

Head Rotations in the Play of Hanuman Langurs (*Semnopithecus entellus*): Description and Analysis of Function

Milada Petrů
Charles University in Prague

Marek Špinka
Institute of Animal Science

Stanislav Lhota
University of South Bohemia

Petr Šípek
Charles University in Prague

Although head rotations are frequent patterns in play behavior in many mammalian species and differ from head movements used in other contexts, they have not been quantitatively described and their function remains unclear. The head rotations occurring in the play behavior of free-ranging Hanuman langurs (*Semnopithecus entellus*) were described from videotaped sequences. The authors tested 2 possible hypotheses about their function. Either the head rotations serve to create unexpected situations and should therefore occur in both solitary and social play and also be very variable, or they serve as play signals and should therefore occur only in social play and be ritualized. If head rotations have both functions, they should be less variable in social play. The data revealed that head rotations were very variable and were present both in solitary and social play. Furthermore, there was no difference in the variability between the head rotations present in the 2 types of play. The results do not support the function of head rotations as play signals but, rather, suggest that head rotations may serve to create unexpected situations in play.

Keywords: play, head rotation, self-handicapping, communication, *Semnopithecus entellus*

Head rotational movements occur in mammalian behavior in various contexts. For instance, sagittal rotations (pitch axis rotations, head tosses) are used in dominant and submissive displays in ungulates and primates (Bolwig, 1978; Dolhinow, 1978; Sade, 1973), rotations in the frontal plane (roll axis rotations, head tilts) occur in ritualized fighting of giraffes and antelopes (Estes, 1992), and rotations in the horizontal plane (yaw axis rotations, head shakes) are employed by carnivorous mammals during prey killing

and tearing. More complex head movements also occur. For example, predatory head shakes may combine rotations in several planes as they fulfill the two functions of disorienting the prey and enhancing penetration by the canines (Pellis & Officer, 1987). Nevertheless, the context in which head rotations—and also torso and whole body rotations—are most prominent and probably also most varied is in play behavior.

To cite just a few examples, head rotations have been reported in the play of degu (*Octodon degus*), choz-choz (*Octodontomys gliroides*), dwarf mara (*Pediolagus salinicola*), harbor seal (*Phoca vitulina*), pygmy hippopotamus (*Choeropsis liberiensis*), giant panda (*Ailuropoda melanoleuca*) (Wilson & Kleiman, 1974), bonobo (*Pan paniscus*; Enomoto, 1990), brown bear (*Ursus arctos*; Fagen & Fagen, 2004), Cuvier's gazelle (*Gazella cuvieri*; Gomen-dio, 1988), various species of canids (Bekoff, 1974), domestic pig (*Sus scrofa*; Donaldson, Newberry, Špinka, & Cloutier, 2002), golden lion tamarin (*Leontopithecus rosalia*; de Oliviera, Ruiz-Miranda, Kleiman, & Beck, 2003), common chimpanzee (*Pan troglodytes*; Nishida & Wallauer, 2003), Siberian ibex (*Capra ibex sibirica*; Byers, 1977), and laboratory rat (*Rattus norvegicus*; Pellis & Pellis, 1983). The diversity of species that display rotational movements while playing suggests that they may be ubiquitous to mammalian play. In a systematic study, Byers (1984) found that head shakes, head jerks, or neck twists were present in the play of the 12 ungulate families investigated. After fast forward movements, they were the second most widely occurring type of behavior in play.

Although references to head rotations in mammalian play are plentiful, quantitative kinematic descriptions of these patterns are lacking. Head rotations have been labeled as head shakes, head jerks, head tosses, or neck twists, but whether these labels refer to

Milada Petrů and Petr Šípek, Department of Zoology, Faculty of Science, Charles University in Prague, Czech Republic; Marek Špinka, Ethology Group, Institute of Animal Science, Prague-Uhřetíněves, Czech Republic; Stanislav Lhota, Faculty of Biological Sciences, University of South Bohemia, České Budějovice, Czech Republic, and Ústí nad Labem Zoo, Ústí n. L., Czech Republic.

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Correspondence concerning this article should be addressed to Milada Petrů, Ethology Group, Institute of Animal Science, Přátelství 815, 104 01 Prague-Uhřetíněves, Czech Republic. E-mail: milada.petru@seznam.cz

kinematically distinct types of head rotations remains unclear. Another unresolved issue concerns the functional significance of head rotations in play. During most kinds of movements, mammals try to stabilize their head orientation. For instance, primates such as gibbons, macaques, and langurs stabilize the head rotationally in space during locomotion (Dunbar, Badam, Hallgrímsson, & Vieilledent, 2004; Hirasaki & Kumakura, 2004). In this way, both gaze stabilization and maintenance of vestibular orientation is achieved. Dunbar et al. (2004) found that head stabilization was much stronger during galloping than during quadrupedal walking, suggesting that keeping a stable head orientation is more important during fast movements. When the head does rotate, other gaze stabilization mechanisms come into effect, such as the vestibular–ocular reflex—antithetic movements of eyeballs in reaction to head rotations (Crane & Demer, 1997; Newlands et al., 1999). During play, however, head or gaze stabilization does not seem to be a priority. Head rotations are frequent, and, in contrast to most nonplay contexts, many head, torso, and whole body rotations seem to be so fast that gaze probably cannot be stabilized; this would result in a retinal slip of the image and, therefore, a deteriorated perception of the 3-dimensional shape of visual stimuli (Gielen, Gabel, & Duysens, 2004).

