★	★	★	★	★
sc-cw	★		★	★	★	
91	77	74	74	82	87	69

Table 3.7 shows the distribution of all observed behaviours across sex, age and rank categories. See Appendix A for behaviour codes and definitions.

Postural congruence was observed to occur in 63 of the 91 behaviours. The behaviours were partitioned into five broad categories, which included social, feed/forage, rest, movement and other behaviours for the analysis. Table 3.8

shows the breakdown of the behaviours into the five broad categories, and the behaviours associated with postural congruence.

Table 3.8: Behaviour and Postural Congruence by Broad Category:

★ Indicates behaviour is associated with postural congruence

SOCIAL		FEED/FORAGE	REST	MOVEMENT	OTHER
★ ag	★ rcd	dr	★ re	★ lo	bou
★ ap	★ rch	★ eb			ca
★ btd	★ rclsp	★ ed			★ cw
cd	★ rds	★ fe			dg
★ ch	res	★ fo			★ el
clsp	★ rgr				ind
★ ds	rgrb				★ li
★ fi	★ rins				★ man
fl	★ rlea				★ mas
★ fol	★ rlp				o/s
★ gr	★ rmap				★ rb
grb	rmou				★ rh
hh	rmt				★ sc
★ ins	★ rpr				★ scr
lea	rres				★ sgr
★ lp	★ rsb				★ ss
★ mag	★ rtou				★ sta
★ map	★ rvcl				stre
★ mbtd	★ sb				★ yn
★ mgr	str				★ sc-cw
★ mlp	★ tou				
★ mmap	vcl				
★ mou	★ vo				
mt	★ wr				
★ nu	btd-tou				
★ pl	rag-lp				
plbi	★ rgr-gr				
pos	rgr-man				
★ pr	★ rgr-mou				
★ rag	★ rgr-sc				
★ rap	rgr-scr				
★ rbtd	rgr-sgr				
64		5	1	1	20

Table 3.8 shows the breakdown of behaviours into the five broad categories and indicates the behaviours associated with postural congruence. See Appendix A for behaviour codes and definitions.

An inspection of the distribution of total seconds spent in postural congruence by the study population indicates that posture sharing occurred mainly in the contexts of social and resting behaviours, as seen in Table 3.9.

Table 3.9: The Distribution of Seconds in Postural Congruence by Broad Behavioural Category

Category	# Posture Sharing Seconds	Percentage (%)
Social	130747	39.3
Rest	129418	38.9
Feed/Forage	22955	6.9
Movement	3113	0.9
Other	46456	14
	332689	100.0%

A chi square test for independence revealed that the amount of time spent posture sharing is dependent on behavioural category ($\chi^2 = 94.01$, df =16, $p<.001$).

4. Discussion

This study has revealed that in addition to a large and diverse repertoire of social behaviours, Tonkean macaques have an extensive inventory of distinct body postures which they use on a regular basis. This is especially important for the purpose of studying the phenomenon of postural congruence, because it reduces the chance that posture sharing is the consequence of random coincidence in body posture due to a small number of regularly observed body postures (Scheflen 1964). This study has shown quantitatively that postural congruence does in fact occur in a nonhuman primate species. The study population of Tonkean macaques spent more than half of the observation time (57.2% of the total time) engaged in posture sharing behaviour with at least one other group member. This finding contrasts with the hypothesis that "complex" communicative behaviours such as postural congruence, are linked to verbal communication (Scheflen 1972), since the study subjects were not capable of verbal interactions and yet exhibited high levels of postural congruence. This complements the Beattie and Beattie (1981) research finding that posture sharing occurs among humans in the near-absence of spoken conversation on a hot, crowded beach, and supports their accompanying suggestion that high levels of posture sharing "cannot be accounted for in terms of basic linguistic communication," therefore, postural congruence must be mediated through visual rather than spoken cues.

An important implication of the evidence for posture sharing among nonhuman primates is that it stands in direct opposition to the enduring assumption that this particular phenomenon, as well as other complex communicative behaviours are specifically human (Scheflen 1972). Like the study of interactional synchrony in capuchin monkeys (Slavoff 1997), the findings of this study on posture sharing in Tonkean macaques lend support to the hypothesis that co-ordinated interaction developed long before vocal communication systems did. This in turn supports a gestural origins theory of language in early human communication development (Armstrong, Stokoe & Wilcox 1995).

