

Do California Ground Squirrels (*Spermophilus beecheyi*) Use Ritualized Syntactic Cephalocaudal Grooming as an Agonistic Signal?

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Animal communication theory holds that many signals have evolved from nonsignal precursors. This field and laboratory study of California ground squirrels (*Spermophilus beecheyi*) provides evidence for the coexistence of such a precursor with its derived display. The precursor is an ancient, endogenously sequenced (syntactic) pattern of cephalocaudal grooming movements (CCGs) shared by all rodent suborders. The following evidence supports the hypothesis that a supernormal version of this pattern has been selected for signal function. Syntactic CCGs in the field (a) were more rigidly stereotyped than ordinary syntactic CCGs in the laboratory; (b) differed from laboratory syntactic CCGs in other ways that enhanced their conspicuousness, in part through exaggeration of the syntactic cephalocaudal pattern; (c) were associated with scent marking and social staring; and (d) were associated with intrasexual agonistic encounters that did not escalate to fighting.

Many animal social signals are thought to have evolved through modification of older noncommunicative behavioral patterns by a process called *ritualization* (Beer, 1977; Tinbergen, 1952). Through ritualization, behavior may be modified in form, pattern, and context of use as it is shaped by selection for communicative function. The concept of ritualization has proven useful in accounting for a diversity of communicative activities. For example, male ducks “sham-preen” during social interactions (Lorenz, 1971); males of many rodent species frequently engage in nonejaculatory intromissions during sexual interactions (Dewsbury, 1988); and many hoofed mammals interact through the use of “intention movements,” or stylized postures preparatory for various activities (Walther, 1984).

Interest in ritualization has been kindled in recent years by new developments in thinking about communicative systems and their origins (Hennessy, Owings, Rowe, Coss, & Leger, 1981; Krebs & Dawkins, 1984; Markl, 1985; Owings & Morton, 1997, 1998). In particular, increased emphasis on the impact of active assessment on communication has led to a better understanding of how signals might originate. Researchers now understand more clearly that communication depends equally on two activities—managing the behavior of others and extracting the cues needed for making decisions in one’s own interest. It is the utility of an act as an inferential cue to self-interested observers that predisposes it for signal function. Ritualization of an act can be driven by selection arising when actors benefit from observers’ use of that act as a cue in making their own behavioral decisions (Hennessy et al., 1981; Krebs & Dawkins, 1984; Markl, 1985; Owings, 1994).

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A large body of literature on the relation between grooming and physiological arousal is consistent with the hypothesis that grooming can be used as such an inferential cue (Hansen & Drake af Hagelsrum, 1984; Kametani, 1988; Scucchi, Maestriperieri & Schino, 1991; Spruijt, Van Hooff & Gispen, 1992) and therefore may have been a candidate for ritualization. Conditions that increase arousal, and thereby modify behavior, can also induce reliable changes in the amount and form of grooming activity (Bulwada, Nyakas, Koolhaas, & Bohus, 1993; Spruijt et al., 1992; van Erp, Kruk, Meelis, & Willekens-Bramer, 1994). This association may stem from and be complicated by the efficacy of grooming as a modulator of arousal (Chance, 1962; File, Mabbutt & Walker, 1988; Spruijt et al., 1992; van Erp et al., 1994).

We present evidence here that a highly stereotyped but common rodent-grooming pattern has undergone ritualization. Many rodent species share a distinctive pattern of a head-to-tail sequence of grooming acts (Berridge, 1990; Richmond & Sachs, 1980), so

stereotyped as to be a modal action pattern (Barlow, 1977). This same pattern has been found in species from a wide range of families within the order Rodentia (Berridge, 1990; Berridge, Fentress, & Parr, 1987; Colonnese, Stallman, & Berridge, 1996; Ewer, 1967; Richmond & Sachs, 1980).

This proposed precursor to communicative behavior is a stereotyped four-phase cephalocaudal sequence of up to 25 grooming actions called a *syntactic chain*, in which the face and head are groomed first and then the torso, using a specific number and sequence of movements (i.e., an *action syntax*; Berridge, 1990; Berridge et al., 1987). Once initial movements are produced, the remaining phases follow to syntactic completion with high predictability (e.g., 80% to 90% for rats; Berridge, 1990). In rats, the entire sequence occurs 13,000 times more frequently than would be expected on the basis of the independent probability of its component movements (Berridge, 1990). The use of the same stereotyped syntactic pattern of cephalocaudal grooming (CCG) by distantly related rodent species indicates that this grooming pattern has long been available for selection, having originated as much as 60 to 100 million years ago, before the divergence of rodent suborders (Kumar & Hedges, 1998; Wilson & Reeder, 1993; but see Foote, Hunter, Janis, & Sepkoski, 1999).

Anecdotal evidence suggests that CCG has undergone ritualization in one rodent species. Durant, Dole, and Fisler (1988) observed CCG by male California ground squirrels (*Spermophilus beecheyi*) interspersed among other agonistic activities such as lateral approaches, flank pushes, fights, and marking behavior. Interpreting this grooming as displacement behavior, they noted that males would break off an agonistic encounter to groom and then either resume the encounter or mark a nearby stake. Having made similar observations, we hypothesized that this grooming does not interrupt agonistic behavior; rather, it is an agonistic display that has been derived through ritualization of the ancient and widely shared syntactic CCG pattern.

This project extended the systematic study of syntactic CCGs to California ground squirrels. Our goal was to examine the following additional evidence relevant to the hypothesis that syntactic CCGs have undergone ritualization: (a) We gathered the first systematic field data on syntactic CCGs in any species; (b) we explored the details of the social context of naturally occurring syntactic CCGs in the field; (c) finally, we compared the microstructure of the hypothesized display to syntactic CCGs by solitary squirrels in the laboratory, the context in which this grooming pattern has been studied in other rodent species. This third part of the project allowed us to confirm the similarity of California ground squirrel syntactic CCGs to the syntactic grooming chain patterns of previously studied species and to assess whether the hypothesized signal version is a distinct modification of this stereotyped syntactic chain pattern.

