



Scan and focal sampling: reliability in the laterality for maternal cradling and infant nipple preferences in olive baboons, *Papio anubis*

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We compared measures of laterality obtained by two observational sampling procedures (a 15-min focal-dyad sampling with continuous recording, and a scan and instantaneous sampling), using 10 mother–infant dyads of captive olive baboons. The two measures of lateral biases for maternal cradling, infant nipple preference, infant head position and maternal carrying, but not those for infant retrieval, were positively and significantly correlated. Our results clearly show that the two sampling procedures produce equally sensitive measures of lateral bias for both the maternal and the infant behaviours. They also provide evidence of asymmetries in mean bout length and therefore suggest that recording bouts is not necessarily the best measure of lateral bias. Taken together, these results show empirically that the scan and instantaneous sampling procedure does not lead to a lack of independence of data points, as previously assumed.

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In the past 10 years there has been a plethora of research on the assessment of lateral bias in hand preference in nonhuman primates (New World monkeys: Hook-Costigan & Rogers 1996; Old World monkeys: MacNeilage et al. 1987; Fagot & Vauclair 1991; Marchant & McGrew 1991; Hopkins & Morris 1993; Ward & Hopkins 1993; Hopkins 1996; McGrew & Marchant 1997). The majority of studies have focused on whether nonhuman primates show population-level handedness in any way that resembles that observed in humans. Population-level handedness is observed when a significant majority of the sample shows the direction in hand use for a specific task or series of tasks. Human subjects are generally considered to show a population-level right-hand preference as indicated by the fact that ca. 90% self-report themselves as being right handed which is much higher than would be predicted by chance.

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The issue of whether nonhuman primates show a population-level hand preference remains highly controversial and there has been considerable debate concerning the assessment and interpretation of hand preference data in various primate species (see McGrew & Marchant 1997; Hopkins 1999, for contrasting views). Specifically, some investigators have suggested that population-level hand preferences are manifest in several primate families including great apes (Hopkins 1996), Old and New World monkeys (Lehman 1993; Westergaard et al. 1993; Diamond & McGrew 1994; Hook-Costigan & Rogers 1996) and prosimians (Ward et al. 1993). In contrast, others have suggested that various methodological and procedural flaws in various studies preclude concluding that any nonhuman primates show population-level hand preferences (Ettlinger 1988; McGrew & Marchant 1997). For example, McGrew & Marchant (1997, page 226) concluded 'that the biggest, simplest conclusion is that there is yet no compelling evidence that nonhuman primates are lateralized at the population level. That is, neither level 4 nor 5 is the norm for any species, task, or setting . . .' In the five-level model (McGrew & Marchant 1997), from level 4, the overall distribution of individuals

in the population is significantly asymmetrical. At level 4, a majority of individuals are significantly but incompletely lateralized, while at level 5, individuals are completely lateralized.

Recently, Hopkins (1999) has argued that the procedural and methodological criteria for the inclusion of many of the nonhuman primate studies reviewed by McGrew & Marchant (1997) are based on arbitrary criteria and do not have any strong empirical or scientific merit. For instance, McGrew & Marchant (1997) did not include any studies in their meta-analysis in which they judged the authors had not controlled for the independence of observations when collecting the hand preference data. The 'independence of observations' problem is when the hand used for a specific response can influence the use of the hand on subsequent responses. In particular, McGrew & Marchant (1997) did not include studies in their meta-analysis in which scan sampling procedures were used to collect frequencies in hand use for specific motor actions (e.g. Colell et al. 1995; Tomaszycycki et al. 1998), presumably because these procedures do not result in independent observations of lateral bias and therefore skew the results in one way or another.