In this study, factors such as sex, age and dominance rank were examined for their influence on postural congruence with a view to evaluating several hypotheses about the expression and function of posture sharing. It is important to note here that the group composition with respect to sex and age, makes it difficult to separate sex and age effects, since 10 out of the 12 adults were female, and 8 out of the 10 immature subjects were male.

The results have shown that females spent more of their time (68.7%) engaged in postural congruence than males did (44%) and that the average length of posture sharing episodes was longer for females than for males. The age data is almost identical to the sex data, with adults spending a greater amount of time posture sharing and showing a longer average duration than immature subjects. Low ranking individuals spent more of their overall time in

postural congruence (69.1%) than high ranking subjects did (52.7%) but the average duration of posture sharing episodes did not vary significantly ($p>.01$) between high and low ranking subjects.

Sex, age and rank did appear to have a significant influence on partner preference. Female focal individuals engaged in posture sharing more often and for longer durations with other females than they did with males. Males engaged in posture sharing more often with other males than with females, but the duration of the episodes did not vary much between male or female partners of male focal individuals. Similarly, adult subjects preferred other adults as partners in postural congruence and the length of posture sharing episodes increased when their partner was also an adult group member. Immature subjects, on the other hand, spread their episodes of postural congruence almost evenly between adult and other immature partners, showing only a slight preference for adult partners. Immature focal subjects engaged in longer episodes of posture sharing with adults than with other immature group members. Dominance rank did not appear to have an effect on the length of posture sharing episodes, but high ranking subjects showed a strong preference for other high ranking posture sharing partners, while low ranking subjects showed only a slight preference for partners also of low rank.

These results show that there is considerable variability in the expression of postural congruence across sex, age and dominance rank categories and with

respect to partner preference. The results of this study on posture sharing in Tonkean macaques show both some agreement with and some contrast to previous work on posture sharing in humans. Specific hypotheses about the functional significance of postural congruence, including posture sharing as an indicator of social status (Scheflen 1964), social roles (Scheflen 1964), and general "relatedness" (Charny 1964), that it functions as a "tie sign" (Beattie & Beattie 1981) and as a mechanism by which one can establish rapport or influence another individual's behaviour (LaFrance & Ickes 1981), are examined in light of the evidence for posture sharing in this macaque group.

The results of the present study are not incompatible with the Scheflen hypothesis that postural congruence is correlated to similarity in social status (Scheflen 1964). The study population was made up of two matrilines, one high ranking and one low ranking, and rank was determined by which matriline the individuals belonged to. Since rank and kinship could not be separated in this study, "social status" in this case incorporated both dominance rank and kinship. High ranking subjects overwhelmingly preferred to engage in posture sharing with other high ranking individuals, favouring high ranking partners for 73% of their posture sharing episodes. Low ranking focal subjects showed a slight preference for partners of similar rank, but divided their episodes more evenly between low (53%) and high (47%) ranking partners. It is not clear whether the preference to engage in posture sharing with individuals of similar social status is rooted in dominance rank, kinship, or both.

Scheflen also hypothesised that in addition to being correlated with similarity in social status, postural congruence is correlated with similarity in social roles (Scheflen 1964). Beattie and Beattie (1981) found no evidence to support this hypothesis in their study of the phenomenon on the beach, since male-female dyads showed much higher levels of posture sharing than male-male dyads did. The present investigation however, did find evidence that lends support to the hypothesis.

Female Tonkean macaques showed a strong preference for female posture sharing partners. They favoured female partners more frequently ($t=11.15$, $p<.01$) and maintained longer episodes of postural congruence with female partners ($t=34.24$, $p<.01$) than they did with male partners. Male individuals also showed a bias in favour of same-sex posture sharing partners, engaging in posture sharing more frequently with other males ($t=9.01$, $p<.01$). Adult subjects also clearly preferred adult partners, engaging in posture sharing behaviour much more frequently ($t=9.24$, $p<.01$) and for longer periods ($t=27.31$, $p<.01$) with other adult group members. Immature focal subjects did not however, show a preference for other immature subjects, exhibiting posture sharing with adults slightly more than with immature subjects.