Method and Materials

Laboratory Observations

Subjects

Twenty-three adult California ground squirrels (*Spermophilus beecheyi*) were observed; the group included the following individuals: (a) Five males and 5 females trapped as juveniles between June and August, 1994, in the East Bay Regional Park District's Camp Ohlone or nearby areas,

Alameda County, California; these squirrels, 2 years old at the time of the study, were housed in groups in 1.8 × 6.4 m outdoor pens at the University of California, Davis (U.C. Davis), until they were tested as adults. (b) Three male and 3 female squirrels from two litters, born in captivity of parents from Camp Ohlone at U.C. Davis in the spring of 1994; these squirrels were 2 years old during the study. (c) Two male and 5 female squirrels trapped as adults in Camp Ohlone in 1993; these squirrels were at least 4 years old during the study. All of the squirrels in the latter two groups were housed individually in the U.C. Davis Department of Psychology animal quarters in cages 56 × 39 × 26 cm high, with attached nest boxes, and were maintained on a 12-hr light–dark cycle with lights on at 7:00 a.m. All squirrels were provided with food (Purina Rodent Chow) and water ad libitum.

Apparatus

Squirrels were videotaped in an enclosure (56.5 × 43 × 54 cm) that provided two views of the subject on the video record of each trial: (a) through a glass wall allowing a direct view of the squirrel and (b) from a mirror beneath a glass floor providing a view from below. A bank of eight 40-W fluorescent bulbs in the ceiling provided illumination. During videotaping, a lamp with a 100-W incandescent bulb was positioned on the floor 46 cm from the glass wall to provide additional illumination. Videotapes were re-recorded using a Panasonic WJ-810 time–date generator to individually label each video frame at 33.33 ms intervals.

Procedure

Individual 2-hr videotaping sessions were conducted between 8:00 and 11:00 a.m. from April through August, 1996. We transferred both penned and caged animals to the testing compartment by giving them access to a dark transfer box that they readily entered. The penned animals were deloused while in this box by dusting with Sevin brand pyrethrins (Ortho, Columbus, OH). We then released the animals into the testing chamber by placing the transfer box there and detaching its floor. Each trial began immediately after the squirrel had been placed in the testing compartment, and squirrels were returned to their home enclosures at the end of each session, again through the use of the transfer box. Squirrels were randomly selected for videotaping both within and between groups, with the constraint that no squirrel was retested until all squirrels within a group had been tested once; as a result, each squirrel participated in two to four 2-hr sessions. Videotaping continued until a total of 200 min of grooming had occurred, summed across all squirrels.

Field Observations

Field Site and Study Area

Squirrels were observed at an established field site approximately 365 m above sea level at Camp Ohlone, Alameda County, California (the same population from which our laboratory squirrels were derived). A description of the site and general methods used for trapping, handling, measuring, and marking the squirrels has been published elsewhere (Hennessy & Owings, 1988).

Procedure

Throughout the study period between April, 1992, and April, 1995, we videotaped 10-min focal animal samples from elevated blinds (Altmann, 1974) to assess the frequency, duration, form, and context of grooming behavior. During each video sample, we recorded the identity and location of the focal squirrel, as well as the date and time. In bimonthly observation sessions lasting 2 to 3 days, we worked to accumulate multiple focal samples on 62 different adult squirrels (35 males and 27 females). Following is a summary of the numbers of squirrels observed each year

(including squirrels that were observed in more than 1 year; the numbers in parentheses refer to mean ages and ranges of ages in years of the squirrels): 1992, 15 males (2.37 ± 0.35 ; 1–4) and 15 females (1.87 ± 0.26 ; 1–4); 1993, 7 males (2.60 ± 0.67 ; 1–5) and 9 females (2.33 ± 0.37 ; 1–6); 1994, 8 males (2.14 ± 0.40 ; 1–5) and 7 females (2.67 ± 0.56 ; 1–4); and 1995, 8 males (2.44 ± 0.42 ; 1–5) and 4 females (2.33 ± 0.43 ; 2–3).

We carried out additional observations during the breeding season of 1995 to assess the social context of grooming. All occurrence sampling (Altmann, 1974) of social interactions was used to describe agonistic encounters in real time on audio cassette. To maximize the proportion of social interactions that we observed, we initiated behavioral recording when squirrels approached to within 2 m of each other and continued recording until squirrels were separated by more than 2 m. To estimate territory sizes and boundaries, we conducted scan samples at approximately 20-min intervals, recording the identity and location of each visible squirrel.

Analyses

Behavioral Video Analysis of Syntactic CCG Microstructure

Video records of 7 laboratory and 6 field squirrels were selected at random from the subset that engaged in syntactic CCGs, analyzed in slow motion, and scored using a computer-aided event-recording procedure and choreographic grooming notation system (Cromwell & Berridge, 1996). Video analyses of microstructure were carried out by four independent, trained observers blind to our hypotheses regarding differences in grooming between laboratory and field conditions. Their results were compared and where there were disparities, that video footage was reanalyzed to identify the source of the disparity and resolve it. A sample choreographic notation of a syntactic CCG chain is shown in Figure 1a and explained in the caption. Grooming behavior was analyzed for the following features.

Occurrence of syntactic CCGs. The beginning of each syntactic CCG was counted to assess the propensity to engage in patterned sequences of action. Syntactic CCG initiation was defined as the occurrence of 1 to 2 Phase-I strokes (1 or 2 small, rapid, bilateral forepaw strokes around the nose and mouth at a rate of 6 to 7 Hz). To qualify as such an initiation, Phase I had to be followed immediately by either a Phase-II stroke (i.e., a unilateral stroke or an asymmetrical bilateral stroke over the vibrissae) or a Phase-III stroke (i.e., large amplitude, unilateral overhand strokes over the eyes or ears). Phase III typically consists of a set of 3 to 10 large-trajectory bilateral strokes.