Rather than continually debate the merits of one procedure over another in the assessment of lateral bias in hand use, what is needed are studies that directly compare different assessment procedures to determine whether the measures of lateral bias differ. The purpose of our study was to compare scan and focal-dyad sampling procedures with instantaneous sampling and continuous recording, in the assessment of lateral bias as well as for maternal and infant asymmetries of posture and hand preferences. Our hypothesis was that focal-dyad and scan sampling procedures would reveal consistent and reliable assessments of lateral bias. Furthermore, we hypothesized that the magnitude of lateral bias would be similarly reliable and consistent between sampling procedures.

In addition, the focal-animal sampling with continuous recording procedure allowed us to collect data on both the frequency and duration of lateral bias. Dividing the total duration data by the frequency allows one to create a measure of the average amount of time each lateralized behaviour occurs. From the standpoint of methodology in the measurement of lateral bias in primates, these data are important because they directly address the issue of whether measuring individual motor actions or bouts of motor actions are more sensitive to the assessment of lateral bias. Specifically, McGrew & Marchant (1997) have argued that measuring bouts of motor actions is a better measure of hand preference because the investigator is thereby controlling for the independence of each observation. In contrast, Hopkins (1999) has argued that asymmetries can occur in bout length or in the average number of events per bout, which are overlooked if one considers only bouts of behaviour. For example, in reaching to pick up food without any intervening behaviour, a subject might successively use its left hand on nine occasions and its right hand on one occasion. If the subject performed this same pattern in 10 separate observation sessions, the total number of left and right hand responses would be 90 and

10 but the number of bouts would be 10 and 10, respectively. Furthermore, the average number of responses per bout would be nine for the left hand and one for the right. In this case, the subject has a clear lateral bias that would not be reflected by recording bouts rather than individual actions. In this study, we tested whether asymmetries in mean bout length were manifest in the expression of lateral bias for maternal and infant postures and preferences. We hypothesized that asymmetries in mean bout length would be evident, suggesting that recording bouts is not necessarily the best way to measure lateral bias, as suggested by others (gorillas: Byrne & Byrne 1991; nonhuman primate species: McGrew & Marchant 1997).

METHODS

Subjects and Housing

The subjects were 10 mother-infant baboon dyads belonging to a social group of 70–90 individuals. All the infants in the study were captive born, and none of the animals was caught specifically for our study. The founders of this group were wild caught in Uganda, more than 10 years ago and kept first at the Wildlife Park of Saint Vrain (near Paris, France). During the spring and summer of 1997, the animals were transferred to Rousset Station, near Marseille, France, to establish a breeding colony of nonhuman primates for use in research by the French government. The females ranged in age from 6 to 12 years, although their exact ages were not known because they were wild caught. All 10 females gave birth at Rousset between December 1997 and April 1998.

The baboons were housed in two large outdoor compounds, connected by a tunnel, each measuring 20 × 25 m and open at the top; each had an attached indoor building that was 7 × 6 m in diameter and 2.6 m high. Each outdoor compound contained a wooden climbing structure with a sliding ramp and a tyre to swing to and fro. A variety of plastic toys and logs were given in the outdoor compounds on a daily basis. The baboons could pass freely between the indoor building and outdoor compound, except during observation periods when they were locked in the outdoor compound. Water was available ad libitum and monkey chow, fresh fruits and vegetables were given in the late afternoon after the day's last test. Three times a week the monkeys were given bananas, white cabbage, oranges and corn.

Procedure

We used scan and focal-dyad sampling techniques to assess lateral bias in maternal cradling, infant position and nipple preference behaviour. These data are part of a longitudinal study aimed at assessing the effect of early maternal and infant behaviours on the development of hand preferences in baboons (Damerose & Vauclair 1999). Previous studies have reported evidence of a left maternal cradling bias in chimpanzees, *Pan troglodytes* (Manning & Chamberlain 1990 but see Hopkins et al. 1993; Dieneske

et al. 1995), as well as left nipple preferences by infants in nonhuman primates (chimpanzees: Nishida 1993; rhesus monkeys, *Macaca mulatta*: Tomaszycki et al. 1998). All of these studies used observational methods (see Damerose & Vauclair, *in press* for details) and therefore these are ideal measures of lateral bias for comparison of different methods of data collection. Each female baboon was identified with a differently coloured ear tag (1 × 3 cm, clipped to the ear). Observations of lateral bias began within 1 or 2 days of birth and continued for the first 6 weeks of the infant's life. We made two observation sessions per week on each mother–infant dyad and for each sampling procedure.