With the exception of the young subjects, the study population of Tonkeana monkeys showed preference for posture sharing partners of the same sex and age category, lending support to Scheflen's hypothesis that postural

congruence indicates similarity in social roles (Scheflen 1964). The disparity between the evidence supporting this hypothesis in the current study, and the lack of evidence to support it in the Beattie and Beattie study(1981) may be attributable to the addition of female-female posture sharing information and age category information available in the present study. A finer grained analysis of social roles (ie. adult females with offspring, high ranking adult males) may yield more information about postural congruence as an indicator of similarity in social roles. However, since this study partitioned only at the coarser levels of sex, age and rank, information about the similarity in social roles was based only on age and sex data. The beach study (Beattie & Beattie 1981) did not include female-female interaction or age information in the sampling.

The results of the present study are consistent with both the general hypothesis that posture sharing indicates "relatedness" (Charny 1964) and the hypothesis that postural congruence functions as a social signal of the bonds between individuals, and defines and demarcates cohesive groups (Beattie & Beattie 1981). Postural congruence in Tonkean macaques was observed to occur in the context of consort pairs, where adult males maintained prolonged contact with oestrus females. By establishing postural congruence, the consort pair may have signalled their pair bond to the other group members, and perhaps specifically to other interested adult males. Similarly, particular individuals had favourite posture sharing partners with whom they spent a great deal of time both in proximity to and in postural congruence with. In this case, posture sharing may

also indicate the social bonds between particular individuals which occur on an ongoing basis, unlike consort relationships which occur at the time of oestrus.

The strong preference for posture sharing partners of the same sex and dominance rank, especially observed among female and high ranking individuals, may support the hypothesis that postural congruence "defines and demarcates cohesive groups," (Beattie & Beattie 1981). The very high levels of posture sharing among female Tonkean macaques and their strong preference for female posture sharing partners may be due to the matrilineal structure of the group, where females make up the stable group core while males emigrate to other groups upon maturity. It may be beneficial and perhaps necessary for core group members to "define and demarcate" their cohesive groups, in this case matrilines, within the entire group structure for maintenance of a stable group over time.

This study did not examine the correlation between postural congruence and rapport, but it should be noted that no evidence was found to refute this hypothesis. In fact, the data suggest that since postural congruence was observed to occur mainly in the context of affiliative social interaction and resting in close proximity, it is compatible with the general hypothesis that a correlation exists where postural congruence either signals rapport (Charny 1966) or functions to establish rapport to influence another individual's behaviour (LaFrance & Ickes 1981). If rapport is established, it may play a role in influencing the behaviour of

the posture sharing partner. Posture sharing and rapport may go hand in hand with the art of persuasion. For example, movement into postural congruence was observed before solicitations for grooming, before individuals attempted to gain access to a desired item such as an infant, and in the context of conflict resolution (This is anecdotal information. Due to ethogram limitations, specific *behaviours* and not *contexts* were recorded.)

This study substantiates many of the findings reported in the naturalistic study of postural congruence by Beattie and Beattie (1981). While both studies showed that the amount of time spent posture sharing is higher for dyads which include female subjects, the levels of postural congruence observed in the Tonkean macaques are much higher than those reported for humans in the beach study. This may be attributable to two factors: (1) the present study included an examination of female-female posture sharing behaviour which accounted for much of the total time spent in postural congruence by the group, and (2) the present study looked at the congruence and incongruence in body posture for three nearest neighbours rather than only one posture sharing partner, which increased the probability that postural congruence would occur. Differences in posture sharing behaviour between humans and Tonkean macaques may also be due in part to species specific factors, such as social structure. Male-bonded hominids and female-bonded macaques may differ in the expression of postural congruence.

It may also be possible that the levels of postural congruence are higher in Tonkean macaques than in other macaque species. Since Tonkean macaques are characterised by high levels of affiliative behaviour and low levels of aggression towards other group members, they might engage more often in posture sharing behaviour than macaque groups who are characterised by weak tolerance for other individuals and high levels of aggression, such as Japanese or rhesus macaques.

5. Conclusions and Directions for Future Research

The investigation into postural congruence in a captive group of Tonkean macaques led to several important findings. Most significant was the discovery that high levels of postural congruence do occur in a nonhuman primate species. Sex, age and dominance rank were found to influence the frequency and duration of posture sharing episodes. These factors were also found to substantially affect partner preference. The Tonkean macaques generally showed a preference for posture sharing partners of the same sex, age and dominance rank category. Adult females were responsible for much of the postural congruence observed in the study population. Postural congruence was observed to occur in 37 of the 73 distinct body postures, and the phenomenon was almost always associated with sitting postures. Over the course of the observation period, 91 behaviours were observed to occur in the study group, and 63 were associated with postural congruence. Posture sharing was most often associated with social and resting behaviours.