Efficacy of syntactic completion. Syntactic CCGs were analyzed for chain completion rates to assess grooming stereotypy in the two contexts. A *syntactically perfect* complete chain has previously been defined as one that progresses through Phases I, II, III, and IV (body licking, in which the animal lowers its head after the last Phase-III stroke and turns sideways to bring its tongue in contact with its flank or back), without interruption and within 5 s of Phase I (Cromwell & Berridge, 1996).

Contextual Analyses

Nongrooming control samples were chosen for each squirrel and matched as closely as possible to syntactic CCG samples for date and time of record. For example, a syntactic CCG that occurred during a focal sample on July 1 at 11:30 a.m. was matched with a focal sample not containing a syntactic CCG chain recorded 3 days earlier, on June 28 at 12:00. Samples were separated by a maximum of 11 days (3.00 ± 1.08). Once the control focal sample was chosen, a 120-s segment of this sample was randomly selected for analysis, subject to the following constraints: (a) The squirrel must have been visible for the entire 120 s, and (b) the segment chosen did not begin within 30 s of the start nor end within 30 s of the end of the sample.

Comparisons of staring and of rubbing against burrow markers, trees, and other stationary objects were made between syntactic CCGs and control samples. Stares were considered to occur if the squirrel's head was within 15° of horizontal and motionless for 3 or more video frames. These comparisons involve the 16 field squirrels that provided syntactic CCG and control samples sufficiently close in time and date.

Tail piloerection. Tail piloerection was assessed as an indication of agonistic motivation (Linsdale, 1946) and was measured as the ratio of on-screen tail width to eye width to control for changing image size. Control data comprised all nonsyntactic CCG tail grooming episodes plus a random sample of measures during which no grooming took place. Thirty-seven squirrels contributed to these comparisons.

Audiotape records. Scan sample locations and social interactions were extracted from the audiotapes by trained assistants. Convex polygon estimates of territorial boundaries were based on 95% of scan samples using HomeRange (Huber, 1999). Measures extracted from the social interactions included squirrel identities, locations, the occurrence or nonoccurrence of syntactic CCGs, rubs against stationary objects (e.g., burrow markers, trees, and rocks), and fights. These records provided data on 11 males.

Statistical analyses. Statistical analyses were conducted using Statview (SAS Institute, 1999) or SuperANOVA (SAS Institute, 1995). Unless otherwise indicated, alpha was set at .05. The distributions of most rate measures were positively skewed; these were square root, natural log, or arcsinroot transformed prior to analyses. However, in text, raw values are presented.

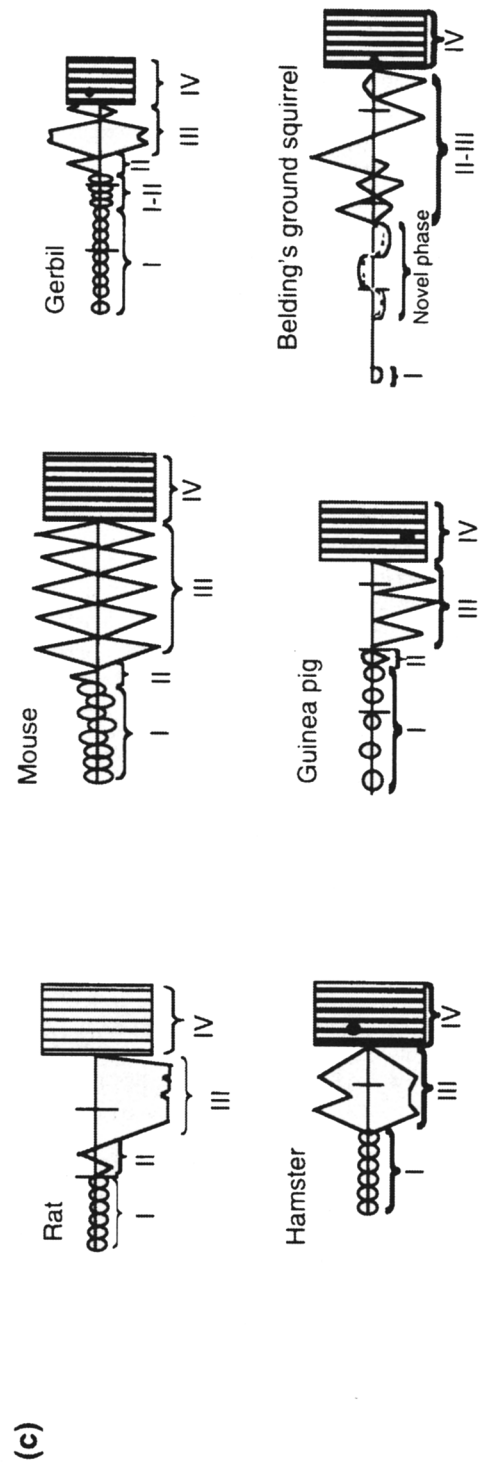
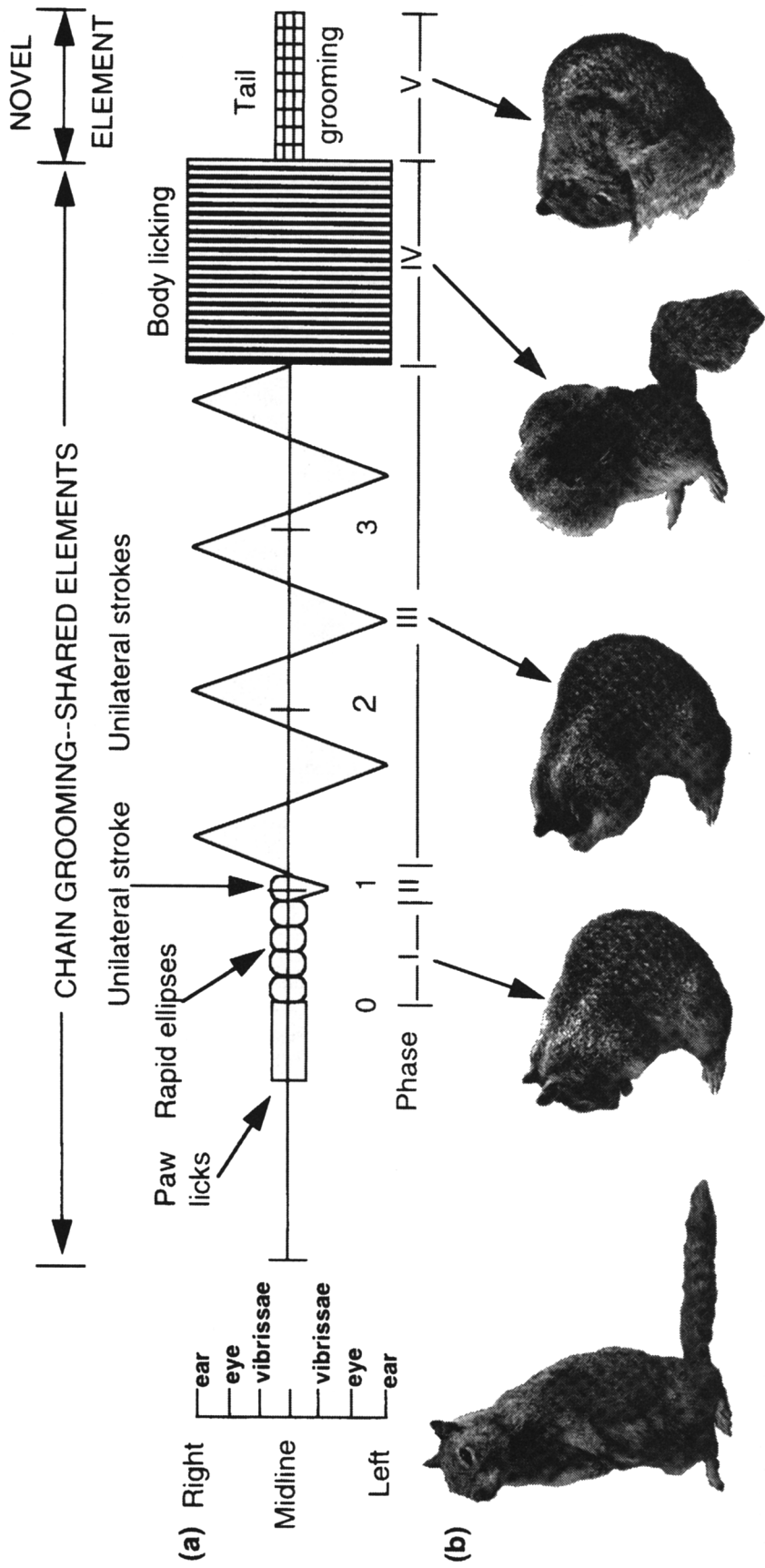
Results