Behaviours of Interest

We recorded five basic measures of lateral bias from either the mother or the infant. These were maternal cradling, maternal carrying, infant retrieval, infant head position and infant nipple preference. We defined maternal cradling as the mother holding the offspring with either her left, right or both hands. It was recorded only when the infant was held ventrally by the mother and she was in a sitting posture. We recorded nipple preferences when the infant suckled from the left or right nipple of the female. No distinction was made between the different suckling phases, such as feeding or nonfeeding nipple contact (e.g. Tanaka 1997). Thus, any and all contact with the nipple by the infant was considered as suckling behaviour. The head position of the infant was assessed in relation to the midline of the body of the mother and was recorded as either left, right or midline (apes: Manning & Chamberlain 1990; humans: Manning & Chamberlain 1991). We included lateral bias in head position in the ethogram because it could occur independently of either the cradling bias of the mother or the nipple preference of the infant. For example, the infant could have its head on the right while suckling on the left nipple. If more than half of the head was on one side of the mother's ventrum, then we considered it a lateralized behaviour (i.e. left or right head position). If the left or right position of the head was unclear, we recorded it as a midline position. Infant retrieval occurred when the infant was apart from its mother and the mother reached to retrieve the infant for any reason. The hand used to retrieve the infant was recorded as left, right or both. Finally, maternal carrying was recorded when females were observed to walk with the infant in a ventral position and simultaneously hold it with one arm (left or right).

We included two additional behaviour categories to make the ethogram mutually exclusive and exhaustive. First, a category of 'no behaviour' was included if the infant or mother was not engaged in any of the operationally defined measures of lateral bias. Second, if the mother or infant was not visible or their behaviour could not be clearly seen from the vantage point of the observer, we simply recorded 'not visible' in the data file. This category represented 12% of our observations.

Sampling Procedures

Instantaneous and scan sampling

For one aspect of the study, we used a scan sampling method with instantaneous sampling for the recording rule (Altmann 1974; Martin & Bateson 1993). Each observation session lasted 1 h and we used a 60-s sample interval for the sample of behaviours of each mother–infant dyad. Consequently, we obtained a total of 60 scans for each observation session. We used a check sheet to collect the data, and we recorded at each scan the lateral bias in maternal cradling, the head position of the infant, the nipple that the infant was suckling, the maternal carrying bias and the infant retrieval. During each sampling interval, the observer scanned the outdoor compounds for the mother–infant dyad and made a note of their behaviour. If a behaviour was the same for several successive 60-s sample intervals, each scan was considered as a separate instance.

On a given day, more than one mother–infant dyad could be observed in the same observation session. Thus, according to the number of mother–infant dyads observed during the 1-h observation session, the observer noted each x s ($x=60/\text{number of observed dyads}$) the behaviours of another dyad. For this, we used a stopwatch (YEMA Memory Chrono) with a timer function, adjustable to 1 s and with an automatic zero-replay. Each scan sample was considered a separate event in terms of the frequency of lateralized behaviours of the infant and the mother.

