

Nature of Proximate Mechanisms Underlying Primate Social Systems: Simplicity and Redundancy

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Understanding the types and qualities of long-term associations, both sought and avoided, is a critical step in elucidating the proximate mechanisms underlying primate social systems. For a complete understanding, we must also take into account the need of group members to coordinate many other activities, such as travel patterns, feeding schedules, and selection of sleeping sites. Individual activity patterns, the manner in which individuals respond to social and nonsocial events, and use of the spatial environment must also be considered. Here, we will illustrate some of the proximate mechanisms contributing to the monogamous and territorial social system of the titi monkey. We will then present a model showing how many relatively simple, error-prone mechanisms can collectively yield stereotypic expressions at the group level.

Given the complexity of primate social systems, it is not surprising that the search for proximate mechanisms is a daunting task. We have long known that the types of social groups that primates form and maintain are characteristic of a given species.¹ It is also clear that social systems emerge from interactions between individuals.² Understanding proximate mechanisms

contributing to social systems, therefore, requires a focus on the tendencies of individual members of a species to interact with one another in particular ways that lead to the production of the species-typical grouping pattern.

At a gross level of analysis, primate social systems can be categorized by the number and sex ratio of adults typically found in the groups. Underlying the most common modal grouping pattern, the multimale-multifemale group, is the tendency for adults to tolerate and even seek like-sex companionship. Other types of primate social groups depend in some part on categorical exclusion of conspecifics.³ For example, in single-male or harem groups males are intolerant of the close proximity of other males, and in monogamous primates both males and females are intolerant of unrelated like-sex adults. In each of these systems, the degree of tolerance of like-sex companions is dependent on circumstances or age. Young males in species characterized by unimale groups often leave their natal groups and form bachelor groups until the opportunity to secure a harem arises. Clearly, the intolerance displayed by

males of these species for like-sex companionship is provisional. Tolerance of conspecifics may also be manifest between groups. In some cases, extensive interactions between animals of neighboring groups lead to elaborate multigroup coordination of activity.⁴ This is seen in extreme form in the Hamadryas baboon (*Papio hamadryas*), which lives in harem groups but shows coordination of sleeping and travel patterns among the scores of harems in a community.⁵ Male-female relationships are also variable, giving rise to distinct qualities of sociality. Squirrel monkeys (*Saimiri sciureus*), for example, live in large multimale-multifemale groups, but males and females do not interact extensively. In contrast, the male-female relationship in the monogamous titi monkey (*Callicebus moloch*) is characterized by a close emotional bond.⁶

Understanding the types and qualities of long-term associations, both sought and avoided, is a critical step in elucidating the proximate mechanisms underlying primate social systems.^{7,8} For a complete understanding, we must also take into account the need of group members to coordinate many other activities, such as travel patterns, feeding schedules, and selection of sleeping sites. Individual activity patterns, the manner in which individuals respond to social and nonsocial events, and the use of the spatial environment must also be considered.

Where do we begin the search for mechanisms? Given the persistence of the species-typical form of social groups across environments and gen-

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erations, there is little doubt that the dispositions that contribute to social systems are represented in the neural and physiological systems of the individual primate. It is tempting, given the stereotypic nature of social expression, to look for comparably stereotypic neurophysiological mechanisms. We consider it unlikely that specific adaptations in support of each species' particular form of social structure exist. It is more likely that proximate mechanisms underlying social proclivities are comprised of numerous, more generalized response tendencies. Moreover, the enormous variability of social systems, even among closely related species, suggests that small evolutionary shifts in one or more tendencies to respond to social and nonsocial stimuli result in large changes in outcome at the group level. Here, we will illustrate some of the proximate mechanisms contributing to the monogamous and territorial social system of the titi monkey. We will then present a model showing how many relatively simple, error-prone mechanisms can collectively yield stereotypic expression at the group level.

SOCIAL DYNAMICS IN TITI MONKEYS

Titi monkeys live in small family groups with an adult male-female pair and 1–3 offspring.⁹ They travel and forage as a group within a small multipurpose territory. Group members are rarely out of sight of one another during daily travel, are usually found in close proximity, and spend considerable amounts of time huddled as a group with their tails entwined. Females give birth to a single infant each year. Infant titi monkeys are carried as much as 90% of the time by their fathers for the first 3 months of life, and then begin to move independently.¹⁰ Although titi monkeys can reproduce by 18 months of age, young adults generally do not participate in reproductive activities, including care of younger offspring, as long as they are living with their parents.¹¹

