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BEHAVIORAL REACTIVITY, DOMINANCE, AND SOCIAL FUNCTIONING IN MALE RHESUS MACAQUES (MACACA MULATTA)

by

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B.S., University of Michigan, 1986
M.A., Hunter College of the City University of New York, 1990

A Dissertation Submitted to the Graduate Faculty
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March 20, 1998
Date

ALEXANDER JAY SKOLNICK
Behavioral Reactivity, Dominance, and Social Functioning in Male Rhesus Macaques (*Macaca mulatta*)
(Under the direction of DOROTHY MUNKENBECK FRAGASZY)

Few studies of individual differences in reactivity to social and nonsocial stimuli in nonhuman primates have adequately addressed the ramifications of these differences for dominance relationships. The present study used objectively-based measures of behavioral reactivity to examine individual differences in changes in dominance relations. Two cohorts of adolescent male rhesus macaques were tested for reactivity to a novel situation before (pretransfer) and after (posttransfer) they were permanently removed from their natal groups. Dominance relationships were monitored for the following 2 years. Dominance rank in the natal group was unrelated to reactivity measures. Pretransfer displacement activity was not correlated with pretransfer dominance but was correlated with posttransfer dominance rank. A composite score of three reactivity measures from both novelty tests was a poor predictor of dominance during the pretransfer and 1-year posttransfer periods, but was a good predictor of dominance at 2 years posttransfer. These results demonstrate a potential role for male rhesus macaques' dispositional characteristics in shaping the outcome of dominance interactions after males emigrate from their natal groups.

INDEX WORDS: Individual differences, Reactivity, Rhesus macaque, *Macaca mulatta*, Dominance, Novelty, Approach, Withdrawal

Dedicated to my parents whom have been putting up with about 30 years of my animal behavior craziness and to Pam who has just been the best at putting up with me.

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Finally, I want to NOT thank myself for NOT thinking of this study about six months earlier than I did. If I had, the study would have been better, my progress exponentially quicker, and my life easier. But that's the way the moon pie crumbled.

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Introduction

Most behavioral and physiological traits vary among individuals and over time. Temperament and personality are two explanatory constructs that address interindividual variation in how humans interact with their social and nonsocial environments. Recently, interest in behavioral variability has been directed at determining whether constructs of temperament and personality as applied to humans might also apply to nonhuman animals. Accordingly, animal research in this area focuses on differences in responsivity to environmental stimuli at both intra- and interspecific levels.

Temperament refers to an individual's behavioral tendencies or response styles that are consistent across varying situations (Bates, 1989; Goldsmith et al., 1987). Essentially, temperament represents the underlying behavioral organization of an organism as inferred from its responses characterized by the threshold, intensity, frequency, and duration of response (Mendoza & Mason, 1989). Temperament variables in nonhuman animals are primarily identified by exposing individuals to unfamiliar situations involving novel and familiar objects, conspecifics, or environments (Box, 1991; Clarke & Boinski, 1995). In both human and nonhuman animal research, however, temperament often lacks a precise definition and has been used synonymously with behavioral tendencies, reactivity, emotionality, and personality. To aid in restricting the construct of temperament to responsivity and to avoid anthropomorphic connotations of terms used to describe human emotionality, the term "behavioral disposition" (Mendoza & Mason, 1989) is preferred when referring to nonhuman animals.

Individual differences in behavioral tendencies

Behavioral dispositions are characteristics of individuals that are relatively invariant regardless of immediate environmental or social contexts. Thus, consistency of individual responses across different situations and over time is expected. For example, cows showed similar fear reactions to an unfamiliar human, a novel object, and an air blast at their feeder (Boissy & Bouissou, 1995). Evidence for such individual consistency has been reported for a number of species in a variety of contexts (cephalopods: Mather & Anderson, 1993; fish: Budaev, 1997; Francis, 1990; Huntingford, 1976; Tulley & Huntingford, 1988; snakes: Herzog & Burghardt, 1988; birds: Jones, Mills, & Faure, 1991; Katzir, 1983; ungulates: Lawrence, Terlouw, & Illius, 1991; Lyons, Moberg, & Price, 1988; carnivores: Adamec, 1991; Durr & Smith, 1997; Fox, 1972; Goddard & Beilharz, 1985; MacDonald, 1983; rodents: Armitage, 1986; Fokkema, Koolhaas, & van der Gugten, 1995; Old World monkeys: Capitanio et al., 1986; Kalin & Shelton, 1989; Mason, 1960; Suomi, 1983; Vochteloo, Timmermans, Duijghuisen, & Vossen, 1991). These studies suggest that behavioral tendencies may be organized in a relatively fixed manner within individuals but may differ among individuals within species.

Reactivity is a much-used construct in research on human temperament (Bates, 1989; Rothbart, 1989; Worobey & Lewis, 1989) and on behavioral dispositions in nonhumans (Clarke & Boinski, 1995; Higley & Suomi, 1989). In such contexts, behavioral reactivity involves an individual's responsivity as defined in terms of approach and withdrawal behavior to unfamiliar situations. At one end of the reactivity continuum are highly reactive individuals with a tendency to more readily show emotional behavior indicative of such as fear (e.g., immobility or withdrawal from novel situations) and that are less likely to approach novel objects. At the other end of the continuum, low reactive individuals require high levels of stimulation before responding fearfully and are more likely to approach novel objects. Several studies with nonhuman primates have shown that avoidance of novelty positively correlates with fearful behavior (Coe, Franklin, Smith, & Levine, 1982; Miller, Bard, Juno, & Nadler, 1986; Vitale, Visalberghi, & De Lillo, 1991; Vochteloo et al., 1991) and that approach to novelty does not (Fairbanks, 1993). Thus, behavioral reactivity is primarily investigated by introducing animals to a mildly-stressful nonsocial challenge involving novel stimuli and scoring fear and stress responses (Clarke & Mason, 1988; Higley & Suomi, 1989; Kalin & Shelton, 1989; Suomi, 1983).

Recently, displacement activities such as scratching, body shaking, and yawning have been used as a measure of fear and anxiety related to approach/withdrawal conflicts. As a measure of fear and anxiety, such displacements may provide a marker of reactivity when there are individual differences in displacement behavior. Displacement activities are known to occur at greater frequencies when animals encounter anxiety-provoking situations (Maestripieri, Schino, Aureli, & Troisi, 1992; van Hoof & Aureli, 1994) such as when in close proximity to dominant animals (Diezinger & Anderson, 1986; Schaub, 1995), after an animal has been the target of aggression (Aureli & van Schaik, 1991), during social disturbances (Baker & Aureli, 1997), in novel situations (Rowell & Hinde, 1963), and when young infants move away from their mothers (Maestripieri, 1993). Additionally, pharmacological evidence supports displacement activities as indicators of anxiety: anxiogenic drugs increase displacement activities and anxiolytic drugs decrease displacement activities (Maestripieri et al., 1992; Schino, Perretta, Taglioni, Monaco, & Troisi, 1996).

Physiological evidence supports the use of reactivity as a meaningful construct. Through a variety of psychophysiological and neuroendocrinological measures, research with both human and nonhuman animals has found activation of limbic and frontal cortical structures underlies approach-withdrawal responsivity, especially to novel or threatening stimuli (Adamec, 1991; Berntson, Boysen, & Cacioppo, 1993; Davidson, 1993; Fox, 1991; Gunnar, 1994; Higley & Suomi, 1989; Stellar, Brooks, & Mills, 1979). Thus, individual differences in behavioral disposition seem founded upon neuroendocrine functioning during times of environmental challenge (Castanon & Mormède, 1994; Gunnar, 1994; Kagan, Reznick, & Snidman, 1988; Sapolsky, 1993; Porges, 1995).

The physical substrates of behavioral dispositions are not usually direct causal agents of behavior, rather they influence the likelihood and intensity of behavior (Mendoza & Mason, 1989). Thus, behavioral dispositions such as reactivity are likely to play a role in modulating species-typical social behavior in animals such as nonhuman primates. These modulatory effects are hypothesized to affect social behavior by processes associated with the types of stimuli or communicatory signals attended to, the evaluation of the behavior of others (Dodge & Crick, 1990), the likelihood of interacting with others (Kagan, Reznick, & Snidman, 1987), and levels of stimulation required to arouse physiological systems involved in an organism's behavior with conspecifics (Benus, Bohus, Koolhaas, & van Oortmerssen, 1991; Mendoza & Mason, 1989). The relationship between these processes and social behavior is only beginning to be addressed.

Furthermore, few studies with nonhuman animals have addressed the significance of individual differences in behavioral responsiveness in terms of ecological, social, or reproductive success. Armitage (1986) showed that individual differences in marmots' (Marmota flaviventris) responses to a mirror were correlated with females' interactions with their neighbors and their tendency to disperse. Pumpkinseed sunfish (Lepomis gibbosus) individuals that differed in their willingness to approach a novel object also differed in a consistent manner in their diet, parasite load, predator risk behavior, and speed of acclimatization to an unfamiliar environment (Wilson, Coleman, Clark, & Biederman, 1993). Budaev (1997) found that consistent individual differences in guppy (Poecilia reticulata) responses to a novel situation were related to their schooling tendencies. In other species of fish, individual differences in response to unfamiliar (Huntingford, 1976; Tulley & Huntingford, 1988) or familiar conspecifics (Magurran, 1986) were predictive of their antipredator responses and chances of survival.

Research on individual differences in behavioral dispositions in nonhuman primates commonly takes an anthropomorphic approach. In nonhuman primates, individuals are usually rated for how much of certain personality characteristics they exhibit (Stevenson-Hinde & Zunz, 1978; Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980). Examples include subjectively rating animals for confidence, apprehension, irritability, and submission. Several studies report that nonhuman primates with certain rated personality traits are more likely to be dominant or subordinate (Bolig, Price, O'Neill, & Suomi, 1992; Buirski, Kellerman, Plutchik, Weininger, & Buirski, 1973; Caine, Earle, & Reite, 1983; Cox, 1989; McGuire, Raleigh, & Pollack, 1994; Stevenson-Hinde et al., 1980). However, these studies are problematic because the measures of personality were subjective and were confounded with the measures of dominance. Instead of providing evidence that individual behavioral tendencies influence social behavior, these traits may merely reflect characteristics of individuals of different dominance status. To date, no study has adequately investigated the role individual differences in behavioral dispositions (as opposed to personality) may play in modulating important species-typical social behavior patterns in nonhuman primates.

Rhesus macaque dominance: a role for behavioral dispositions?

Given the primacy of dominance relationships in many primate species, objectively investigating how dispositions affect dominance relationships is a useful place to begin to understand the relationship between behavioral dispositions and social functioning. In species such as macaques and vervet monkeys (Cercopithecus aethiops), body size and fighting ability play minimal roles in establishing and maintaining social dominance relationships (Bernstein, 1981; Lee & Johnson, 1992; McGuire, Raleigh, & Johnson, 1983; Sugiyama, 1976). Instead, an individual's social relationships within a certain social context are the crucial ingredients in dominance relationships (Bernstein & Gordon, 1980; Mason, 1993).

Rhesus macaque (Macaca mulatta) dominance patterns and social systems are well-studied. Dominance rank of juvenile rhesus macaques reflects maternal dominance rank, ranking just below their mothers (Datta, 1988; Kaufman, 1967). Males usually disperse from their natal group during early adolescence and attempt to join a new group (Colvin, 1986). When males leave their natal group, they leave behind their existing social support and must rely on their individual social skills to join new groups (Berard, 1990; Drickamer & Vessey, 1973; Lindburg, 1969; Neville, 1968). Males tend to enter the new group's dominance hierarchy at or near the bottom, presumably due to their lack of relationships with resident males and females. However, observations on both captive (Bernstein, Gordon, & Rose, 1974; Bernstein & Gordon, 1980) and free-ranging (J. D. Berard, personal communication, 1995; Drickamer & Vessey, 1973; Perloe, 1993) populations find some animals quickly obtain higher dominance rank than would be expected by their tenure in the group, suggesting other factors such as the behavioral dispositions of certain individuals may be involved.

Dominance relationships are central to rhesus macaques social organization, influencing many aspects of group living. Dominance relationships modulate male-male interactions (Colvin, 1983). Compared with subordinate animals, dominant animals are less constrained in their behavior and tend to have priority of access to resources such as food, water, sleeping sites and sexual partners (Brennan & Anderson, 1988; Furuichi, 1983; Manson, 1997; Wrangham, 1981). Animals must cope with interactions with dominant and potentially threatening individuals on a daily basis. Social success under these circumstances can be examined by how group-living animals cope with the inevitable interindividual conflicts that arise and that often lead to agonistic interactions (Mason, 1993). Many conflicts are readily resolved through the expression of the appropriate signal (dominant or subordinate) that reinforces established dominance relationships (Bernstein, 1981), while other potential conflicts are avoided altogether by maintaining large interanimal distances. It is hypothesized here that the behavioral dispositions of primates are manifested in the responses to conflict and potential conflict situations.

If a behavioral disposition such as reactivity does affect behavior in a general way, then animals differing in reactivity should differ in their behavior across multiple settings, including novel social circumstances. Animals more responsive to an unfamiliar situation are postulated to be more "anxious" as indicated by more frequent displacement behavior (Maestripieri et al., 1992), more disturbed by the behavior of other potentially threatening animals, and more prone to withdrawal responses than low-responsive animals. High-reactive individuals are more easily discomposed by the behavior of others than low-reactive individuals; and they should be more compromised in their ability to maintain their dominance relationships. They may also be less able to respond appropriately or obtain allies due to their tendencies to withdraw.

The present study investigated the hypothesis that behavioral reactivity of male rhesus macaques, measured in terms of the levels of fear-related behavior observed during exposure to an unfamiliar situation, influences success in establishing and maintaining dominance relationships. As time passes after males leave their natal group, a reactivity model suggests that behavior becomes less related to natal (matrilineal) dominance relationships and more related to an animal's intrinsic ability to develop and foster social relationships. Individual behavioral reactivity in two captive groups of adolescent rhesus macaques was determined before and after they were permanently moved from their natal groups into all-male housing. Behavioral reactivity was assessed by isolating each male in his home enclosure with a novel stimulus and scoring approach and withdrawal responses. Dominance interactions were recorded during social group interactions.

The following predictions relating reactivity measures to changes in dominance relationships were tested in a cross-lagged design and analyzed using logistic regression models. First, behavioral reactivity was predicted to be stable between two testing situations. Second, behavioral reactivity measured prior to removal from the natal group was predicted to correlate with dominance rank after separation from potential familial support, but be uncorrelated with dominance rank in their natal group. It was further predicted that males challenging dominant animals and successfully resisting challenges from subordinate animals would display lower behavioral reactivity, while males that yielded to challenges from subordinate animals would display higher behavioral reactivity.

Methods

Subjects

Twenty 4-year-old male rhesus macaques from two social groups (A1 and A4) housed at the Field Station of the Yerkes Regional Primate Research Center of Emory University in Lawrenceville, GA served as subjects. Group A1 had 95 members and group A4 had 93, excluding infants born in the most recent birth season. The subjects included 15 males from A1 and 5 males from A4 (Table 1). Five males in A1 and two males in A4 were orphans prior to the start of the study. As part of an ongoing study, the subject males were routinely separated from the group as a whole for a variety of procedures and were trained to enter the indoor quarters on command. Thus, separating the males from the group was done rapidly (1-3 min) and with minimal stress to the animals.

The 20 males were also subjects in a program of research involving the effects of neonatal testosterone manipulations. At birth the males were treated with either a GnRH antagonist, GnRH antagonist plus a testosterone preparation, or control vehicle (Mann et al., 1994). These treatments were considered unlikely to confound the results of the present study as a previous study on the subject males at 2 years of age found negligible effects of the early hormonal treatments on behavior (Wallen, Maestripieri, & Mann, 1995). In a separate cohort of male rhesus macaques, similar neonatal hormone treatments did not influence acquisition or maintenance of dominance relationships (Eisler, Tannenbaum, Mann, & Wallen, 1995). In the present study, neonatal hormone treatment was unrelated to 1996 posttransfer dominance ranks ($\underline{KW} = .273$, $\underline{p} > .05$; $\underline{N} = 20$) or to 1997 posttransfer dominance ranks ($\underline{KW} = .257$, $\underline{p} > .05$; $\underline{N} = 20$).

Housing

The two natal groups occupied separate grassy compounds (38 x 38 m) with attached heated/air conditioned indoor quarters for sleeping and avoiding inclement weather. The

Table 1.
Characteristics of the Male Subjects.

