Straight-Aggression and Appeal-Aggression in *Macaca fascicularis*

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Summary. A quantitative analysis of temporal associations between the behaviour elements shown by 8 individual Java-monkeys (*Macaca fascicularis*) confirmed the distinction between two categories of aggressive behaviour: straight-aggression and appeal-aggression.

Recently three independent analyses, both qualitatively by others[2,3] and quantitatively by ourselves[4,5], have indicated that it is possible to distinguish in the aggressive behaviour of Java-monkeys two categories which may be designated as *straight-aggression* and *appeal-aggression*. During their agonistic actions against the opponent, straight-aggressors exclusively pay attention to this opponent, whereas appeal-aggressors intermingle their agonistic actions against the opponent with particular non-agonistic behaviour elements towards third group-members who almost invariably are dominant in relation to the agonistic actor and to the reactor. Appeal-agressors show – so to speak – 'two-frontal behaviour'[6,7]. The non-agonistic components directed to the third party were called *sub-directed behaviours*.

As our quantitative analysis mentioned above[4,5] was of a rather global nature, an investigation of much greater detail (both observationally and analytically) was carried out in order to test the correctness of the distinction between two types of aggression in Java-monkeys.

Method. With the help of a tape-recorder we recorded all behaviours of selected single members of a Java-monkey group. Each individual was followed 15 times for half-an-hour. We used a list of 85 behaviour codes. A simultaneously registered time-signal divided the running protocol into periods of 5 sec: i.e. 'the cells'. The data were collected from 8 individuals: 2 adult males (Aam, Cam), 1 adolescent male (Som), 2 juvenile males (Rum, Cum) and 3 adult females (Daf, Laf, Zaf). These monkeys lived in either of our two monkey groups, each of which is of a near-to-natural age and sex composition and is lodged in a rather large cage[5,8].

Analysis (I). This analysis was performed in order to delineate the category of agonistic behaviour. To this end, the behaviour element *lunge* (L) was a priori defined as being of an aggressive nature and the element *bared-teeth* (B) as being of a fearful nature (De Waal et al.[5] gave descriptions of these and other behaviour elements). For each monkey under analysis, the behaviour elements which are temporally associated with the aggressive element L were determined as follows: The observed number of coincidences of a behaviour element X with L (i.e. the frequency with which they occurred together in the same cell) was compared with the number of such coincidences that would be expected on the basis of independent occurrence of both elements in time (being the number of cells containing at least one time X multiplied by that containing at least one time L, divided by the total number of cells: i.e. $15 \times 360 = 5{,}400$). Since the behaviour elements in

The procedures of analysis as illustrated by their application to the data on animal Aam

Analysis I. The temporal associations with 'aggressive' element L (N.B. Aam never performed 'fear' element B)

Behaviour element	Frequency	Coincidences with L: Expected e	Coincidences with L: Observed o	Poisson-tables p (%)
L, Lunge	32	–	–	–
O, Open-mouth	67	0.40[a]	23	$\leqslant 0.1$
S, Staring	123	0.73	22	$\leqslant 0.1$
H, Headbob	36	0.21	8	$\leqslant 0.1$
G, Grunt	12	0.07	5	< 0.1
C, Chase	6	0.03	3	< 0.1
T, Tug	8	0.05	3	< 0.1
K, Shoulderbob	8	0.05	2	< 0.2

[a]Computation: $67 \times 32/5{,}400 = 0.397$

In addition, the element 'Groundslap' (D) occurred 22 times of which only 1 time together with L ($e = 22 \times 32/5{,}400 = 0.13$; $o = 1$; $p \gg 5\%$). However, in all 22 cases it occurred in a cell containing at least one of the elements listed above; there were 160 of such cells ($e = 22 \times 160/5{,}400 = 0.65$; $o = 22$; $p \ll 0.1\%$). Therefore, element D is added to Aam's 'around-L' category.

Analysis II. The distribution of coincidences between all 9 agonistic elements

	L	O	S	H	G	C	T	K	D	Σ
L	■	**23**	22	8	5	3	3	2	1	67
O		■	**43**	14	8	2	4	4	10	108
S			■	**32**	11	2	5	4	16	135
H				■	0	0	2	0	8	64
G					■	0	0	1	0	25
C						■	1	0	0	8
T							■	1	0	16
K								■	1	13
D									■	36

Total number of coincidences: 472

In bold print are numbers of coincidences for which $q \geqslant +2$. For example, coincidences of element S with element H: $o = 32$; $e = 135 \times 64/472 = 18.3$; $q = (32-18.3)/\sqrt{18.3} = +3.2$

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question are comparatively shortlasting and rare occurrences, the probability distribution of their coincidences can be regarded as a Poisson-distribution. Therefore, the probability that the observed number of coincidences of X with L did arise by chance has been determined from Poisson tables. If this probability appeared less than 5%, the element X was considered to be temporally associated with L and to belong to the so called 'around-L' category of elements. Furthermore, elements which did not appear to associate with L in this direct manner, but which often occurred (according to the same statistical criterion) within cells containing at least one of the elements of the 'around-L' category were added to this category (see Table for an elaborated example).

In exactly the same manner, the elements temporally associated with fear element B (the 'around-B' category) were determined.

Behaviour elements occurring in less than 6 cells of an individual's protocol were excluded from the analysis.