Focal-dyad sampling with continuous recording

In addition to the instantaneous and scan sampling procedure, we used a 15-min focal-dyad sampling procedure for each of the mother–infant dyads. The different behavioural measures of lateral bias of the mother (maternal cradling, infant retrieval, maternal carrying) and the infant (nipple preference and infant head position) were recorded continuously over a 15-min period. For the focal-dyad sampling, the observer used a portable computer (PC CompuDyne with a 386 SX processor at 25 MHz) to record the mother's and the infant's behaviours. A computer program was written in QuickBasic 4.0 that allowed for continuous and simultaneous recording of the frequency and duration of each behavioural category. Keys on the computer keyboard represented the different behavioural categories and the lateral bias in the behaviour. The onset and offset of specific behaviours were recorded when the observer depressed the different keys representing each behavioural category. One mother–infant dyad was recorded during each 15-min session and each dyad was observed for two sessions per week. We began an observation session only if any two of the three main behaviours were present (i.e. maternal cradling, infant head in contact with the ventrum of the mother, nipple preference). Of particular interest was the nursing behaviour of the mother–infant dyad, so we attempted, with this constraint, to increase the probability of sampling these behaviours. When the mother was carrying the infant under the ventrum, we coded

only the laterality of this behaviour and ignored all other aspects of laterality.

Data Analysis

For the scan sampling procedure, we summed the total frequency of left- and right-sided responses for the 12 observation sessions for each measure of lateral bias. For the focal-dyad sampling procedure, we calculated the total duration, the number of bouts and the mean bout length of left- and right-sided responses for each measure of lateral bias, summed over the 12 observation sessions. For each behavioural unit and sampling procedure, we derived a measure of lateral bias, *LB*, from the formula $LB = (R - L) / (R + L)$, where *R* is the number of right-sided responses and *L* the number of left-sided responses. The *LB* scores ranged from -1.0 to 1.0 with positive values reflecting a right-side bias and negative values a left-side bias. The absolute value of the *LB* score (referred to as *ABS-LB*) reflected the magnitude of asymmetry for each measure. Population biases were assessed with one-sample *t* tests for each measure and the *LB* scores were compared to a normal distribution with a mean of zero. To evaluate the reliability between sampling procedures, we calculated a Pearson product-moment correlation coefficient for the *LB* score derived for each sampling procedure.

For the instantaneous and scan sampling procedure, we analysed maternal cradling, nipple preference and head position of the infant as a percentage (per individual and per h), that is, the ratio of the lateralized acts (right and left) to the time of the observation session (1-h observation session) multiplied by 100. The rate is defined as the frequency of a behaviour's occurrence per specified unit of observation time, such as frequency/h. The carrying and the infant retrieval data were analysed in terms of mean bouts/individual and mean bouts/h.

RESULTS

Inter- and Intrarater Reliability

Prior to data collection, we assessed intra- and inter-rater reliability for the focal-dyad sampling procedure using a kappa coefficient (see Lehner 1996 for an example of how to calculate a kappa with a record of several behavioural categories). Two 15-min observation sessions were videotaped and subsequently scored independently by the three observers. The kappa coefficients between the three observers were all above chance (observer 1 versus 2: kappa=0.76; observer 1 versus 3: kappa=0.85; observer 2 versus 3: kappa=0.83). Intrarater reliability was assessed 2 months after the initial record and was also significantly above chance (kappa=0.93).

Consistency in Lateral Bias between Sampling Procedures

With the exception of infant retrieval (mean of 0.01 events per observation session), there were highly signifi-

Table 1. Intercorrelations between the lateral bias scores from the instantaneous scan sampling and the focal-dyad sampling procedures

Instantaneous rate	Focal-dyad measures		
	Total duration	Number of bouts	Mean bout length
Nipple preference	0.973****	0.937****	0.768*
Maternal cradling	0.900****	0.863**	-0.474
Infant carrying	0.923****	0.880***	0.511
Infant head position	0.962****	0.921****	0.252
Infant retrieval	0.384	0.360	0.433

* $P < 0.05$; ** $P < 0.005$; *** $P < 0.001$; **** $P < 0.0001$.