Male	Mother's Dominance Rank	Pretransfer Dominance Rank	Mother Present?	# of Months Orphan	Pretransfer Body Weight (kg)	Post-transfer Body Weight (kg)
Group A1						
An3	13[a]	5[b]	Yes	--	8.39	9.92
Ck3	11	3	Yes	--	6.12	7.17
Dn3	Low[e]	14	No[c]	28	6.96	9.75
Em3	Low[e]	12	No[c]	31	6.61	9.59
Gm3	12	4	No[d]	during study	8.41	9.94
Kl3	3	1	Yes	--	6.56	8.09
Ll3	22	9	Yes	--	7.01	9.22
Nf3	15	6	Yes	--	7.16	8.59
Qi3	4	2	Yes	--	6.96	8.85
Tm3	26	10	Yes	--	7.89	10.02
Uf3	Middle[e]	8	No	14	7.99	10.28
Un3	Low[e]	11	No	34	6.20	8.90
Yl3	33	15	Yes	--	7.30	9.32
Ym3	20	7	Yes	--	6.25	8.09
Yn3	Low[e]	13	No	24	7.88	11.41
Group A4						
Fh3	High[e]	1	No	2	7.75	10.43
Ml3	High	2	Yes	--	6.90	8.93
Qm3	Low	5	Yes	--	5.82	10.27
Rk3	Middle[e]	3	No	34	6.36	8.59
Vh3	Middle	4	Yes	---	6.82	9.59

Notes:

[a]: Ranks among 34 adult females based on unpublished data from D. Maestripieri;

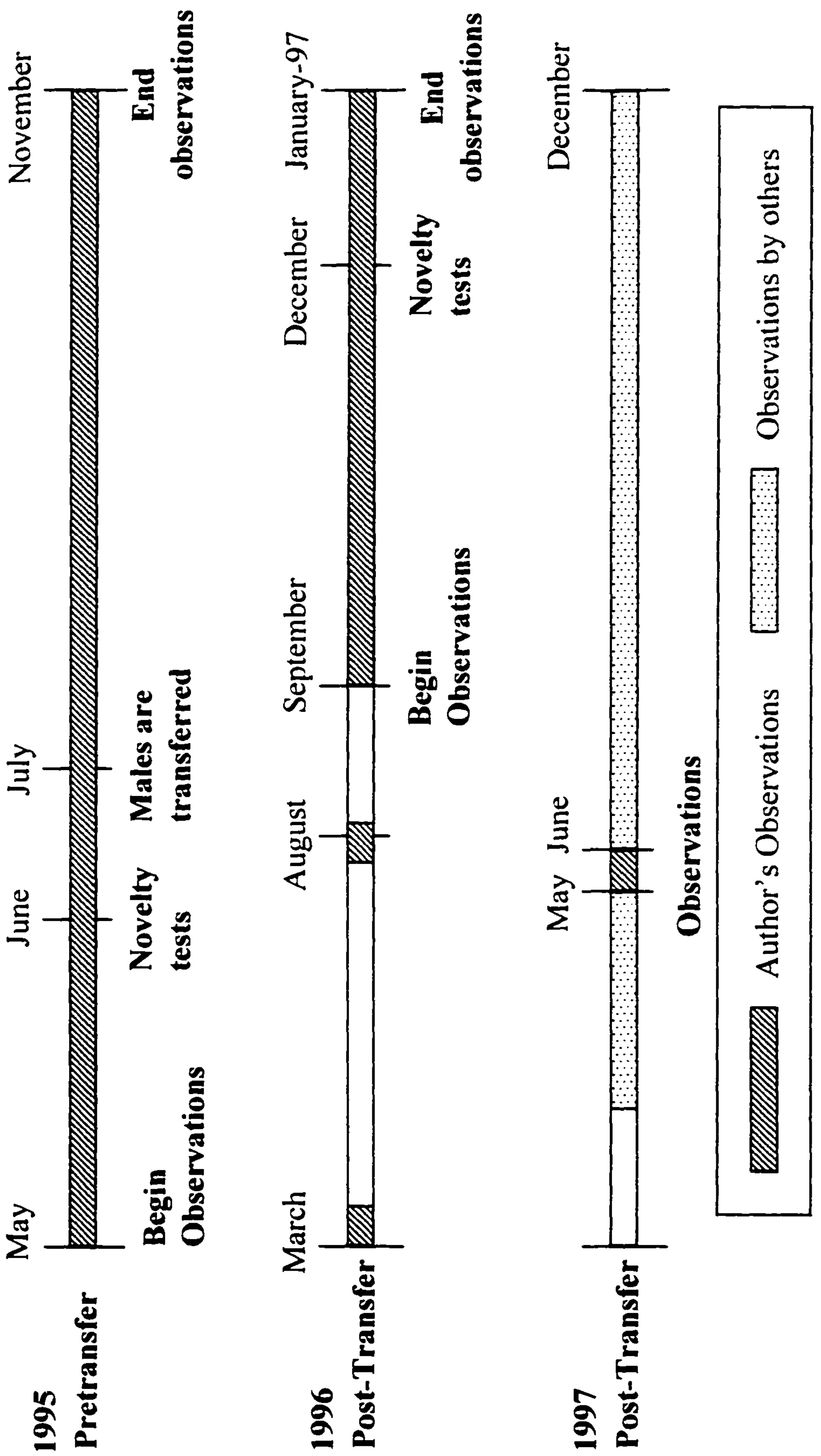
[b]: Natal ranks among subject males based on unpublished data from D. Maestripieri;

[c]: Mother killed during overthrow;

[d]: Mother required medical treatment during pretransfer study;

[e]: Relative rank of mother when she died or was removed, based on unpublished data of D. Maestripieiri.

Figure 1. Timeline of the study.


1995
Pretransfer
May
June
July
November
Begin Observations
Novelty tests
Males are transferred
End observations
1996
Post-Transfer
March
August
September
December
January-97
Begin Observations
Novelty tests
End observations
1997
Post-Transfer
May
June
December
Observations
Author's Observations
Observations by others

two compounds contained metal climbing gyms connected by fire hoses. Animals were fed twice daily with commercial monkey chow and once daily with sliced oranges. Water was available ad libitum. When the two groups were transferred out of their natal groups, they lived in two separate smaller but similarly equipped outdoor compounds (15 x 15 m). During observations the animals were locked out of their indoor quarters. Animals were viewed with and without binoculars, from a tower providing an unobstructed view.

Procedure

Overall design. As illustrated in Figure 1, adolescent males in two natal groups were observed for dominance interactions and singly tested for behavioral reactivity to novelty. After 2 months of observations, the two cohorts of males were transferred to all-male housing where they were observed for changes in dominance relationships. Approximately 1.5 years later, the males were tested again for their reactivity to novelty and their social behavior was monitored as before. Dominance relationships were evaluated again 2.5 years after transfer to all-male housing.

Social Behavior. During all phases of the study, behavioral observations established levels of displacement behavior, activity, sociability (proximity to others), and dominance interactions. The males were observed for 231 pretransfer and 237 posttransfer 10-min focal animal samples with continuous recording of behavior (Altmann, 1974). All data were recorded into a tape recorder and/or Toshiba laptop computer using the Data Collection System (DCS, available from Dr. K. Wallen, Emory University) that time stamps all entries. All data were ultimately transcribed using the DCS. During the posttransfer period, focal observations continued to determine dominance changes. Table 2 lists the behavior items used to assess dominance and baseline behavior of the males for all phases of the study. Interobserver reliability coefficients calculated for the primary observer in comparison to another trained observer ranged from 0.80 (lean) to 0.98 (threat) using kappa coefficients (Martin & Bateson, 1993).

Dominance Relationships. Dominance relationships were assessed from approach-avoidance and agonistic behavior recorded from focal observations and serendipitously throughout the study. If a third monkey joined an aggressing individual, the outcome of that interaction was not used in the determination of dominance. Animals were arranged hierarchically in a matrix based on the directionality of dominant and submissive signals such that each animal only received submissions from those animals ranked lower than himself (Bernstein, 1968). Dominance rank changes were scored when formerly dominant males showed subordinate behavior (e. g., grimace, avoid) to a previously subordinate individual. A male was scored as a challenger if he was observed to direct threatening or aggressive behavior to a dominant animal. A male was scored as resisting a challenge if no change in dominance relationship resulted from being challenged.

Dominance relationships during the pretransfer period (1995) were recorded and compared to their mother's rank (D. Maestripieri, unpublished data). Posttransfer observations were made during the 4 months immediately after the males moved into all-male housing and during the fall of 1996 (9/96 - 1/97); posttransfer 1996 analyses of dominance rank are based on ranks as of 1/97. Analyses of 1997 rank relationships are based on observations made 5/97 and on data from ongoing research with the subjects.

Novelty Test. The tests began by separating three subject males from the rest of the group (this procedure was repeated over several days to accommodate the 20 males) and holding them in transport boxes until tested (this was deemed least stressful since the males have regularly experienced the transport boxes as part of another study since they were born). The rest of the group was run into the indoor quarters. Two sets of stimuli (inverted, standard-sized blue plastic milk crate with known desirable foods including sliced apples, bananas, oranges, potatoes, and peanuts placed on top and underneath) were set up 7 m and 15 m from the doorways. These distances were shortened to 4 m and 11 m when used in the smaller posttransfer enclosures. The subject male was released into the enclosure and his activities were video-taped

Table 2.

Behavior Scored During Group Observations.

Behavior	Description
Locomote.	Includes walking and walking briskly in compound when not in proximity to others.
Stop ongoing behavior	at the approach of another. In whatever position they are in, they stop activity and often become immobile. Sometimes leads to slow avoid.
Scratch	self: rake fur with hands or feet in a rapid manner. Not methodical picking through fur like grooming.
Yawn.	Wide opening of the jaws.
Body shake.	Animal shakes whole body (in wet-dog-like fashion).
Circling.	Locomoting repeatedly over the same path.
Approach.	Locomote in direction of other animal.
Threat.	Directed open-mouth threat face. Usually includes a head jerk and sometimes includes barks.
Supplant.	Occupy spot of animal that avoids approach.
Chase.	Initiate chase of another, running after another.
Lunge.	Quick body movement over short distance directed at another. Can include threats.
Bite.	Common definition. Not scored during attack.
Attack.	Combinations of severe physical contact to other animal: grabbing, biting, etc.
Join.	Join ongoing aggression against other.
Defend.	Join victim of ongoing aggression against perpetrators.
Ignore threat.	No visible agonistic response to a threat.
Avoid.	At approaching animal and move out of path, or, at close approach, leap away.
Lean.	While sitting when another approaches, shifts body and motions to get up or to avoid (but doesn't). Also scored when animal shifts body without getting up from spot to clear path of approaching animal.
Jerk body.	When animal is approaching it jerks its body away from other but does not move away (no avoid).
Run from.	Run away from other either during lunge or chase.
Present	rear to other. Animal stands with tail up in direction of other animal.
Grimace.	Bared teeth to other animal when remaining in location.
Squealing.	High-pitched vocalizations, that are often accompany grimacing when being chased or attacked.

Table 3.

Behavior Scored During the Novelty Test from Videotape.

Behavior	Description
Sitting still.	Sitting quietly and looking around.
Locomoting.	Walking around enclosure.
Feeding at the stimulus.	Hand to mouth eating.
Scratching.	Rapid raking across fur, not methodical picking of fur.
Yawning.	Gaping movement of the mouth lasting a few seconds.
Body shakes.	Shaking movement of the entire body.
Urination.	Common meaning.
Vocalizing.	“Coos” or peeps.
Threat (nothing).	Direct threat facial expression/head jerk to open area, not to other individual.
Pacing.	Locomoting repeatedly over the same pathway or in a circle around edges of the compound. Scored for each bout of pacing separated by 15 s by another behavior.

for 20 min. After the 20 min, the males were reunited with the other animals and the next male was released. The order was determined by each male's preferred order for being boxed. This procedure was repeated 1.5 years after transfer from the natal group, giving the males time to become accustomed to their new surroundings and changes in social status. The same methods were followed in the posttransfer test except that the stimulus boxes were white and the testing arena was smaller. The order of release of the animals was counterbalanced based on the first test.

The video-tapes were scored by one observer before the males' posttransfer dominance hierarchies were set into a matrix. Reliability coefficients were established with another trained observer from a random sample of the videotapes. Reliability coefficients for the behavioral measures were all high (≥ 0.91, kappa coefficients). Using the videotape, behavior related to the subjects' initial immobility, activity, exploration of the novel situation, and distress and displacement activities (Table 3) were recorded using an IBM laptop computer and the DCS. Five derived measures of the males' response to the unfamiliar experience were used for analyses: a measure of "initial immobility" was defined as *latency to leave the release point (LRP,* the time from when the male settles down in one spot to the time it locomotes at least three body lengths away); a measure of "approach to novelty" was defined as *whether they approached the stimulus and took food*; a measure of "exploration" was defined as *time spent in the open area of the test compound (%OA,* percent of time from LRP to the trial's end spent in the open area of the compound after (i.e., away from edges and corners); a measure of activity during the test was defined as *total duration of locomotion (L-DUR,* sum total of locomotion bouts); and a measure of "anxiety" during the test was defined as *frequency of displacement and distress behavior (DD,* combined score of scratches, yawns, body shakes, pacing, distress vocalizations, threats, urination).

Validity. The five measures used here are presumed to be indicative of behavior when animals face potential threats or novel stimuli. Animals exhibiting longer periods of time sitting still at the release point, less locomotion around the enclosure, less time spent in the open, few approachs to desirable food associated with a novel stimulus, and greater number of displacement activities are hypothesized to reflect greater reactivity. Research shows individuals exhibiting increased periods of immobility when facing threatening stimuli also show high levels of behavior that indicate fear in other tests (Boissy & Bouissou, 1995; Jones & Waddington, 1992; Kalin & Shelton, 1989; Lawrence et al., 1991; Lyons et al., 1988) and increased physiological responses to novelty, such as changes in heart rate and cortisol measures (Coe et al., 1982; Kalin & Shelton, 1989; Lyons et al., 1988; Suomi, 1983). Similarly, avoidance of open areas of testing arenas and little locomotion are also correlates of fear-related behavior (Boissy, 1995). Displacement actvities are observed when primates are in uncertain and novel situations (Maestripieri et al., 1992; Rowell & Hinde, 1963). In order to determine if these measures of responsiveness are measuring a similar construct of reactivity, cross-correlations among the measures were performed.

Animals that differ in their general activity levels may also differ in their activity during the novelty test. To rule out the possibility that the novelty test latencies and locomotion are measures of their activity, rather than their reactivity, the latency was compared with the males' activity levels in the group. Activity levels were measured by mean frequency of locomotion bouts during group observations. If no correlation exists between group locomotion levels and the latency to leave the release point, then it is unlikely that general activity levels are being measured in the novelty test.

Design and analysis.

Predictions concerning the relationship between pretransfer and 1996 posttransfer reactivity measures and dominance status were investigated in a cross-lagged design. Stability of measures was assessed by correlating pretransfer with 1996 posttransfer reactivity measures. The relationship between reactivity measures and dominance ranks was assessed by cross-correlations between pretransfer reactivity and posttransfer dominance, and between posttransfer reactivity and pretransfer dominance. To test the directional hypothesis that reactivity scores are factors in dominance interactions, and not the reverse, differences among the cross-correlations were tested statistically using

Fisher Z-transformations in one-tailed comparisons (Zar, 1984). All other statistical tests were two-tailed. All correlations between dominance ranks and behavioral measures of reactivity were conducted with Spearman rank-order correlation coefficients (Siegel & Castellan, 1988). Pearson product-moment correlation coefficients were used to assess normal and transformed data.

The derived reactivity measures were moderately skewed and transformations were applied to approximate normal distributions. Square-root transforms were performed on latency to leave the release point (LRP), duration of locomotion (L-DUR) and displacements/distress (DD) items, and %OA was arcsine transformed (Zar, 1984; Martin & Bateson, 1993). Since DD's skewness decreased but was not eliminated, nonparametric analyses were always used on this measure. Paired t-tests and Wilcoxon signed-rank tests were used to detect group differences in behavior between pre- and 1996 posttransfer tests.

The effects of orphan status on reactivity measures and dominance changes were analyzed with nonparametric phi correlations and chi-squared tests, respectively (Siegel & Castellan, 1988). The effects of the neonatal hormone treatment on dominance rank and reactivity was assessed by nonparametric and parametric one-way analyses of variance. Body weight of the males was correlated with dominance rank at each stage of the study. To rule out aggressiveness of the males as a factor responsible for dominance changes, aggressiveness during pretransfer and posttransfer observations was calculated using mean number of aggressive acts (threats, lunges, chases, grabs, bites, & attacks)/10-min focal and correlated with dominance ranks for each period. Baseline activity was calculated as total frequency of locomotion per male divided by the number of 10-min focal samples separately for pretransfer and posttransfer periods. Locomotion frequencies/male were correlated to the males' L-DUR and LRP during the two novelty tests to rule out general activity level accounting for measures under study.

All analyses involving reactivity measures and dominance were performed only on the larger group because the smaller group exhibited no changes in dominance during the study. The predictive nature of reactivity measures on dominance ranks, as well as on which males actively challenged dominant animals or not and resisted challenges or not, was tested with logistic regressions for categorical and ranked variables run using SAS LOGISTIC (SAS Institute, 1995; Tabachnick & Fidel, 1996). SAS LOGISTIC tests a constant-only model against a constant model with factors added for significant prediction improvement of response variables. Significance is tested with Wald chi-squares. LRP and L-DUR were not entered into the same analyses because the measures were not orthogonal to each other (Tabachnick & Fidel, 1996).

Since no novelty test was run after the 1997 dominance changes occurred, an average score from the previous two novelty tests ([pretransfer score + posttransfer score]/2) was generated for each of three measures of the males' activity in the novelty test (%OA, L-DUR, and DD). LRP was excluded because it was not orthogonal to L-DUR and was not correlated with the other two measures. The three averages were ranked and a mean rank composite score was generated for each male to predict pretransfer, 1996 posttransfer, and 1997 dominance rank. The hypothesized least reactive score received a rank of 1 and most reactive score received a rank of 15. This composite score takes into account multiple components of the males' behavior and differences in how individual males may express their reactivity to the novelty test itself. For this analysis, each period's dominance ranks were divided into three equal rank classes (high, middle, low). The three males no longer living in the group (Figure 2) were not included in the 1997 dominance hierarchy.

Results

Displacement and distress behavior scored during the pretransfer novelty test was unrelated to the males' pretransfer (natal) dominance relationships but was significantly correlated with dominance status of the males after changes in dominance occurred during the 1996 posttransfer period. The other reactivity measures were not predictive of 1996 posttransfer dominance ranks. Three reactivity measures averaged over the two tests better predicted dominance ranks during 1997 posttransfer period than the 1996 posttransfer or pretransfer periods.

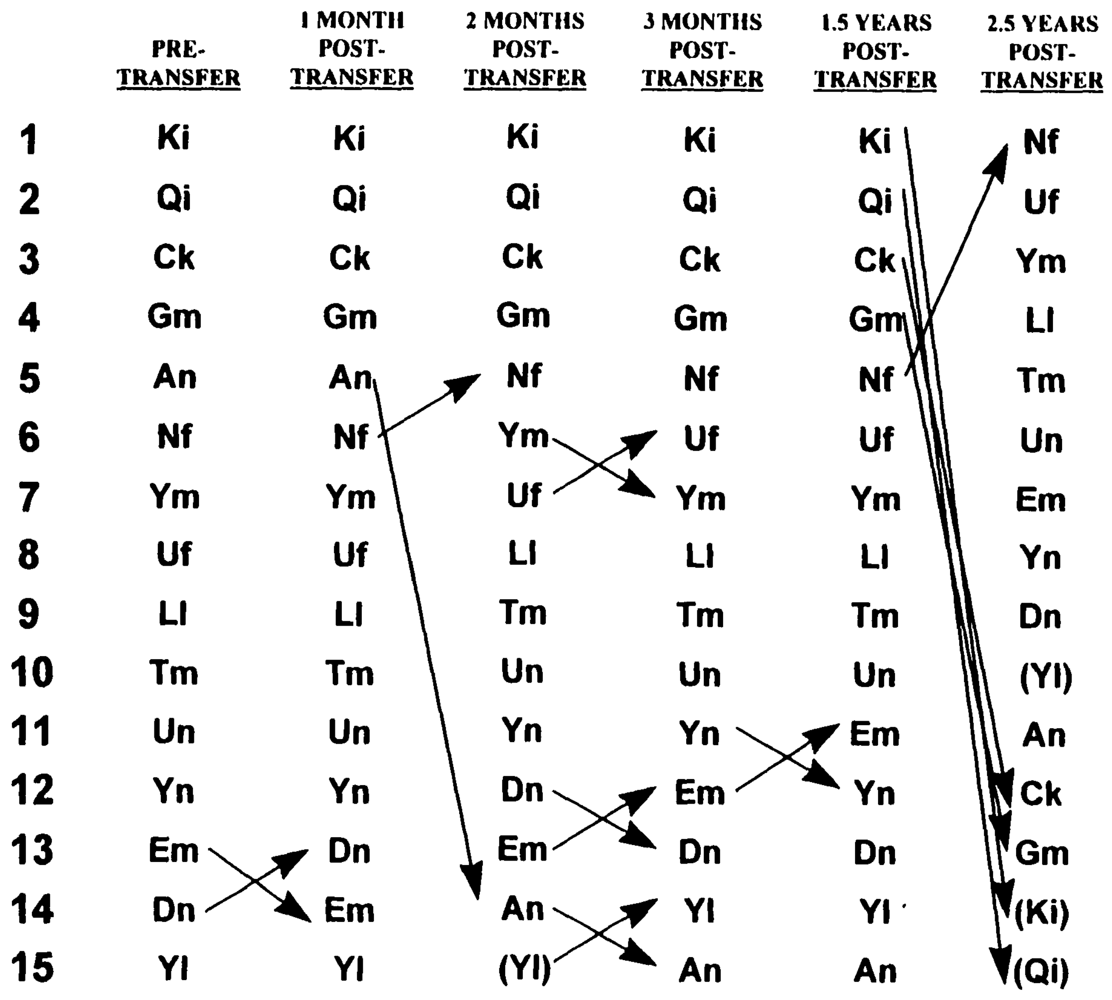
Dominance

The pretransfer dominance hierarchies for the 15 group A1 males and 5 A4 males were constructed such that no reversals of individuals displaying submissive behavior occurred (A1 males: based on 142 dyadic interactions; A4 males: 57 dyadic interactions). The A1 males' ranks based on these observations correlated perfectly with the males' mother's ranks (r_s (10) = 1.0, $p < .001$) excluding the orphaned males. For the A4 females, only the relative ranks based on matriline membership were known; dominance ranks within matrilines were not known. However, the dominance ranks of the A4 males also correlated with their mother's relative ranks (high, middle, low; see Table 1). Orphans in both groups essentially had the ranks of their mothers before they died. This suggests that the dominance ranks of the males during the pretransfer period were derived from their relationship with their matrilines.

