

Play Signaling and the Perception of Social Rules by Juvenile Chimpanzees (*Pan troglodytes*)

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Prescriptive social rules are enforced statistical regularities. The authors investigated whether juvenile chimpanzees (*Pan troglodytes*) recognize and use enforced statistical regularities to guide dyadic play behavior. They hypothesized (a) that proximity of adults, especially mothers of younger play partners, to play bouts will increase the play signaling of older partners and (b) that when juvenile–juvenile play bouts occur in proximity to adults, older partners will play at a lower intensity than when no adults are present. They found that older and younger partners increase their play signaling in the presence of the mothers of younger partners, particularly as the intensity of play bouts increases. In contrast to their hypothesis, older partners played more roughly when the mothers of younger partners were in proximity. These results suggest that juvenile chimpanzees increase play signaling to prevent termination of the play bouts by mothers of younger partners.

Chimpanzee society is characterized by a rich set of social dynamics in which adults negotiate and maintain their relationships through coalition formation, reconciliation, conflict intervention, and even conflict mediation (de Waal, 1982, 1989a, 1989b; Newton-Fisher, 1999; Watts, 2000). That chimpanzees can successfully engage in these types of complex interactions suggests that they have considerable understanding of their social environment. Little, however, is known about which information in the social environment is salient to chimpanzees or how chimpanzees learn to use this information to regulate their behavior in response to or in anticipation of the behavior of others. Numerous qualitative reports in the literature have suggested that chimpanzees perceive and act in accordance with social rules. One example of a quantitative study is that of de Waal (1989a), which reported that chimpanzees are more likely to share food with individuals that have just groomed them and less likely to share with individuals that have just been groomed by them. This suggests that a turn-taking rule underlies food-sharing decisions.

Despite such reports, however, there have been few systematic attempts to identify social rules in the societies of chimpanzees or other nonhuman primates. This is doubly surprising (a) given the utility that a study of social rules might have for addressing whether nonhuman primates have the capacity to understand causal relations in social interaction patterns (for a review of the evidence for causal understanding in primates, see Visalberghi & Tomasello, 1998) and (b) despite the growing theoretical literature on the importance of rules and rule enforcement to the evolution of certain forms of cooperation (e.g., Axelrod, 1986; Boyd & Richerson, 1992; Nowak & Sigmund, 1998; Simon, 1990). For example, Simon (1990) suggested that it is precisely the ability to learn social norms and prescriptive rules that facilitates the evolution of cooperation. Flack and de Waal (2000a, 2000b) proposed that this capacity is an important building block of moral systems. The goal of this study was therefore to determine whether prescriptive social rules are unique to human society by systematically investigating whether any can be identified in the societies of our closest living relative, the chimpanzee.

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What Is a Social Rule?

The term *social rule* can be used in either the descriptive or prescriptive sense. The term *descriptive social rule* is used to describe a typical response to a specific social situation, such as when females protect their offspring from the aggression of conspecifics (cf. de Waal, 1991). Such rules describe statistical regularities in social interaction patterns. When individuals perceive, comply with, and/or enforce statistical regularities so that the regularities instruct social interaction patterns, the term *prescriptive social rule* is applied.

One question that arises when distinguishing between prescriptive and descriptive social rules is what level of cognitive complexity is required for an individual to perceive a prescriptive social rule. At the very least, an individual must be able to (a) perceive a statistical regularity in social interaction patterns and (b)

anticipate the consequences to itself of deviating from that regularity. In other words, it must perceive the contingencies between its own behavior and that of others. Many studies, both experimental and observational, have demonstrated that these capacities are present in a number of species from rats to primates. Moreover, there is a substantial literature showing that this type of causal relationship can be learned without any sophisticated causal understanding—for example, through the Rescorla–Wagner learning rule (Rescorla & Wagner, 1972) or through specialized innate learning programs that are essentially “causal detectors” (see Kummer, 1995). Thus, if we are to adhere to the above definition of a prescriptive social rule, it is likely that a variety of different learning rules, or algorithms, can lead to its formation and that they might be found in the social repertoire of species other than humans.

There has been little empirical work on prescriptive social rules in natural settings (exceptions have included long-tailed macaques [Kummer & Cords, 1991], Rhesus macaques [Bernstein & Ehardt, 1986], Barbary macaques [Silk, 1992], chimpanzee [de Waal, 1989a, 1997; Hemelrijk, 1994], and hamadryas baboon [Sigg & Falett, 1985]). Many of these studies have investigated social rules only indirectly. For example, the “respect of possession” studies on macaques by Kummer and Cords (1991) and on baboons by Sigg and Falett (1985) studied the proximate cues of ownership but assumed (with justification) that a possession rule existed in the repertoire.

One reason for the lack of research on prescriptive social rules is that social rules imply the existence of expectations, which are not directly observable (de Waal, 1991). There are, however, at least two potential ways of studying prescriptive social rules and the expectations that underlie them. One is to assume the existence of an expectation and then to violate it—a tactic used by Tinklepaugh (1928), who showed that monkeys learn to expect particular reinforcers: Individuals given a leaf of lettuce showed disappointment when they were expecting a slice of banana. Another is to use communication as a window into the mind—as suggested by Griffen (1978) and applied by Cheney and Seyfarth (1990). Cheney and Seyfarth used the alarm calls of vervet monkeys to investigate what monkeys know about the relationship between escape routes and predator types.

Here we explored rule perception in juvenile chimpanzees by investigating whether juvenile communicatory behavior during social play is affected by adult presence and intervention. We chose juvenile chimpanzees as our subjects because the socialization of young chimpanzees is assumed to be a dynamic process requiring both adults and youngsters to take an active part in the teaching of and learning about social rules (Adang, 1985). We focused on juvenile play because previous studies suggested that it is closely monitored by adults, who have been reported to intervene into play bouts when these become too rough (e.g., Hayaki, 1985). We focused on communicatory behavior during play because of the possibility that senders emit signals to preempt the anticipated behavior of their play partners or of nearby adults who might be monitoring the interaction.