We know that in play behavior, rotational movements are not only common, but also very frequent and often fast. But what we still do not know is their function. Why, in play behavior, do mammals use rotational movements so often and with such vigor?

One clue to this enigma may reside in the fact that rotational movements during play are typical self-handicapping patterns. Self-handicapping happens when an individual actively performs a behavior pattern that puts it into a disadvantageous position or situation (Bekoff, 2001a, 2001b). Rotation of the head in more than one plane probably impairs sensory perception and may lead to loss of spatial orientation and temporary loss of control of the movements. It is therefore probably safe to call it a *self-handicapping pattern*. However, head rotations are not the only self-handicapping elements in play. For instance, in playful social interactions, animals can limit their competitive ability by using positions such as lying on their backs or hanging with their heads down. Self-handicapping may thus occur in both social playful situations and solitary play (Bauer & Smuts, 2006; Bekoff, 2001a, 2001b; Donaldson et al., 2002; Fontaine, 1994; Watson & Croft, 1996).

Two adaptive functions have been proposed for the self-handicapping elements in play. First, self-handicapping movements may serve as play signals. Therefore, their adaptive function may reside in the fact that they promote the initiation or continuation of a playful interaction between partners (Bekoff, 1995). When an animal perceives another animal in a compromised position or performing a self-handicapping movement, this provides information of that animal's reduced capability to attack. Therefore, self-handicapping movements are good candidates to become play signals through ritualization (Špinka, Newberry, & Bekoff, 2001).

It is widely accepted that during the evolution of a visual signal, the signal becomes more and more unambiguous as the variability of the form decreases; thus, the form becomes conspicuous and more distinguishable from signals carrying different messages. Traditionally, this process has been called *ritualization* (Cullen, 1966; Lorenz, 1966; Morris, 1966). Hence, if head rotations serve as visual signals, they should be relatively uniform in appearance.

Second, through self-handicapping, animals can actively seek and create unexpected events; in this way, they learn how to regain

control in situations when an external force has kicked them out of the normal flow of movements (Špinka et al., 2001). According to this hypothesis, head rotations are part of the general suite of self-handicapping movements that are performed to create unexpected positions, situations, and perspectives. If so, then head rotations should be highly variable.

The first aim of this study was to describe head rotations occurring in the play behavior of Hanuman langurs (*Semnopithecus entellus*) and to examine whether they represent one behavior pattern with variable form or two or more distinct behavior patterns.

The second aim of this study was to test the two functional hypotheses outlined above and determine which better accounts for the head rotations present in the play behavior of Hanuman langurs. Three predictions about the occurrence and variability of head rotations were examined:

1. If the head rotations serve as play signals, then they should be rather uniform and should occur only in social play;
2. If the head rotations serve to create unexpected events, then they should be highly variable and should occur both in social and solitary play;
3. If head rotations serve both purposes, then they should occur in both types of play but be less variable during social play. That is, the kinematic properties of head rotations in the two types of play should reflect their different functions.

Method

Videorecording

The analysis was based on video records of the play behavior of free-ranging Hanuman langurs (*S. entellus*), habituated to human presence, in Alwar district in Rajasthan, Northwest India. Play behavior was recorded in three groups during 8 months (May–November 2002, April–June 2004). Each group consisted of 1 adult male, approximately 30 adult females, and 15 young individuals. These conditions provided good opportunity to collect numerous play bout recordings. The videotapes were collected using a handheld Panasonic VHS-C camera from a distance of approximately 1–20 m. The animals were not individually recognized, and the sex of the playing individuals was not systematically recorded. However, the approximate age of the individuals playing could be categorized from the videotapes (see below).

On each observation day, we focused on one of the three troops and attempted to videorecord any playful activity that occurred throughout the day. Altogether, 46 hr of videotapes containing play bouts were obtained. Play behavior was recognized by the characteristics of the movements as defined by many authors (Bekoff, 1974; Burghardt, 1999; Fagen, 1981; Loizos, 1967): Movements were exaggerated, the body posture relaxed, and the play bouts were interspersed with rotational movements of the body and play signals, such as the play face.

Videanalysis

The videotapes were digitalized and then analyzed in the program Observer 5.0.25 (Noldus Information Technology, The Netherlands). For the purpose of the study, two types of play were distinguished. *Solitary (locomotory) play* was defined as any playful activity that involved only one animal, that is, play during which no

Table 1
Occurrence of Head Rotations in Solitary and Social Play

Type of play	Age category	Total number of play bouts	Number of head rotations	Probability that head rotation occurred during play bout	Total duration of play bouts (s)	Number of head rotations/hr
Social	II	82	1	.012	1,775	2
Social	III	399	6	.015	8,205	3
Social	IV	961	50	.043	22,310	8
Solitary	II	17	1	.067	365	10
Solitary	III	167	8	.048	8,315	3
Solitary	IV	15	0	0	225	0

Note. Extracted from 10 hr of video-recorded play behavior. Each play bout in social play was counted twice (once for each individual). Age categories: II = approximately 1 week to 3 months old; III = between 3 and 5 months old; IV = 5 or 6 months old or older.

interaction with another individual, whether involving contact or not, was observed. This play included running, jumping, hanging on trees, pivoting, somersaulting, and so forth. *Social play* was any playful activity directed to or reacting to another animal. This included play chasing, wrestling, and other forms of play in which contact or other types of interaction between two or more animals were visible.