The primary objective of this research was to determine whether or not postural congruence occurs in a nonhuman primate species, directly testing the Scheflen assumption that it is a human specific phenomenon. Scheflen's hypothesis that posture sharing is linked to verbal communication and is mediated through spoken language (1972) can be dismissed on the basis that posture sharing was shown to occur at high levels among a group of nonhuman primates.

Similarly, his evolutionary scheme of communication which reserves "complex" communication for human interaction cannot be corroborated. However, the Beattie and Beattie (1981) hypothesis that posture sharing is not mediated by speech, but by visual cues is strongly supported by the present study.

Four hypotheses regarding the expression and functional significance of postural congruence to be evaluated in light of the data from the present study, were laid out in chapter one. Based on the results of this study, several conclusions were drawn.

(1) The results of this study lend support to the hypothesis that postural congruence is correlated with similarity in social status and social roles (Scheflen 1964) and (2) are compatible with the hypothesis that posture sharing functions as a general indicator of relatedness and rapport (Charny 1966). (3) Results from the present study of posture sharing in Tonkean macaques are in accordance with the Beattie and Beattie (1981) hypothesis that posture sharing acts as a signal of the bonds between individuals and serves to define and demarcate cohesive groups. Finally, (4) the results of this investigation lend credence to the hypothesis that postural congruence functions to establish rapport and/or influence the behaviour of another individual (LaFrance & Ickes 1981).

The present study was exploratory in nature. It fulfilled its main objectives to establish whether or not postural congruence occurs in a nonhuman primate species (confirming the existence of posture sharing in a *M. tonkeana* group), to

evaluate various hypotheses about the expression and function of postural congruence, and to add another naturalistic study to the small number of original research projects devoted to postural congruence. However, it also led to a number of new questions about the phenomenon of posture sharing in both human and nonhuman primates.

Plate 5.1: Postural Congruence In an Access Situation?

An adult female has established postural congruence with another adult female possibly in an attempt to gain access to her infant, September 1996

The natural contexts in which posture sharing behaviour occurs has largely been ignored in the studies of postural congruence. Among the Tonkean macaques, postural congruence was often observed in three noteworthy

contexts: social learning, reconciliation, and in attempts to gain access to desirable items such as infants or novel objects. In each of these contexts, postural congruence as an indicator of mutual identification or rapport may be a useful strategy to employ in order to achieve the goal of a particular interaction (learning, conflict resolution, access to the desired item). A study which incorporates contextual information into the sampling procedure in addition to behavioural information may be helpful in understanding the social benefits of posture sharing behaviour.

A comparative study of postural congruence in various primate species may reveal information about the way in which posture sharing is expressed and whether or not the type of social organisation has an effect on posture sharing behaviour. It may also lead to a better understanding of the development of communication systems and social behaviours of group living animals. Future primatological research may be instrumental in coming to understand the scope and the function of postural congruence.

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Appendix A: Behaviour Codes and Definitions

The ethogram is made up of 57 "core" behaviours where the focal subject is actively engaging in the behaviour, 20 "received" behaviours, where the focal individual is the recipient of another individual's behaviour, 5 "mutual" behaviours, where the focal subject is engaged in giving and receiving the same behaviour as the individual with whom it is interacting, and 9 "simultaneous" behaviours, where the focal subject is actively engaging in two behaviours simultaneously, or engaging in one and receiving another simultaneously.