Background

Oddly defined as motor patterns directed at another individual, play appears to have no instrumental purpose in that there is no

material or social goal associated with it as in, for example, foraging. Play typically involves wrestling, hitting, pinching, and slapping—behavioral elements shared with agonistic interactions (e.g., Bateson, 1956; Bekoff & Byers, 1981; Fagen, 1981). Facial markers, spatial cues, body postures, reversibility in direction, and “relaxedness” of movement are usually taken into account in order to distinguish play from aggression, especially as play bouts become more intense (i.e., Pellis & Pellis, 1997). When such markers and cues are used in determining playful versus aggressive encounters, the vast majority of incidents can be reliably classified by observers (e.g., Smith & Lewis, 1985).

This observation has prompted researchers to speculate that to the primates themselves, play signals are actually metacommunicatory devices (Bateson, 1956) or intentional signals (e.g., S. A. Altmann, 1962; Bekoff & Allen, 1992; Hauser & Nelson, 1991; Millikan, 1984), the function of which is to clarify the meaning of ambiguous, potentially agonistic, behavior. In support of this hypothesis, data from studies using sequential analyses indicate that play signals are exchanged more if partners are engaged in contact play than in locomotory play (long-tailed macaques, lion-tailed macaques, Barbary macaques, and Tonkean macaques [Preuschoft, 1992, 1995]; canids [Bekoff, 1995]), suggesting that signaling increases as the likelihood of escalation to aggression increases. Despite the use of such signals, play does in fact sometimes escalate to actual conflict (Fagen, 1981), and conflict tends to invite interventions by third parties. As such, it seems likely that chimpanzees engaged in play should be attentive to information in their social environments, especially play signals of their partners and the proximity of third parties to their play bouts, so that they can appropriately regulate their behavior—including their own play signaling—and avoid interruptions by protective outsiders.

The regulation of play behavior is likely to occur at two levels: *dyadic* (between the partners themselves) and *triadic* (in response to outside influences). At the dyadic level, the needs of each partner should influence play intensity and how and by whom play is initiated. Four observations of play among wild chimpanzees have supported this hypothesis. Hayaki (1985) observed instances of *self-handicapping*, or restraint, by older individuals toward younger partners during play (for a review of self-handicapping, see Spinka, Newberry, & Bekoff, 2001). Hayaki also found that approximately one quarter of attempts by older individuals to initiate play with younger partners failed, perhaps reflecting fear on the part of the younger partners. Hayaki noted as well that older relatives of younger play partners sometimes intervened on their behalf. Mendoza-Granados and Sommer (1995) found that the older individual in a play dyad was more likely than the younger partner to have initiated the bout. This result was interpreted as evidence that younger partners were hesitant to initiate play because they feared rough responses. Taken together, these results suggest that at the dyadic level, play is a continually negotiated interaction that requires learned adjustment of one partner to the needs of the other.

Learned adjustment, which might occur through the reduction of play intensity or perhaps through the increase in play signaling, probably involves conditioning to the avoidance of an aversive stimulus that occurs if younger partners protest, scream, or pull away when the potentially agonistic features of play increase in frequency (de Waal, 1996). The occurrence of such self-handicapping (e.g., S. A. Altmann, 1962) has also been reported in

bonobos (Enomoto, 1990), chimpanzees (Goodall, 1986; Loizos, 1969), hamadryas baboons (Pereira & Preisser, 1998), canids (Bekoff, 1995), and red-necked wallabies (Watson & Croft, 1996). Surprisingly, hamadryas baboon juveniles are reported to play roughest when in proximity to adult males and to self-handicap most frequently when out of proximity with these males (Pereira & Preisser, 1998). Whether primates or other animals self-handicap or self-regulate during play remains an open question because all studies thus far have been qualitative or limited demographically. Two goals of the present study were to assess if play partners actually do exercise restraint in play intensity dependent on the relative age of their play partner and if play partners are more likely to increase their rate of signaling as play intensity increases.

At the triadic level, juveniles should adjust the intensity of their play behavior or the frequency of their play signals when particular adults are nearby if these adults systematically interfere in play bouts with certain characteristics. For example, if a juvenile lessens the intensity or reduces the agonistic components of play with a younger partner when the partner's mother approaches, it might be doing so to avoid impending punishment if rough play tends to lead to an agonistic intervention by the mother of the play partner. Alternatively, an older juvenile might increase the frequency with which it emits play signals, such as play faces, when playing with a younger individual whose mother is close by if doing so signals to the mother that what is occurring is play and not an agonistic bout that would otherwise warrant an intervention.

Hypotheses

In this study we assessed whether prescriptive social rules influence the play behavior of juvenile chimpanzees. We tested seven hypotheses:

1. The larger the age difference between two juvenile play partners, the less roughly the older juveniles will play (i.e., older juveniles will self-handicap).
2. As play becomes more intense, play signals such as the relaxed open-mouth display and/or panting laugh are more likely to be emitted. (We refer to these two expressions, described by van Hooff, 1972, as *play-face* and *laugh*.)
3. When playing with younger partners, older juvenile partners will be more likely than younger partners to emit play signals.
4. Adults are more likely to intervene in play bouts that are of a higher intensity.
5. Adults performing interventions in play bouts are more likely to intervene against the older partner on behalf of the younger partner.
6. The proximity of adults, especially mothers of younger partners, will increase the play signaling of older partners.
7. The proximity of adults, especially mothers of younger partners, will affect the intensity of juvenile–juvenile play bouts such that older partners will play at lower intensity than when adults are distant.

Method

Study 1

Study subjects. The first outdoor chimpanzee (*Pan troglodytes*) colony of the Yerkes National Primate Research Center's Field Station was established in 1978 and during the period of Study 1 included up to 16 individuals: 1 adult male, 7 adult females, and 8 juveniles. All juveniles were born and raised in the group and were of various ages between 3 and 6 years. All juveniles present in the colony were subjects of this study.