The animals were divided into four categories according to their age (Hrdy, 1977): I—newborn pink-faced young (in the 1st week of life); II—brown, black-faced young (approximately from 1 week to 3 months old); III—black-faced young, whose fur color is changing from black to gray (between 3 and 5 months old); and IV—black-faced young or adults, which are completely gray (from the 5th or 6th month onward).

Relative Head Rotation Frequency

For the purpose of quantifying the relative occurrence of head rotations in social and solitary play, the last 10 hr of our videorecordings were screened for play bouts. This sample was chosen because of the best quality of records (resulting probably from the accumulated experience in videorecording in the field) and good representation of both types of play and all age categories. A play bout was defined as a period of time from the beginning of play behavior until the animals had stopped playing for at least 5 s. Altogether 1,183 play bouts were identified. In 263 play bouts, we were not able to determine either the type of play or age category, and these play bouts were omitted from

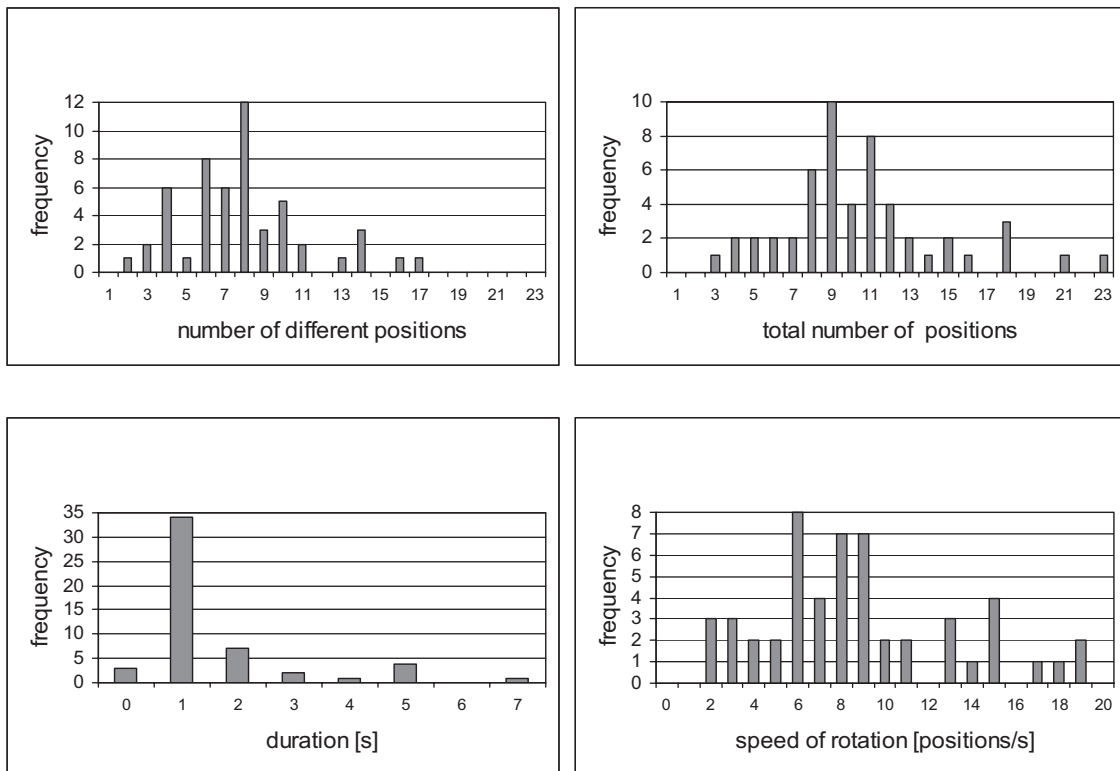


Figure 1. Descriptive parameters of 52 head rotations. Duration and speed rounded on integral numbers.