Table 2. Intercorrelations between the lateral bias scores for the three measures from the focal dyad sampling procedure

	Number of bouts	Mean bout length
Total duration		
Nipple preference	0.956**	0.808*
Maternal cradling	0.930**	-0.485
Infant carrying	0.956**	0.610
Infant head position	0.910**	0.361
Infant retrieval	0.944**	-0.161
Number of bouts		
Nipple preference		0.601
Maternal cradling		-0.767*
Infant carrying		0.326
Infant head position		-0.054
Infant retrieval		0.392

* $P < 0.01$; ** $P < 0.0001$.

cant positive correlations between the *LB* scores from the instantaneous scan sampling and the total duration and the number of bouts *LB* scores from the focal-dyad procedure (Table 1). In contrast, instantaneous scan sampling *LB* scores did not correlate significantly with the mean bout length *LB* scores from the focal-dyad procedure, except for infant nipple preferences (Table 1). The total duration and the number of bouts *LB* scores from the focal-dyad procedure were significantly and positively correlated across all of the behavioural categories but were not consistently correlated with the mean bout length *LB* scores (Table 2).

Asymmetries in Mean Bout Length

A central focus of this paper is the assessment of asymmetries in mean bout length. For each behavioural measure we calculated a mean bout length value, for left and right defined as total duration/number of bouts. Following our previous *LB* score calculation, in a post hoc analysis, we calculated a new lateral bias score using the mean bout length values for each side, following the equation below:

Table 3. One-sample *t* test for each lateral bias and absolute lateral bias scores and sampling procedures

	Lateral bias score			Absolute lateral bias score		
	<i>t</i>	<i>df</i>	<i>P</i>	<i>t</i>	<i>df</i>	<i>P</i>
Instantaneous rate						
Maternal cradling	-0.64	9	0.541	3.93	9	0.003
Nipple preference	-1.17	8	0.276	7.58	8	0.0001
Infant head position	1.75	9	0.115	4.01	9	0.003
Infant carrying	-1.38	9	0.201	4.51	9	0.001
Infant retrieval	-1.09	8	0.309	4.89	8	0.001
Focal-dyad						
Total duration						
Maternal cradling	-0.50	9	0.628	3.09	9	0.013
Nipple preference	-0.80	8	0.445	5.90	8	0.0001
Infant head position	1.64	9	0.136	4.39	9	0.002
Infant carrying	-0.56	9	0.587	4.17	9	0.002
Infant retrieval	-0.55	7	0.599	4.62	7	0.002
Number of bouts						
Maternal cradling	-0.28	9	0.785	2.07	9	0.068
Nipple preference	-0.55	8	0.598	5.67	8	0.0001
Infant head position	0.54	9	0.605	3.21	9	0.011
Infant carrying	-0.62	9	0.551	3.24	9	0.010
Infant retrieval	-2.04	8	0.076	2.56	8	0.034
Mean bout length						
Maternal cradling	0.36	9	0.730	2.23	9	0.052
Nipple preference	-0.60	8	0.567	5.99	8	0.0001
Infant head position	2.83	9	0.020	3.96	9	0.003
Infant carrying	-0.49	8	0.635	3.05	8	0.016
Infant retrieval	0.128	7	0.241	3.83	7	0.006

Lateral bias scores indicate directional biases; absolute lateral bias scores reflect strength in lateral bias, irrespective of direction and are calculated by taking the absolute value of the lateral bias score.

$$LB_m = \frac{m_R - m_L}{m_R + m_L} = \frac{\frac{d_R}{b_R} - \frac{d_L}{b_L}}{\frac{d_R}{b_R} + \frac{d_L}{b_L}} = \frac{d_R \times b_L - d_L \times b_R}{d_R \times b_L + d_L \times b_R}$$

where LB_m =lateral bias for the mean bout length measures, m_R =mean bout length for right measures; m_L =mean bout length for left measures, d_R =total duration for right measures, d_L =total duration for left measures, b_R =number of bouts for right measures, b_L =number of bouts for left measures.

We then took the absolute value (noted ABS- LB_m) of the LB_m score to assess whether the asymmetries differed from a normally distributed set of scores. Significant asymmetries were found for cradling ($t_9=2.23$, $P<0.05$), infant nipple preference ($t_8=5.99$, $P<0.01$), infant head position ($t_9=3.96$, $P<0.01$) and infant retrieval ($t_7=3.83$, $P<0.01$). Thus, the mean bout lengths were asymmetric for four of the five measures, suggesting that bouts, by themselves, may not capture the entire dimension of lateralized behaviours in monkeys.