We argued elsewhere that proximate mechanisms contributing to the monogamous, territorial lifestyle of titi monkeys can be categorized ac-

ording to three major dimensions: 1) temperament, or the characteristic response to environmental events; 2) categorical responses to conspecifics, such as familiar vs. unfamiliar, male vs. female, and adult vs. juvenile vs. infant; and 3) dynamics of social relationships.^{3,6,12} The studies that led to these designations were performed as a part of a research program comparing the monogamous titi monkey with the polygynous squirrel monkey. Squirrel monkeys are referred to here only as necessary to illustrate the distinctive traits of titi monkeys; a separate treatment of them is provided elsewhere.¹³

Temperament

In comparison to squirrel monkeys, titi monkeys are more sedentary, cautious, and reluctant in their approach to the environment. Titi monkeys travel within their relatively small territories along habitual pathways.⁴ They are slow to incorporate new travel routes, and when provided with shortcuts to desired goals, they rarely utilize them.¹⁴ They will often travel a considerable distance in order to maintain contact with a familiar route or substrate.¹⁵ Titi monkeys do not differ from squirrel monkeys in performance on standard cognitive tasks, but they are slower to contact novel objects or tasks, they are more cautious in approaching new problems, and their behavior is less varied than that of squirrel monkeys.^{16,17} Titi monkeys are even reluctant to take a highly desirable food item when presented in a context that deviates only slightly from familiar conditions (Mason, unpublished observations).

The sedentary and cautious lifestyle of titi monkeys is supported by the activity and reactivity of their physiological systems. Titi monkeys exhibit less sympathetic activity than squirrel monkeys, and sympathetic responses in titi monkeys but not squirrel monkeys are quickly counteracted by a rapid and substantial opposing parasympathetic response.¹⁸ Changes in the environment that will lead to activation of the pituitary-adrenal response to stress are more subtle in titi monkeys than in squirrel monkeys,¹⁹ but the stress response, once activated, is greater and more prolonged

in squirrel monkeys than in titi monkeys.²⁰ The physiological, like the behavioral, response to challenge and change is characterized by strong inhibitory reactions in titi monkeys, in contrast to the more vigorous behavioral and physiological activation characteristic of squirrel monkeys in comparable situations.

Categorical Responses

Adult male and female titi monkeys react strongly to other animals. In the absence of familiar companions, a titi monkey will interact positively with an unfamiliar conspecific of the opposite sex. Even like-sex conspecifics may become the focus of affiliative interactions if no other social alternatives are available. Given a choice between multiple alternatives, however, titi monkeys will interact selectively with a single animal of the opposite sex. As with the nonsocial environment, titi monkeys are highly sensitive to familiarity in the social environment, and their interactions are more cautious and tentative with unfamiliar than with familiar animals. The tendency to interact cautiously with an opposite-sex stranger is particularly prominent in females and persists even if the mate has been absent for several days prior to the encounter.²¹ For titi monkeys that are living with a mate, the response to unfamiliar conspecifics of the same sex is usually agonistic, particularly when the mate is also present, and can lead to activation of autonomic and pituitary-adrenal activity.^{21–23} For an adult titi monkey, then, there appears to be a strong motivation to establish affiliative interactions with another animal. Whenever possible, these affiliative interactions are directed toward a single animal of the opposite sex. In nature, titi monkeys will occasionally seek interactions with opposite-sex animals from neighboring groups.²⁴ When an unfamiliar rival is encountered close to the mate, jealousy reactions are often severe. On the rare occasion when this occurs, antagonism can be directed to the mate as well as towards the stranger. Males, in particular, have been observed to actively restrain their mate.^{4,24,25}

Adult titi monkeys also respond to

young animals categorically. When presented with either their own offspring or an unfamiliar age-matched animal, titi monkeys respond to infants less than 6 months of age with greater elevations in heart rate than to juveniles 12–18 months of age. In a choice situation, parents do not differentiate their own offspring at either age from an unrelated infant or juvenile titi monkey, either behaviorally or physiologically.²⁶ The stimuli presented by infants or juveniles form distinct categories for adults, but the distinction here between familiar and unfamiliar is less robust than that between familiar and unfamiliar adults.

Dynamics of Social Relationships

Perhaps the most striking feature of the social dynamics of titi monkeys is the close emotional bond established between the adult male and female that form the nucleus of the social group. In nature, the activity of the adult pair members is highly coordinated, and each member frequently looks toward the mate during travel and feeding. Encounters with neighboring troops are highly ritualized and include simultaneous and coordinated displays between mates.⁹ Laboratory studies have confirmed the tendencies to coordinate travel, feeding, and other activities between pair-mates.^{4,27–29} Separation of mates is a substantial stressor for adult titi monkeys, and the behavioral and physiological response to novelty is somewhat attenuated by the presence of the mate.^{19,22,23,30} The close emotional bond between the adult male and female members of the family group resembles the filial bond found in most other primate species.