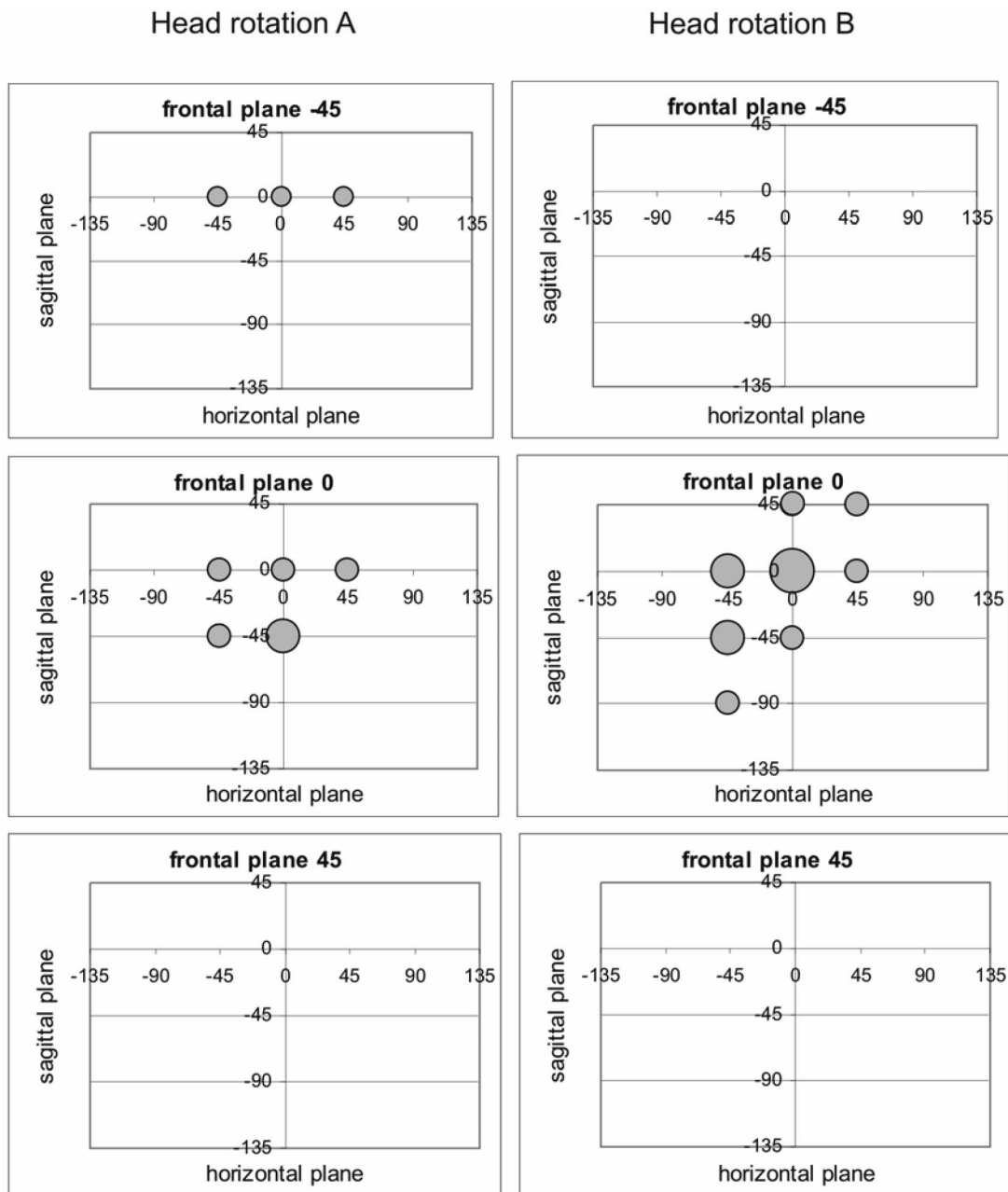


Figure 2. Positions of the head in four examples of head rotations are displayed according to the three perpendicular planes. Size of the circle represents the number of times the head passed through the specific position.

further analyses. As a result, 721 bouts of social play and 199 bouts of solitary play were analyzed (see Table 1). Each of the social play bouts was counted twice, for each of the two play partners separately. We recorded the number of head rotations, the duration of each play bout, the type of play, and the age categories of the animals.

Kinematic Analyses of Head Rotations

Not every video record of a head rotation was of sufficient quality for the detailed analysis of head positions during the

rotation. Therefore, we selected 52 head rotations of good quality from the videotapes. Out of these, 25 rotations were from social play and 20 were from solitary play; in 7 head rotations, we were not able to determine the type of play with certainty.

The bouts of head rotation were analyzed in their entirety. The beginning of a bout was defined as when the head began to move from a stabilized natural position (i.e., from -45° to $+45^\circ$ in the horizontal plane, 0° or $+45^\circ$ in the sagittal plane, and 0° in the frontal plane). The end of a head rotation bout was defined as when the head again returned to a stabilized position and remained in that position for at least 5 s. The body position varied for different