Population Asymmetries and Comparison with Other Findings

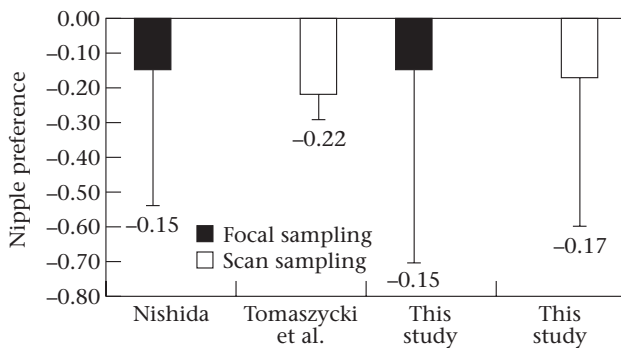
We assessed population-level biases for each behavioural measure with one-sample *t* tests and *Z* scores. With respect to the LB scores, no significant population-level

biases were found, although some of the measures did approach statistical significance (Table 3). We also classified subjects as either left or right sided based on the sign of their LB score for each sampling procedure. Subjects with negative values were classified as left sided and subjects with positive values as right sided. Table 4 gives the number of subjects classified as left or right sided. There were significantly more infants classified as having a right than left head position for the instantaneous and scan sampling. The focal-dyad data showed nonsignificant trends towards a left nipple preference and a right head position for the sample.

Although we failed to find population-level directional asymmetries for the measures of lateral bias with the LB scores, our results are consistent with other findings in monkeys and apes. For example, Fig. 1 compares the mean LB scores for nipple preferences in a sample of 34 chimpanzees (Nishida 1993) and 39 rhesus monkeys (Tomaszycki et al. 1998) with our own findings in nine baboons. Among the 10 mother-infant dyads that we followed, one mother had only a right nipple, so these data were not included in the analysis of asymmetries in the nipple preference. As can be seen, the mean LB scores are comparable between the species, suggesting a common mechanism in the expression of nipple preferences in Old World monkeys (but see Rogers & Kaplan 1998 for a contrary view in common marmosets, *Callithrix jacchus*, and Damerose & Vauclair, in press, for a more detailed review).

Table 4. Classification of the lateral bias scores

	Focal-dyad total duration			Instantaneous rate		
	Left	Right	Z	Left	Right	Z
Nipple preference	7	2	-1.67†	6	3	-1.00
Infant head position	2	8	1.90†	1	9	2.53*
Maternal cradling	7	3	-1.26	6	4	-0.63
Maternal carrying	6	4	-0.63	7	3	-1.26
Infant retrieval	3	5	0.71	6	3	-1.00

† $P < 0.1$; * $P < 0.05$.**Figure 1.** Mean (+SD) of left nipple preference and sampling procedures for different studies (Nishida 1993; Tomaszycski et al. 1997; this study).

DISCUSSION

Our results are relatively straightforward. In the assessment of lateral bias for maternal cradling, maternal carrying, infant nipple preference and infant head position, instantaneous and scan sampling and focal-dyad sampling procedures reveal comparable levels of lateral bias. Furthermore, individual variation in both strength and direction of lateral biases are highly consistent using both procedures. Our findings are in accordance with other studies on animal behaviour. Rhine & Ender (1983) found a high correlation, using a Monte Carlo simulation, between duration and instantaneous sampling for an observation interval up to 120 s. They defined the duration as the proportion of the total observation time during which the behaviour was recorded as occurring. An instantaneous score is the proportion of defined instants in time, such as the end of 30-s intervals at which the behaviour is observed in progress. According to our data analysis, their duration scores (Rhine & Ender 1983) are equivalent to our measures from the focal-dyad sampling with continuous recording. Similarly, their instantaneous scores (Rhine & Ender 1983) are equivalent to our measures from the instantaneous and scan sampling. Rhine & Flanigan (1978), with stump-tailed macaques, *Macaca arctoides*, and Leger (1977), with chimpanzees, both found that instantaneous rate was highly correlated with duration ($r=1.00$, $r=0.99$, respectively).