Although clearly capable of forming intense emotional bonds, adult titi monkeys surprisingly do not form a close bond with their offspring. Neither mother nor father titi monkeys respond to separation from their young with behavioral distress or activation of the physiological stress response.³⁰ Parents respond to infant vocalizations, and perhaps other forms of infant distress, by moving to the source, and they will retrieve a separated infant.^{30,31} Their response

to the infant does not appear to be specific to their own offspring, however, and they do not display the highly organized parental behaviors seen in chimpanzees or macaques that function to relieve infant distress. In fact, parental care in titi monkeys primarily consists of simply allowing infants to cling. For mothers, tolerance of infant contact is generally limited to brief periods surrounding nursing. In mothers and older siblings, prolonged infant contact leads to clear signs of agitation, attempts to dislodge the clinging infant, and often biting of its hands and feet. This pattern of parental behavior clearly contrasts with the otherwise close and harmonious relationships among family members in titi monkey groups.

In response to differential treatment, infant titi monkeys quickly learn to move to the mother for brief nursing bouts, to avoid siblings, and to remain with their fathers most of the time. The tendency for parents (and other group members) to maintain close proximity with one another facilitates the infant's movement between the tolerant father and the nursing mother. By the end of the first week of life, titi monkeys are fairly skilled in making the transitions and do so without the assistance of either parent. In choice tests, 6-month-old infants generally choose the father instead of the mother.³⁰ When tested for their response to separation from their parents, 3–5-month-old infants show a substantial pituitary-adrenal response to separation from their fathers, even when their mother is present during the separation period. In stark contrast to squirrel monkeys, infant titi monkeys do not respond to separation from their mother if their father is present during the separation period.³² Titi monkey infants thus form an emotional attachment bond with their fathers that is not reciprocated.

The emotional bond between the young and the father persists into adulthood. Young adults living in their natal group respond to separation from their parents (presumably, most strongly from their father) with a sustained increase in pituitary-adrenal activity, regardless of whether

they remain with their siblings in the familiar home environment or are placed alone in an identical cage.^{33,34} Elevations in cortisol may persist for as long as 4 weeks of separation. The fact that the pituitary-adrenal response is sustained suggests that the normally efficient negative feedback mechanisms are rendered inoperative during the separation period. Upon reunion with parents, cortisol levels rapidly return to pre-separation values. It is interesting to note that restoration of pre-separation cortisol levels can also be achieved by providing the young adult titi monkeys with a new, unfamiliar heterosexual companion.³⁴ In contrast to the intolerance female titi monkeys and siblings display toward a clinging infant, other interactions between mothers and offspring and interactions among siblings are amicable, often including prolonged periods of passive contact with tail-twining. Aggressive interactions among family members are rare.

Summary

Given our current understanding, we can use numerous factors or determinants that contribute to the monogamous, territorial system of titi monkeys (Fig. 1). The factors listed range from regulation of autonomic balance organized in the hypothalamus or brain stem³⁵ to social perceptions that are likely organized in forebrain areas such as the frontal lobe or amygdala.³⁶ Some characteristics that help to define titi monkey lifestyle are not listed. For example, a preliminary comparison of the brains of a titi monkey, squirrel monkey, and macaque revealed that the hippocampus of both the titi monkey and the squirrel monkey was nearly two times larger than the macaque hippocampus, in spite of the larger overall brain and body size of macaques. Because the hippocampus is known to be involved in processing spatial information, this may reflect the arboreal lifestyle of these New World monkeys. Moreover, the titi monkey hippocampus occupies a proportionately larger amount of neural tissue than that of the squirrel monkey, perhaps reflecting a greater emphasis on spatial details in titi monkeys. These findings offer a promising avenue for explor-

Temperament	
D ₁	neophobic
D ₂	habit driven
D ₃	focus on contextual details
D ₄	behavioral inhibition
D ₅	parasympathetic dominance
D ₆	low stress response threshold
D ₇	efficient negative feedback inhibition
Categorical Responses	
D ₈	high social motivation
D ₉	xenophobic
D ₁₀	focus social motivation on single animal
D ₁₁	heterosexual attraction
D ₁₂	responsive to infant stimuli
Relational Dynamics	
D ₁₃	adult male-female attachment
D ₁₄	biparental care
D ₁₅	paternal tolerance
D ₁₆	maternal, sibling intolerance to clinging
D ₁₇	infant attachment to father
D ₁₈	friendly familial relations

Figure 1. Individual factors or determinants (D) underlying emergence of a monogamous, territorial system in titi monkeys. Determinants are organized according to three major dimensions that influence how titi monkeys interact with their environment, both social and nonsocial.

ing the neurobiology of species differences in use of space (e.g., Clayton³⁷). It is unlikely, however, that the highly developed hippocampus can explain other aspects of their monogamous, territorial lifestyle. Although there is much to be learned about how the organization of the nervous system contributes to the distinctive lifestyle of titi monkeys, it is clear that their social system is a multiply determined trait that is dependent on diverse neurobiological systems.