No changes in dominance rank were observed in group A4 males during the 2 years following the transfer to all-male housing. Further, no subordinate male was observed to challenge a dominant male. In group A1, however, several changes in dominance relationships (two dyads reversed rank and one male fell in rank below 10 males) were observed during the three months following the transfer of the subject males out of their natal groups into all-male housing (Figure 2). In the time between the 1995 and 1996

Figure 2. Dominance ranks of A1 males over the course of the study. Arrows show the direction of change in male rank. ( ) = male was out of the group during this period. In 1997, Yl removed due to severe arthritis, Ki removed due to severe wounding after fall in dominance status. Qi died while resisting challenges to dominance.

DOMINANCE RANK



	PRE-TRANSFER	1 MONTH POST-TRANSFER	2 MONTHS POST-TRANSFER	3 MONTHS POST-TRANSFER	1.5 YEARS POST-TRANSFER	2.5 YEARS POST-TRANSFER
1	Ki	Ki	Ki	Ki	Ki	Nf
2	Qi	Qi	Qi	Qi	Qi	Uf
3	Ck	Ck	Ck	Ck	Ck	Ym
4	Gm	Gm	Gm	Gm	Gm	Ll
5	An	An	Nf	Nf	Nf	Tm
6	Nf	Nf	Ym	Uf	Uf	Un
7	Ym	Ym	Uf	Ym	Ym	Em
8	Uf	Uf	Ll	Ll	Ll	Yn
9	Ll	Ll	Tm	Tm	Tm	Dn
10	Tm	Tm	Un	Un	Un	(Yl)
11	Un	Un	Yn	Yn	Em	An
12	Yn	Yn	Dn	Em	Yn	Ck
13	Em	Dn	Em	Dn	Dn	Gm
14	Dn	Em	An	Yl	Yl	(Ki)
15	Yl	Yl	(Yl)	An	An	(Qi)

observations, two more changes occurred (1 male fell, 1 male rose). Dominance ranks between the pretransfer and 1996 posttransfer periods were significantly correlated (r_s $(15) = .79$, $p < .001$) but were not correlated between pretransfer and 1997 posttransfer periods (r_s $(12) = -.39$, $p > .05$). Beginning three months after the end of direct observations (1/97), the four highest ranking males were overthrown during the next seven months. All subsequent analyses will concern only the dominance changes involving 15 A1 subject males.

Pretransfer aggressiveness in the social group was unrelated to pretransfer (r_s $(15) = -.28$, $p > .05$), 1996 posttransfer (r_s $(15) = -.11$, $p > .05$), and 1997 posttransfer dominance rank (r_s $(12) = .09$, $p > .05$). Aggression during the posttransfer period was also unrelated to 1996 posttransfer (r_s $(15) = -.25$, $p > .05$) and 1997 posttransfer (r_s $(12) = -.33$, $p > .05$) dominance rank.

Reactivity during novelty tests

The males' behavior during the 1996 posttransfer novelty test differed somewhat from the pretransfer test. In the smaller posttransfer testing arena, males tended to begin locomoting earlier from the release point ($M_{pre} = 8.1$; $M_{post} = 4.1$ min, $t(14) = 2.06$, $p = .06$), locomoted for longer periods ($M_{pre} = 2.5$; $M_{post} = 7.1$ min, $t(14) = 4.23$, $p < .001$), have longer bouts of locomotion ($M_{pre} = 0.36$; $M_{post} = 0.79$ min, $t(12) = 2.29$, $p = .04$), and display less displacement and distress behavior ($M_{pre} = 4.1$; $M_{post} = 2.0$, $z = 2.93$, $p = .004$). These differences did not preclude individual consistency in the males' behavior: DD scores were significantly correlated between pretransfer and posttransfer tests (r_s $(15) = .56$, $p < .05$). However, individual consistency on the whole was not found for LRP (r $(13) = .36$, $p > .05$), L-DUR (r $(13) = -.19$, $p > .05$) and %OA (r $(13) = .45$, $p = .07$). Approaching the stimulus boxes with food was also not stable across tests. In the pretransfer novelty test, 13 of the 15 males spent time looking at the stimulus boxes with the desirable food, but no one approached a box. This is in contrast to the posttransfer test when 8 of the 15 males approached a box and took food from it. Consideration of the behavioral measures of reactivity as dispositional characteristics of the subjects requires that stability in the measures

Table 4.

Pearson and Spearman Correlation Coefficients (r) for Novelty Test Measures.

Measure	1	2	3	4
Pretransfer Novelty Test				
LRP	--	-.73**	-.22	-.28
L-DUR		--	.36	.43
%OA			--	.60*
DD				--
Posttransfer Novelty Test				
LRP	--	-.48	-.23	-.26
L-DUR		--	.30	.63*
%OA			--	-.22
DD				--

Note. LRP = Latency to leave release point. L-DUR = Duration of locomotion. %OA = Percentage of time after first locomotes spent in open area. DD = Total displacements and distress behavior.

* $p \leq .02$, two-tailed Spearman rank-order correlation.

** $p < .005$, two-tailed Pearson product-moment correlation.

between the two tests be established. Therefore, DD was the primary measure addressed in cross-lagged analyses.

Extraneous factors were tested to assure they did not compromise validity of the measures. Neonatal hormone treatment, body weight, and orphan status were not statistically associated with any measure of reactivity in either the pre- or posttransfer novelty tests (hormone treatment: all ps $\geq .07$; body weight: all ps $\geq .07$; orphan status: all ps $> .20$). Latency to first leave the corner and duration of locomoting were not merely measures of general activity as LRP and L-DUR during the novelty tests were not significantly correlated with mean activity levels in the social group (LRP: pretransfer: $r(13) = -.04$, $p > .05$; posttransfer: $r(13) = .29$, $p > .05$; L-DUR: pretransfer: $r(13) = -.38$, $p > .05$; posttransfer: $r(13) = .23$, $p > .05$). Intercorrelations among the novelty test reactivity measures are shown in Table 4. DD was significantly associated with %OA during pretransfer and with L-DUR during 1996 posttransfer period. Pretransfer LRP was negatively correlated with L-DUR, but this relationship was not unexpected since males with longer latencies to leave the release point had less time to spend locomoting during the test than males with shorter latencies.

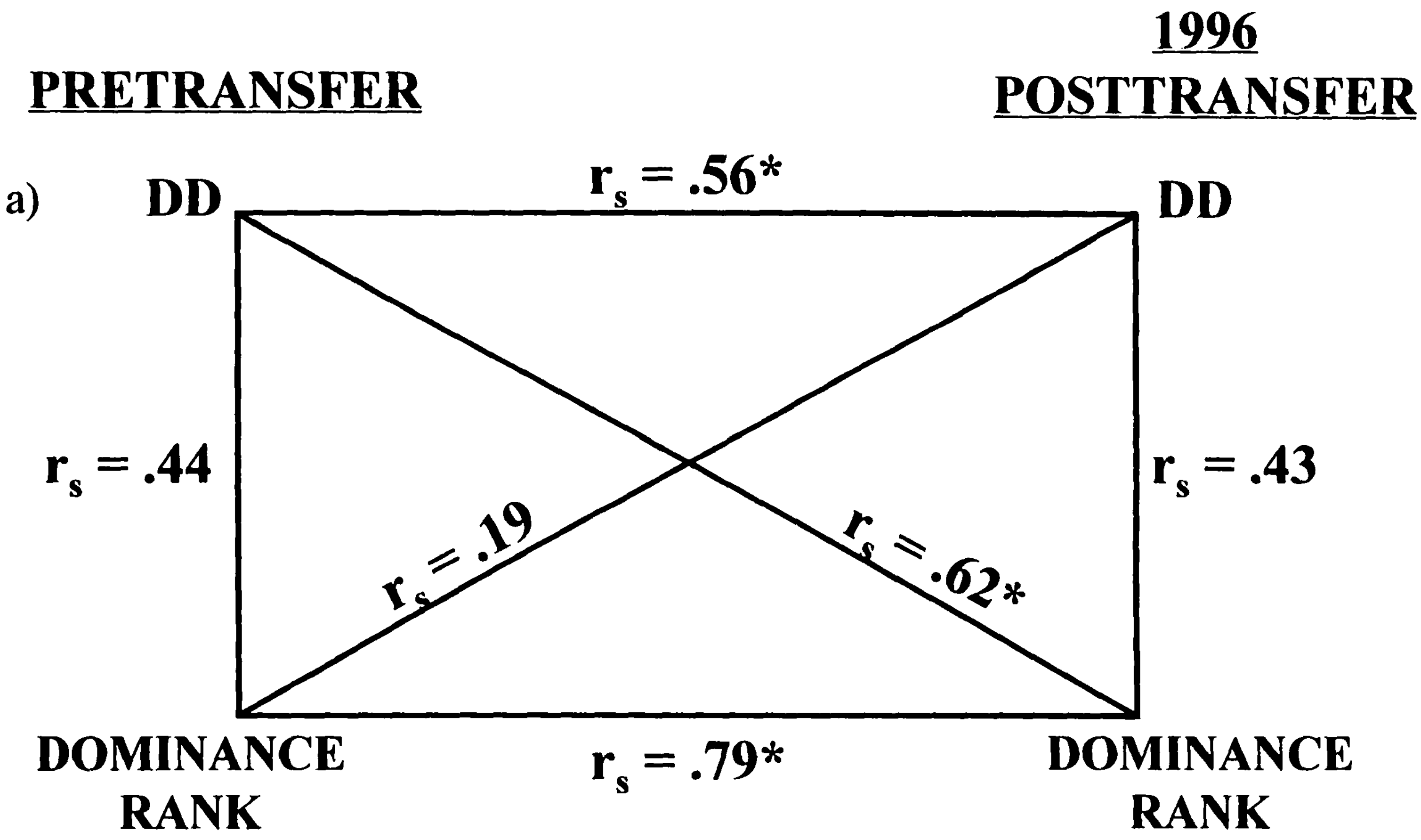
Predicting 1996 dominance relationships. Cross-lagged correlational analyses (Figure 3a) of DD in relation to pretransfer and 1996 posttransfer dominance shows that males exhibiting higher levels of DD in the pretransfer tests were lower ranked in the posttransfer period ($r_s(15) = .62$, $p < .05$) but not in the pretransfer period ($r_s(15) = .44$, $p > .05$). Furthermore, posttransfer DD was unrelated to both pretransfer dominance rank ($r_s(15) = .19$, $p > .05$) and 1996 posttransfer dominance rank ($r_s(15) = .43$, $p > .05$). The hypothesis that reactivity plays a greater role influencing dominance relationships than dominance relationships influence reactivity (i.e., DD), was tested by comparing the correlation coefficient for pretransfer DD - posttransfer 1996 dominance (.62) to the coefficient for posttransfer DD - pretransfer dominance (.19) and to pretransfer DD - pretransfer dominance (.44). The correlation coefficient of pretransfer DD - posttransfer dominance was significantly greater than posttransfer DD - pretransfer dominance ($z = 1.82$, $p = .03$, one-tailed) but not greater than pretransfer DD - pretransfer dominance ($\underline{z} = 0.87$, $\underline{p} > .05$). This set of analyses generally supports the hypothesis that this measure of reactivity recorded during the pretransfer period was unrelated to pretransfer (i.e., natal) dominance rank but was predictive of later changes in dominance relationships.

Figure 3b-d shows that the three other measures of reactivity were either unrelated to any dominance ranking (LRP, L-DUR) or the pattern of correlations was inconsistent with the reactivity hypotheses (%OA). Consistent with the stated model of reactivity-dominance relationships, pretransfer %OA was not significantly correlated with pretransfer dominance ranks ($\underline{r}_s$ (15) = .26, $\underline{p} > .05$) but was significantly correlated with the posttransfer dominance ranks of the males ($\underline{r}_s$ (15) = .55, $\underline{p} < .05$), with males spending a greater percentage of time in the center of the compound had lower ranks in 1996 posttransfer period. However, posttransfer %OA was significantly correlated with both pretransfer dominance ($\underline{r}_s$ (15) = .55, $\underline{p} < .05$) and posttransfer dominance ranks ($\underline{r}_s$ (15) = .53, $\underline{p} < .05$). There was no difference between the cross-lagged correlations.

In testing a model of pretransfer measures as predictors of 1996 posttransfer dominance, pretransfer dominance rank, DD, %OA, L-DUR, LRP were entered sequentially into a logistic regression. While a model with these five factors was significantly different from a constant-only model (Wald χ^2 (3, $\underline{N}$ = 15) = 14.79, $\underline{p}$ = .0001), only pretransfer rank (Wald χ^2 (1) = 14.81, $\underline{p}$ = .0001) and DD (Wald χ^2 (1) = 3.90, $\underline{p}$ = .048) were significant predictors of posttransfer 1996 dominance rank. Given that pretransfer rank was highly correlated with posttransfer rank and the positive results of the DD cross-lagged analysis, this pattern of results was not surprising. None of the other reactivity measures added reliable predictability to this model or other regressions performed without pretransfer rank as a factor. When three reactivity measures (DD, %OA, LRP or DD, %OA, L-DUR) were entered as factors in two separate logistic regressions, only DD was identified as a marginally significant predictor of 1996 posttransfer rank (Wald χ^2 (1) = 3.74, $\underline{p}$ = .057; Wald χ^2 (1) = 4.35, $\underline{p}$ = .035, respectively).

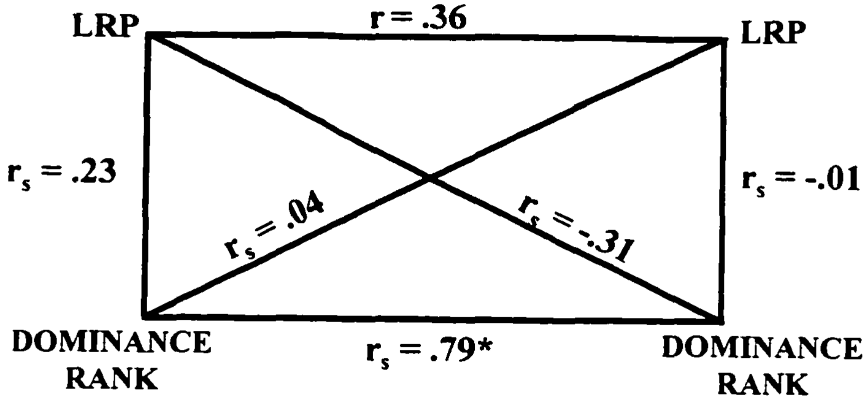
Figure 3. Cross-lagged analyses for four reactivity measures. a. DD = displacement and distress behavior. b. LRP = latency to leave the release point. c. L-DUR = Total duration of locomotion. d. %OA = percent of time spent in open area. r_s = Spearman rank-order correlation coefficients. r = Pearson product-moment correlation coefficients.

* = $p < .05$, two-tailed.

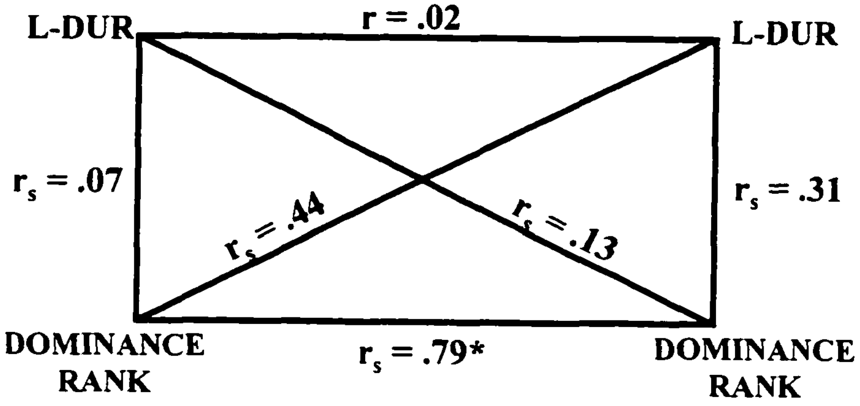

1996
PRETRANSFER
POSTTRANSFER
a)
DD
$r_s = .56*$
DD
$r_s = .44$
$r_s = .43$
$r_s = .19$
$r_s = .62*$
DOMINANCE RANK
$r_s = .79*$
DOMINANCE RANK

PRETRANSFER **1996 POSTTRANSFER**

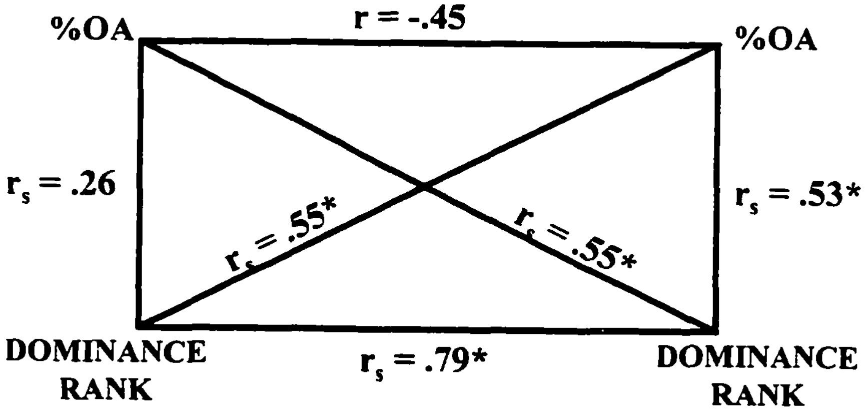
b)



c)



d)



Predicting 1997 dominance relationships. Pretransfer (natal) dominance rank was predicted to have a decreasing influence and individual differences in reactivity an increasing influence over time, leading to changes in dominance relationships. Dominance ranks at the three stages of the study were predicted by using a composite score of each male's behavior in the reactivity tests, and by the reactivity measures averaged as predictors in a logistic regression model. This composite score takes into account multiple components of the males' behavior and differences in how individual males may express their reactivity to the novelty test itself.