Overview of Grooming

Captive squirrels maintained in the laboratory differed significantly from those held in outdoor pens by only one measure, which is not one discussed in this article; Phase-I strokes were 0.28 versus 0.39 s long, respectively. Consequently, we combined the data from the laboratory groups. Squirrels in the field and laboratory spent approximately the same percentage of time engaged in all types of grooming: $2.90 \pm 0.38\%$ and $3.50 \pm 0.68\%$, respectively; $t(83) = 0.45$, *ns*. However, field squirrels engaged in more frequent grooming bouts: $0.26/\text{min} \pm 0.04$ versus $0.04/\text{min} \pm 0.01$ for laboratory squirrels; $t(83) = 10.7$, $p < .0001$; but these bouts were shorter: 7.40 ± 1.02 s versus 73.20 ± 19.73 s for laboratory squirrels; $t(83) = 5.41$, $p < .0001$. Grooming took a variety of forms; the most frequent non-CCG acts were scratching the head and body with the hind foot, licking the hind foot, licking or biting the body, and licking the forelegs. Not all squirrels engaged in syntactic CCGs; 19 of 62 (31%) did so in the field, whereas 16 of 23 (70%) did so in the laboratory. For those that did produce syntactic CCGs, this category of grooming comprised a small and similar percentage of total grooming time in the field and laboratory: $11.0 \pm 3.5\%$ and $8.0 \pm 1.7\%$, respectively; $t(33) = 1.29$, *ns*. Syntactic CCGs were not a routine part of nonsocial grooming in the field.

Variation in Sequential Organization of Syntactic CCGs

The prototypical rodent syntactic CCG pattern is highly stereotyped, consisting of four successive phases progressing from head to flank (see Figure 1). In our laboratory results, syntactic CCGs embedded within autogrooming behavior were similar to the syntactic chains seen previously in other rodents (rats, mice, gerbils, hamsters, guinea pigs, Belding's ground squirrels, voles, and de-



gus; Richmond & Sachs, 1980; Berridge, 1990). One exception to this overall similarity was the occasional inclusion of a novel fifth phase by California ground squirrels; 33% of syntactic CCGs included a bout of tail licking on the side ipsilateral to the last Phase-IV body lick.

Syntactic CCGs observed in the field were even more invariant than those recorded in the laboratory (Figure 2a). For example, squirrels in the field never included nonsyntactic CCG elements, but a variety of such elements were common in the laboratory. Ten of the 16 laboratory squirrels that produced syntactic CCGs included one or more of five different types of nonsyntactic CCG elements, $\chi^2(1, N = 16) = 18.97, p < .0001$ (scratching with the hind foot, licking the hind foot, licking the ventrum, low-amplitude forepaw brushing motions at the corners of the mouth, and biting/licking of the forearms). This inclusion of nonsyntactic CCG elements was characteristic of a number of laboratory syntactic CCGs (22 of 110 episodes). The more consistent inclusion of Phases IV and V in field syntactic CCGs also contributed to their greater invariance (Phase IV: 91% in the field but only 79% in the laboratory; Phase V: 95% in the field and 33% in the laboratory; see Figure 2a and 2b).