"Core" Behaviours

ag - aggression towards an individual including threats but no physical contact
ap - approach an individual, looking at and moving toward another individual
bou - bounce display, jumping into the air and landing on all fours, with knees and elbows stiff
btd - silent bared teeth display, an affiliative display where upper lip or both lips are vertically retracted to expose the teeth
ca - carry an object or individual
cd - contact deterrence, pushing away another individual in response to their behaviour
ch - chase, an individual runs after a fleeing individual
clsp - clasp an individual, an affiliative behaviour where an individual clasps another individual with one or both hands
cw - chew food or objects
dg - drag an object or individual
dr - drink, usually water from a spigot provided in the indoor enclosure
ds - displace, an individual approaches another which moves away
eb - eat bark or wood, swallowing bark or wood stripped from trees, logs or wooden items in the park
ed - eat dirt, swallowing soil usually after digging in it
el - eliminate, excreting urine or faeces
fe - feed, eating commercial monkey chow, plants or insects
fi - fight with an individual, aggressive physical contact including slapping, pushing and biting
fl - flight, fleeing from a threatening or attacking individual
fo - forage, search for food out of doors
fol - follow an individual, walking or running after a moving individual
gr - groom an individual, removing debris from the skin and hair of a partner
grb - grab, grabbing an object and taking it from an individual or grabbing and pulling and individual by the hair or a limb
hh - hiphold, grasping the hips of another individual, usually preceding mounting
ind - indeterminable activity

ins - inspect, closing looking at and/or smelling the anogenital region of another individual
lea - leave, an individual moves away from another individual
li - lick, licking an object, another individual or own hands
lo - locomote, moving from place to place within the parks
lp - lipsmack, an affiliative display where the lips are pursed and the lower jaw moves up and down, often producing a "smacking" sound
man - manipulate, handling an object
map - mouth approach, an affiliative behaviour where an individual brings its mouth towards the mouth of another individual, sometimes touching
mas - masturbation, genital self-stimulation
mou - mouth an object or individual, touching with the lips
mt - mount, a copulatory and/or affiliative behaviour where an individual climbs ventrodorsally upon a partner
nu - nurse, an individual gives or receives suckle
o/s - out of sight, focal individual is out of sight
pl - play, an individual engages in relaxed and/or enthusiastic patterns of climbing, swinging, rolling, dragging, jumping, pirouetting, pulling, grasping, slapping etc. alone or with other individuals in the context of play
plbi - play bite, an individual gently bites another individual in the context of play
pos - positioning, an individual grasps the pelvic region of another individual orienting it towards itself for anogenital inspection or mounting
pr - present, an individual orients its hindquarters towards another individual, often in an invitation for anogenital inspection or mounting
rb - rub, an individual rubs the ground or an object under or between hands
re - rest, an individual remains in a relaxed posture, with eyes open or closed, in a state of inactivity
res - restraint, an individual prevents another individual (usually an infant) from leaving by grasping a limb
rh - rub hands, an individual rubs its hands together
sb - sit beside, an individual sits beside and sometimes in contact with another individual
sc - scan, an individual surveys the environment
scr - scratch, an individual rubs its skin to relieve an itch or in response to stress
sgr - self groom, an individual removes debris from its own skin and hair
ss - support shake, a display which involves the violent shaking of an environmental object such as a branch
sta - stare, a visual fixation on another individual and acts as a mild threat
str - struggle, an individual attempts to break contact with an individual who is restraining it
stre - stretch, an individual extends its body and/or limbs
tou - touch, an individual makes contact with another individual, by touching it with its hand
vcl - ventral cling, an individual (usually an infant) clings to the ventral surface of another individual

vo - vocalise, an individual emits a vocalisation
wr - wrestle, an individual engages in prolonged, playful body contact with another individual while grasping each other and rolling
yn - yawn, an individual makes a gaping movement with the mouth in the context of drowsiness or sometimes agonistic interactions

"Received" Behaviours

rag - receive aggression, focal individual receives aggression from another individual, including threats but no physical contact
rap - receive approach, another individual who is looking at the focal individual moves toward the focal individual
rbtd - receive silent bared teeth display, the focal individual receives the affiliative silent bared teeth display from another individual
rcd - receive contact deterrence, the focal individual is pushed away by another individual with whom it is trying to interact
rch - receive chase, the focal individual is pursued by another running individual
rclsp - receive clasp, the focal individual is clasped by another individual with one or both hands, in an affiliative context
rds - receive displace, the focal individual moves away when another individual approaches it
rgr - receive groom, another individual removes debris from the skin and hair of the focal individual
rgrb - receive grab, another individual takes an object from the focal individual or the focal individual is grabbed by the hair or limb and pulled by another individual
rins - receive inspect, another individual looks closely at and/or smells the anogenital region of the focal individual
rlea - receive leave, another individual moves away from the focal individual
rlp - receive lipsmack, another individual lipsmacks at the focal individual
rmap - receive mouth approach, another individual brings its mouth towards the mouth of the focal individual, sometimes touching, in an affiliative context
rmou - receive mouthing, another individual touches the focal individual with its mouth
rmt - receive mount, another individual climbs ventrodorsally upon the focal individual in the context of copulation and/or affiliation
rpr - receive present, another individual orients its hindquarters towards the focal individual, often in an invitation for anogenital inspection or mounting
rres - receive restraint, another individual prevents the focal individual from leaving by grasping one or more of its limbs
rsb - receive sit beside, another individual sits beside and sometimes in contact with the focal individual
rtou - receive touch, another individual makes contact with the focal individual, by touching it with its hand
rvcl - receive ventral cling, another individual (usually an infant) clings to the

ventral surface of the focal individual.