Observational methods. Juvenile chimpanzees were observed from March 15 to November 22, 1993. Summer observations occurred between 0700 and 1000 to avoid periods of extreme heat and low activity levels; otherwise, observations were distributed evenly across the hours from 1000 through 1500. Data were recorded onto a hand-held tape recorder and were transcribed into computer files as soon as possible. Behavioral durations were recorded using a handheld digital stopwatch and were made from an observation tower above a large, indoor–outdoor compound that offered complete visibility. During observation hours, the chimpanzees were confined to the outdoor portion of the compound, which contained shade and play structures as well as two sheet metal barriers that provided the chimpanzees with some privacy from one another by preventing visual monitoring of the entire compound at once. Each group received primate chow in the mornings and primate chow and fruit after 1500.

Approximately 26 focal hr of observation were conducted for each juvenile for a total of 205 hr. Focal observations on each individual (J. Altmann, 1974) lasted 20 min each, and observation sessions usually included eight focal bouts, one for each juvenile in the group. The focal sampling method was used to obtain frequencies for a range of juvenile social behavior, including play, competition, teasing, agonism, nursing, and affiliative behavior, such as grooming. Measures of both dyadic and triadic interactions were taken. Dyadic entries included identity of initiator and recipient, proximity and visibility of mothers (see below), types and sequence of behaviors, and how dyads were terminated. Triadic entries (i.e., a third party becomes involved in the original dyad) were coded within the context of the original dyadic entry and included information about the identity of all three individuals, the behavior that was occurring at the time that the third party became involved, the action by the third party, the reaction of the members of the original dyad, and the net effect of the interruption on the original dyad (see below).

Operational definitions. A *play bout* was operationally defined as a dyadic interaction between either two juveniles or one juvenile and one adult, in which one individual approached another and either performed a play invitation (defined below) that was then followed by a play response by the second individual or directly engaged in play behavior that was followed by a play response by the second individual. Play behavior included chasing, grappling, tumbling, gnawing, stomping, tackling, slapping, dragging by limbs, and slamming to the ground, as long as body movements by both partners were relaxed and did not serve any other apparent purpose, such as food acquisition or the initiation of grooming.

Juvenile–juvenile and juvenile–adult interactions, including play bouts, were broken into phases. A phase change occurred when the type of interaction changed (e.g., play to aggression) or when a third party intervened in the play bout. The highest play intensity for each partner within a phase was recorded. Play was defined in terms of four levels of intensity, the latter three of which constituted contact play. (a) *Play chase* (PC) was defined as nonagonistic chasing characterized by relaxed body movements and no contact. (b) *Low-intensity* play (P1) was defined as slow and relaxed movements that did not serve any other apparent purpose (such as grooming or transfer of objects) and included the behavioral elements of tickling and/or slow grappling. (c) *Mid-intensity* play (P2) was defined by the behavioral elements of fast grappling, tumbling, and gnawing. (d) Lastly, *high-intensity* play (P3), the roughest play, included the behavioral elements of tackling, stomping, audible slapping, dragging by limbs, and

slamming to the ground. Each partner's play intensity was assessed independently for each bout.

A play index was developed for some analyses (see Results) that took into account both the intensity of contact play (Levels P1–P3) and the proportions (in terms of relative frequency) of the occurrence of each level of roughness. This play index (PI), which increased with increased play intensity, was calculated for each individual in a dyad as follows (where f = frequency of each play intensity for individual i in dyad j , and where n = total number of play bouts for dyad j):

$$PI = [(1 * f_{P1}) + (2 * f_{P2}) + (3 * f_{P3})] / n_j$$

Following van Hooff (1972), play signals were recorded independently of play intensity and included *no signal*, defined as no discernible expression during play; *play face*, defined as an open mouth, with upper teeth covered by lips; and *laughing*, defined as a vocalization consisting of panting, sometimes aspirated. Two other aspects of play were also recorded: *play–distress vocalizations*, defined as any nonlaugh vocalization that occurred in the course of play, including whimpers and screams, and *play–invite*, which was defined as including any combination of the following: slapping the back of another individual and then running away, looking between legs at play partner, falling down in front of partner, and attempting to tickle partner, all with relaxed body movements. Play–invite was only recorded if mutual play did not follow the invite.

For each dyadic interaction, the proximity and visibility of the mother of each juvenile was recorded. Although behavioral codes were more detailed, for the purpose of the analyses presented in this article, mother presence for each juvenile was classified into three categories: *close* (within 2 m of dyad and in view of juveniles); *in view* (visible to juveniles, and between 2 m and 10 m away from the bout); and *far* (farther than 10 m from play bout regardless of whether in view or not). Visibility was taken into account because the chimpanzee compound contained sheet metal barriers that made it difficult for an individual to view the entire compound at once.

Several other categories of behavioral interactions were also recorded during Study 1, including agonistic and triadic behavior patterns. These behavioral measures are defined as follows.

Agonistic behavioral measures. Agonistic behavior was characterized in terms of both degree of intensity of agonism and response of partner. We followed the definitions laid out in de Waal and van Hooff (1981), which distinguish between *quasi-agonistic behavior* (clearly apparent conflict but with no strict agonism, no contact, no intention movements, and no response from partner); *silent bluff display* (pilo-erection, swagger, charge, etc., but no strict agonism); *vocal bluff display* (bluff display with vocalization); *agonistic interaction without contact* (chasing, lunging); *contact aggression* (pushing, slapping, punching, nipping, etc.); and *serious contact aggression* (sustained biting of > 5 s, hitting, or trampling). Also collected was the response of the recipient of aggression, including withdrawal, flight, yelping, screaming, or counter-aggression.