Infant retrieval, as a measure of lateral bias, does not appear to be highly correlated between sampling procedures. Although we found a positive correlation, it

was not significant. Infant retrieval occurred at a much lower frequency than the other behavioural categories, which could explain why the reliability of the infant retrieval measure was not significant. Rhine & Ender (1983) have argued that the number of hits in a sampling session, defined as the number of times the behaviour is recorded as occurring, is important. A low number of hits tends to yield low reliability and low comparability. Furthermore, the infant retrieval behaviour is an event, because this behaviour category has relatively short behaviour patterns (Martin & Bateson 1993), with a mean bout length of 1.7 s; while the other behavioural categories are states. A behavioural unit is considered as a state when it can be timed with a stopwatch and has an appreciable duration (Lehner 1996). Therefore, recording bouts of events and total duration of states appears to be not equivalent for the two sampling procedures. In this case, we would argue that when a behavioural unit has a low occurrence, then recording the total duration and the frequency by focal-dyad sampling and instantaneous and scan sampling procedures would not yield comparable results.

As instantaneous and scan sampling is a sampling procedure of states and not events (Altmann 1974), and as focal-dyad sampling with continuous recording is also a sampling procedure of states, we argue that measuring the frequency of bouts of states is equivalent to totalling the duration of bouts of states. The comparison between total duration and number of bouts obtained with the focal-dyad sampling procedure for each *LB* and *ABS-LB* score confirms this assumption. In fact, recording the total duration appears to be comparable to counting the number of bouts of maternal cradling, infant head position, nipple preference and maternal carrying. So when the behavioural unit is a state (i.e. like these four behavioural units), calculating a rate is equivalent to counting a total duration, independently of the sampling procedure used. However, when the behavioural unit is an event (i.e. like infant retrieval), only with focal-dyad sampling are the number of bouts and the total duration equivalent.

Our results do not support McGrew & Marchant's (1997) hypothesis that studies involving scan sampling procedures are subject to a lack of independence of data points which biases the laterality results. Our results clearly show that the two sampling procedures produce equally sensitive measures of lateral bias for both the

maternal and the infant behaviours. Therefore, there is no reason to assume that scan sampling procedures bias the laterality effects, at least as it pertains to the measurement of maternal cradling, maternal carrying, infant head position and infant nipple preference. Our results further suggest that recording the frequency of 'bouts' of response asymmetries without consideration of the individual events is not recommended because significant asymmetries can occur in the number of individual responses per bout. In short, there can be asymmetries in mean bout length as was evident in the behavioural measures we used (Table 3). Taken together, these results show empirically that some of the criteria used to include or exclude studies in the meta-analysis of hand preference used by McGrew & Marchant (1997) are not warranted. This, in turn, may have led to a selection bias which resulted in their concluding that asymmetries in hand preference are not evident in nonhuman primates.

In conclusion, we obtained equivalent degrees of asymmetry from the instantaneous and scan sampling procedure and the 15-min focal-dyad sampling with continuous recording procedure. However, because continuous recording data can be further subdivided into frequency and duration, analyses of a more molecular nature (McDowell 1973) are possible (e.g. mean bout length, sequential organization of behavioural patterns). Hence, using the mean bout length is by no means trivial because it can potentially provide a measure of hand skill rather than preference per se, an important dimension of laterality that has largely been overlooked in the literature on nonhuman primates compared with human hand preference. Therefore, focal-dyad sampling with continuous recording would be recommended over instantaneous and scan sampling, particularly for preliminary studies of an observational nature such as the one described here.

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