"Mutual" Behaviours

mag - mutual aggression, the focal individual and another simultaneously show mutual aggression towards each other, including threats but no physical contact

mbtd - mutual silent bared teeth display, the focal individual and another simultaneously direct the silent bared teeth display toward each other

mgr - mutual groom, the focal individual and another simultaneously engage in removing debris from each other's skin and hair

mlp - mutual lipsmack, the focal individual and another simultaneously direct lipsmacking displays toward each other

mmap - mutual mouth approach, the focal individual and another simultaneously bring their mouths toward each other, sometimes touching, in an affiliative context

"Simultaneous" Behaviours

btd-tou - silent bared teeth display and touch, the focal individual simultaneously directs the silent bared teeth display towards another individual while touching it with its hand

rag-lp - receive aggression and lipsmack, the focal individual receives aggression from another individual and simultaneously directs lipsmacks towards the aggressor or another individual

rgr-gr - receive groom and groom, the focal individual receives grooming from an individual while simultaneously grooming another individual

rgr-man - receive groom and manipulate, the focal individual receives grooming from another individual while simultaneously manipulating an object

rgr-mou - receive groom and mouth, the focal individual receives grooming from another individual while simultaneously mouthing an object or another individual

rgr-sc - receive groom and scan, the focal individual receives grooming from another individual while simultaneously scanning the environment

rgr-scr - receive groom and scratch, the focal individual receives grooming from another individual while simultaneously scratching itself

rgr-sgr - receive groom and self groom, the focal individual receives grooming from another individual while simultaneously grooming itself

sc-cw - scan and chew, the focal individual simultaneously scans the environment while chewing food or an object

Appendix B: Posture Codes and Definitions

The posturogram is made up of 73 distinct body postures observed as regular components in the postural repertoire of the Tonkean macaques at the Strasbourg Primate Centre. Sitting, standing, laying, movement and clinging postures are included in the posturogram, and variations are noted on the arm, leg, and head positionings.

Arm Positionings:

closed - both arms tucked in against the front of the body
open - both arms extended along the sides of the body
half open - one arm tucked in against the body, and one arm extended along the side of the body
reach - both arms reaching away from the body
half reach - one arm reaching away from the body, the other in the open or closed position
cat - arms straight, hands planted on substrate in front of body

Leg Positionings:

closed - both legs bent at the knees tucked against body
extension - both legs straight, extended away from the body
half extension - one leg straight, extended away from the body, the other tucked against body (closed)
v - both legs angled upward, resting against substrate
half v - one leg angled upward, resting against substrate, the other tucked against body (closed)
chair - both legs dangling downward from a substrate
half chair - one leg dangling downward from substrate, the other tucked against body (closed)
v extension - one leg angled upward, resting on substrate, one leg straight, extended away from body
v chair - one leg angled upward, resting on substrate, one leg dangling downward from substrate

*when no specific leg position is indicated, the leg or legs are in the "closed" position, tucked against the body

Head Positionings:

ball - head is down and chin is tucked onto chest
up - head is up, and the chin is off the chest

*unless the "ball" position is indicated, the head is in the "up" position

Sitting Postures:

cs - closed sit, both arms and both legs are "closed"
os - open sit, arms are "open", legs are "closed"
hos - half open sit, arms are "half open", legs are "closed"
bl - ball, arms and legs are "closed", chin is resting on chest
ob - open ball, arms are "open", legs are "closed" and chin is on chest
hob - half open ball, arms are "half open", legs "closed" chin is on chest
cat - cat position, arms are "cat", legs are "closed"
ocat - open cat position, one arm is "open", the other arm is "cat", legs are "closed"
ccat - closed cat, one arm is "closed", the other arm is "cat", legs are "closed"
rcat - reach cat, one arm is "reach", the other arm is "cat", legs are "closed"
catex - cat extension sit, arms are "cat", legs are "extension"
cex - closed extension sit, arms are "closed", legs are "extension"
chex - closed half extension sit, arms are "closed", legs are "half extension"
cvex - closed v extension sit, arms are "closed", legs are "v extension"
oex - open extension sit, arms are "open", legs are "extension"
ohex - open half extension sit, arms are "open", legs are "half extension"
hoex - half open extension sit, arms are "half open", legs are "extension"
hohex - half open half extension sit, arms are "half open", legs are " half extension"
cch - closed chair sit, arms are "closed" legs are "chair"
och -open chair sit, arms are "open", legs are "chair"
chch - closed half chair sit, arms are "closed", legs are "half chair"
hoch - half open chair sit, arms are "half open", legs are "chair"
hohch - half open half chair sit, arms are "half open", legs are "half chair"
ohch - open half chair sit, arms are "open", legs are "half chair"
rea - reach sit, arms are "reach", legs are "closed"
hrea - half reach sit, arms are "half reach", legs are "closed"
reaex - reach extension sit, arms are "reach", legs are "extension"
reahex - reach half extension sit, arms are "reach", legs are "half extension"
hreaex - half reach extension sit, arms are "half reach", legs are "extension"
hreahex - half reach half extension sit, arms are "half reach", legs are "half extension"
cv - closed v sit, arms are "closed", legs are "v"
ov - open v sit, arms are "open", legs are "v"
hov - half open v sit, arms are "half open", legs are "v"
chv - closed half v, arms are "closed", legs are "half v"

ohv - open half v sit, arms are "open", legs are "half v"
hohv - half open half v sit, arms are "half open", legs are "half v"
cvb - closed v ball, arms are "closed", legs are "v", chin is on chest
ovb - open v ball, arms are "open", legs are "v", chin is on chest
reav - reach v sit, arms are "reach", legs are "v"
reahv - reach half v sit, arms are 'reach", legs are "half v"
hreav - half reach v sit, arms are "half reach", legs are "v"
hreahv - half reach half v sit, arms are "half reach", legs are "half v"
reach - reach chair sit, arms are "reach", legs are "chair"
reahch - reach half chair sit, arms are "reach", legs are "half chair"
hreach - half reach chair sit, arms are "half reach", legs are "chair"
hreahch - half reach half chair sit, arms are "half reach", legs are "half chair"
cvch - closed v chair sit, arms are "closed", legs are "v chair"
hovch - half open v chair sit, arms are "half open", legs are "v chair"

Standing Postures:

qs - quadrupedal stand, standing on all four limbs
tri - tripedal stand, standing on 3 limbs
cr - crouch, standing on all four limbs with the hindquarters squatting
bicon - bipedal stand, standing with hands in contact with an individual or object

Laying Postures:

lat - lateral lay, laying with side of the body in contact with ground
sup - supine lay, laying with the back of the body in contact with ground
spr - sprawl, laying with front of body in contact with ground, limbs extended
pc - prone crouch, laying with front of body in contact with ground, head and upper body raised, resting on forearms
cu - curl, laying with front of body in contact with ground, arms and lugs tucked under body and head resting on ground
uex - upper extension lay, laying with front of body in contact with ground, legs tucked under body and arms extended in front of body
lex - lower extension lay, laying with front of body in contact with ground, arms tucked under body and legs extended behind body
tw - twist, body twisting at the waist, half supine and half lateral laying position

Movement Postures:

r - run
w - walk
clu - climb up substrate
cld - climb down substrate

qucl - quadrupedal cling, clinging to an individual or substrate using both hands and feet
tricl - tripedal cling, clinging to an individual or substrate using 3 limbs
ja - jump across to substrate
jd - jump down from substrate
sus - suspension from substrate
vcl - vertical cling, clinging vertically to a substrate
sli - slide, sliding down a hill or tree on limbs and/or torso