Variation in Microstructure

Microstructural features of field syntactic CCGs rendered them much more visually distinctive than laboratory syntactic CCGs, at least to the human observer. Field syntactic CCGs contained more large-amplitude Phase-II and -III strokes (7.40 ± 0.50 Phase-III strokes) than did laboratory syntactic CCGs: $5.10 \pm 0.46, t(11) = 3.26, p < .01$ (Figure 2a and 2b). Consistent with this shift toward greater conspicuousness, field syntactic CCGs contained fewer small-amplitude Phase-I strokes (1.40 ± 0.61) than did laboratory syntactic CCGs: $3.80 \pm 0.54, t(11) = 2.90, p < .02$. The resulting bias toward larger strokes made field syntactic CCGs more noticeable to human observers.

Field syntactic CCGs also substantially shortened Phase IV (field = 1.40 ± 0.19 s; laboratory = 3.02 ± 0.63 s), $t(11) = 2.29,$

$p < .05$ (Figure 2a and 2b). This helped to compress the duration of the entire sequence to one-half its laboratory form (field = 5.24 ± 1.26 s; laboratory = 10.13 ± 1.73 s), $t(11) = 3.76, p < .0008$, enhancing its continuity and thereby giving it a rapid distinctive appearance (Figure 2a and 2b). This effect was further augmented by the more consistent addition of Phase-V (tail) grooming to field syntactic CCGs (see above), a visual flourish that substantially extended the cephalocaudal pattern by progressing from the base to the tip of the tail while adding minimally to the duration of the syntactic CCG (average durations: total of Phases I through IV = 3.46 s; Phase V = 1.78 s).

Finally, syntactic CCGs in the field always consisted of the syntactic chain pattern by itself, without other grooming movements either before or after. By contrast, of the 55 syntactically perfect CCGs in the laboratory, only 8 occurred in isolation from other grooming, whereas 47 were embedded within other grooming bouts: $\chi^2(1, N = 114) = 9.16$ (for syntactic CCGs) or $\chi^2(1, N = 25) = 34.05$ (for squirrels), $p < .0001$ (Figure 2b). In general, the unique alterations seen in syntactic CCGs emitted in the field made the entire sequential pattern seem quite dramatic, punctate, and distinctive, at least to human eyes, and possibly to other squirrels.

Social Context of Displays

Syntactic CCGs in the field were emitted only by particular squirrels (19 of 62 = 31%). In contrast, a majority of squirrels emitted syntactic CCGs during autogrooming in the laboratory (16 of 23 = 70%): $\chi^2(1, N = 85) = 11.1, p < .001$. All field syntactic CCGs were intrasexual, and most were emitted during male-male interactions (88% of field syntactic CCGs), Mann-Whitney $U, z = 2.19, p < .03$; the remaining 12% of syntactic CCGs were between females. No comparable male bias was noted in the laboratory; 8 of 10 males (80%) and 8 of 13 females (62%) produced syntactic CCGs: $\chi^2(1, N = 23) = 0.87, ns$. The males that emitted syntactic CCG chains in the field did so at a higher

Figure 1. (opposite). a: Choreographed syntactic chain representation of a cephalocaudal grooming (CCG) sequence. A choreographic transcription of a prototypical syntactic grooming chain shows the moment-by-moment trajectories of forelimb strokes over the face and the occurrence of other grooming actions. The axis represents the position of the squirrel's nose, and stroke trajectories over the face are depicted relative to the nose. Deviations of the lines above (right paw) and below (left paw) the horizontal axis represent the elevation (level of the eye, the ear, etc.) reached by each forepaw during a stroke. To read the choreographic transcription, note that time proceeds from left to right and that vertical tick marks on the axis represent seconds. Phase I: a series of one to six rapid, tight, ellipse strokes at the tip of the nose made simultaneously by both paws; Phase II: one or several unilateral strokes over the vibrissae; Phase III: a series of large-amplitude strokes over the eyes or ears, typically by both paws; Phase IV: tucking of the head and shifting of torso to engage in flank licking; Phase V: manipulation of the tail, typically with both paws and mouth and proceeding from the base to the tip of the tail. Phases I through IV are elements shared with other rodent species, whereas Phase V tail grooming is unique to California ground squirrels (*Spermophilus beecheyi*). From "Comparative Fine Structure of Action: Rules of Form and Sequence in the Grooming Patterns of Six Rodent Species," by K. C. Berridge, 1990, *Behaviour*, 113, p. 25. Copyright 1990 by Brill Academic Publishers via the Copyright Clearance Center. Adapted with permission. b: A squirrel engaged in a syntactic CCG display. The first figure depicts a California ground squirrel immediately before beginning the display; the remaining figures depict the squirrel in Phases I, III, IV, and V, respectively. c: Representative choreographs of syntactic chain grooming by six rodent species observed in the laboratory. From "Comparative Fine Structure of Action: Rules of Form and Sequence in the Grooming Patterns of Six Rodent Species," by K. C. Berridge, 1990, *Behaviour*, 113, pp. 30-32. Copyright 1990 by Brill Academic Publishers via the Copyright Clearance Center. Reprinted with permission.