Predictability of dominance ranks from the males' composite score ranks increased over the study periods (Table 5). Pretransfer dominance class was not predicted for any male by their composite score (0/15). For posttransfer 1996 dominance rank class, only 27% (4/15) of the males were correctly predicted by their composite score. However, posttransfer 1997 dominance rank class was predicted for 75% (9/12) of the males, a significantly greater proportion of correct assignments than for the other two periods (proportions test: 1997 vs. pretransfer, $\underline{z} = 4.08$, $\underline{p} < .0001$; 1997 vs. 1996, $\underline{z} = 2.50$, $\underline{p} = .012$).

Membership in high, middle, and low dominance classes for each period (pretransfer, 1996 posttransfer, and 1997 posttransfer) was also tested by sequential logistic regression analyses using the males' ranks for each of the averaged reactivity measures (%OA, L-DUR, DD) entered as predictors. For pretransfer dominance rank class, a model using these predictors did not differ from a constant-only model suggesting no relationship between the predictors and pretransfer dominance. A statistically reliable model was found for posttransfer 1996 dominance class prediction (χ^2 (1, $\underline{N} = 15$) = 5.22, $\underline{p} = .022$), but only the averaged DD score significantly contributed to the model (Wald χ^2 (1) = 4.47, $\underline{p} = .035$), corroborating the previously discussed cross-lagged analyses. A logistic regression model for posttransfer 1997 dominance using all three reactivity measures was statistically significant (χ^2 (3, $\underline{N} =$ 12) = 11.25, $\underline{p} = .011$). Only a combination of all three predictors as a set (%OA: Wald χ^2 (1) = 4.06, $\underline{p} = .044$; L-DUR: Wald χ^2 (1) = 4.96, $\underline{p} = .026$; DD: Wald χ^2 (1) = 4.43,

Table 5.

Dominance Class Compared to Composite Reactivity Scores for Each Period.

Class	Male	Pre-Transfer Rank	Composite Score Rank	Male	1996 Post-Transfer Rank	Composite Score Rank	Male	1997 Post-Transfer Rank	Composite† Score Rank
HIGH	Ki	1	15	KI	1	15	Nf	1	1*
	Qi	2	7	Qi	2	7	Uf	2	9
	Ck	3	14	Ck	3	14	Ym	3	3*
	Gm	4	13	Gm	4	13	Ll	4	2*
	An	5	12	Nf	5	1*	Tm	5	4
MEDIUM	Nf	6	1	Uf	6	11	Un	6	7*
	Ym	7	3.5	Ym	7	3.5	Em	7	6*
	Uf	8	11	Ll	8	2	Yn	8	5*
	Ll	9	2	Tm	9	5	Dn	9	8
	Tm	10	5	Un	10	9*	(Yl)	--	--
LOW	Un	11	9	Em	11	8	An	11	10*
	Yn	12	6	Yn	12	6	Ck	12	11*
	Em	13	8	Dn	13	10*	Gm	13	12*
	Dn	14	10	Yl	14	3.5	(Ki)	--	--
	Yl	15	3.5	An	15	12*	(Qi)	--	--
Dominance Class Correctly Predicted			0% (0/15)			27% (4/15)			75% (9/12)

Note. * correctly predicted dominance class. ( ) = male out of group during this period. † = Composite scores for 1997 Posttransfer period are ranked based on the 12 males remaining in the group.

p = .036) reliably distinguished the three dominance classes. These analyses suggest that males who were higher ranked in 1997 tended to show a combination of the following characteristics in the two novelty tests: exhibited less displacement and distress behavior, spent more time locomoting around the compound, and spent a greater proportion of their time away from the corner in the open areas of the compound.

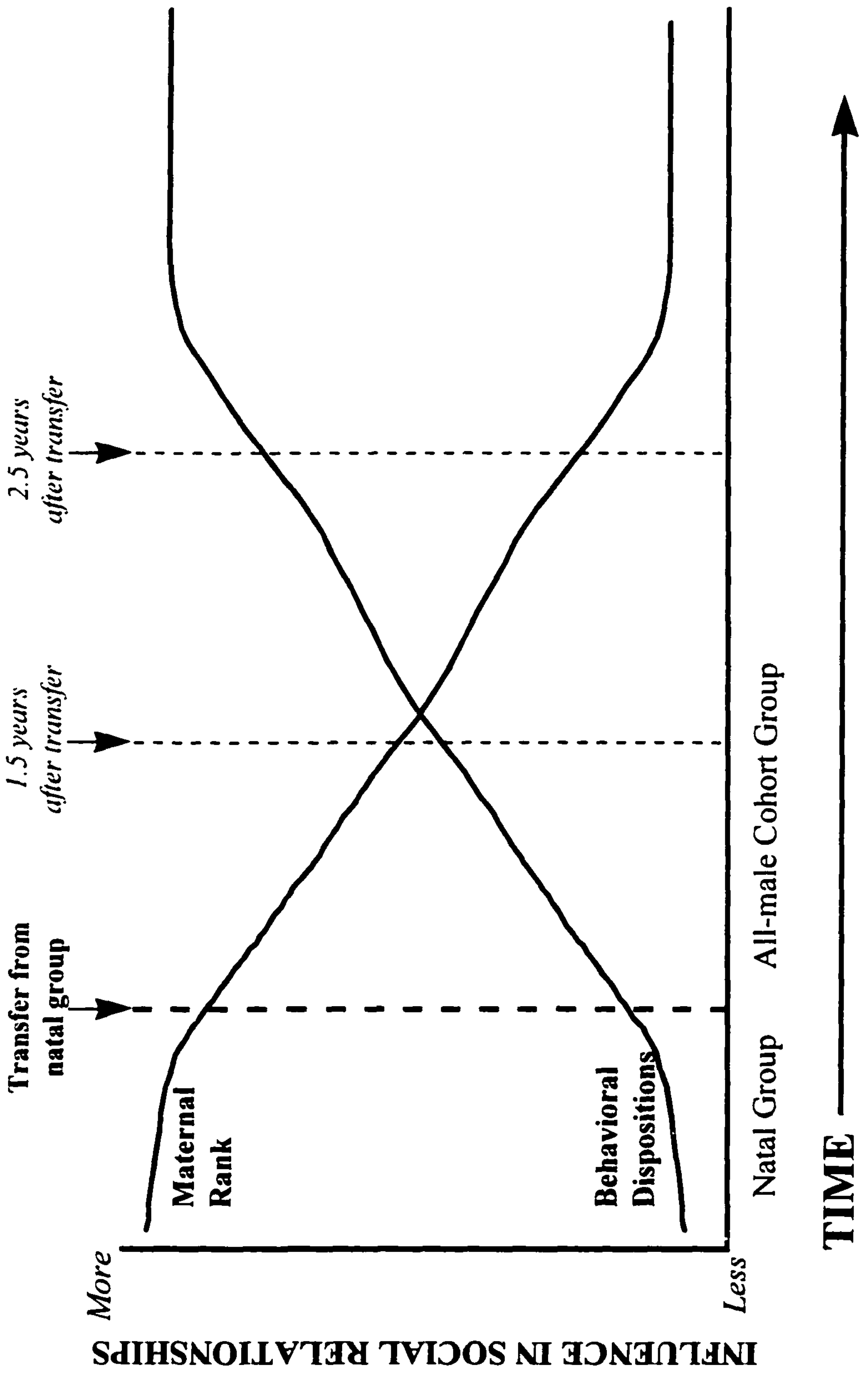
Predicting Challengers and Resisters. Whether pretransfer reactivity measures could be used to predict which males would actively challenge dominants or not and which would resist challenges from subordinates was tested for both 1996 and 1997. The likeliness of subordinate males to challenge dominant males was not predicted by any combination of the reactivity measures in a logistic regression model. The ability to resist a challenge from subordinates, however, was reliably differentiated for the 1997 posttransfer period when pretransfer rank, DD, %OA, and L-DUR were entered as predictors (χ^2 (3, N = 14) = 9.86, p = .043), but not when LRP was added to the model. No single predictor significantly improved upon the model; only the combination of pretransfer rank, DD, %OA and L-DUR differentiated resisters from nonresisters. These analyses suggest that males who resisted challenges as of 1997 tended to show a combination of the following characteristics: were lower ranked in the hierarchy, performed fewer DD activities, spent more time locomoting, and a greater proportion of their time in the open.

Discussion

The results support a model of decreasing influence of the male rhesus macaques' matrilineal dominance relationships paralleled by an increasing influence of individual behavioral dispositions on dominance relationships once separated from their natal group (Figure 4). A measure of reactivity (DD) varied among the males and was relatively consistent across testing sessions 1.5 years apart. Thus, DD is a stable characteristic of the males and likely to be a manifestation of a behavioral disposition. Displacement activities, including scratching and yawning, have been shown to occur in nonhuman primates under different situations involving approach/withdrawal conflicts and anxiety-provoking stimuli (Baker & Aureli, 1997; Maestripieri et al., 1992; van Hoof & Aureli, 1994; Schaub, 1995). Individual differences in the tendencies to show displacement behavior seem to reflect individual differences in how the males perceived the novelty test situation as fear- or anxiety provoking (e.g., Laudenslager & Boccia, 1996). This reactivity measure recorded during the pretransfer novelty test correlated well with the male's future dominance relationships but not with their natal dominance. An average of DD from both novelty tests was also a significant predictor of 1996 posttransfer dominance rank and of 1997 posttransfer dominance rank along with two other putative reactivity measures.

While residing in the natal group, male dominance ranks are similar to their mother's or matriline's rank (Bernstein & Williams, 1983; Datta, 1988; Kaufman, 1967). When males migrate out of their natal groups to new groups their rank is rarely influenced by relatives (a possible exception is emigration with a brother, Meikle & Vessey, 1981) and they must forge new social relationships. In the present study, the males were transferred as an intact cohort and although they lost potential matrilineal support, they did not have to forge new relationships with unfamiliar animals. Without other group members, including relatives, to reinforce pretransfer relationships the

Figure 4. Hypothetical changes in relative influences of natal rank and behavioral dispositions on developing male rhesus macaques.


INFLUENCE IN SOCIAL RELATIONSHIPS
More
Less
Transfer from natal group
1.5 years after transfer
2.5 years after transfer
Maternal Rank
Behavioral Dispositions
Natal Group
All-male Cohort Group
TIME

status quo would only be maintained by the social inertia of prior relationships amongst themselves. Some males, however, differing in their abilities to function socially with others, acted against the status quo and challenged their pretransfer relationships. The present study shows that males that changed dominance rank during the study either by successfully challenging a dominant male or by unsuccessfully resisting a challenge could be differentiated based on individual measures of reactivity. These measures of reactivity are assumed to reflect some underlying disposition that influenced the male's behavior during these social interactions.

If dominance itself is not an attribute of an animal but the outcome of two animals interacting (Bernstein, 1981; Barrette, 1993), how is it that reactivity in the form of displacement activities – theoretically reflecting an attribute of an animal – was associated with changes in dominance relationships? The interpretation herein is not that displacement activities were directly involved with changes in the male's dominance relationships, rather the propensity to show displacement activities under novel situations merely reflected aspects of individual behavioral dispositions. It is presumed that the males' behavioral dispositions modulated (see Appendix A) the nature of social interactions with dominants and subordinates in everyday interactions around resources (e.g., food, water, shady spots) and conflict situations. It is also likely that dispositions such as tendencies toward fearfulness or boldness influenced animals' behavior during major conflict situations. These influences possibly extend to whether a male responds to a challenge effectively or whether a male would actively challenge dominant animals.

The cross-lagged analyses suggest that individual reactivity influenced dominance rank, not the reverse. This conclusion is warranted because a) pretransfer displacement and distress responses correlated with the males' new posttransfer dominance ranks after some relationships changed a year later and b) pretransfer (matrilineally-derived) dominance ranks were unrelated to displacement and distress responses in either pretransfer or posttransfer periods. The two findings together indicate that reactivity measures were predictive and dominance ranks were not. When manipulation of subject variables, such as a male's reactivity level or dominance relationship status, is difficult, cross-lagged designs offer some confidence in identifying causal relationships (Kenny, 1979; Rosenthal & Rosnow, 1991). However, further experimental work is required to confirm the reactivity-dominance relationship. A likely experimental avenue may include determining an animal's reactivity in a novelty situation followed by pairing unfamiliar animals based on reactivity scores such that each member of the pair would have an opposite score; the direction of the dominance relationships established could then be documented.

The 1996 posttransfer dominance ranks reported were stable for at least 9 months. The changes in dominance relationships taking place in 1997 offered a further test of the reactivity hypothesis of dominance relationships. Lacking a concurrent test of reactivity after the changes in dominance took place, a composite score of reactivity measures was used to predict changes in dominance relationships. This analysis supported the reactivity hypothesis as the composite measures predicted 1997 posttransfer dominance rank. In contrast, the composite reactivity measures did not predict pretransfer or 1996 posttransfer dominance rank (apart from that already predicted by displacement activities). It is worth noting that 2.5 years after the transfer, while reactivity nicely predicted 1997 dominance rank, pretransfer matrilineally dominance was no longer a influential factor. Thus, over time, dominance status was increasingly predicted by reactivity measures and decreasingly influenced by natal matrilineal rank (Figure 4).

Several confounding factors in the study were rejected as alternatives to reactivity correlating with dominance. Like most studies of rhesus macaques (Bernstein & Gordon, 1980; Drickamer & Vessey, 1973) body weight (Table 1) was irrelevant to dominance, as smaller males dominated larger and larger males were not necessarily resistant to challenges (e.g., An did not resist and was one of the largest males; Figure 2). Although orphans tended to be lower ranking in pretransfer dominance, being an orphan was not related to any future changes in dominance that took place. Additionally, males that were ultimately high ranking were not the most aggressive since there were no associations between frequency of aggression and dominance rank in any period.

The stability of DD scores over time supports the claim that this response is based on an intrinsic characteristic of the males. Lack of stability in LRP, L-DUR, and %OA suggests they were labile and possibly dependent on changes that occurred during the year between tests such as age, dominance, or social experience. Age differences in reactivity have been found, usually with younger juveniles displaying less reactivity and more curiosity than older juveniles (Bernstein, 1966; Fairbanks, 1993; Joubert & Vauclair, 1986). However, in the present study, the males seemed less reactive (more likely to approach the novel stimulus, more likely to locomote around open areas, lower frequency of displacement behavior) when they were older (5 years old).

Alternatively, differences in these response parameters may have been due to differences in testing situations. Although the two novelty tests were made as similar as possible (isolated in their own enclosure with similar stimuli), physical differences in the testing arenas may account for the variability of the reactivity measures across the two tests. The pretransfer and posttransfer enclosures differed in size (1444 m^2 vs. 225 m^2) and in layout of the animal access doors. In novel or threatening situations many animals tend to avoid open areas and head for sheltered spots (e.g., Bernstein, Schusterman, & Sharpe, 1963; Menzel, 1969). In the larger enclosure, the sheltered corner utilized by 13/15 males was adjacent to the access doors. In the smaller posttransfer enclosure, there was no comparable sheltered corner and several males locomoted early to sit in the nearest corner away from the access doors. This difference in the enclosures was a likely contributing factor to the lack of stability across the two tests in both the latency to leave the release point (LRP) and possibly the total duration locomoting (L-DUR) as well. The fact that the most stable measure, displacement behavior (DD), was consistent over the tests and was also the only measure recorded not directly affected by the size of the testing arena further supports this hypothesis. A methodological improvement, which was not logistically possible in the present study, would be to test the males in the same neutral (i.e., non-home) arena at both points in time.

How much can be said about this pattern of reactivity and dominance in other groups of rhesus macaques or other species? It is difficult to know all the variables that factor into the decision-making process of whether to challenge a dominant male or how to respond if a position is threatened. The relationship between a male's behavioral dispositions and his behavior in a social environment is probabilistic rather than deterministic (Mendoza & Mason, 1989). The social context also plays an important role in setting the limits on the behavior of the individuals in that context. For example, male dominance rank in rhesus and Japanese macaques (Macaca fuscata) is usually determined for new group members by the presence of animals already in the process of maintaining relationships (Bernstein & Gordon, 1980; Bernstein, 1981; Sugiyama, 1976). Thus, the social context usually overrides the potential for dispositions to influence the outcome of dominance interactions. Thus, given these parameters, there is no necessary relationship between certain behavioral dispositions and the prescribed behavior of an animal.

The present study attempted to examine dominance changes in male rhesus macaques in a situation in which some social contextual factors were removed. Examining an intact cohort of males transferred together from their natal group helped avoid the 'seniority effect' that usually sets the basic rank of new males to the lowest position (Bernstein & Gordon, 1980; Drickamer & Vessey, 1973; Sugiyama, 1976). Yet, the males from A4 were not observed to challenge the status quo over the 2 years of the study. The social context may have overridden the potential for challenges because the highest ranking pair of males (ranks 1 & 2) were the most aggressive in the group and the lowest ranking males were the least aggressive during the pretransfer period (r_s (5) = -.90, p > .05). It was the observer's impression that the other group males actively stayed away from the dominant pair, reinforcing their pretransfer relationships.

Theoretically, behavioral dispositions can modulate behavior in any nonhuman primate species in which dominance interactions are not established solely by size and fighting ability. In vervet monkeys, for example, male dominance acquisition is related to how effectively the males interact with the females and gain their support (Raleigh & McGuire, 1989). Part of the attraction of the females to the males is the manner in which they behave affiliatively or aggressively. Affiliative males showing less impulsive aggression were more likely supported by females (Raleigh, McGuire, Brammer, Pollack, & Yuwiler, 1991). Individual differences in behavioral dispositions, therefore, quite likely correlate with the quality of the male's social interactions with females.

At the very least this study shows that reactivity can be dissociated from current dominance relationships. This is in marked contrast to studies that attempt to measure personality in primates through subjectively rating their behavior on personality items at a single point in time in a single environment. Past studies examining personality in primates have concluded that there are specific personality characteristics (e.g., confidence, competence, fearfulness) that coincide with being either dominant or subordinate in rank. These studies, however, can not dissociate personality from dominance because the same behaviors assessed for rating the animals are used to assign dominance ranks. Therefore, when Bolig et al. (1992) found high ranking rhesus macaques were also high on a "confident-popular" personality dimension, they could not disentangle the rated personality as a potentially intrinsic characteristic of the animals from an aspect of their behavior that any dominant animal would show once acquiring dominance status. Indeed, McGuire et al. (1994) measured personality in vervet monkeys before and after changes in dominance occurred and found that 16/18 animals that changed rank also received different scores on the "social competence" personality dimension. Thus, future studies should employ, as this one did, a before-after design with more objective measures of behavioral dispositions taken at different points in time if intrinsic characteristics of animals are to be measured and compared to their dominance relationships or other aspects of their social functioning.

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Appendix A

Individual Differences in Behavioral Dispositions in Nonhuman Primates

Variation in the genes and experiences of organisms contributes to the development of unique individuals. In research, this uniqueness is mostly treated as noise and its repercussions lessened through design and statistical procedures. While intraspecific variability has long been known, only recently has a framework been established to examine the nature and function of individual behavioral variability and its importance in behavioral evolution (Clark & Ehlinger, 1987; Stamps, 1991; Wilson, Clark, Coleman, & Dearstyne, 1994). Although random intraspecific variation can be found on almost any behavioral trait, some current research links specific psychological and physiological processes related to consistent individual variability in responsiveness to change in environmental stimuli. Evidence suggests that individuals differ in behavioral and physiological responsiveness from an early age and these differences can persist into adulthood (Suomi, 1991). These individual tendencies to respond to certain stimuli are the focus of the following review.