Triadic behavioral measures. Triadic measures were designed to record the sequence of events in a triadic interaction, including the events that preceded the involvement of the third individual. Additionally, the nature of the involvement of the third individual was also recorded. Such involvement was classified as an *impartial intervention* if directed at both of the original dyad members or as a *directed intervention* if behavior was directed at only one of the two original dyad members (de Waal & van Hooff, 1981). Impartial and directed interventions were defined as *agonistic interventions* if the third party used pinching, grabbing, slapping, tackling, biting, pushing, or directed a threat vocalization at one or both play partners and if the intervener's body movements were tense rather than relaxed. *Gentle interventions* were defined as those in which the third party restrained or distracted one play partner. The following information was recorded for these triads: initiator and recipient identities for original dyad members, identity of the initiator of the triadic interaction, type of

Table 1
Percentage of Play Signaling by Younger or Older Play Partner Depending on Distance to the Younger or Older Partner's Mother

Signal	Far %	In view %	Close %
YMOS			
	$n = 446$	$n = 462$	$n = 200$
No signal	22.4	14.3	12.5
Play face	69.5	72.5	72.5
Laughter	08.1	13.2	15.0
YMYS			
	$n = 349$	$n = 263$	$n = 142$
No signal	17.8	12.9	12.0
Play face	72.7	75.7	68.3
Laughter	09.5	11.4	19.7
OMOS			
	$n = 291$	$n = 194$	$n = 88$
No signal	18.2	16.0	11.4
Play face	73.5	76.3	76.1
Laughter	08.3	07.7	12.5
OMYS			
	$n = 367$	$n = 221$	$n = 105$
No signal	16.7	15.8	11.5
Play face	72.4	73.3	71.4
Laughter	10.9	10.9	17.1

Note. YMOS = location of younger partner's mother, older partner signals; YMYS = location of younger partner's mother, younger partner signals; OMOS = location of older partner's mother, older partner signals; OMYS = location of older partner's mother, younger partner signals.

dyadic activity, triadic pattern type, behavioral action by third party, target of this action, and effect on the original dyad (Table 1).

Interobserver reliability. For the judgment of play intensity, which is critical for our analyses, an interobserver reliability check was performed between the main observer, Lisa A. Jeannotte, and a longtime technician familiar with the same chimpanzees, Michael Seres, to confirm that these categories of play intensity are discrete and can be used to consistently describe play interactions. Ten videotaped play interactions and 26 live observations of varying levels of play intensity and a variety of partner combinations (involving juveniles, adults, and infants) were used. The two independent observers agreed on the intensity of 33 out of these 36 play bouts. Cohen's Kappa for this comparison was calculated at .85, considered "excellent" by Bakeman and Gottman (1997).

Study 2

Study 2 was expressly designed to increase the sample size of interventions by adults into play bouts.

Study subjects. Individuals in two chimpanzee groups were observed in Study 2. These individuals included the 8 juveniles in the "old group" observed in Study 1 as well as 6 additional juveniles in a more recently established colony at the Yerkes National Primate Research Center's field station. This new group, which was established in 1993, included 19

individuals: 2 adult males, 7 adult females, 6 juveniles, and 3 infants and subjuveniles. Juveniles ranged from 2 to 4 years in age. All juveniles present in this colony were subjects of Study 2. In contrast to juveniles in the old group, 4 of the 6 juveniles in the new group had been nursery reared at the Yerkes Main Station nursery and thus, in comparison with all other juveniles in the study, had no mothers present in the group.

Observational methods. A total of 50 one-hour sampling periods were performed on each group, for a total of 100 hr of observation in Study 2. Because Study 2 was developed to increase the sample size of adult interventions into juvenile interactions, the all-occurrences method of sampling behavior (J. Altmann, 1974) was chosen to collect a more focused set of data. Despite these differences, the protocol used to collect data in Study 2 closely followed that used in Study 1. All operational definitions used were the same for both studies. Each group was observed for 1 hr on each observation day, and observation periods were distributed evenly between 0700 and 1400, with summer observations conducted mainly in the first half of this period. As with Study 1, observations were recorded on a handheld recorder and transcribed as soon as possible onto computer files.

Analyses (Studies 1 and 2)

A matrix permutation analysis (Dow, Cheverud, & Friedlaender, 1987; Schnell, Watt, & Douglas, 1985) was used to test for correlations in the case of matrix-based data. This method of analysis accounts for the data interdependencies within matrices that normally prevent evaluation of the probability of a correlation against a normal distribution. Each analysis was conducted using the software program MatMan developed by de Vries, Netto, and Hanegraaf (1993). The matrices were permuted 10,000 times, meaning that the smallest probability of an observed correlation was 0.0001.

For those hypotheses in which we were analyzing frequencies, we used the *G* test (depending on the analysis, either the replicated *G* test or the independent *G* test; see Sokal & Rohlf, 1995) instead of the corresponding chi-square tests because the *G* test is generally considered a stronger test that is computationally simpler and, in the case of the replicated tests, has the property of being additive. The *G* test is chi-square distributed.

Results

Descriptive Results

Focal animal data revealed that play between juveniles accounted for 37.1% of all observed dyadic behavioral bouts involving at least 1 juvenile. Excluded from this calculation are play initiation attempts by 1 partner that were not followed by mutual play.

Play Initiation

Using focal data from Study 1, rates of successful and unsuccessful play initiation attempts for 8 juveniles, regardless of partner, were examined using a heterogeneity *G* test (replicated goodness-of-fit test; Sokal & Rohlf, 1995). The data indicate that the ratios of successfully initiated play to unsuccessfully initiated play were not homogenous but heterogenous (*h*), suggesting that some juveniles were more likely to successfully or unsuccessfully initiate play, $G_h(7) = 18.27, p = .01$. Partitioning *G* into contributions on the basis of individual samples revealed that 2 males (M_1 and M_2) were more likely to successfully than unsuccessfully initiate play given the expected ratio, $M_1: G(1) = 5.98, p = .01$; $M_2: G(1) = 4.16, p = .04$. (For calculations throughout this article, $\alpha = .05$.) No significant differences were found for the other 6

juveniles given the expected ratio. The expected ratio was given by the average ratio of successful to unsuccessful attempts to initiate play for all 8 juveniles. A row-wise matrix permutation procedure in which rows were permuted 10,000 times (see de Vries et al., 1993) revealed no significant relationship between the frequency with which dyad partners successfully initiated play and their absolute age difference ($r_{\text{row-wise}} = -.25, p = .10$).