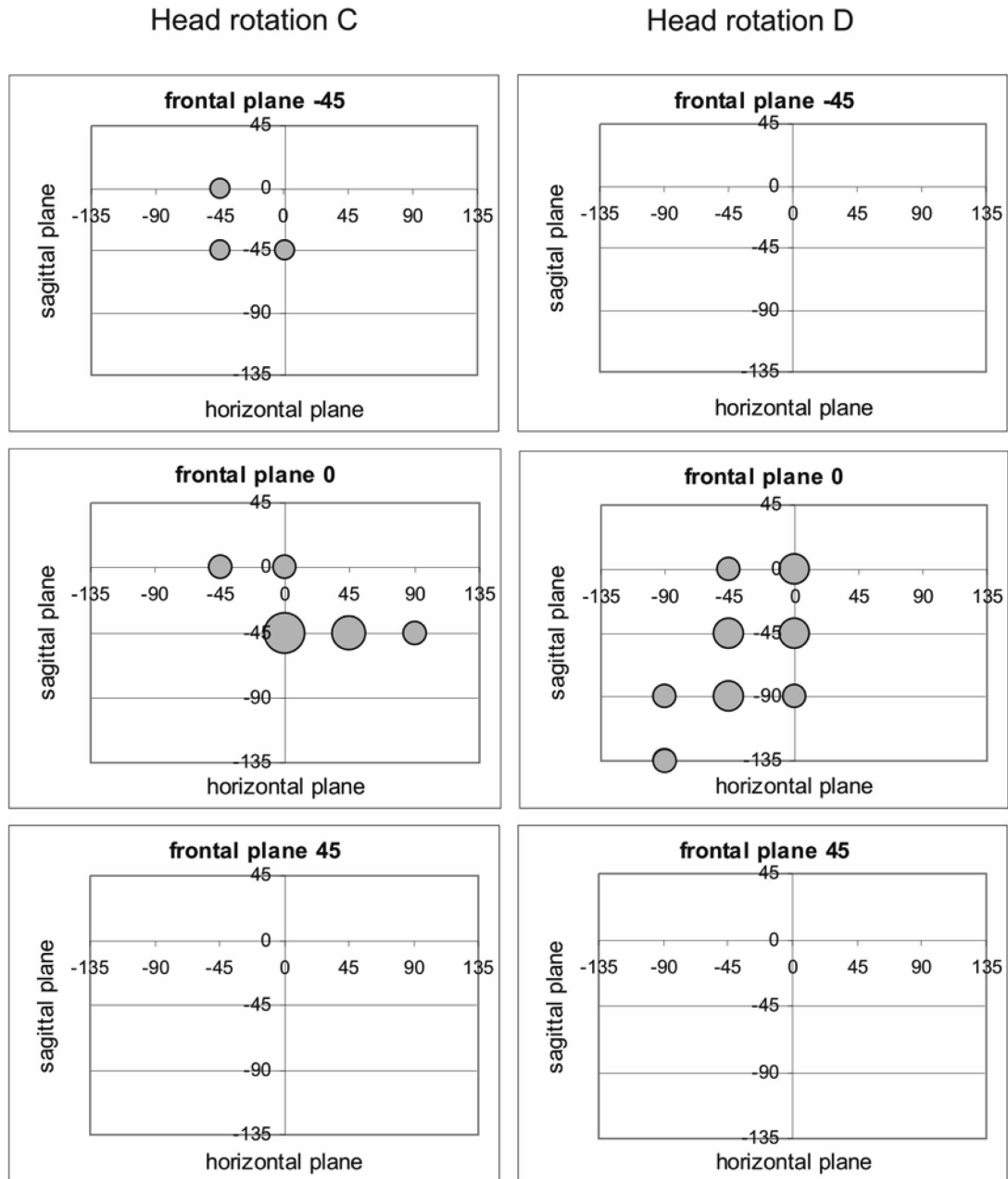


Fig. 2. (Continued)

head rotation bouts. Therefore, we always analyzed the position of the head in relation to the backbone.

The analysis of head positions during the head rotations was conceptually based on a system of three perpendicular planes: the horizontal, sagittal, and frontal planes. Using Observer software, we went through each head rotation in three runs, in each case, recording changes in the head orientation in one of the three planes. The precision of head orientation on each plane was to the nearest 45°, and the time accuracy was to the nearest video frame, that is, 0.04 s. The overall sequence of head positions resulted from the overlapping of the analyses of the individual planes. Theoret-

ically, the head could occur in 105 possible positions combined for all of the three planes; 7 in the horizontal plane (from -135° to +135° by 45°), 5 in the sagittal plane (from -135° to +45°), and 3 in the frontal plane (from -45° to +45°).

The number of different positions, total number of positions, duration, and speed (defined as the total number of positions divided by duration) were calculated for each bout of head rotation. As an additional way of quantifying the diversity of each rotation, we calculated the most commonly used diversity index—the Shannon index—as $H = -\text{SUM}\{p_i \cdot \ln(p_i)\}$, where p_i is the probability of each head position in a given head rotation (Magurran, 1988).

Statistics

Using a logistic regression, we assessed whether head rotations occurred with different probability in social play bouts and in solitary play bouts. Type of play (social vs. solitary), age category of the animal, and the duration of the play bout entered the model as fixed factors. The Type of Play \times Age Category interaction was also included in the model.

General linear models (PROC GLM, SAS 9.1) were used to assess differences in variation in head rotation between solitary and social play. The number of different positions, total number of positions, and the Shannon diversity index in one rotation bout were used as the dependent variables, and the type of play, age category, and the interaction between type of play and age category were the explanatory variables.

A chi-square test was applied to examine whether the two types of play differed in the probability of including a tilted head position in the frontal plane. This was done because rotation in the frontal plane is especially typical of play behavior (Sade, 1973) and so may shed further insight into the function of head rotations.

Results

Description of Head Rotations

For each head rotation, we analyzed its duration, the number of different positions, the total number of positions, and the speed of rotation (see Figure 1). The bar graphs show that the number of different positions, the total number of positions, and the speed of rotation were approximately normally distributed. Most of the rotations lasted between 0.5 and 1.5 s. These results suggest that head rotations represent one behavioral element that is continuously variable rather than two or more distinct behavioral patterns. The mean speed of rotation (8.79 positions/s) also illustrates that the head achieves a quite high angular velocity. As the positions were 45° apart, the average angular velocity was approximately 390°/s ($8.79 \times 45^\circ = 395.55^\circ$), with the swiftest rotation achieving 19 positions or 855°/s.

Occurrence of Head Rotations in Solitary and Social Play

Table 1 shows the occurrence of head rotations in play bouts extracted from 10 hr of videorecording. The rotations occurred both in social and solitary play. The logistic regression model showed that neither the type of play nor the age category nor the interaction between them influenced the occurrence of head rotations. The occurrence of head rotations was strongly dependent on duration of the play bout ($p < .0001$).