Behavioral variability of responses to environmental changes is approached using concepts from research on humans, namely temperament and personality. Temperament is discussed and argued to play a modulatory role in social interactions in both humans and nonhumans. Physiological systems involved in responses related to environmental changes (including 'stress') and emotion are then highlighted and shown to be similar in humans and nonhuman primates. Methods of studying personality and temperament in nonhuman primates is critiqued and suggestions for improving our understanding of these variables are made. Finally, the argument is made that understanding how temperament and physiology vary across animals allows for better understanding of individual differences in sociophysiological processes.

Behavioral tendencies

The study of behavioral variation mostly centers around how animals interface with their physical and social environment. It is during these interactions when potential life-challenging situations occur involving responses to potential food, predators, mates, conspecifics, habitats, and the like. Two general behavioral characteristics most often discussed and evaluated are 1) reactivity (or responsiveness) to stimuli, especially to novelty or change, and 2) responsiveness to potentially hazardous or risky situations (Clark & Ehlinger, 1987; Clarke & Boinski, 1995; Greenberg, 1989; Kagan, Reznick, & Snidman, 1987; Wilson et al., 1994). How animals respond in these situations is characterized along approach-withdrawal dimensions (Schneirla, 1959; 1965). For the purpose of this review only reactivity will be addressed because it is not always clear when risk is separable from novelty, as certain novel situations may be interpreted as being potentially hazardous. The initial research into behavioral tendencies arose from trying to understand differences between species and only recently has attention turned to differences within species.

Interspecific differences in behavioral tendencies

The usefulness of comparing species based on their reactions to both novel and threatening stimuli was recognized long ago (e.g., Yerkes, 1913). Characterizing response styles of species aids in identifying relevant psychological and physiological variables that underlie species differences. Two areas of study into species differences in responsiveness to stimuli are aggression and mother-infant interactions (Clarke & Mason, 1988; Maestripieri, 1994; Mason, Long, & Mendoza, 1993; Thierry, 1985; de Waal & Luttrell, 1989; see Clarke & Boinski, 1995; Mason & Mendoza, 1989; for review). For example, Maestripieri (1994) found that behavioral indicators of emotional reactivity (e.g., scratching) in macaque mothers correlates with species differences in levels of protectiveness mothers show toward their infants. Examining species differences allows for the characterization of species in terms of their basic response parameters. That is, one species may be more reactive, more hostile, more curious, more affiliative, more impulsive, or more restrictive with infants than another.

Intraspecific differences in behavioral tendencies

The new focus on behavioral variability has spawned research that through various methods describes the extent organisms vary in a wide range of taxa (Tables 1 & 2). The behavioral tendencies addressed usually are related to reactivity, inhibition or fearfulness in response to changes in nonsocial and social stimuli (Wilson et al., 1994; Clarke & Boinski, 1995). In order to show that behavioral tendencies are characteristics of individual animals and not solely dependent on the immediate environmental or social contexts, the consistency of individual behavioral tendencies across different situations and over time must be examined. Cross-situation consistency in responsiveness of individuals can be found when contrasting predator versus conspecific or social versus nonsocial stimuli (fish: Huntingford, 1976; Tulley & Huntingford, 1988; birds: Katzir, 1983; Jones, Mills, & Faure, 1991; ungulates: Lyons, Moberg, & Price, 1988a; Lawrence, Terlouw, & Illius, 1991; Boissy & Bouissou, 1995; wolves, Canis lupus: Fox, 1972; Old World monkeys: Suomi, 1983; Vochteloo, Timmermans, Duijghuisen, & Vossen, 1991). Individual consistency over time in behavioral tendencies is also found in a range of vertebrates (fish: Francis, 1990; garter snakes, Thamnophis melanogastor: Herzog & Burghardt, 1988; wolves: MacDonald, 1983; Old World monkeys: Suomi, 1983; Capitanio et al., 1986; Kalin & Shelton, 1989; Vochteloo et al., 1991; Borries, Sommer, & Srivastava, 1994). Overall, these studies suggest behavioral tendencies are organized in a relatively fixed manner within individuals but differ between individuals.

To strengthen the argument that intra- or interspecific differences are meaningful and not just convenient labels assigned because the observed patterns of responsiveness have a superficial resemblance to human responses, recent work has focused on concomitant physiological underpinnings. It is generally hypothesized that systematic patterns of neuroendocrine functioning are associated with intraspecific behavioral tendencies (Suomi, 1983; Cacioppo, 1994; Gunnar, 1994; Clarke & Boinski, 1995). Mendoza & Mason (1989) argue that the physiological systems involved in how animals respond to their environment are significant for understanding behavioral tendencies in

Table 1

Studies Documenting Individual Differences in Behavior in Nonhuman Animals.

Species	Behaviors examined	Individual differences (factors, % variance explained)	Reference
Octopus rubiscens	Responses to alerting, threatening & feeding tests	3 factors, 45%	Mather & Anderson, 1991
Three spined sticklebacks (Gasterosteus aculeatus)	Aggression in response to conspecifics and predators across the breeding cycle. Response to unfamiliar environment.	Correlations between aggression and boldness-timidity factors	Huntingford, 1976
Three spined sticklebacks	Behavior during and after predator encounters	8 factors, 70%	Huntingford & Giles, 1987
Minnows (Phoxinus phoxinus)	Responses to a model predator	1 factor, 45%	Magurran, 1986
Midas cichlids (Cichlasoma citrinellum)	Aggression tests using a mirror	18-month stability in individual scores	Francis, 1990
Pumpkinseed sunfish (Lepomis gibbosus)	Response to novelty (a net). Multiple tests used to discriminate between shy vs. bold fish.	Differences in behavior between shy and bold fish	Wilson et al., 1993
Guppies (Poecilia reticulata)	Response to new environment, open-field test, predator inspection test, schooling tendencies.	2 main dimensions of Activity/ Exploration and Fear/Avoidance	Budaev, 1997
Mexican garter snakes (Thamnophis melanogaster)	Reactivity (strike patterns) to moving and nonmoving predator stimuli.	Individual stability during first year	Herzog & Burghardt, 1988
Japanese quail (Coturnix c. japonica)	Open field, hole-in-the-wall-test, & tonic immobility	1 factor, 35%	Jones et al., 1991
Black-tailed prairie dogs (Cynomys ludovicianus)	Time allocation patterns	5 factors, 100%	Loughry & Lazari, 1994

Table 1. Continued.

Yellow-bellied marmots (Marmota flaviventris)	Mirror-image stimulation; maze behavior	3 factors, 85%	Armitage, 1986a, b
Dairy goats (Capra hircus)	Five measures of human-goat interactions	1 factor, 76%	Lyons et al., 1988a
Domestic pigs	Reactivity to handling tests	Consistency of responses	Lawrence et al., 1991
Friesian cows	Reactivity to open field, novel object, feeding conflict test, & surprise test.	Moderate individual consistency across 4 tests correlating w/ fear.	Boissy & Bouissou, 1995
Domestic cats	Subjective personality ratings	3 factors	Feaver et al., 1986
Domestic cats	Tested aggressive & nonaggressive cat's responses to rats, mice, & a novel environment.	4 consistent patterns of approach-withdrawal responses across conditions.	Adamec & Stark-Adamec, 1989
Domestic cats	Tested with novel stimuli, novel animals in groups and individually.	Found consistency in novelty responses but no effect of dominance of the cats.	Durr & Smith, 1997
Domestic dogs	Responses to dog-dog, dog-human encounters	2 factors, 51%	Goddard & Beilharz, 1985
Wolf cubs (Canis lupus)	Reactivity to novel objects & people, competition test	Stability in scores increased with age	MacDonald, 1983
Brown Bears (Ursus arctos)	Subjective personality ratings	Found 5 dimensions on which bears varied.	Fagen & Fagen, 1996

Table 2

Studies Documenting Individual Differences in Behavior in Nonhuman Primates.

Species	Age	N	Behaviors examined	Differences	Individual Explained	% Variance Comments	Reference
Rhesus macaques (Macaca mulatta)	JF,M	168	Durations of play, A/W, explore, contact, hostility, fear.	3 factors: -fearful* -hostile -sociable	NA	Peer-reared animals	Chamove et al., 1972
Anubis baboons (Papio anubis)	all	7	EPI: subjective ratings based on 12 paired adjectives.	Large differences in emotional profiles	NA	No profiles correlated	Buirski et al., 1972
Chimpanzees (Pan troglodytes)	AF,M	23	EPI: 45 sets of paired trait words.	NA	NA	Dominant more aggressive, less timid.	Buirski et al., 1978
Rhesus macaques	I	46	Subjective ratings based on 25-33 adjectives on a 7-point scale.	3 factors: -confident-fearful -active-slow (excitable) -sociable-solitary	63-69%	4 years of scores on animals	Stevenson-Hinde & Zunz, 1978; Stevenson-Hinde et al., 1980
Pigtail macaques (Macaca nemestrina)	I	15	Observational measures: 28 behavioral & 6 physiological measures.	Levels of activity & nature of mother-infant relationships varied.		Physiological measures inter-correlated & correlated with behavior	Reite & Short, 1980
Pigtail macaques	JF,M	10	Subjective ratings based on 21 adjectives on a 3-point scale; Competition test.	Correlated items with factors of [S].	NA	Dominant animals more confident & solitary, less fearful.	Caine et al., 1983
Japanese macaques (Macaca fuscata)	J-A	14	EPI: subjective ratings based on 12 paired adjectives.	Interyear stability of ratings from different observers	NA	Examined procedures & reliabilities.	Martau et al., 1985
Rhesus macaques	I	NA	Neonatal test batteries; social separation.	High vs. low reactive	NA	Interactions of mom's caregiving behavior & infant's reactivity correlated with peer dominance.	Suomi, 1987

Table 2. Continued.

Stumptailed macaques (Macaca arctoides)	AF,M	10	Subjective ratings based on 27 adjectives on a 7-point scale.	Same factors as [S]		Dominants more sociable & confident.	Cox, 1989
Rhesus macaques	I	23	Neonatal battery assessment at 1-month & problem solving, motor function, & behavior rating at 8 months.	4 factors: -activity -orientation -state control -motor maturity	NA	1-month bold-fear scores differentiated subjects at 8 months.	Schneider et al., 1991
Rhesus macaques	all	22	Subjective ratings based on [S] Rated reactivity on 3 point scale.	4 factors: -solitary -confident-tense -motherly-playful -aggressive-irritable	80%	Dominants more confident, less tense	Bolig et al., 1992
Olive baboons (Papio anubis)	AM	25-45	Observational measures: sex, affiliation, & male interactions.	5 clusters: -consortship behavior -grooming trends -male-male conflict -initiation of aggression -differentiation of social signals	NA	Clusters of behavioral styles correlated with basal cortisol levels.	Sapolsky & Ray, 1989; Ray & Sapolsky, 1992
Vervet monkeys (Cercopithecus atheiops)	all	97	Subjective ratings based on 12 \adjectives on a 5-point scale; 5 overt behaviors scored.	3 factors: -competent -curious -opportunistic	70%	Competent animals more dominant. Changes in dominance changes factor scores.	McGuire et al., 1994
Rhesus macaques	AF,M	33	Subjective ratings based on [S].	4 scales: -sociable -equable -confident -active	NA	Factors predictive of immune parameters.	Capitanio et al., 1994
Gorillas (Gorilla gorilla)	all	298	Subjective ratings based on [S].	4 factors: -fearful -extroverted -dominant -understanding	>50%	No other behaviors examined.	Gold & Maple, 1994

Notes. A = adult; J = juvenile; I= infant, F = female, M = male; NA = not available; EPI = Emotions Profile Index; [S] = Stevenson-Hinde et al., 1980

• = Factor labels are presented to provide a sense of the results. Commonality in factor label does not make studies directly comparable because factors are based on different loadings of behavior.

both inter- and intraspecific comparisons of behavior. These include activation of the hypothalamic-pituitary-adrenal (HPA) axis, the autonomic nervous system (ANS), neuroregulatory hormones (such as catecholamines and serotonin), and central neural processing of emotional responses. The HPA axis and the ANS are both involved in rapid physiological responses to environmental stimuli perceived as a stressor, readying the body for immediate and possibly prolonged action. Comparisons at both the species and individual levels show preliminary evidence for consistent associations between behavioral and physiological systems.

Presentation of a novel stimulus to a variety of animal species leads to similar physiological changes in systems involved in (emotional) arousal and stress responses. In rodents, ungulates, carnivores, and primates, exposure to novelty activates the HPA axis to produce glucocorticoids and the sympathetic-adrenomedullary system to release catecholamines (Levine, Coe, & Weinberg, 1989; Broom & Johnson, 1993; Boissy, 1995). Some species have been shown to exhibit significant correlations between individual differences in behavioral reactivity and physiological responses (e.g., mice: Benus, Bohus, Koolhaas, & van Oortmerssen, 1991; goats, Capra hircus: Lyons, Price, & Moberg, 1988b; wolves: Fox & Andrews, 1973; Old World monkeys: Suomi, 1983; Higley & Suomi, 1989; Kalin & Shelton, 1989; Sapolsky & Ray, 1989; humans: Kagan, Reznick, & Snidman, 1988). Thus, the presence of variability in reactivity responses found across a wide spectrum of species and evidence that corresponding underlying physiological processes are similar across species suggests significant evolutionary continuity for behavior-physiology relationships.

Temperament and behavioral dispositions: definitions

The basis for understanding tendencies for different reactive responses in nonhumans relies on research into individual variation of temperament and personality in humans. While definitions of these two terms differ according to the user, a general consensus is that temperament refers to behavioral tendencies or style of response to the environment across a wide spectrum of situations (see Bates, 1987, 1989; Goldsmith et al., 1987; Rothbart, 1989). Temperament describes how an individual responds to its physical and social environment rather than what its response is. although the temperamental character of an organism potentially influences the discrete type of responses shown. The concept of temperament is an intervening variable (Hinde, 1989) for a complex set of psychological and physiological interactions that influence the overall response of an organism interacting with its environment. Likewise, Mendoza and Mason (1989) conceptualize temperament as organismic constraints that affect the probabilities that certain behaviors will occur under certain conditions.

Temperament is supposed to represent the intrinsic or fundamental response pattern of an individual (or species). For most theorists, this means that temperament is evident when animals are immature and it is rooted in underlying 'biological' processes with little nonbiological input. Several researchers have even advocated that temperament be restricted to those responses that are due to differences in genotype and not related to differences in experience (Goldsmith et al., 1987; Kagan, 1994). Hinde (1989) argued that requiring a genetic component as part of the criteria for temperament is untenable on a number of grounds. Research has also shown that there can be significant prenatal (Clarke & Boinski, 1995) and postnatal effects (Suomi, 1987; Mason & Capitanio, 1988; Fairbanks & McGuire, 1993; Clarke & Boinski, 1995) on both behavioral and physiological indices of temperament in both humans and nonhuman primates. Therefore, for the purpose of this review, temperament will be considered an 'intrinsic' aspect of the character of the individual as a the result of the integration of genes and experience during development. "Intrinsic" in this formulation means that the response tendencies have become relatively fixed in the individual and not dependent on immediate social contexts.

In the primate literature there is little consistency in the usage of the terms "temperament" and "personality"; they are often used interchangeably and to characterize both intra- and interspecific variation. I advocate the use of definitions supplied by Clarke and Boinski (1995) for the delineation of the terms 'temperament' and 'personality' when applied to nonhuman animals. They define temperament as a response style to novel stimuli or challenging situations considerably independent of social or volitional influences. Thus, temperament is the animal's basic or inherent response to stimuli. When applied to nonhuman animals, however, the term 'behavioral' or 'social disposition' (Mendoza & Mason, 1989) may be preferable to 'temperament'. Personality, on the other hand, refers to social characteristics of individuals, (i.e., how playful, affiliative, aggressive, etc.). While it's commonly assumed that there is some continuity between humans and nonhuman animals in the psychological and biological processes underscoring behavioral styles (see below), several of the factors involved in the determination of temperament and personality in humans lack any obvious parallel in animals. Thus, in this review, temperament and personality will be employed when describing human behavior and behavioral disposition and behavioral style, respectively, will be adopted to describe behavior of nonhuman animals as defined above.

How are behavioral dispositions characterized?

Emotions are integral ingredients for most characterizations of the component dimensions of behavioral dispositions. There is no universally excepted definition of "emotion" but among researchers with a biological slant there is some agreement in the view of emotions as organism-environment interactions: emotions ready the body for a behavioral or physiological response to an environmental change (e.g., Fox, 1991; Heller, 1993; Lang, 1995). As responses to environmental changes, emotions are products of psychologically or physiologically based disruptions in the steady-state functioning of an organism. Such disruptions can be positive (facilitating approach responses) or negative (facilitating withdrawal responses) (Schneirla, 1959; Fox, 1991; Davidson, 1993). Disruptions can also take the form of attention to rewarding stimuli (Depue et al., 1994), prevention of motivated behavior (Lang, 1995), discrepancies of perception (Mandler, 1990), or uncertainty that results from lack of control or predictability of situations (Frankenhaeuser, 1986; Levine et al., 1989; Gunnar, Marvinney, Isensee, & Fisch, 1989; van Hoof & Aureli, 1994). Based on this view, emotional processes require perception with evaluation of environmental change, plus arousal to respond behaviorally and physiologically to such a change. While emotion and behavioral dispositions are closely linked behaviorally and physiologically, they can be distinguished by focusing on relatively momentary specific affect states or motor acts in the former and relatively stable general behavioral tendencies in the latter.

Individuals are differentiated by the expression of various component dimensions of behavioral dispositions. The component dimensions upon which individuals are shown to vary are usually described as a continuum from one extreme of the dimension to the other. The dimensions that most researchers suggest represent behavioral dispositions include reactivity (highly responsive/aroused to unresponsive/unaroused to change in stimuli), inhibition (uninhibited/bold to inhibited/fearful in response to unfamiliar stimuli), inhibitory control (easily inhibit arousal to difficult to inhibit arousal), sociability (approach others to withdraw from others), and activity (active to inactive) (Bates, 1989; Rothbart & Ahadi, 1994). Theoretically, many behavioral differences among individuals can be attributed to the expression of combinations of these dimensions. The influence of these components shapes the behavior of the organism by acting on its psychological processes such as attention, perception, assessment of the physical and social environment, adaptation to stimuli, and social bonding among conspecifics.

One example of human temperament research uses responses to unfamiliar objects, people, or situations to identify stable temperamental characteristics in children (Kagan et al., 1987, 1988). In response to unfamiliar stimuli, children at one extreme responded in a shy or fearful manner (referred to as behaviorally "inhibited") while children at the other extreme of responsiveness appeared bolder or fearless (behaviorally "uninhibited"). Kagan et al. (1987, 1988) also provide evidence for inhibited/uninhibited temperament being a stable attribute of children's behavior across several years. These two groups of children also exhibited consistent differences in several physiological indices of HPA and ANS function, including different salivary cortisol, urinary norepinephrine, and cardiac (heart rate and vagal tone) measures. Kagan et al. (1988) concluded that differences in thresholds of amygdala-hypothalamic arousal to unfamiliar stimuli underlies temperament differences seen among these children.