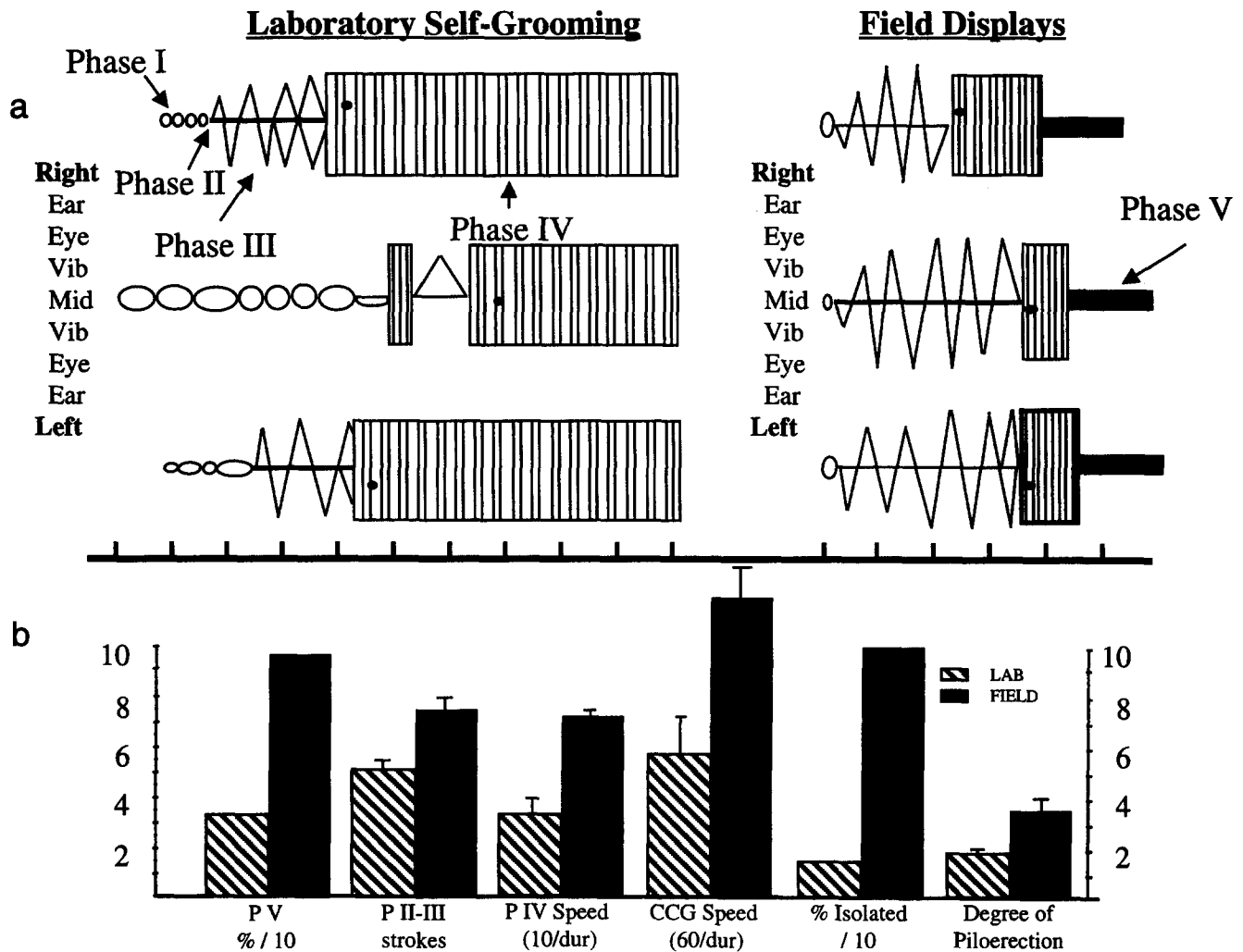


Figure 2. a: Choreographs of selected syntactic cephalocaudal grooming (CCGs) illustrating the differences between chains performed by California ground squirrels (*Spermophilus beecheyi*) in the laboratory (left) and in the field (right). The position of the paws in relation to the face during each stroke is indicated by the stroke-amplitude marker near the second chain for each group. Time (in seconds) is shown at the bottom. Phase-I through Phase-IV components are indicated near the first laboratory chain choreograph; the novel field Phase-V component is indicated near the second field choreograph. The closed circle near the beginning of Phase-IV grooming indicates which side of the body is licked; vib = vibrissae. From "Comparative Fine Structure of Action: Rules of Form and Sequence in the Grooming Patterns of Six Rodent Species," by K. C. Berridge, 1990, *Behaviour*, 113, p. 25. Copyright 1990 by Brill Academic Publishers via the Copyright Clearance Center. Adapted with permission. b: Field CCGs (solid bars) were more pronounced than laboratory CCGs (striped bars) in several respects. P V = percentage of CCG bouts completed to Phase V divided by 10; P II-III strokes = number of individual grooming strokes performed during Phase-II through Phase-III grooming; P IV Speed = 10 divided by Phase-IV duration; CCG Speed = 60 divided by CCG duration; % Isolated = percentage of CCGs performed in isolation from other grooming divided by 10. For an explanation of degree of piloerection, see the Method and Materials section of the text.

rate ($0.095/\text{min} \pm 0.020$) than did laboratory squirrels ($0.026/\text{min} \pm 0.006$): $t(33) = 2.38, p < .03$.

Male ground squirrels are territorial and relatively intolerant of male trespassers, resisting intrusion through agonistic interactions (Boellstorff & Owings, 1995; Owings, Borchert & Virginia, 1977). Syntactic CCGs were most common near territorial boundaries (see Figure 3) and were an integral part of

agonistic encounters between males. We observed 101 interactions involving 18 different pairs of males (mode = 4 interactions per pair, range = 2-13; 11 different males were involved). Interactions between males that contained at least one syntactic CCG were less likely to contain a fight than interactions between the same 2 males that lacked a syntactic CCG (conditional probabilities = 0.06 and 0.27, respectively, $p < .02$,