Play Intensity

In order to examine whether the contact play intensities (P1–P3) of partners were similar, we used the focal data from Study 1 to calculate play indices for each juvenile in each of its juvenile–juvenile dyads (i.e., in the Sk–Dn dyad, an index was calculated for individual Sk as well as individual Dn based on their respective play intensities in their play bouts with one another only). We then performed a row-wise matrix permutation analysis (10,000 permutations; de Vries et al., 1993) to test if the average play intensity per bout for one dyad partner was correlated with the average play intensity per bout of the other dyad partner. We found that partner play intensity was highly correlated ($r_{\text{row-wise}} = .89, p < .01$). However, using the heterogeneity *G* test (Sokal & Rohlf, 1995), we found that some dyads were more or less likely than others to match their play intensities, $G_h(27) = 64.73, p < .01$. Visual inspection of the results did not suggest any pattern, except that of the six dyads in which the ratio of matched bouts to unmatched bouts differed significantly, four involved the youngest female, Dn. In three of these dyads, the partner of Dn played more roughly than Dn, and in one dyad, the play intensities of the partner and Dn were nearly identical.

Intervention Data

Because of the low frequency of adult interventions into juvenile play bouts, focal data from Study 1 were combined with global data from Study 2. These intervention data from Study 2 are the only data from Study 2 used in this article. Across these two studies, a total of 623 interventions were observed (focals, 535; globals, 88) into dyadic interactions involving at least one juvenile. A total of 117, or 18.8%, of these interventions were by adults into juvenile–juvenile behavior, and 86 of these 117, or 73.5%, were into juvenile–juvenile play behavior. The mothers of play bout partners intervened into 25 play bouts, or 0.02% of all juvenile–juvenile play bouts, and in all cases except one were within 2 m of the play bout prior to intervention. In 84.0% of these interventions, the mother's intervention either terminated or reduced the intensity of the bout. However, 56.0% of mother interventions were not aggressive or were ambiguous in terms of intended target. In 8 interventions, the mother attacked her offspring's play partner, who in all cases was an older partner. In one case, a mother attacked her own offspring, who was the younger partner. Distress vocalizations occurred in only 0.01% of all play bouts and, of bouts with distress vocalizations, 25.0% led to intervention by an adult.

Of the 25 interventions performed by mothers, 17 of these were into play bouts in which play partners matched their play intensities and used the same play signal. Three of the interventions were into bouts in which individuals used different play signals, and 2 interventions were into bouts in which the intervener's offspring

had not signaled, although its partner had. Two interventions were into play bouts in which the play partners were using different intensities and, in both cases, the offspring of the intervener was using the lower intensity. In one of these cases, the offspring emitted a distress vocalization.

Hypothesis Testing

1. The larger the age difference between two juveniles, the less roughly the older juvenile will play (i.e., older juvenile will self-handicap).

The relationship between contact play intensity (P1, P2, P3) and age difference of the 8 juvenile play partners was assessed using a nonparametric matrix permutation analysis (10,000 permutations; de Vries et al., 1993). The absolute play partner age difference, defined as age of younger partner in months subtracted from age of older partner, for a dyad was correlated with the average intensity per bout of the older partner's play behavior for the same dyad. Absolute age difference did predict the older partner's average intensity per bout ($r_{\text{row-wise}} = .44, p < .01$), indicating that older partners played less roughly the greater the age discrepancy with their younger partner.

2. As play becomes more intense, play signals, including the play face and laughter, are more likely to be emitted.

For this analysis, we investigated whether frequency of play signaling per bout, which included both play face and laughter, changed as a function of contact play intensity (P1, P2, P3). The analysis was conducted at the individual level ($n = 8$). Using Friedman's method of randomized blocks (Sokal & Rohlf, 1995), we found that the effect of play intensity on frequency of play signaling per bout was significant, $\chi^2(2, N = 8) = 13.00, p < .01$. Multiple comparisons among the treatment means revealed significant differences between all three groups (Mann-Whitney U for P1 and P2: 64, $M = 55.8\%$, $p < .01$; for P1 and P3: 64, $M = 89.1\%$, $p < .01$; and for P2 and P3: 43, $M = 91.6\%$; $p < .01$ for all U s), such that play signaling increased with each play intensity level (Figure 1).

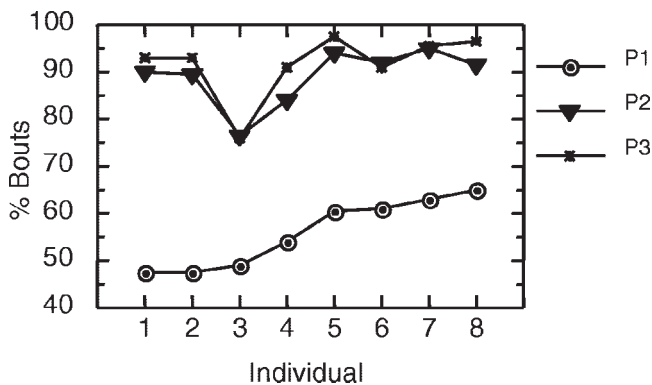


Figure 1. The percentage of bouts, at each play intensity level, in which juveniles emitted signals. P1 = low-intensity contact play; P2 = mid-intensity contact play; P3 = high-intensity contact play.

3. Older partners are more likely to emit play signals than younger partners.

To test this hypothesis, we used the heterogeneity G test (Sokal & Rohlf, 1995). The analysis was conducted at the dyadic level. We did not find significant heterogeneity among the 28 juvenile–juvenile dyads, $G_n(27) = 7.93, p = .99$, and the overall pooled result indicated that the data did not fit the expected ratio, $G_{\text{pooled}}(1) = .03, p = .86$. The data therefore indicate that older partners are not more likely to emit play signals than their younger counterparts.