Do behavioral dispositions influence social behavior?

Infants and children are the primary focus of temperamental research in humans because they are thought to be minimally influenced by volitional and societal factors. The huge body of research on temperament in infants and children has centered around the delineation of temperament and its predictive value in identifying behavioral problems later in development. A few research programs have examined and revealed influences of temperament in behavioral contexts related to functioning in social interactions, such as attention, perception, development of attachment relationships, social adaptation, and responses to stressful situations. These effects will first be explored in humans and compared with findings from primate research in following sections.

The first psychological processes that interface with environmental stimuli are perceptual processes such as evaluation and attention. Any response to an unfamiliar event requires some form of appraisal of the situation in order to identify the situation as novel and/or threatening. If differences exist among organisms in their perception of similar events (due to differences in dispositions), different behavioral responses should be expected. For example, differences in the perception of the social behavior of others could lead to differences in aggressive responses as exhibited by aggressive children (Quiggle, Garber, Panak, & Dodge, 1992). Such aggressive children differ from nonaggressive children in several components of how they process social information (Dodge, 1991), such as in encoding and interpreting environmental cues (Dodge & Crick, 1990; Quiggle et al., 1992). The competence children show in distinguishing between rough-and-tumble play and aggression was one factor that increased the likelihood that play bouts would lead to aggression (Pellegrini, 1988). Physiological responses to stressful situations are also influenced by the individual's perception (Sapolsky, 1992; Broom & Johnson, 1993). Rothbart, Derryberry, and Posner (1994) suggest that differences in the ability to control attention allows some children to attend to positive emotional states and develop coping mechanisms to stressful situations. Thus, if the perceptual capabilities of an organism are influenced by behavioral dispositions, response biases are expected to occur.

Individual differences in levels of reactivity to novel situations may have important ramifications for social interactions in children. The willingness to approach novel situations or conspecifics when 2 to 3 years old was shown to be associated with a child's willingness to interact with peers when 5.5 years old and with a friendly adult when 7.5 years old (Kagan, 1989). This shows the stability of the trait and the potential for influencing social interactions. Inhibition or withdrawal in response to arousing situations, such as unfamiliar settings or conspecifics, may represent a organism's method of adapting or coping with overly unpredictable and overly arousing events (Gunnar, 1994). Fox, Calkins, and Bell (1994) suggest social interactions with peers may be difficult for inhibited children because they lack the necessary approach behaviors to initiate interactions with others. Strong withdrawal in social situations, however, may put limits on the development of social skills available to a child or young animal.

Variation in the tendencies to interact socially could be related to children's abilities to adequately cope with stress in social domains. Organisms normally maintain their internal environment at species-typical homeostatic levels. Moment-to-moment fluctuations in arousal in either direction (positive or negative) are countered via adaptive processes involving activation of the ANS, HPA axis, and behavioral responses. When faced with provocative stimuli that either increase or decrease arousal, organisms can behave such that arousal is regulated (Thompson, 1994). For example, an infant's arousal level strongly influences where it directs its attention: aroused infants shift attention away from intense stimuli and vice versa (Gardner & Karmel, 1995). Variation in the ability or style of emotional regulation may influence social interaction among children. Rubin, Coplan, Fox, and Calkins (1995) found that individual differences in emotional regulation and sociability in children placed in unfamiliar same-sex groups were predictive of their tendencies to adapt socially to the unfamiliar social situations. Among children who interacted with others at low levels, the ones better at regulating emotions showed fewer anxious behaviors (appeared more comfortable) in this social situation than children that were poor emotional regulators.

Physiological correlates of behavioral dispositions

The idea that individual characteristics in humans have concomitant physiological bases has a long history, going back at least to the time of Hippocrates (Rothbart, 1989). Individuals that differ in their response to changing stimuli are assumed to have accompanying differences in the central nervous and neuroendocrine systems that regulate neurological and hormonal functioning during times of environmental challenge (Sapolsky, 1993b; Castanon & Mormède, 1994; Gunnar, 1994; Porges, 1995). Modern attempts to examine psychobiological aspects of behavioral dispositions have focused on physiological systems related to emotional functioning, such as the HPA axis, ANS, neuroregulatory catecholamines and indolamines, and central neural processing and control (Rothbart, 1989; Gunnar, 1990). The relationship between each of these physiological systems and behavioral dispositions is reviewed in humans and nonhuman primates in order to highlight the parallels between the two groups. The implications of such parallels are that as physiology serves dispositional characteristics in humans, similar physiology-behavior relationships exist in nonhuman primates and other mammals as well.

Stress and the HPA. Throughout daily activities, animals continually regulate their physiological functioning such that the body is maintained within tolerable limits (homeostasis). When the animal encounters either physiological or psychological disruptions to homeostasis, the body reacts with several different systems to counter the disruption depending on its nature (adaptation). If they are unable to adapt (or cope) and disruptions remain at intolerable levels, pathological repercussions likely follow (Sapolsky, 1992; Broom & Johnson, 1993). Thus, an organism experiences 'stress' when stimuli (usually some adverse condition or 'stressor') overtax homeostatic control systems and activate two major neuroendocrine systems (stress response) in the adaptation process (Sapolsky, 1992; Broom & Johnson, 1993). Both the sympathetic-adrenomedullary (SAM) and the HPA systems are involved in the mobilizing of energy and the rapid responding of the organism. The SAM system is activated more rapidly; in a matter of seconds catecholamines are released from nerve endings throughout the sympathetic nervous system (norepinephrine) and from the adrenal medulla (epinephrine). When a stressor is detected the HPA axis quickly begins its own cascade of hormonal events beginning with the release of corticotropin releasing hormone from the hypothalamus. A short time later adrenocorticotropic hormone is released from the anterior pituitary and travels through the bloodstream and stimulates the release of glucocorticoids (e.g., cortisol) from the adrenal glands several minutes later.

The predominant psychological conditions leading to stress responses involve uncertainty for an organism (Levine et al., 1989) and/or negative emotional reactivity (J. Mason, 1975; Gunnar et al., 1989; Stansbury & Gunnar, 1994; Boissy, 1995). Most evidence points to uncertainty as the prime activator of HPA responses to stress, and even stress responses seemingly induced by emotional reactivity may be modulated by uncertainty as well (Gunnar et al., 1989; Stansbury & Gunnar, 1994). Stimuli become psychologically stressful when they become unpredictable, when an organism loses the capacity to make active responses to relieve itself of the situation (lack of control), when an organism loses the ability to obtain information after making a behavioral response (lack of feedback) or when an organism is prevented from achieving a desired goal after a period when it was obtainable (frustration) (Levine et al., 1989). Behavior patterns leading to conditions that maintain some level of predictability and control tend to relieve the effects of psychologically stressful circumstances (Hanson, Larson, & Snowdon, 1976; Gunnar, Gonzalez, & Levine, 1980; Misslin & Cigrang, 1986; Levine et al., 1989; Hennessy, Mendoza, Mason, & Moberg, 1995).

Given that behavioral dispositions essentially constrain or influence the probabilities that certain behavior will be expressed (Mendoza & Mason, 1989), dispositions are likely fundamental for an animal's response to stimuli considered arousing and/or stressful. Behavioral dispositions can influence how animals respond to stress by modulating the perception of the situation (e.g., in determining how threatening the situation is) or by modulating the extent to which a behavioral response is effective in reducing the stressful situation. Parameters of the stress response are considered to be stable within individuals, vary across individuals, and be linked to behavioral reactivity

(Suomi, 1983; Higley & Suomi, 1989; Gunnar, 1994; Porges, 1995). Evidence from human infants, for example, supports this notion. When exposed to novel or threatening situations, infants differing in certain temperamental dimensions such as reactivity and inhibition also exhibit consistently different HPA stress responses (Kagan et al., 1988; Lewis, 1992; Gunnar, 1992; Gunnar, 1994) and autonomic cardiac responses (Porges, 1995; Snidman, Kagan, Riordan, & Shannon, 1995; Stifter & Jain, 1996). Individual differences in adrenal reactivity to a stressor also correlates with dispositional measures related to loss of situational control in infants (Gunnar et al., 1995).

Although less well studied, similar relationships between individual dispositions and stress responsivity have been theoretically and empirically linked in nonhuman animals. Common brain structures, such as components of the limbic system, may be involved in the activation of both dispositional characteristics such as inhibition and neuroendocrine systems of stress (Kagan et al., 1987, 1988; Berntson, Boysen, & Cacioppo, 1993). Greater HPA activity in response to a stressor is associated with greater inhibition in animals such as quail (Coturnix coturnix; Jones, Satterlee & Ryder, 1994), goats (Lyons et al., 1988a), mice and rats (Benus et al., 1991; Fokkema, Koolhaas, & van der Gugten, 1995), and rhesus macaques (Macaca mulatta; Suomi, 1983). In infant rhesus macaques, levels of HPA and sympathetic responses to stress were predictive of tendencies for extreme behavioral reactivity when separated from others (Suomi, 1983).

The ANS and reactivity. The ANS consists of two reciprocally activated systems that continually function to maintain internal homeostasis: the sympathetic system activates the visceral muscles and glands during stress and readies the body for emergency responses and the parasympathetic system maintains the steady-state functioning of the body and promotes functions associated with growth and restoration (Porges, 1995). These two systems are influenced by changes in the CNS and due to their connections to limbic pathways (Jansen et al., 1995) are key elements in emotional functioning and responding to stress. Two indices of underlying ANS contributions to individual differences have been examined in relation to dispositions: aspects of cardiac functioning and measures of SAM output (epinephrine and norepinephrine).

Cardiac activity is sensitive to changes in orientation and attention contingent on external stimuli of both social and nonsocial nature (Cacioppo, 1994). The sympathetic system increases heart rate and blood pressure while the parasympathetic system decrease heart rate once the sympathetic system has reduced its activation. Cardiac measures below baseline indicate parasympathetic dominance (or tone) while measures above baseline indicate sympathetic tone. The differential contribution to cardiac measures of the two ANS divisions can be obtained by statistically dividing out the variance in heart rate due to vagal nerve innervation to the heart (parasympathetic system). The variance due to parasympathetic control is called vagal tone (Porges, 1995). Thus, measures indicating shifts from homeostatic cardiac activity would index the relative contributions of the two systems in cardiac regulation and potentially identify physiological bases for individual differences in behavior.

Several measures of cardiac responsivity are associated with emotional functioning and dispositional differences in children (Kagan et al., 1987; Fox, 1989; Snidman, 1989) and adults (Cacioppo, 1994). Infants with lower cardiac vagal tone (more sympathetically activated) as compared with high vagal tone (more parasympathetically activated) were less likely to look at novel stimuli and were more easily distracted (Fracasso, Porges, Lamb, & Rosenberg, 1994), displayed fewer self-regulatory abilities at 5 months-old, were slower to approach a stranger, more likely to be rated by their mothers as difficult, and seemed poorer at adapting to a challenging social situation (i.e., their first week at nursery school) (Fox, 1989). When assessing the role of ANS activation in the cardiac measures of inhibited children, Snidman (1989) found heart rate variability more likely to be sympathetically influenced than in uninhibited children. Stifter and Jain (1996) suggest that high vagal tone is associated with approach behavior (anger, interest) while low vagal tone is related to withdrawal behavior (fearful, inhibited behavior). Thus, in infants and children individual differences in behavioral indices of temperament correlate with cardiac vagal tone and the relative amount and type of ANS input.

Few studies have examined heart rate indices of individual differences among primates. Consistent interindividual variability was a prominent feature of heart rate data of infant pigtail macaque (Macaca nemestrina) over several months (Reite & Short, 1980). Baseline heart rate measures predicted both behavioral and physiological reactions to maternal separation in infant pigtail macaques (Boccia, Laudenslager, & Reite, 1995). In free-ranging rhesus macaques held in captivity (an acute stressor), males with slower heart rates exhibited endocrine changes suggesting more adaptive responses to the stress than males with quicker heart rates (Rasmussen & Suomi, 1989). In rats, blood pressure was correlated with dispositional levels of aggressiveness (Fokkema et al., 1995). These few studies provide some evidence for similarities to data for humans in ANS function related to dispositional factors.

Monoamines and impulsivity. The dispositional dimension of impulsive-restrained behavior is not well studied in children but may be important for understanding behavioral dispositions in other species. Impulsivity and pathological aggressivness seem to be inversely correlated with peripheral serotonin levels in humans (Kruesi et al., 1990). Recently, similar behavior-serotonin relationships have been examined in primates either by correlating naturally occurring serotonin levels with aggression and impulsive behavior (rhesus macaques: Mehlman et al., 1994, 1995) or by controlled pharmacological manipulations (vervet monkeys, Cercopithecus aethiops: Raleigh et al., 1991). Both studies find that animals with lower serotonin levels exhibit either escalated aggression (Mehlman et al., 1994) or inappropriate aggression (e.g., as aggression directed at females which are potential allies; Raleigh et al., 1991). In the latter study, individual differences in serotonin levels predicted which male would become dominant in the absence of the normally dominant male. The psychological mechanism responsible for these behavior changes is unknown but serotonin may be acting on components of the animal's behavioral dispositions by altering thresholds to respond aggressively, aggression levels, and/or possibly the animal's perception of social situations.

Central processing and behavioral dispositions. Emotional responses are integral components of behavioral dispositions (above). Neocortical processing of aspects of emotion functioning (processing emotional stimuli and expression) has been found to be mostly associated with frontal cortex in both human and nonhuman animals (Kolb & Taylor, 1990). Additionally, evidence for asymmetries in hemisphere function related to emotion in humans is accumulating from clinical and experimental literature (Heller, 1990; 1993; Fox, 1991; Davidson & Sutton, 1995). The left hemisphere appears more involved in positive emotions and approach-related behaviors whereas the right hemisphere appears to play a greater role in negative emotions and withdrawal-related behaviors (Fox, 1991; Davidson, 1995). The right hemisphere is also uniquely associated with several measures of autonomic functions that are linked to emotion, such as ANS pathways that regulate heart rate and limbic pathways influencing the stress response (Heller, 1993; Porges, 1995).

Consistent hemispheric asymmetries in frontal cortex processing represent tendencies toward positive or negative emotionality (Fox, 1991; Davidson, 1993) and may reflect behavioral dispositions. Through the use of brain electroencephalograph (EEG) patterns, relationships between emotionality and approach-withdrawal tendencies are revealed in both children and adults. Children of different temperaments can be differentiated by asymmetrical patterns of EEG activation (Fox, 1991; Davidson, 1993; Dawson, 1994). Fox, Bell, and Jones (1992) found infants exhibiting more right frontal activation were more likely to be distressed by maternal separation than infants with more left frontal activation. Samples of extremely inhibited and uninhibited children displayed opposite patterns of hemispheric activation; inhibited children showed greater right than left activation and uninhibited children showed greater left than right activation (Davidson, 1993). In another study, infants that showed greater right frontal EEG asymmetry when 9 months of age were shown to be more inhibited at 14 months of age (Fox et al., 1994).

Evidence that primates show similar lateralized function related to emotional responses has been examined only recently. Hauser (1993) found that the left side of the face appears more expressive than the right in rhesus macaque fear grimaces. Hopkins and Bennett (1994) showed approach-avoidance behavior to novel objects in chimpanzees (Pan troglodytes) can be differentiated based on their trends in handedness; right-handed chimpanzees were less fearful of the objects and approached the objects more readily than the left-handed chimpanzees. Finally, split-brained rhesus macaques (with a severed corpus callosum) were more responsive when viewing emotionally laden images with their right hemisphere than with their left (Ifune, Vermeire, & Hamilton, 1984). These findings suggest that some similarities with evidence for lateralized emotional processing in humans.

Whether nonhuman primates also exhibit asymmetries in frontal cortex function was investigated in rhesus macaques through the pharmacological manipulation of fear-related behavior. In infant rhesus macaques, benzodiazepines are important in controlling fear-related freezing responses (Kalin & Shelton, 1989). When given benzodiazepines, infant rhesus reduced their freezing and vocalizations in response to threatening stimuli (i.e., they reduced their reactivity). Davidson, Kalin and Shelton (1992) administered diazepam (a benzodiazepine) to infant rhesus and measured EEG patterns when restrained. Benzodiazepines increased frontal asymmetry by increasing left-frontal activation. This result is consistent with the human data (above) that suggests left hemispheric function is related to approach components rather than reactivity behaviors. Davidson, Kalin and Shelton (1993) used infants' freezing responses to threatening stimuli as an index of their variation in fear prior to measuring EEG patterns. The size of the increase in asymmetry due to diazepam and individual differences in the duration of freezing were significantly correlated. The longer the duration of freezing, the greater the difference in hemispheric activation. Thus, these studies suggest that behavioral inhibition in rhesus shows a similar relationship to frontal cortex functioning as is found in humans.

Summary

The consistent yet sparse evidence presented allows for the tentative conclusion that similar behavior-physiology relationships exist in both human and nonhuman primates in regards to emotional responding and behavioral dispositions. These parallels can also be seen in the conservative nature of physiological functioning related to emotional and stress responses across mammalian taxa. As emotional processes are related to approach-withdrawal processes (Tobach, 1970; Fox, 1991; Davidson, 1993; Lang, 1995) and approach-withdrawal was argued by Schneirla (1959, 1965) to be a universal component of behavior, these parallels across taxa should not be surprising. Berntson et al. (1993) among others argue that the evolutionary continuity in these traits is due to a common mammalian neural organization underlying approach-withdrawal processes and other evaluative functions in the central nervous system.

Behavioral dispositions in primates

Researchers working with primates are struck by their individuality. This perception of individuality probably stems from the flexibility of primate responses (due to their relatively long developmental periods and large brains that facilitate the influential effects of life experiences during development), the complex ways that primates interact with each other, and the perceived behavioral similarities between humans and nonhuman primates (e.g., Goodall, 1986). The perceived similarity between humans and nonhuman primates has inspired researchers to apply terms and methods used to examine individual differences in humans to nonhuman primates (below). Thus, individual differences in primate behavior are examined within a framework of both human personality and temperamental factors.

As emotionality is an important component for measure of temperamental dispositions in humans, they may be equally important in examining nonhumans as well. The task of inferring emotions or dispositions from behavior is, perhaps, more difficult in primates than in humans because we belong to different species. We can not directly inquire as to what an animal experiences due to differences in communication abilities. Therefore, we make inferences based on observed behavior and ultimately assume similarities between species where there may not be any. When an animal is "agitated", for example, the expression of the agitation could be different from its expression in humans. Also, there may not be one-to-one correspondence between emotions experienced and their expression (Hinde, 1985). Therefore, caution is warranted when making conclusions concerning the similarities among individual characteristics among human and nonhuman primates.

Smuts (1985) observed that differences among male olive baboons (Papio anubis) in their ability to refrain from becoming "unnerved" and lashing out at rival males (i.e., inhibitory control) seemed to differentiate males that could maintain a consortship with a female and those that could not. Most research in this area, however, is not as anecdotal as this observation. Table 2 briefly describes the nonhuman primate studies that make inferences of behavioral dispositions and style. Two general approaches have been applied in these studies: 1) observing animals in social group situations, and 2) implementing a rating scale where observers estimate where animals rank on behavioral/emotional dimensions relative to everyone else. This latter technique essentially creates a personality profile of the animals, but does not necessarily represent behavioral dispositions. Both techniques rely on factor analyses to pare down a number of behavior items or rating scales into a smaller set of dimensions of behavior that characterize the animals.