Variability of Head Rotations

Head rotations were very variable (see Figure 1). The average number of different positions used in one rotation was 7.88 (95% confidence interval [CI] = 6.97, 8.80), and the average total number of positions was 10.48 (95% CI = 9.33, 11.63). Thus, one head rotation usually consisted of a sequence of unique positions with little repetition in any of them. The four examples of head rotations displayed in Figure 2 show that the positions used differed from one rotation to another. For instance, Rotations A and C included positions tilted in the frontal



Figure 3. Example of sequence of one head rotation performed by animal of age category IV in social situation. The sequence of the head positions is displayed from the left to the right. The most highlighted position represents the extreme position +45° in the horizontal, -135° in the sagittal, and 0° in the frontal planes. (Drawing by I. Fedorjaková.)

plane, whereas Rotations B and D did not. Rotation B was balanced between -90° and 45° in the sagittal plane, whereas Rotation D involved a deep backward bend of the head of up to -135°. Rotation D was left-biased in the horizontal plane, whereas the other three were not. Figure 3 shows an example of one head rotation with description of the most tilted position. Figure 4 shows that, altogether, 51 different head positions of 105 possible positions were noted. The positions were quasi-normally distributed around the most frequent position of -45° sagittally, 0° horizontally, and 0° frontally. Thus, it seems that in individual rotations, the monkeys used arbitrary combinations of head positions, each with decreasing probability as they deviated more and more from the central "normal" position.

Comparison of Variability of Head Rotations in Social and Solitary Play

We did not find any difference in the variability of head rotations occurring in the two types of play. Head rotations in solitary play and social play did not differ in terms of number of different positions per head rotation ($F_{GLM,1,39} = 0.22, p = .64, n = 45$), total number of positions ($F_{GLM,1,39} = 0.21, p = .65, n = 45$) in one rotation, average duration ($F_{GLM,1,39} = 0.02, p = .88, n = 45$), or speed (number of positions in 1 s) of the rotation ($F_{GLM,1,39} = 0.22, p = .64, n = 45$). The Shannon diversity index also was not different for head rotations occurring in the two types of play ($F_{GLM,1,39} = 0.79, p = .38, n = 45$; see Figure 5). Furthermore, we did not find any effect of the animal's age on the number of different positions per head rotation ($F_{GLM,2,39} = 1.36, p = .27, n = 45$), total number of positions ($F_{GLM,2,39} = 0.43, p = .65, n = 45$) in one rotation, average duration ($F_{GLM,2,39} = 1.31, p = .28, n = 45$), or speed (number of positions in 1 s) of the rotation ($F_{GLM,2,39} = 2.69, p = .08, n = 45$). The Shannon diversity index also did not differ according to age ($F_{GLM,2,39} = 1.21, p = .31, n = 45$).