4. Adults are more likely to intervene into play bouts that are of a higher intensity.

To test this hypothesis, we used the Wilcoxon signed-ranks test to evaluate whether adults were more likely to intervene in high-intensity (P2, P3) or low-intensity (P1, P3) bouts. To increase the sample size, we included interventions by adults into juvenile–juvenile and juvenile–adult play bouts ($n = 7$). Because no low-intensity juvenile–juvenile or juvenile–adult play bouts occurred during Study 2, only intervention data from Study 1 were used here. To correct for differences in the frequency with which high-intensity and low-intensity bouts occurred, each adult's frequency of intervention into low- and high-intensity bouts was divided by the total number of low- and high-intensity bouts, respectively. Although adults intervened into only 65 of 1,424 juvenile–juvenile and juvenile–adult play bouts, they intervened into significantly more high-intensity bouts than low-intensity bouts ($T+ = 6, T- = 1, z = 2.197, p = .03$).

5. Adults performing partial agonistic interventions into play bouts are more likely to intervene against the older partner on behalf of the younger partner.

In this analysis we included data from both Study 1 and Study 2 on adult ($n = 9$) partial interventions into juvenile–juvenile play bouts. Partial interventions included those interventions in which an adult targeted one play partner and used either restraint, moderate, or severe aggression against that target (see Method section). Using the Wilcoxon signed-ranks test, we found that adults were not significantly more likely to target the older play partner (sum of all positive ranks $[T+] = 3$, sum of all negative ranks $[T-] = 6$), $z = 1.611, p = .054$.

6. Older play partners will signal more frequently if adults, particularly mothers of younger play partners, are in proximity to their play bouts than if adults are farther away.

Data from Study 1 were used to assess the relationship between distance of mothers to play bouts and signaling by play partners. We independently analyzed four conditions: (a) signaling by the older partner considering the location of the older partner's mother (OMOS); (b) signaling by younger partner, location of older partner's mother (OMYS); (c) signaling by older partner, location of younger partner's mother (YMOS); and (d) signaling by younger partner, location of younger partner's mother (YMYS). For each of these conditions, we constructed a 3×3 contingency table to assess the relationship between the occurrence of play signal (no

signal, play face, laughter) and the distance (close, in view, far) of the mother to the bout.

In the YMOS condition, we used data from 7 of 8 juveniles (the oldest had no older partner). The independent G test indicated that older play partners signaled significantly more frequently when the mothers of their play partners were close by (88% of bouts) or in view (86% of bouts) than when these mothers were far away (78%), $G(4) = 20.19, p < .01$. As shown in Table 1, play face occurred more frequently than either laughter or no signal in all three conditions. However, only laughter increased in frequency over each of three mother distances; play face increased in frequency from far to in view but remained the same from in view to close.

In the YMYS condition, we used data from 6 of 8 juveniles (the youngest had no younger partner, and, during this condition, 1 other female had no mother in the group). The independent G test indicated that younger play partners signaled significantly more frequently when their own mothers were close (88.0% of bouts) or in view (87.1%) than when their mothers were far (82.2%), $G(4) = 12.09, p < .025$. However, as shown in Table 1, the percentage of play faces increased from the far to the in view condition but decreased in the close condition. Laughter increased over all three conditions, with the biggest change between the in view and close conditions.

In the OMOS condition, we used data from 5 of 8 juveniles (the oldest had no older partner, and, during this condition, 2 juveniles had no mother in the group). The independent G test indicated that older play partners did not signal significantly differently depending on the location (close = 88.6%; in view = 84.0%; far = 81.8%) of their mother, $G(4) = 3.82, p < .50$. As shown in Table 1, laughter increased slightly over the three distance conditions, and play face increased slightly from far to in view, but in view and close were highly similar.

In the OMYS condition, we used data from 5 of 8 juveniles (the youngest had no younger partners, and, during this condition, 2 juveniles had no mother in the group). The independent G test indicated that younger play partners did not signal significantly differently depending on the location (close = 88.5%; in view = 84.2%; far = 83.4%) of their older play partner's mother, $G(4) = 4.22, p < .50$. As shown in Table 1, the percentage of laughter in the far and in view conditions was highly similar, but laughter increased in the close condition. Play face was relatively similar across the three distance conditions.

Overall, these data support our Hypothesis 6. The presence of the younger partner's mother increases the frequency of signaling by both the younger and older partner. The presence of the older partner's mother does not have any affect on the signaling patterns of either partner.

7. The proximity of adults, especially mothers of younger partners, will affect the intensity of juvenile–juvenile play bouts such that older partners will play at lower intensity than if adults are absent.

Data from Study 1 were used to assess the relationship between distance of mothers to play bouts and play intensity by play partners. We independently analyzed four conditions: (a) play intensity of the older partner considering the location of the older partner's mother (OMOI); (b) play intensity of the younger part-

ner, location of older partner's mother (OMYI); (c) play intensity of the older partner, location of younger partner's mother (YMOI); and (d) play intensity of the younger partner, location of younger partner's mother (YMYI). For each of these conditions, we constructed a 3×3 contingency table to assess the relationship between play intensity (P1, P2, P3) and the distance (close, in view, far) of the mother to the bout.

In the YMOI condition, we used data from 7 juveniles (the oldest juvenile had no older partners). The independent G test indicated that the play intensity of older partners differed significantly depending on the location of the younger partner's mother, $G(4) = 12.86, p < .01$. However, as shown in Table 2, the percentage of bouts in which the older partner played roughly (P3) increased the closer the mother of the younger partner was to that bout, which is in contrast to our hypothesis.