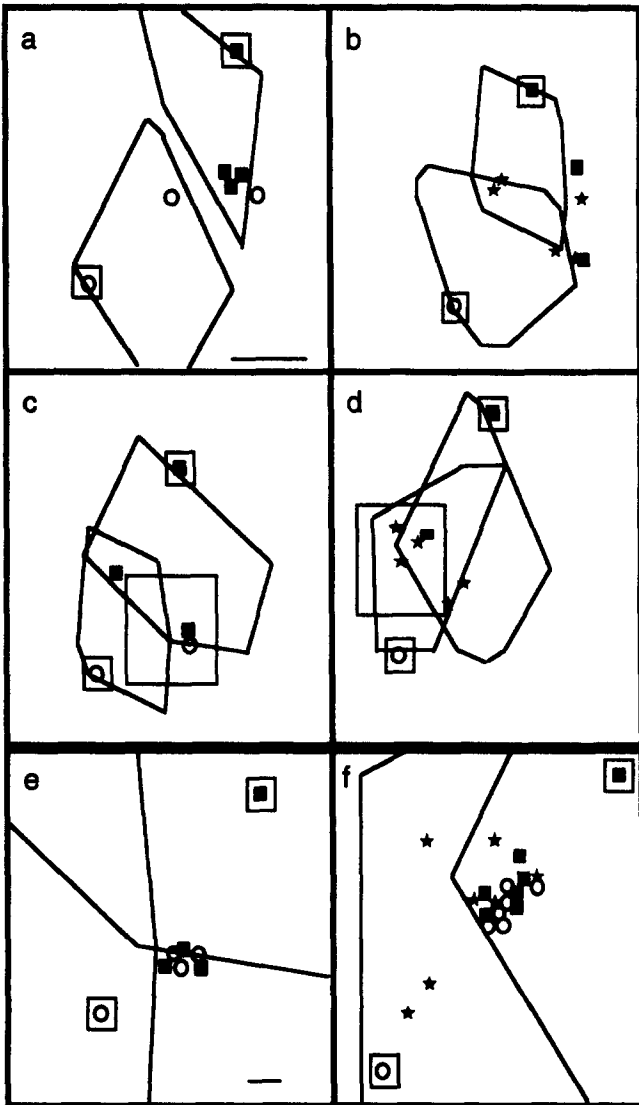


Figure 3. Location of syntactic cephalocaudal grooming (CCG) sequences and fights for four pairs of interacting male California ground squirrels (*Spermophilus beecheyi*) with respect to territorial boundaries. Boundaries are indicated by the two polygons in each of Panels a through d. Territory ownership is indicated by the small inset boxes on a boundary of each home range (Panels a through d). Panels e and f provide detailed plan views of locations of interactions represented in the large boxed areas in Panels c and d. Filled squares and open circles represent syntactic CCGs by either squirrel; stars represent fights. Scale: Panels a through d = 10 m (indicated by the horizontal line in Panel a) and Panels e and f = 1 m (indicated by the horizontal line in Panel e).

paired sign test), suggesting that syntactic CCG displays might curtail agonistic escalation.

Field syntactic CCGs were preferentially associated with other nonfighting agonistic behaviors such as tail piloerection; stares directed at the adversary; and scent rubs against stationary objects, for example, burrow markers, burrow mounds, or trees (for descriptions of agonistic behavior in this species that includes these components, see Durant et al., 1988; Linsdale, 1946; Owings et al.,

1977). Tail piloerection during Phase V of syntactic CCGs by field squirrels was nearly twice that of laboratory squirrels (field = 3.75 ± 0.27 ; laboratory = 1.92 ± 0.12), *LSD* $p < .0001$ (Figure 2b). This difference was largely the result of increased piloerection by field squirrels only during syntactic CCGs: control field piloerection = 2.26 ± 0.05 ; interaction $F(1, 36) = 37.3$, $p < .0001$. Field stares associated with syntactic CCGs were shorter in duration (2.63 ± 0.58 s) than at other times (6.83 ± 1.24 s): $t(15) = 2.91$, $p < .02$. Finally, the 16 squirrels that provided focal samples both with and without syntactic CCGs rubbed at a greater rate within 15 s of syntactic CCGs ($0.502 \pm 0.150/\text{min}$) than during matched samples that did not contain syntactic CCGs ($0.038 \pm 0.020/\text{min}$): $t(15) = 3.47$, $p < .002$. (A movie clip of syntactic CCGs in the field is available at <http://www.cameron.edu/~stanleyb/squirrel.rm>).

Discussion

In both the field and laboratory, California ground squirrels engaged in a wide variety of grooming activities. In these two contexts, syntactic CCGs comprised a similarly small percentage of all forms of grooming. Syntactic CCGs in the laboratory were similar to the moderately variable sequences performed by other rodents observed in the laboratory (Berridge, 1990). Therefore, the rodent-typical syntactic chain pattern used in self-grooming has been retained by California ground squirrels.

However, syntactic CCGs in the field differed from those in the laboratory in several ways, all of which tend to make field syntactic CCGs more visually dramatic and noticeable than ordinary, rodent-typical syntactic CCGs:

1. They were less variable than laboratory syntactic CCGs, both in their more consistent completion through Phases IV and V and in their total exclusion of nonsyntactic CCG elements.
2. They were also about 50% shorter in overall duration, causing them to be perceived by human observers as a rapid and distinct event. This difference in duration was generated by a reduction in the number of Phase-I strokes and shorter Phase-IV durations, changes more than sufficient to offset their greater number of Phase-II and -III strokes and the much more frequent addition of Phase V.
3. They involved greater levels of tail piloerection.
4. Finally, field syntactic CCGs were typically an integral part of agonistic encounters, accompanied by the brief stares and head and body rubbing also characteristic of such interactions and negatively associated with escalation to fighting.

We propose that these structural changes in field syntactic CCGs are a result of ritualization of this ancient grooming pattern. Support for the ritualization hypothesis is, in our opinion, strong enough for rejection of alternative, by-product hypotheses, that is, that social syntactic CCGs are no more than by-products of physiological processes subserving some noncommunicative function (cf. Blumberg & Alberts, 1997). Although social syntactic chaining may have originated as a by-product, a number of observations indicate that ritualization has since taken this pattern beyond by-product status.

Social syntactic CCGs have been modified in several ways that have enhanced their conspicuousness, at least to humans and probably to squirrels, and thereby made them more effective as signals. In a generic sense, social syntactic CCGs appear more

conspicuous because they involve greater tail piloerection, as well as a trade of some of the small-amplitude Phase-I strokes for more large-amplitude Phase-II and -III strokes. In a rodent-typical sense, this CCG pattern is a supernormal exaggeration of its precursor pattern, the syntactic CCGs used in the care of the body surface, which makes it even more conspicuous than the precursor pattern (which itself is the most conspicuous and stereotyped sequential pattern that occurs during rodent grooming). Several features contribute to this exaggeration, including the total absence of all nonsyntactic-CCG elements, more consistent inclusion of Phases IV and V, and the amplification of the cephalocaudal pattern by the rapid tail-base-to-tip progression of Phase V, combined with the simultaneous abbreviation of the duration of the entire syntactic CCG; these last two features contribute to a more coherent and extensive excursion from head to tail. Such exaggeration could be an adaptation to a perceptual prototype of grooming in the assessment systems of signal targets, which could in turn be an adaptation to capitalize on this useful cue (as argued in the first section of this article; Hennessy et al., 1981; Ryan & Keddy-Hector, 1992). The evolutionary abbreviation of field syntactic CCGs, especially the body-lick (Phase-IV) component, could have been made possible by the reduction of a body-care function during the acquisition of signal function.