If we examine all the factors identified in Figure 1 and seek to understand how a monogamous, territorial system is created, another problem arises. The contribution of each factor is only probabilistic. That is, most titi monkeys display most of the traits characteristic of the species most of the time. Any given monkey, however, is unlikely to display all features completely, and for any given feature only about 80–90% of the animals tested show the trait in a given situation. For

example, some fathers are not very tolerant of infant clinging, and some mothers are very tolerant. Similarly, new travel routes are sometimes incorporated into daily routines, and occasionally daily routines are abandoned altogether. In some cases, the tendencies animals display are not internally consistent. Thus, a titi monkey female will on occasion make a mad dash into the neighboring territory, outrunning her mate, to copulate with another male, and yet a female titi monkey will typically avoid interactions with unfamiliar males even in the absence of her mate. None of the traits that we propose as contributing to the titi monkey lifestyle is absolute, and none is expressed in the same reliable fashion as the monogamous, territorial social system. We propose that the factors contributing to a monogamous, territorial system do so semi-independently. Because of the sheer number of factors, monogamy is virtually an inevitable outcome, even though each factor is itself error-prone.

To illustrate how social systems are produced from underlying proximate mechanisms, we present two alternative models. The linear model assumes that all determinants of a social system are additive and necessary. The redundant systems model, which we advocate, assumes that determinants are independent and that not all need to be in place for the outcome to be realized.

THE LINEAR MODEL

If each individual factor were necessary for the emergence of a social system, then the factors would be considered additive, each contributing to and required for the expression of complex behavioral patterns. This can be represented by:

$$D_1 + D_2 + D_3 + D_4 + \dots \neq D_n$$

= Emergence of
Complex Social System

where D₁–D_n are the individual factors or proximate mechanisms (e.g., as listed in Fig. 1). In reality, we know that any one factor is not necessarily expressed at all times, nor present in all individuals. This becomes prob-

lematic for the linear model. For example, if each of five factors is expressed only 80% of the time, the probability that the species-typical social system will emerge is equal to the probability that all factors are present, which is quite low:

$$0.8 * 0.8 * 0.8 * 0.8 * 0.8 = 0.32.$$

With this model, the social system is hence expected to be expressed only 32% of the time. Addition of more factors would further reduce the probability of expression. Thus, the linear model does not explain how these social systems emerge in such a reliable and stereotypic fashion.

REDUNDANT SYSTEMS MODEL

In this model, each factor can contribute to the emergence of the behavior in question, but not all are necessary. The model can be represented as:

$$D_1 \text{ or } D_2 \text{ or } D_3 \text{ or } D_4 \text{ or } \dots \neq D_n$$

= Emergence of
Complex Social System.

Rather than calculating the probability that all factors will be expressed simultaneously, we can calculate the probability that all will *fail* simultaneously:

$$0.2 * 0.2 * 0.2 * 0.2 * 0.2$$

= 0.00032.

The probability that all factors will simultaneously fail is 0.00032, so the probability that one or more will be operable and contribute to the outcome is 0.99968, or 99.9%. The addition of more factors will increase the probability of the outcome being expressed.

The redundant systems model allows us to reconcile the fact that simple behavioral patterns and other proximate determinants are *not* expressed reliably, yet more complex behavioral patterns (including social systems) can emerge from these dispositions with predictable regularity. Thus, a number of relatively simple response tendencies or factors (the more the better), each of which is somewhat error-prone, can function together to generate a species-specific

social system that is relatively impervious to error. Redundancy in the proximate mechanisms underlying primate social systems ensures that social organization persists in spite of failures that might, and regularly do, occur in the elements that create the system.

CONCLUSIONS

To understand proximate mechanisms underlying primate social systems, we must first identify the components of sociality for individual primates. Our research over the past three decades has successfully identified numerous factors important to the monogamous, territorial lifestyle of titi monkeys. In taking the next steps and asking how these factors are represented in the brain and physiology of the species, we have barely scratched the surface. It is clear that numerous systems are involved and distributed throughout the brain. The search for proximate mechanisms of social systems at the neurobiological level will be most successful if each behavioral disposition contributing to social expression is examined individually, and its contribution to social systems is determined independently. In our opinion, combining the results of this essential analytic task with continuing efforts at synthesis is the most effective path toward understanding the neurobiology of social systems.

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