In the YMYI condition, we used data from 6 juveniles (the youngest juvenile had no younger partners, and, in this condition, 1 juvenile had no mother in the group). The independent G test indicated that the play intensity of younger partners was not significantly different depending on the location of the younger

Table 2

Percentage of Each Play Intensity Used by the Younger or Older Partner Depending on the Distance to the Younger or Older Partner's Mother

Play intensity	Far %	In view %	Close %
YMOI			
	<i>n</i> = 466	<i>n</i> = 480	<i>n</i> = 203
P1	22.5	15.4	14.8
P2	62.5	65.8	63.1
P3	15.0	18.8	22.1
YMYI			
	<i>n</i> = 366	<i>n</i> = 278	<i>n</i> = 146
P1	25.1	18.7	17.1
P2	59.8	67.3	67.1
P3	20.7	14.0	15.8
OMOI			
	<i>n</i> = 301	<i>n</i> = 204	<i>n</i> = 91
P1	18.9	21.6	29.7
P2	66.5	64.2	58.2
P3	14.6	14.2	12.1
OMYI			
	<i>n</i> = 380	<i>n</i> = 232	<i>n</i> = 109
P1	20.2	19.8	21.1
P2	62.3	67.8	59.6
P3	16.8	13.4	19.3

Note. P1 = low-intensity contact play; P2 = mid-intensity contact play; P3 = high-intensity contact play; YMOI = location of younger partner's mother, intensity of older partner; YMYI = location of younger partner's mother, intensity of younger partner; OMOI = location of older partner's mother, intensity of older partner; OMYI = location of older partner's mother, intensity of younger partner.

partner's mother, $G(4) = 6.48, p < .25$. As shown in Table 2, the percentage of mild play (P1) by the younger partner was highest in the far condition and relatively similar in the in view and close conditions. The percentage of mid-intensity play (P2) by the younger partner increased from the far to the in view conditions, but did not change much between the in view and close conditions. The percentage of rough play (P3) by the younger partner was highest in the far condition and relatively similar in the in view and close conditions.

In the OMOI condition, we used data from 5 juveniles (the oldest had no older partners, and, in this condition, 2 juveniles had no mothers in the group). The independent G test indicated that the play intensity of older partners did not significantly differ depending on the location of their own mother, $G(4) = 4.56, p < .50$. Although this result is nonsignificant, Table 2 shows that older partners tend to play more intensely the closer they get to their own mothers.

In the OMYI condition, we used data from 5 juveniles (the youngest had no younger partners, and, in this condition, 2 juveniles had no mothers in the group). The independent G test indicated that the play intensity of younger partners did not significantly differ depending on the location of the older partner's mother, $G(4) = 3.00, p < .75$. As shown in Table 2, the data on play intensity display no obvious pattern across the three conditions. It is interesting to note, however, that percentage of rough play by younger partners was highest when the bout was close to the mother of the older partner.

Overall, these data do not support our hypothesis. Older partners play more roughly if the mothers of their younger partners are close by.

Discussion

The primary goal of the present study was to explore whether the perception of social rules underlies changes in rates of play signaling and levels of play intensity among juvenile chimpanzees. In particular, we were interested in determining how the presence of potential rule enforcers affects juvenile play. Overall, our results suggest that juvenile chimpanzees (a) respond to social pressures, such as maternal interventions, about what is acceptable play behavior to engage in with play partners and (b) acknowledge to third parties their influence by increasing their play signaling rate as play becomes more intense, especially if third parties are nearby and able to see them. These two findings suggest that juvenile chimpanzees recognize prescriptive social rules about play. Our results also support the conclusion that play signals are intentional signals (e.g., Hauser & Nelson, 1991) used by individuals to modulate the behavior of others. Before discussing this in more detail, we first review what the results of this study suggest about the play behavior of juvenile chimpanzees.

How Do Juvenile Chimpanzees Play?

To tackle these issues, we had to assess whether and how juvenile chimpanzees learn what behavior is acceptable when playing with younger partners. For example, if juvenile chimpanzees self-handicap during play with younger partners, this would suggest an ability to assess the capacities of their playmates and/or recognize withdrawal responses in the form of learned adjustment

to the needs of others (de Waal, 1996). Several studies on play behavior have suggested that primates and many other mammal species, from wallabies to elephants, show self-handicapping (e.g., chimpanzees [Goodall, 1986; Hayaki, 1985; Loizos, 1969; Mendoza-Granados & Sommer, 1995; Merrick, 1977]; hamadryas baboon [LeResche, 1976; Pereira & Preisser, 1998]; squirrel monkey [Biben, 1989]; whiptail wallaby, wallaroo, red-necked wallaby, red kangaroo, rufous wallaby [Watson, 1998; Watson & Croft, 1996]; and African elephant [Moss, 1988]). Our results are consistent with the existing literature: The larger the age difference between play partners, the more likely it was for older play partners to play at a lower intensity. However, our results also indicate matching on the part of both partners. We were not able to determine who initiates the matching; it seems to be a complementary process. That our data support both self-handicapping and intensity matching favors Hayaki's (1985) speculation that restraint on the part of the older partner goes hand in hand with facilitation on the part of the younger partner rather than the possibility that older partners actively maintain lower intensity play bouts when playing with younger juveniles.

The occurrence of play intensity matching in combination with apparent self-handicapping by the older partner suggests that juvenile chimpanzees have the ability to assess each other's capacities but do not follow a strict rule about what intensity to use when playing with younger partners. In other words, play intensity is partly determined by both the age and size difference between the partners and by the partners' responses to one another. Both self-handicapping and play intensity matching appear to functionally hinge on continual cooperative probing and negotiation that occur during the course of the play bout as suggested by Bekoff (1998). Support for the idea that cooperative probing and negotiation characterize intensity matching is provided by the data indicating that as play intensity increases, so does the frequency with which partners emit play signals. Whether, however, this increase in signaling as play intensity increases is due to a corresponding increase in arousal, to an understanding of the increased need to communicate one's intentions as the boundary between play and aggression blurs, or to some combination of the two is a question that remains to be addressed.