The ritualization hypothesis also helps explain why field syntactic CCGs are performed in a social context, are negatively associated with escalation to fighting, and accompany scent marking and abbreviated stares. Benefits that have accrued to target and signaler, related to preventing agonistic interactions from escalating into full-blown fights, may have driven the exaggeration of syntactic CCGs into the more stylized pattern that now exists in this species (Ryan & Keddy-Hector, 1992). Perception of unritualized syntactic CCGs might have had a calming effect on potential adversaries if production of the precursor is associated with a relaxed state, as we propose below. The associated cheek-to-back pattern of apparent scent marking is also used for dusting (Owings et al., 1977) and so may provide another example of a display derived from patterns used in the care of the body surface (Bursten, 1998). Brief stares may function in the acquisition of social feedback regarding the impact of syntactic CCGs and other agonistic displays.

Why Should Unritualized Syntactic CCGs Be Stereotyped?

The syntactic CCG pattern may have been selected as an agonistic display partly because of its original high level of stereotypy, a feature that could have enhanced its distinctiveness and therefore its utility as a cue to the behavioral dispositions of potential adversaries. But what accounts for this original stereotypy?

The answer may lie in one particular time frame in which grooming is organized. Grooming is frequently assumed to work reactively, serving to dislodge ectoparasites as they are detected (Bell, Jellison, & Owen, 1962; Bennett, 1969; Lewis, Christenson, & Eddy, 1967; Rozsa, 1993; Tanaka & Takefushi, 1993). Two aspects of our laboratory results seem paradoxical under this assumption: (a) Even though the laboratory squirrels were free of ectoparasites and field animals were not (Bursten, Kimsey, & Owings, 1997), they groomed the same proportion of time; (b) grooming in the laboratory is relatively stereotyped, an unexpected

feature of a reactive system. However, these results are paradoxical only under the reactive grooming assumption.

A complementary form of defense is to groom prophylactically, partly to prevent successful attachment by blood-feeding parasites (B. L. Hart, Hart, Mooring, & Olubayo, 1992; L. A. Hart, Hart & Wilson, 1996). Prophylactic grooming would necessarily involve internally programmed grooming schedules (B. L. Hart et al., 1992; L. A. Hart et al., 1996). Prophylactic grooming might also be less variable than reactive grooming because it is less influenced by variable peripheral feedback and perturbation and because such reduced immediate modulation could permit internal programming of optimal sequencing. The prophylactic-grooming idea is consistent with evidence that peripheral stimulation is not necessary for development and maintenance of cephalocaudally organized grooming activities by mice and rats (Berridge et al., 1987; Fentress, 1988), and that the neural substrates for serial ordering of grooming motor acts are distinct from those associated with the production of the acts (Aldridge, Berridge, Herman, & Zimmer, 1993; Berridge, 1989; Colonnese et al., 1996; Cromwell & Berridge, 1996).

Programmed, prophylactic grooming might occur in anticipation of future needs and should be of low priority, appearing only when other, more immediate needs have been met. Therefore, the grooming exhibited by the laboratory squirrels may have been prophylactic, because they were freed not only of ectoparasites, but also from the demands of higher priority systems, such as acquiring food, socializing, avoiding predation, and so forth. Indeed, laboratory episodes of grooming seldom looked reactive. In contrast, a far greater proportion of nonsyntactic CCG grooming in the field involved abrupt grooming starting at an apparent locus of irritation rather than at the head (e.g., scratching the flank with a hind foot; Bursten, 1998).

It seems unlikely that field syntactic CCGs were deployed in response to immediate irritation. Were this the case, we would expect less, not more stereotypy in comparison with laboratory syntactic CCGs. Instead, the field syntactic CCGs observed in this study eclipsed the laboratory syntactic CCGs in their consistency of sequencing. So, the process of ritualization may have freed grooming in a social context even further from the moderate peripheral modulation of sequencing (Fentress, 1976) expected in prophylactic grooming. As a consequence, the central pattern generator of syntactic CCG sequencing might have gained even less disturbed access to the motor patterns of grooming when they are used in the agonistic context.

Conclusions and Limitations

This study is unique in that it compared a similar behavioral pattern of grooming under two conditions: during undisturbed social interactions in the field and in the laboratory context in which it has typically been studied. Our results provide strong support for the hypothesis that all syntactic CCGs seen in the wild are ritualized visual displays derived from the ancient four-phase syntactic CCG pattern that virtually all rodents display during ordinary self-grooming. We are much more tentative about our hypothesis that the more variable syntactic CCGs in the laboratory reflect prophylactic grooming, because there is no evidence as yet that ectoparasites influence the emission of this behavioral pattern. That remains a topic for future research.

Our conclusion that this species of ground squirrel currently has two forms of the syntactic CCG pattern, the rodent-typical form used in prophylactic grooming and the even more stereotyped display form used in agonistic social encounters, is conditional on the supposition that these ground squirrels, like other rodents, use the ordinary syntactic CCG in prophylactic grooming. We did not see much prophylactic grooming in the field, perhaps because we were able to see the field squirrels only when they were above ground. Presumably, most prophylactic grooming occurs under other conditions, for example, in their home burrows. Home conditions do seem conducive to grooming in general; laboratory rats observed in their home cages spent as much as 40% of their active time grooming (Bolles, 1960), a value far greater than that reported in this or any other rodent study. Future studies could confirm that a squirrel uses two different forms of syntactic CCGs, one in display and another in prophylactic grooming, by comparing syntactic CCG patterns emitted by the same squirrels in both agonistic social encounters (display form) and artificial home burrows (prophylactic form).

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