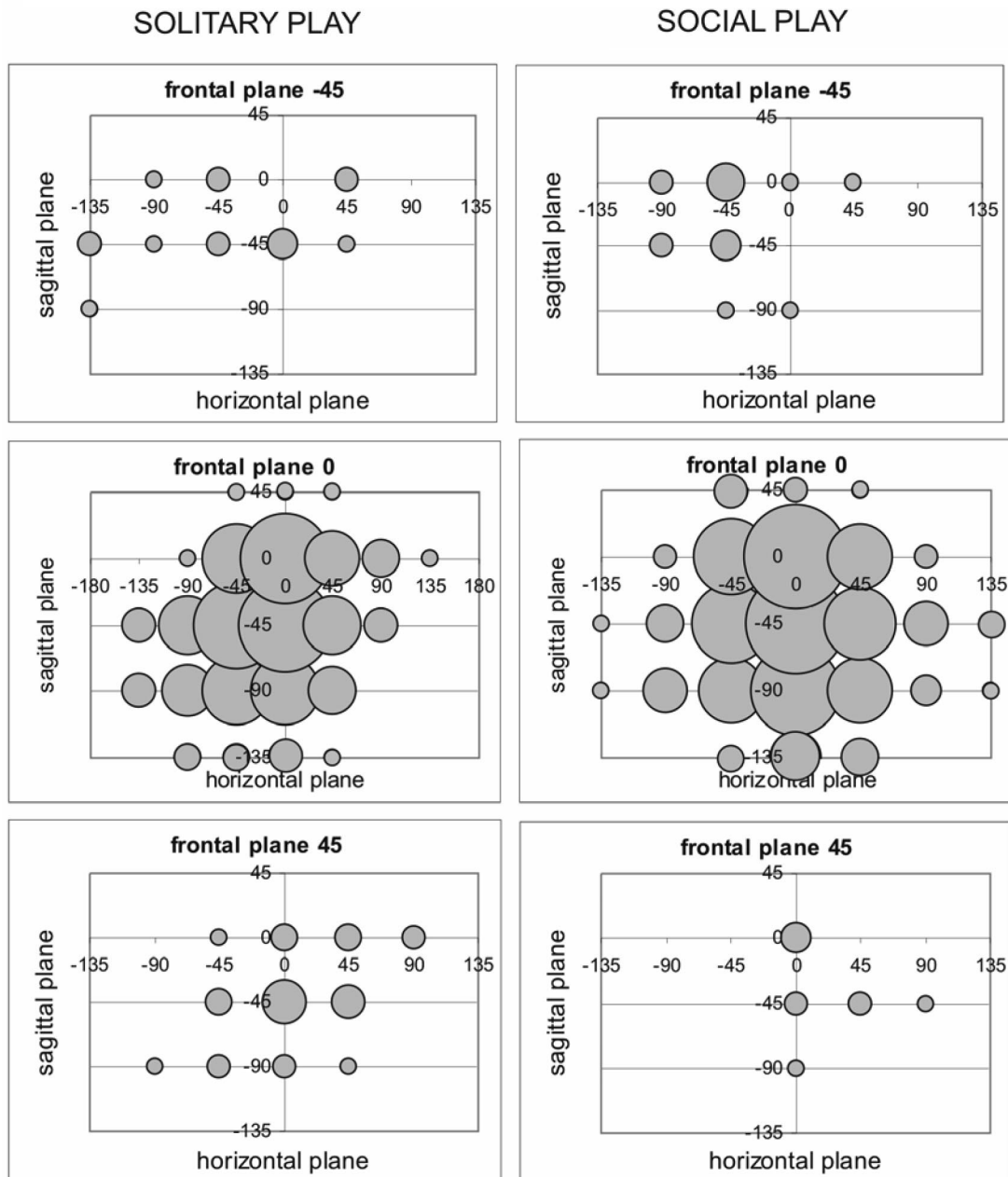


Figure 4. Positions of the head displayed according to the three perpendicular planes. Size of the circle represents the number of times the head passed through the specific position, summed over all head rotations.

The only difference between the two types of play was related to head tilting in the frontal plane (see Table 2). Head turning in the horizontal plane and head lifting and lowering in the sagittal plane were present in almost all of the analyzed rotations and, in this respect, there was no difference between solitary and social play. However, head tilting in the frontal plane was less frequent generally (21 of 45 rotations = 47%), and it also occurred more often in solitary play (13/20 = 65%) than in social play (8/25 = 32%), $\chi^2_1 (n = 45) = 4.87, p = .03$ (see Table 2).

Discussion

This study presents a description of head rotations in the play behavior of Hanuman langurs and examines the possible functions of such behavior. To our knowledge, nobody has yet attempted a quantitative kinematical description of the actual head movements during play, either in langurs or in other mammalian species. Therefore, it remains unclear whether such labels as head shakes, head tosses, and neck twists in the literature refer to distinct behavioral elements or are just different names for a single behav-

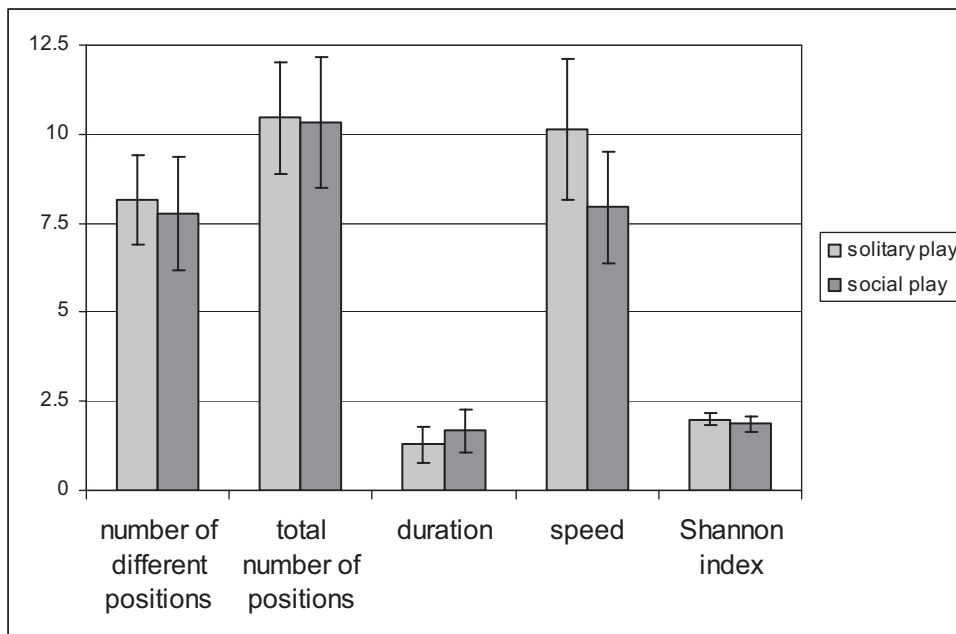


Figure 5. Descriptive parameters of head rotations occurring in solitary ($n = 20$) and social ($n = 25$) play. Least square means and 95% confidence intervals.

ioral pattern. In our detailed analysis of 52 rotations, we did not find any evidence for there being two or more distinct patterns. The analyses revealed that the characteristics of the rotations (i.e., number of different positions, total number of positions, and speed of the movement) were normally distributed and that the rotations were all in at least two planes; therefore, there were no easily recognizable classes of patterns, such as sagittal head bobbing or horizontal head shaking. Together, these data suggest that head rotations occurring in play represent a single behavioral pattern that is highly variable.

Extreme positions combining the maximal deviation in both horizontal and sagittal planes were missing, as well as many positions combining tilting in the frontal plane with the two other planes. It is not clear whether these positions were just very improbable and, therefore, not captured in our sample, whether they are physically impossible for the langurs to achieve, or whether they are possible but the animals do not employ them because they are too self-handicapping.