Chamove, Eysenck, and Harlow (1972) were first to attempt to establish personality factors in primates by applying factor analyses to overt behaviors of juvenile rhesus. The majority of studies since then, however, employ subjective rating methods by Stevenson-Hinde and Zunz (1978) and Stevenson-Hinde, Stillwell-Barnes, and Zunz (1980). In these studies, the behavior of rhesus macaques from captive colonies was rated annually by observers familiar with the animals. The rating scales consisted of a number of adjectives (e.g., "popular", "confident", "equable", "tense") that the raters scored for how well they described each animal. Adjectives with high reliabilities among raters were entered into principal components analyses that reduced the scores down to three factors that accounted for over 60% of the variance among individuals. The three main factors were described as "confident", "excitable", and "sociable" based on the ratings (adjectives) that loaded onto each factor. In these and other studies, interobserver ratings of animals are judged fairly reliable (based on interobserver correlations) and valid (based on comparisons with observed behaviors) (Stevenson-Hinde et al., 1980; Martau, Caine, & Candland, 1985; Bolig et al., 1992).

Rating the behavior of primates has been subsequently used to investigate behavioral style and dispositions in a number of species of primates (Table 2). Studies on Old World monkeys generally find three or four factors that seem to represent similar dimensions of behavior, such as confidence or competence, and active or curious. Where possible, individual variation on the factors is correlated with dominance status of the animals. Regardless of how dominance was measured (water competition test: Caine et al., 1983; matrilineal rank: Cox, 1989; Bolig et al., 1992; success in agonistic encounters: McGuire, Raleigh, & Pollack, 1994) all studies find significant correlations between dominance and at least one factor (usually one that represents confidence or sociability).

The use of subjective ratings to identify differences in dispositions or style of behavior is limited in its usefulness. Rating animals may indicate more about the common conceptions people have about personality features rather than the actual features of the animals being rated. Stevenson-Hinde et al. (1980) tried to account for the possibility that ratings reflect the raters' own implicit theories by correlating six rating scales with similar quantifiable behaviors (e.g., the rating playfulness with the total frequency of play). While all six matched behaviors correlated significantly, the correlation coefficients were all 0.73 or below, suggesting that only half the variance (53%) was accounted for by the ratings. This suggests, validity may be compromised to some extent. A related problem is that in several of the studies, raters discussed the ratings before hand, possibly biasing ratings toward a group conception.

Perhaps, a greater problem with rating behaviors is a confound with dominance relationships. That is, many of the adjectives used for ratings describe actions and reactions of animals involved in dominance interactions. Rating scales may therefore be based on the style of response or responses due to the position dependent on dominance relationships. Thus, it is no wonder that confident animals are also the dominant ones, part of the ratings that usually load onto a confidence factor include effective (gets own way; can control others), aggressive (causes harm), assertive (direct; forceful), and fearful (grimaces, retreats readily from others). Showing that confident animals are usually dominant is more likely showing that dominant animals are confident. In support of this conclusion, McGuire et al. (1994) found that all vervet monkeys that changed dominance status (either increased or decreased) during their study also showed altered personality measures. Therefore, what they described was not a factor intrinsic to the animals but a factor dependent on their dominance relationships.

A final problem with subjective rating scales was pointed out early on by Stevenson-Hinde and Zunz (1978). During the first two years of their study, their rating scales reduced to two factors accounting for about 64% of the variance in scores (Table 2). The following years new items were added to the rating scales which subsequently produced a third factor, although the amount of variance accounted for overall remained similar indicating the variance was divided up differently. They suggest that the new factor was merely derived from the addition of the new items and no big changes occurred in the behavior of the animals. They concluded that the derived factors are not entities independent of the method of assessment. Consequently, studies that use different rating scales can not be easily compared.

Less subjective methods are also used to examine variation among individuals in primates. Schneider (Schneider, Moore, Suomi, & Champoux, 1991) implemented tests developed to examine temperamental responses in human neonates on infant rhesus macaques. They found rhesus infants vary over four dispositional dimensions (orientation, state control, motor maturity, activity) during the first few weeks of life. Suomi and colleagues presented infant rhesus monkeys with novel situations and distinguished individual monkeys by their levels of reactivity to social separation and other tests (Suomi, 1987). Reite and Short (1980), through a combination of behavioral and physiological indices, documented individual profiles of infant pigtailed macaques that were relatively stable across a period of several months. McGuire et al. (1994) supplemented ratings of behavior with overt behaviors to generate factors that described the behavioral style of vervet monkeys. And finally, Sapolsky and Ray (1989; Ray &

Sapolsky, 1992) used clusters of scores of behavior to document the style of dominance exhibited by male olive baboons. They found among dominant males, that glucocorticoid profiles correlated with the display of behaviors variable in degree of control and predictability over social contingencies. Thus, the inclusion of more objective measures of behavior is warranted over subjective rating methods.

The representation of an amalgam of behavioral traits with a subjective rating may also misrepresent the nature of the subjects. For example, when rating a monkey as fearful because it often displays a fear grimace or retreats readily from others (two characteristics of the fearful rating), the animal may be intrinsically fearful or alternatively, the animal may be low ranking within its group causing it to perform these behaviors to avoid conflicts. Another possible explanation is that this seemingly fearful animal may in fact be "bold" because it continually approaches and shows fear responses to the most dominant animal in the group. Thus, an animal that may appear fearful due to the amount of behavior it exhibits, may in fact, be socially adept and not intrinsically fearful by expressing submissive signals at appropriate times while making affiliative connections with a dominant animal. Through objective quantification of the performance of these "fearful" behaviors, elucidation of timing and identification of social contexts, one could begin to identify how that animal expresses whatever fear it experiences. This approach would better lend itself to establishing a dispositional profile (as defined above) of an animal, rather than describing behavior in more global terms, as used in rating behavior.

One strategy to separate individual differences in the behavioral and physiological responses from responses due to environmental and social factors is to measure these responses in one context and then change the context and measure them again. For example, McGuire et al. (1994) measured behavioral style of vervet monkeys in one set of groups and then separated them into smaller groups and measured them again. Another design is to take repeated measures over significant periods of time. For example, Suomi (1983) reports that physiological reactions to stress at early ages (22-28 days) in rhesus macaques were highly correlated with behavioral and physiological reactions later in development. Finally, animals may be tested for responsiveness in one context and then for social interactions in another. For example, in rats (Blanchard, Hori, Tom, & Blanchard, 1988) and marmosets (Callitrix jacchus; Saltzman, Schultz-Darken, & Abbott, 1996) animals were tested for individual differences in responsiveness to conspecifics in one situation and then put together into social groups in another. In both species, levels of aggressiveness during confrontations with conspecifics were predictive of later dominance interactions.

Conclusion

The preceding review addresses the importance of individual differences of behavior in primates and argues that its study is useful in understanding the organization of behavior in relation to physiology. By understanding the factors by which animals show variability and the associated physiological functions will enable a better appreciation of organization of behavior both within and between species. The use behavioral dispositions to elucidate this variability is a first step in the unveiling the mechanisms and functions of sociophysiological processes.

Appendix B

Psychological Aspects of Dominance Relationships in Nonhuman Primates and Rhesus Macaques in Particular

Dominance is a ubiquitous concept in animal behavior, used to describe interanimal relations. However, there is some debate on the definition of dominance and in how it should be measured. Many authors have tried to elucidate the essential nature of the concept of dominance in primates (e.g., Rowell, 1974; Hinde, 1978; Bernstein, 1981; Drews, 1993). Bernstein (1981) stressed that the nature of the relationships among interactants is paramount to dominance. Dominance relationships are learned relationships between two individuals based on a history of past experience of agonistic interactions where one interactant reliably submits at the onset of an encounter (Bernstein, 1981). Included in this formulation are two aspects often left out of other definitions; discrimination between different opponents and a learning component evidenced when one interactant changes behavior based on its history of interactions with the opponent. Based on this definition, if two animals fight each time they encounter each other and one of them reliably wins the fight, the winner would not necessarily be dominant because neither animal shows evidence that a consistent relationship has formed. The winner is considered dominant and the loser subordinate when the loser changes its behavior. When the loser assesses the interaction and signals its end (e.g., by avoidance, cower, vocalization, facial expression, etc.) then there is evidence that a relationship has formed, i.e., one of the animals has learned something from the encounter (Bernstein, 1981) and no escalation in aggression is required by the dominant animal to "win" the encounter (Drews, 1993).

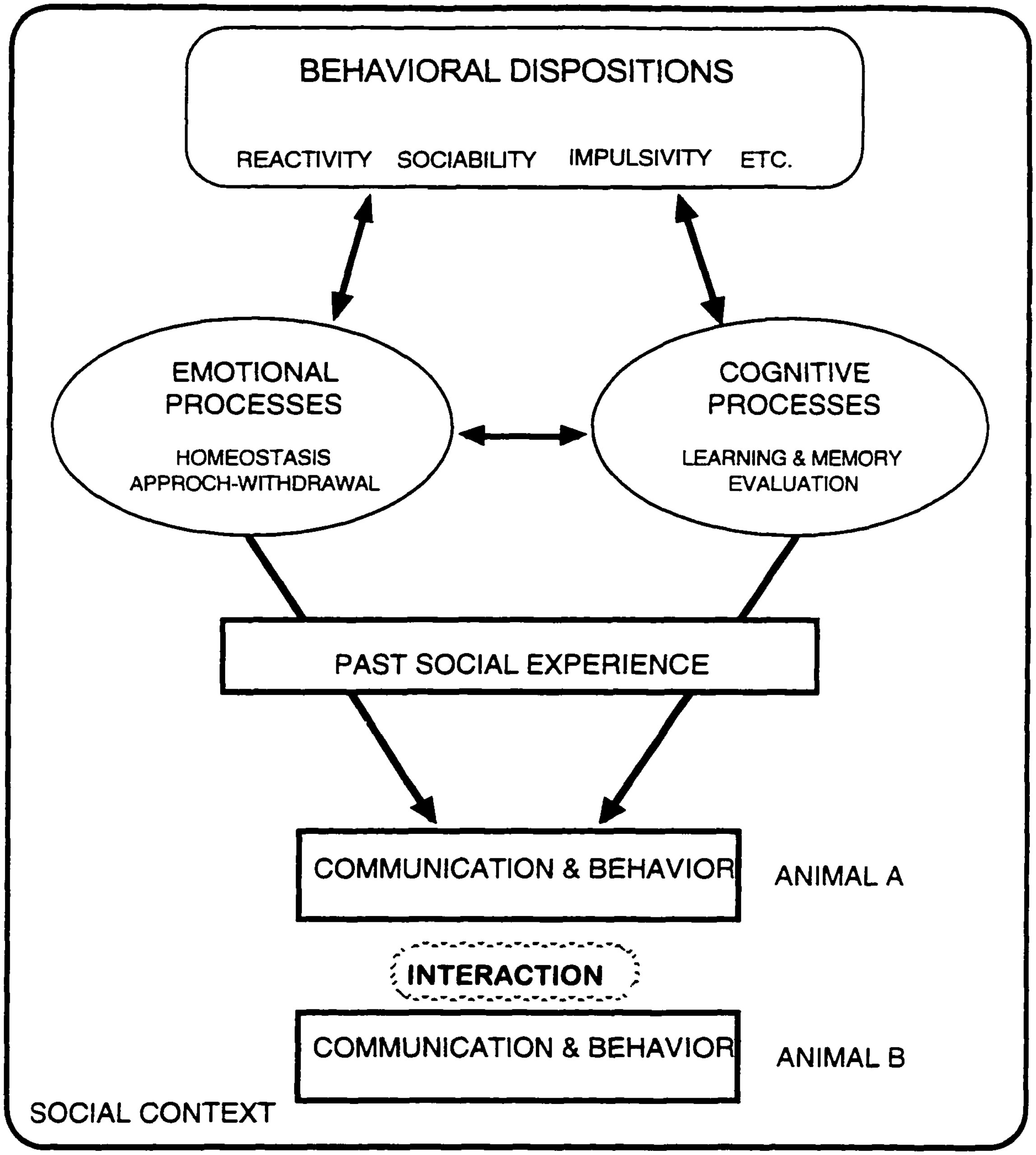
In many primates and some other vertebrate groups, dominance is not merely based on components of aggression such as body size, canine size or fighting ability. While dominance is mostly based on the history and direction of aggressive interactions, other factors in the expression of dominance have been shown to be pervasive such as the social context (Bernstein & Gordon, 1980; Mason, 1993), tolerance and affiliative behavior (De Waal, 1986; 1989) and social ties between individuals established through interactions such as grooming, sitting in proximity and through long term interactions among kin (Hinde, 1983; Chapais, 1992; Lee & Johnson, 1992). In species that exhibit marked levels of sociality, many social interactions involve more than a pair of interactants. In these cases, the social ties among individuals also becomes critical and the "social skills" of individuals in facilitating other group-members to defensively or offensively come to another animal's aid may become more important than aggression alone in determining dominance relationships. In captive vervet monkeys for example, the males' affiliation with females rather than their aggressive behavior plays an important role in determining which of two subordinate males will become the most dominant (Raleigh & McGuire, 1989).

Although dominance is relative among individuals (Bernstein, 1981) dependent on social structure and context, certain characteristics of interactants that influence social skills may be crucial for its establishment and maintenance. These include the animal's basic response tendencies or temperament, recognition of individuals; social experience in evaluating other group-members' behavior and social signals; ability to enlist aid when needed, etc. It is the culmination of these characteristics in the expression of social affect (e.g., fear responses) and aggression that may be most important in influencing which animals become dominant over others and which successfully maintain these relationships. That is, how animals interpret and respond to approach and withdrawal-type behaviors of rivals may be the critical feature for success in social interactions with conspecifics.

A model of the psychological processes involved in dominance relationships

In the model in Figure 1, I attempted to account for the fundamental psychological processes that potentially influence the outcome of social interactions leading to dominance relationships in primates. According to this model, when two animals interact the responsiveness of each actor is initially determined by its

Figure 1. Model of psychological processes influencing a dominance interaction in nonhuman primates. Presumably, Animal B has similar processes occurring.


BEHAVIORAL DISPOSITIONS
REACTIVITY
SOCIABILITY
IMPULSIVITY
ETC.
EMOTIONAL PROCESSES
HOMEOSTASIS
APPROCH-WITHDRAWAL
COGNITIVE PROCESSES
LEARNING & MEMORY
EVALUATION
PAST SOCIAL EXPERIENCE
COMMUNICATION & BEHAVIOR
ANIMAL A
INTERACTION
COMMUNICATION & BEHAVIOR
ANIMAL B
SOCIAL CONTEXT

behavioral dispositions (intrinsic levels of aggression, fear, inhibition, boldness, impulsivity, etc.). Animals with tendencies to become anxious or fearful may be more susceptible and more vulnerable to effects of stress and less able to effectively cope in social situations. The animal's current emotional state will therefore interact with its normal response tendencies to modulate the evaluation of the social environment, social communication, and social experience.

Cognitive processes in social situations are important when one animal interacts with another in either stressful or affiliative interactions. Primates need to evaluate the relative abilities of opponents based on whatever behavioral cues available (e.g., the way one walks, the loudness of vocalizations, etc.), showing appropriate social signals to avoid conflict and establish or maintain social ties. Individuals may need to assess the social environment for the presence of potential allies or competitors. As any relationship between two animals will depend on their history of interactions, this history will shape what the animal knows/remembers about another animal and the consequences of interacting with it. Ultimately, the manner in which their affective state and intentions are communicated to another will have important ramifications on each animals' response to the other.

This model highlights the potential importance that behavioral dispositions can play in the acquisition and maintenance of dominance relationships. While the focus of the present research is on male rhesus macaques, the model is theoretically applicable to any organism for which dominance depends somewhat on individual characteristics and not predominantly on other structuring mechanisms, such as maternal relationships. Unlike male rhesus macaques, in female rhesus macaques, like many other species with female philopatry (Holekamp & Smale, 1991), dominance is highly structured around maternal relationships. Daughters acquire similar dominance status with their mothers based on how other individuals in the group respond to them and on their own aggressive behavior (Datta, 1988; Chapais, 1992). The psychological variables associated with female dominance relationships developing from this system probably differ from those described in this model. Thus, this model would be less applicable to the processes underlying dominance interactions in female rhesus macaques than it is to males outside of their natal group.

Maternal relationships are also major determinants of male rhesus macaque dominance relationships during preadult residence in their natal groups (Lee & Johnson, 1992). Males usually leave their natal groups when they reach adolescence and try to enter new groups. Once they have left their familiar groups, males lose any support in agonistic interactions they enjoyed in their natal groups and must depend on only their own characteristics to establish new dominance relationships in a new group. While research has shown that the social context of male interactions is important in the establishing of relationships (Bernstein & Gordon, 1980), when there is no overriding structure males must establish new relationships using only what they bring to each interaction.

Components of the Model

Behavioral Dispositions

Studies examining the formation of dominance relationships between unfamiliar male rhesus monkeys find that asymmetrical relationships form in a matter of hours or minutes (Bernstein & Gordon, 1980; Mendoza & Barchas, 1983; Mendoza, 1993). While the factors responsible for such relationship formations are elusive, suggestions have included the rapid evaluation of opponents and the adherence to straightforward rules of social interaction (Bernstein & Mason, 1963; Mendoza, 1993). However, not all animals are identical in their tendencies to interact and form relationships with others. It is suggested here that differences among males in behavioral dispositions can influence the outcomes of initial encounters.

Research is convergent on the idea that interspecific differences in the style of dominance relationships displayed has its basis in differences in responses that occur across a wide array of social and environmental situations (Thierry, 1985; Clarke & Mason, 1988; Mendoza & Mason, 1989; de Waal & Luttrell, 1989; Butovskaya, 1993). De Waal & Luttrell (1989) found that style of dominance in two macaque species, for example, could be distinguished by tendencies to act conciliatory after conflict, to approach others without negative outcomes, and to be socially tolerant at a resource. A comparison of three macaque species responses to the presence of a passive human, Clarke & Mason (1988) showed species could be differentiated by measures of overall responsiveness, fear, and hostility. Given that such factors may influence species differences in dominance patterns, it is also likely that similar factors may differentiate individuals' dominance styles within species. For example, Bernstein, Gordon, and Rose (1974a) found that whether a male rhesus macaque resisted or accepted reduction in dominance rank upon reintroduction into a former group after a period of absence, was dependent on individual differences in response patterns.

Behavioral dispositions, as discussed above, can influence several other components of this model, including the perception and evaluation of the social communication of others and tendencies to regulate certain emotional responses during social situations involving stress (van Hoof & Aureli, 1994). For example, after the removal of a dominant male in small vervet monkey groups, the subordinate male that becomes the new dominant male is the one that is able to establish affiliative relationships with the females in the group (Raleigh & McGuire, 1989). Through the pharmacological manipulation of serotonin levels in subordinate males, Raleigh and McGuire (Raleigh et al., 1991) showed that individual differences among males in serotonin levels could form the basis of differences in behavioral styles that influences the attractiveness of the males to the females to interact with them.