Miscellaneous:

ind - indeterminable posture
o/s - out of sight

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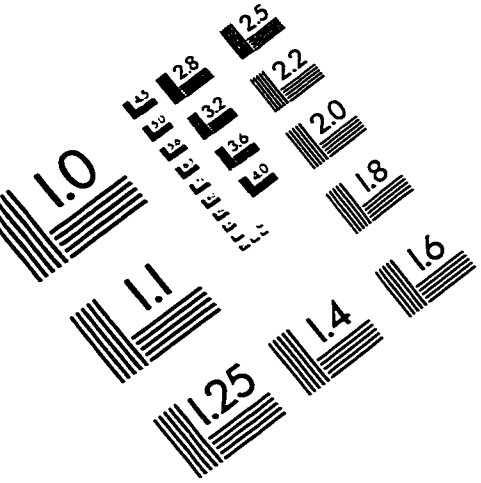
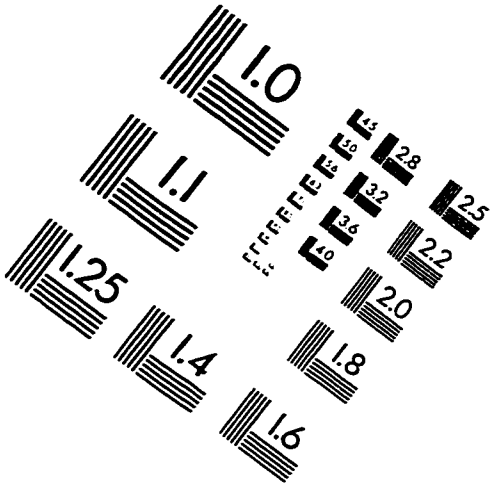
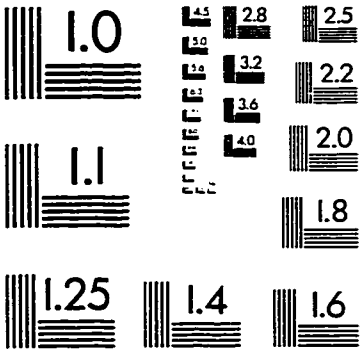
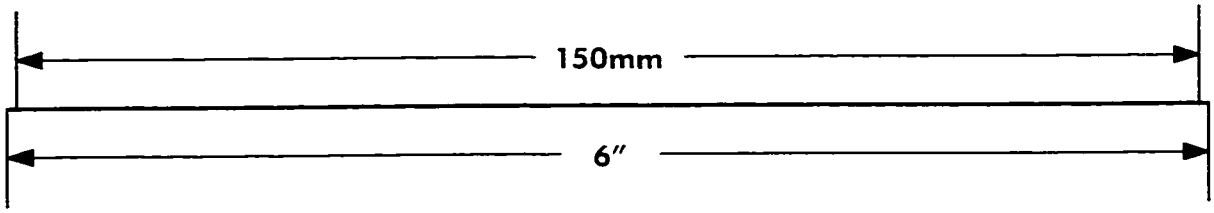
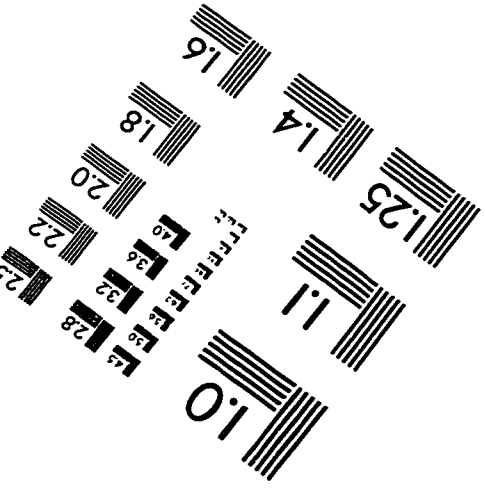
TEST TARGET (QA-3)

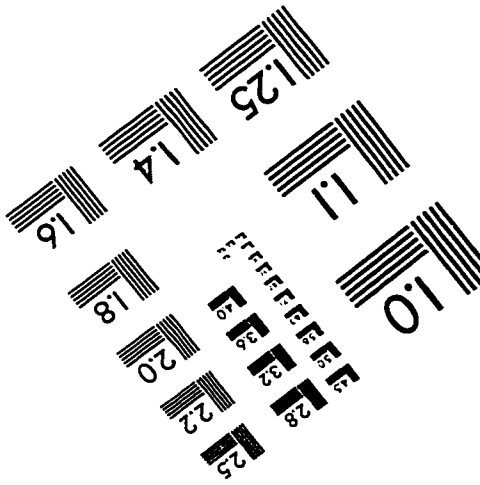












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