The next question concerned the function of head rotations in play behavior. Because head rotations are common in play and occur much less, if at all, in other behavioral contexts, one obvious

possibility is that they serve as play signals. If so, then head rotations should mostly occur in social play. Contrary to this prediction, we found head rotations to be present in both solitary and social play. Furthermore, the probability for a head rotation to occur was not higher in social than in solitary play bouts. These data indicate that at least some head rotations—especially those occurring in nonsocial contact—are likely to serve a noncommunicative function. We then tested two alternative hypotheses, using the “design feature approach” as defined by Burghardt (2005, p. 114). First, during play, head rotations may serve to create unexpected positions and situations and thus facilitate training for the unexpected (Špinka et al., 2001). For this function, head rotations should be highly variable both in social and in solitary play. Second, head rotations can serve both functions. Then they should occur in the variable form to create unexpected situations in both solitary and social play and in the ritualized form to serve as communication in social play. In this case, the head rotations should be less variable on average in social play.

We did not find any significant difference between these two types of play in the number of different positions, total number of positions, duration, speed, or the Shannon diversity index. The rotations also showed a large overall variability, each consisting of a unique sequence of nonrepetitive positions, which is not a design that would be predicted for an element with a communicatory function. That head rotations are highly and equally variable in both solitary and social play provides further evidence against the play signal hypothesis while providing support for the “training for the unexpected” hypothesis. The angular velocity of head rotations was quite high; therefore, it is probable that through the fast and variable head rotations, the animal creates sudden deterioration of its own orientation. Thereby, the langur may train how to cope with situations of this type later in life, for example, after stum-

Table 2
Number of Head Rotations According to Rotations in the Three Planes

Type of play	Total rotations	Horizontal plane		Sagittal plane		Frontal plane	
		Rotation	No rotation	Rotation	No rotation	Rotation	No rotation
Social	25	23	2	24	1	8	17
Solitary	20	20	0	18	2	13	7

bling, slipping, being knocked over, or hitting accidentally an obstacle with the head. Nevertheless, on the basis of the results of this study, we cannot simply reject the hypothesis that head rotations can serve as communication between play partners or at least that play partners react to head rotation of the other animal. Further investigation such as sequential analysis would be useful.

Of course, it is possible that head rotations serve functions other than those already considered. Two most commonly invoked theories for the function of play are general exercise (Fagen, 1981) and training of specific adult motor patterns (Biben, 1998; Byers, 1998; Fagen, 1981; Loizos, 1967; Poirier & Smith, 1974). It is difficult to see how the head rotations can contribute to either of them. First, head rotations are insufficiently frequent and intensive to fulfill a general exercise function. Second, because head rotations of the type observed in play do not occur in nonplay behavior, it is unlikely that they are performed as training for aggression or for other specific movement patterns of adult behavior. Another possibility is that head rotations could help to maintain play among partners of uneven size, age, or social status through their self-handicapping character. According to this hypothesis (which would apply only to social play), either the dominant, older, larger, or stronger animals could use the head rotation as reassurance signals, or the subordinate, younger, smaller, or weaker animals could use it as submission or appeasement signals (Wiper & Semple, 2007; see also Pellis & Pellis, 1997). On the other hand, certain types of head rotations might also serve to terminate play (Burghardt, 2005, p. 96). Further studies examining the effects of head rotations on initiation, continuation, and termination of play, especially when the partners are mismatched, involving larger and more detailed data sets are needed to evaluate this possibility fully. Such studies will combine the design feature approach with correlational evidence about the effects of head rotations on play behavior stream and will thus provide more powerful evidence about function of head rotations (Burghardt, 2005, pp. 114–115).

Head rotations displayed during play often include rotation in all three planes and thereby differ from head movements displayed in other contexts (but see Pellis & Officer, 1987, for an example of diversity of predatory head shakes). Rotation in the frontal plane seems to be especially typical for play behavior (Sade, 1973). During “normal” locomotion, the head is stabilized and rotates within a limited range in the sagittal plane so as to compensate for translation of the body and serves an important role in stabilizing the gaze during locomotion (Dunbar et al., 2004; Hirasaki & Kumakura, 2004). Rotations in the horizontal plane occur when animals are looking to the right and left. Tilting the head is avoided in “serious” behaviors because it results in the two eyes being positioned at different heights and may thus hinder accurate binocular vision. In our study, about half of the head rotations involved tilting in the frontal plane. In this respect, there was a difference between social and solitary play. Whereas in solitary play most of the head rotations were tilted in frontal plane (13 of 20), in social play, much fewer of them were (8 of 25). Our possible explanation for this difference is that tilting the head adds an extra degree of self-handicapping and unpredictability to the play sequence and hence may be avoided in vigorous social play in which enough variability and unpredictability is caused by the behavior of the play partner. Analogously, Byers (1977) also observed that locomotory play was performed at a level of risk avoided in social play. In his study, Siberian ibex kids played

socially on flat surfaces, whereas their locomotory play occurred on sloped surfaces.

In conclusion, this study shows that the head rotations occurring in the play of Hanuman langurs are highly variable and are present in both social and solitary play, which indicates that they may serve to create unpredictability during play.

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