Emotional processes Emotions in humans are accessed through communication, action, and physiological responses. However, in nonhuman primates, the extent that emotions can be accessed through these methods is hampered by the fact that observers don't have a full understanding of these modes of expression (Hinde, 1985). Emotionality is usually determined from the expression of changes in the physiological and/or cognitive state of the organism in response to external stimuli that result in a disruption of ongoing behavior. Emotional responses occur only to the perceived aspects of environmental stimuli, such that a stimulus may not be threatening per se, but could cause an emotional response (fear or anxiety) based solely on a perceived threat. Emotional responses are likely in situations where the actions of others are unpredictable or unexpected, for example, after agonistic encounters when further aggression is possible (Aureli & van Schaik, 1991; Maestripieri et al., 1992).

An organism's current emotional state can influence the cognitive evaluation of social communication (e.g., emotional content of facial expressions) and other events and memories (LeDoux, 1986, 1993; Rolls, 1992), while the emotional content of stimuli influence learning and memory processes directly (Gaffan, 1992; LeDoux, 1993). Moment-to-moment homeostatic regulation of the internal state of the organism can interact with certain response tendencies resulting in changes in one direction or another. The interaction of an individual's social dispositions that set the general affective tone of the animal, with its emotional responses to social stimuli can play a modulatory role in such responses. For example, bonnet macaque mothers are "socially disposed" to be less likely to prevent others from interacting with their infants than rhesus mothers (Mason et al., 1993), but this permissiveness could be reduced if the individual interacting with the infant generated some emotional response (e.g., fear) in the mother.

Emotional responses probably play their role indirectly by affecting the cognitive processes involved in social responses. For example, differences among rhesus macaque mothers in emotionality are reflected in their mothering styles and perception of risk for their infants (Maestripieri, 1993). Furthermore, after a fight between female baboons (Papio cynocephalus ursinus), subordinate females responded differently to screams of dominant females they just fought with, depending on whether the dominant female reconciled with her or not (Cheney, Seyfarth, & Silk, 1995). The assumption is that without reconciliation, the emotional state of the subordinate female may still be heightened so the subordinate would interpret the screams of the dominant females differently, i.e., as representing potential attack. Although Cheney et al. (1995) base this assumption on cognitive factors alone, interpreting their findings in terms of emotional changes is more parsimonious with the current discussion and less assumptive of the cognitive capacities of the baboons.

The regulation of emotional responses may be critical for normative social functioning in the face of social conflict. Social conflict is inevitable in group living primates (Mason, 1993) and has the potential to greatly alter the emotional state of the animals involved (van Hoof & Aureli, 1994). Thus, when conflicts arise and threaten the stability of social relationships, individuals in some species may be able to reduce their aroused states and maintain/restore these relationships through reconciliatory behaviors or redirection (de Waal, 1986; van Hoof & Aureli, 1994). Individual differences in this behavior has not been explored previously. Theoretically, animals able to regulate emotional changes due to intense social interactions through reconciliation or redirection behaviors would therefore be able to cope with competitive situations better than animals that are less able to regulate their arousal.

Regrettably, little is known about the role of emotional responses in primate social relationships. While some authors suggest variables related to individual differences in emotionality are involved in relationships between mothers and infants (Altmann, 1980; Goodall, 1986; Maestripieri, 1993, 1994; Schino, D'Amato, & Troisi, 1995), emotional inputs into processes involved in dominance interactions are hypothetical at this point. Future research in the area should be able to elucidate its contribution through biotelemetric monitoring of physiological correlates of emotional function in freely behaving animals. This may allow us to discover that animals successful in dominance relationships act bold rather than fearful, are better able to overcome a state of fear when conflict situations require action, are better able to evaluate its opponent's emotional state, or can remember what behavior patterns lead to successful outcomes over certain opponents under uncertain situations.

Communication: Aggression Aggression or aggressive behavior is usually defined as an attack or the threat of attack (threat of physical harm). Physical aggression has the potential to cause serious harm to the individuals involved, whether they are the victors or losers of the interaction. This potential for injury may be an evolutionary impetus for the establishment of less potentially harmful forms of aggression such as those communicated without physical contact (Bernstein, 1981). Aggressive behavior in primates can be expressed in many forms such as physical contact, vocalizations, scent markings, facial expressions, body postures, and ritualized movements. The form and intensity of aggression depends on many factors, such as the species (Bernstein, Williams & Ramsay, 1983b; Thierry, 1985), social contexts set by the social organization of the group and the immediate social environment (Bernstein et al., 1974a; Mason, 1993), probability of retaliation (Thierry, 1985; de Waal & Luttrell, 1989), perception of the behavior of other animals departing from the normal social patterns (Bernstein & Gordon, 1974a; Mason, 1993), current emotional states (e.g., rage, fear, anxiety), and the animal's social dispositions (Mendoza & Mason, 1989).

Much research finds aggression plays an important role in establishing relationships in some species of primates (Bernstein, Gordon, & Rose, 1974b; Mendoza & Barchas, 1983; Bernstein & Ehardt, 1985; de Waal, 1986). Dominance relations are initially influenced by aggression if the aggressive behavior of one animal increases the likelihood that another will produce submissive signals indicating that it will not respond aggressively. Once asymmetry in the response patterns is produced, dominance relationships can develop (Bernstein, 1981). Aggression is strongly tied to dominance interactions during the initial formation of groups and during periods of social instability (Sapolsky, 1983). But aggression is not always an important determinant of dominance nor are dominance and aggression necessarily linked (Bernstein & Gordon, 1980; Francis, 1988; Keverne, 1992; Mason, 1993) due to social pressures that can override individual attributes (Bernstein & Gordon, 1980; Bernstein, Gordon, & Rose, 1983a). This is especially true once dominance relationships have been established. In many primate species, therefore, the most dominant animals are not the most aggressive and the most aggressive are not the most dominant.

Communication: Expression of dominance In many vertebrate species that display dominance interactions, ritualized displays facilitate the communication of the expression of dominance. The social signals that function in these displays include vocalizations, scent marking, facial expressions (e.g., open-mouth, tongue flick), body movements (e.g., head jerks, distinctive movements, genital flashes), mounting, grooming, etc. These communicatory acts are thought to function by providing receivers with information about the animal's affective state (agitated, fearful, calm) or probable responses (intention) (Hinde, 1985; Mason, 1993). Animals gain information about others from directly experiencing these social signals directed at them, or through monitoring the communicatory actions among other animals. While the clear expression of an animal's intentions to act aggressive should facilitate clear unidirectional dominance interactions (de Waal, 1986), displays do not always provide reliable information (Mason, 1993). Furthermore, in conflict situations, several factors can alter the intensity of a signal or modulate the behavioral response of the receiver, such as the value of a contested resource (e.g., food, shady spot), the social relationship among interactants (strong or weak), and the immediate social environment (i.e., whom else is present).

In group-living species, social competence may be derived from both cognitive and regulatory skills during interactions with others. The expression of emotion, whether through vocalizations, facial expressions, body movements, or pheromones, provides conspecifics with information about the current state of an animal. Group members are attuned to this information as evidenced by the difficulties some individuals have relating to group members with impaired behavior (Mason, 1985). In social contexts, emotional responses may be misinterpreted by conspecifics leading to negative outcomes, such as aggression or ostracism. In vervet monkeys, for example, less impulsively aggressive males are more attractive as social partners to females than are more impulsively aggressive males (Raleigh & McGuire, 1989; Raleigh et al., 1991). Bernstein and Gordon (1974) emphasized that animals expressing "inappropriate" signals (a perceived violation of normal social functioning) in certain situations are responded to with aggression. They suggest that aggression may result when the actions (or position) of a conspecific are perceived by another as a challenge to their social relationship. Individual differences in tendencies to display certain emotions or display them at levels deviating from normal social functioning may therefore encourage aggression against certain individuals more than others (Mason, 1985). These effects may distinguish individuals who have difficulties in the social milieu from those who are more savvy.

<u>Perceptual processes: Interpretation of social signals</u> For many primate species, the cognitive evaluation of the social environment is important for the establishment and maintenance of relationships (Bernstein & Gordon, 1980; Bernstein et al., 1983a; Cheney, Seyfarth, & Smuts, 1986; Sapolsky & Ray, 1989; Ray & Sapolsky, 1992; de Waal, 1993). Evidence comes from studies showing animals that are adept at differentiating social signals of others are likely to be successful in social interactions. Examples include how the actions of others are perceived as either threatening or not (Sapolsky & Ray, 1989), the distinguishing of winning and losing a fight (Sapolsky & Ray, 1989), the evaluation of the state of relationships (De Waal, 1993), the ability to process information about an animal's relationships with others involved in alliances and coalitions (Harcourt, 1992), and the ability to select favorable contexts for competition (Chapais, 1988).

The same event perceived by one organism as threatening maybe perceived by another as benign or attractive. Several studies obtained data indicating either the importance of social cognition in physiological responses (Sapolsky & Ray, 1989; Ray & Sapolsky, 1992) or dominance rank differences in social perception (Capitanio, Boccia, & Colaiannia, 1985). Different glucocorticoid profiles in male olive baboons, for example, correlate with their tendencies to respond differentially to neutral or threatening stimuli (Sapolsky & Ray, 1989). In a different paradigm, Capitanio et al. (1985) used attentiveness and disturbance to videotapes of conspecifics either displaying aggressive or submissive displays as a measure of perception in female pigtailed macaques. They found that middle ranked animals differed from both high and low ranked animals regardless of the type of stimuli, suggesting that dominance relationships influence the evaluation of social signals and individual differences in how the behaviors were received. If individual differences in perception can arise from dominance relations, then potentially, other sources (e.g., dispositional variables) of these differences may be likely as well.

Learning and memory Also critical for the structuring of dominance relationships are learning and memory processes: animals must be able to remember the consequences of their past interactions with others for consistent relationships to be formed. Knowledge of an opponent's fighting abilities, number of allies that come to its aid, and the exact social context may be important in cases where the presence of other individuals can alter the outcome of certain interactions. For example, if animal A submits the first time it meets animal B when B's mother was present to protect B, remembering this fact would be beneficial the next time A encounters B. Animals that are quick to learn about their social milieu may have an advantage in social interactions. This learning may begin at an early age when infants are experiencing their mother's social environment and other group members are learning to identify the mother-infant pair (Holekamp & Smale, 1991; Chapais & Gauthier, 1993).

Predictability and uncertainty As discussed above, high levels of uncertainty, unpredictability, or lack of control in social situations can be psychologically stressful (Levine et al., 1989). Individual differences in he susceptibility to arousal from uncertainty and, in the ability to adequately cope with the stress may form the basis for differentiating individuals in their success in dominance interactions. One source of predictable outcomes is long term, stable and familiar social relationships where the past experience with the behavior of other, is the best predictor of future behavior (Bernstein, 1981; Levine et al., 1989). Dominance relationships themselves offer some stability if the direction of ritualized dominant and subordinate signals are relatively consistent. For example, in rhesus macaques 86% of all aggressive interactions were followed by the appropriate (i.e., submissive) responses (Bernstein & Ehardt, 1985). However, ambiguous communication between dominants and subordinates can lead to the perception by either animal that their relationship is unstable, aggression can escalate (in the above study a third of the inconsistent agonistic interactions involved continued aggression), and the predictability in the relationship breaks down. Many of the cognitive aspects of social interactions related to dominance relationships (mentioned above) are germane to reducing uncertainty as well.

Background for proposed studies

Dominance relationships in rhesus macaques This model suggests that among the psychological functions that underlie the behavior of males during social interactions that either influence or is influenced by dominance relations, behavioral dispositions can be important. However, given the nature of rhesus macaque societies there may be a few distinct periods in a males' life when aspects of his style of behavior could greatly influence his dominance relationships. This is due to the fairly rigid social structure that is set by the social context in the establishment of dominance relationships (Bernstein & Gordon, 1980). Dominance relationships are based on maternal relationships when young and a seniority system when adult, leaving little room for the influence of individual characteristics to play a great role in dominance acquisition.

Rhesus monkeys show the ubiquitous cercopithecine pattern of female philopatry and natal male dispersal during the peripubertal period (Melnick & Pearl, 1987). Dominance relationships in rhesus macaques conform to the pattern shown by other species with similar social systems (Holekamp & Smale, 1991) in that like their congeners, juveniles show maternal rank inheritance for females and males, ranking below their mothers (Datta, 1988). As juvenile males reach adolescence, their contacts with their matrilines slowly weaken, in part by targeted aggression from adults (Bernstein, Judge, & Ruehlman, 1993). The majority of males migrate from their natal group during adolescence (3-4 years old, Colvin, 1986) and attempt to integrate into other groups. Even into adulthood, male rhesus macaques will disperse to new groups repeatedly (Lindburg, 1969; Drickamer & Vessey, 1973).

When rhesus males leave their natal group during adolescence they are less constrained by a group's historical structure. While within their natal group males may receive social support from matrilineal members during social conflicts. In contrast, migration entails surviving during the time between groups, and using their social skills to either join small all-male groups or heterosexual groups (Lindburg, 1969; Drickamer & Vessey, 1973; Berard, 1990; Fernald et al., 1995). Upon natal migration males lose any support from either matrilineal members or other animals that aided him during conflicts. However, Meikle and Vessey (1981) suggested that males could continue to receive support by emigrating to groups containing maternally-related brothers. This may not match the condition in the wild because Meikle and Vessey studied males on an island where migration was confined to a choice of only three other groups to possibly enter. In at least one wild population, rhesus males showed random choices in groups with respect to former group members when choosing among more than three groups (Melnick, Pearl, & Richard, 1984).

While little is known about the processes of entering a new group, acceptance and/or tolerance by female rhesus macaques seems to be an important factor in group integration (Wilson & Gordon, 1979; Tannenbaum, Eisler, & Wallen, submitted). Introduction studies suggest that new males have to handle themselves in the face of aggression from resident males and females (Bernstein et al., 1974a; Southwick, Siddiqi, Farooqui, & Pal, 1974) and establish affiliative contacts with adult females (Tannenbaum et al., submitted). Variation in males' behavioral dispositions could lead to variation in the method or success in integrating into a new group. The typical pattern observed in males is to remain at the periphery of a group and slowly establish relationships with other females and males (Lindburg, 1969; Berard, 1990; Fernald et al., 1995). Other methods are possible: one migrating male was observed to actively challenge others, including high ranking males, only submitted when facing a number of opponents (e.g., Perloe, 1993). However, this method was unsuccessful due to the large number of adult males that allied against him (Perloe, personal communication, 1995).

When rhesus males join a group, they usually do so at the bottom of the established dominance hierarchy (Drickamer & Vessey, 1973; Bernstein & Gordon, 1980). This is most probably due to their lack of relationships with resident males and females. However, variation in this pattern has been found both in captive (Bernstein & Gordon, 1980) and free-ranging (Drickamer & Vessey, 1973; Berard, 1990) populations. Berard (personal communication, 1995) suggests that when a male hierarchy is unstable, some emigrating males are able to obtain the highest ranking positions over resident males. Thus, if behavioral dispositions influence social skills of males then individual variation in males' dispositions can play a role in dominance acquisition in new groups.

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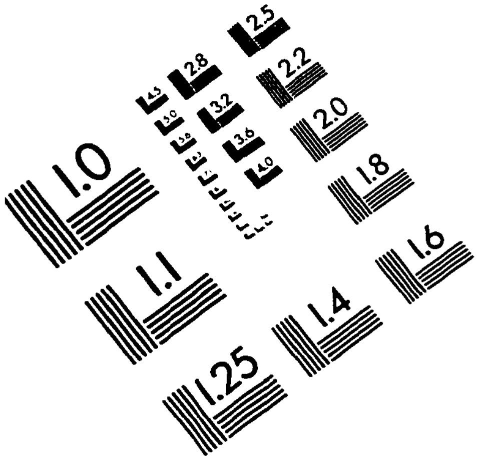
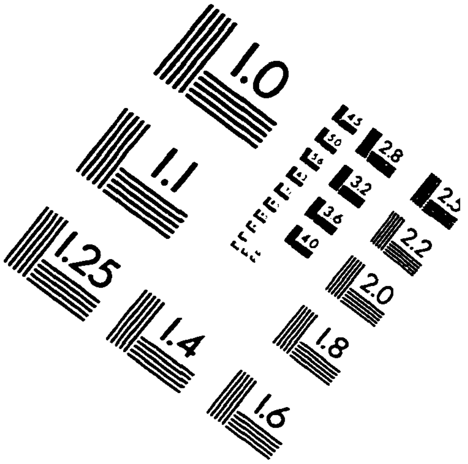
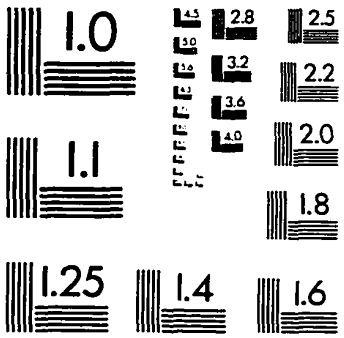
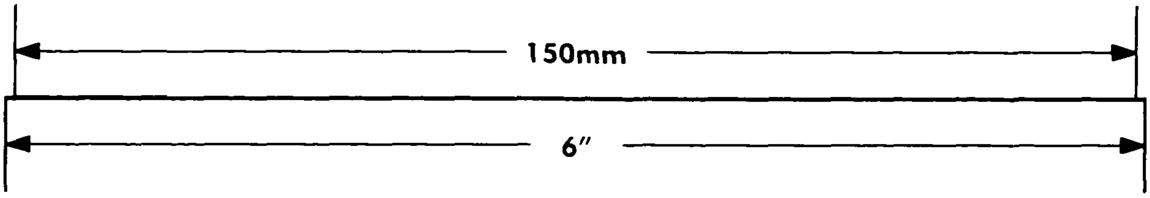
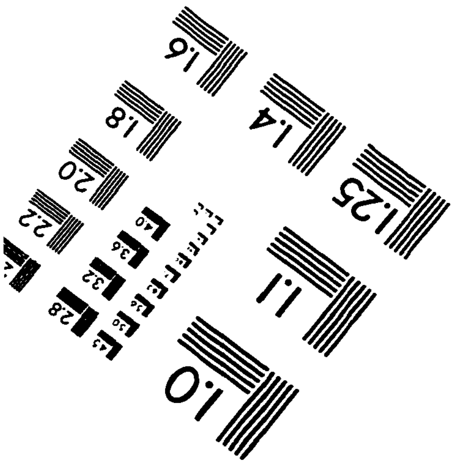
IMAGE EVALUATION TEST TARGET (QA-3)

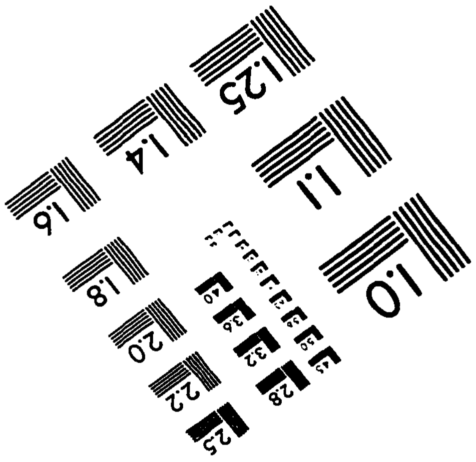












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