Signaling and Play

As shown in Table 1, juvenile chimpanzees use play faces approximately three times more frequently than they use laughter or no signal during play bouts. If play signals are intentional signals used to reduce the uncertainty of play partners and third parties about the nature of the play bout, then it is not surprising that play faces occur more frequently. Play faces are a more conspicuous signal for third parties than is laughter, particularly if the play bout is too far away for laughter, a low-pitched vocalization, to be audible. Correspondingly, the discrepancy in the frequencies with which these two play signals are used might be attributable to observer bias for a visual signal over a difficult-to-hear auditory one. It is also important to note that it is not clear what physiological mechanisms underlie play faces and laughter—in particular, whether there are differences in the degree to which each signal is under voluntary control.

Do Juvenile Chimpanzees Perceive Social Rules?

Determining whether individuals recognize statistical regularities and thus perceive social rules that then influence their behavior is somewhat easier if behavioral changes are assessed in the presence of third parties rather than only in dyadic contexts. One way that this question can be approached in polyadic contexts is to examine how individuals involved in dyadic interactions change their behavior toward their partners in response to anticipated actions of third parties who might be monitoring how the dyadic interaction unfolds.

In the present study, a significant relation was found between the frequency with which an older play partner emitted play signals and the proximity of the younger play partner's mother to the play bout. Our data also indicate a significant relation between the frequency with which a younger play partner emitted play signals and the proximity of the younger partner's mother to the play bout. That the increase in signaling by the play partners was due to the presence of the younger partner's mother is supported by five related results. (a) Play signaling by the older partner did not increase in the presence of its own mother. (b) Play signaling by the younger partner did not increase in the presence of the older partner's mother. (c) Adults intervened more frequently into higher intensity play bouts. (d) Bouts in which the older partner was using a high intensity occurred most frequently in close proximity to the younger partner's mother. It is not clear whether this was due to the presence of the younger partner's mother or was the cause for it. Given that there was no significant relation between the younger partner's intensity and the location of either its mother or its partner's mother, nor any significant relation between the older partner's intensity and the location of its mother, the latter possibility seems more likely. (e) Finally, the majority of interventions by adults terminated or disrupted the play bout. It is important to note that the change in behavior by the older and younger play partners was highly specific to a particular context—that is, to the presence of an adult inclined to intervene if the play bout became too intense.

The change in the signaling patterns seems to reflect an understanding that the younger partner's mother might intervene in the play bout either to attack the older play partner or to remove the younger one, in both cases ending it so as to prevent it from spinning out of control. Both the younger and older partner have an interest in preventing an intervention that might terminate or disrupt their play bout. Therefore, a reasonable explanation for the increased signaling by the older and younger partners is that it serves to provide the mother with appeasing information about what kind of dyad her offspring is involved in. The increased rate of play signaling thus reduces the mother's uncertainty, which has the effect of preempting the need for intervention. If this interpretation is correct, then play signals qualify as predictive, intentional signals (Hauser & Nelson, 1991) in the sense that they provide reliable information about the sender's subsequent behavior and intent and that they are emitted in the presence of individuals likely to be checking this information.

Social Rules and Causal Understanding

Because play signals were only observed to occur during play, particularly during social play with contact components (for ma-

caques, see also Preuschoft, 1992, 1995), and have rarely been observed to function as appeasement signals in agonistic, nonplay contexts, it is unlikely that presence of the younger partner's mother involuntarily elicits play signals from the older partner. Considering that the intervention frequency by adults into play bouts is so low, it seems unlikely that associationist learning rules, such as the Rescorla–Wagner learning rule (Rescorla & Wagner, 1972), can account for the increase in signaling. This is because it is difficult to conceive how an association between the stimulus (intervention) and the behavior (increase in signaling) could form considering that (a) the stimulus occurs infrequently and inconsistently and (b) tends to involve termination of the play bout by removal of the younger partner rather than aggression directed at the older partner, and (c) the signaling behavior is not naturally connected to the stimulus (e.g., Rescorla & Holland, 1982), as would be the case when an aggressive signal serving as a stimulus is then followed by a withdrawal response.

How is it that juveniles learn that there is a statistical regularity between their own behavior and the mother's response if intervention occurs with such low probability? It is possible that they have learned to recognize the statistical regularity through punishment administered by mothers who either attack older partners or remove younger partners from play bouts that are characterized by rough play and little signaling. We feel this explanation is unlikely because in order for the learning to be attributable to punishment, the older partner must exhibit a decrease in the behavior that leads to the punitive reaction by the third party. However, older partners played more roughly and signaled more frequently when the younger partner's mother was present.

Play signaling rate might have been negatively reinforced by the mother's behavior, such that the older partner increased the frequency with which it emitted the play signals when in proximity to the younger partner's mother because doing so discouraged the younger partner's mother from ending the play bout. Although learning through negative reinforcement is well documented in many species in experimental settings, it is not clear whether negative reinforcement would be sufficient in a "noisier" setting to learn to associate two behaviors that are not naturally related to one another. In chimpanzees, a play signal is not a natural response to the anticipated agonistic behavior of others in any context, yet it increases in frequency in the presence of potential interveners, who in actuality almost never intervene. Considering these factors, the relationship between play signaling and prevention of intervention might be too complex for an individual to grasp through learning based only on the formation of associations; some causal understanding seems to be required. The possibility that chimpanzees have a causal understanding of social rules is consistent with recent data on causal understanding in monkeys. In Zuberbühler's (2000) data from playback studies of crested guinea fowl, leopard alarm calls to Diana monkeys indicate that the Diana monkeys have the ability to recognize the causes of another species' alarm calls rather than just associating the call with a particular predator.

These data suggest that juvenile chimpanzees perceive prescriptive social rules and use these to regulate their signaling behavior in play contexts. These results are significant because they demonstrate that prescriptive social rules, which have been proposed as an important building block of moral systems (Flack & de Waal, 2000a, 2000b), are not unique to humans. Studies are now needed that systematically identify other social rules in the societies of

chimpanzees and other species, investigate the degree of cultural variation in the expression of rules, and assess whether causal understanding is likely to account for this kind of causal knowledge.

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