Results (I). The behaviour elements that appeared to belong to the 'around-L' and/or the 'around-B' category constituted the *agonistic category* of elements. Figure 1 shows the 31 behaviour elements present in the agonistic categories of one or more of the individuals investigated: each element being present on the average in 3.6 of the 8 individual agonistic categories. In the large majority of cases (i.e. 83%, $n = 112$) where an element appeared to belong to an individual's agonistic category, this occurred by direct association with either L or B. Of the 136 cases where an element did not appear to belong to an individual's agonistic category, whereas it belonged to this category of at least one of the other individuals, this was mostly (i.e. 88%) due to its low frequency of performance by this individual. So, there is no reason to ascribe this to individual differences in programmatic rules. The size of the agonistic category ranged from 7 elements in individual Zaf to 19 in both Cam and Daf (see blacks dots in Figure 1). The frequency of performance of agonistic elements ranged from 171 times by Zaf to 785 times by Rum.

Temporal associations of elements with L, but directed at another partner than the one at which L was aimed, occurred with respect to 4 elements; these have been indicated by an asterisk in Figure 1. Two of these particular elements (*lip-smacking* and *presenting*) even turned out to be associated also with B. These 'double associations' were independent, as coincidences between B and L never occurred.

Analysis (II). The purpose of this analysis was to find further differentiation within the category of agonistic behaviour. For each individual, we counted the numbers of coincidences between each pair of elements belonging to its agonistic category (as defined above). These values were compiled into a matrix of coincidence frequencies (see Table, for an example). The discrepancy between the observed numbers (o) in this matrix and the numbers expected (e) on the basis of random coincidence was expressed by the quotient[9]: $q = (o-e)/\sqrt{e}$ which represents the root of one term of the X^2-formula. The expected number of coincidences between elements X and Y equalled the product of their marginal totals in the coincidence matrix, divided by the total number of coincidences in the matrix. (Cases with $e \leq 0.1$ were left

[9] J. VAN HOOFF, in *Social Communication and Movement* (Eds. M. VON CRANACH and I. VINE; Academic Press, London, New York 1974), p. 75.

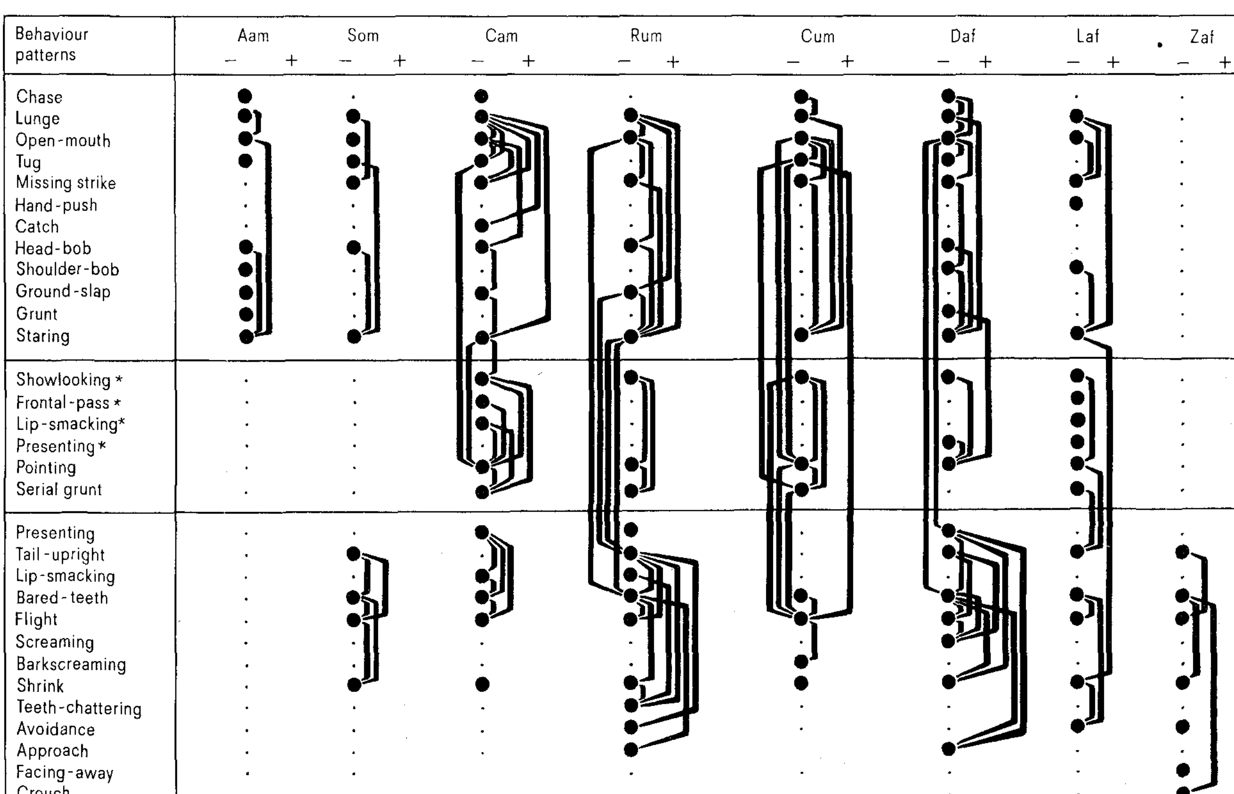

Fig. 1. Relatively often (+) and rarely (–) observed combinations between agonistic behaviour elements shown by 8 individual monkeys (further explanation see text).

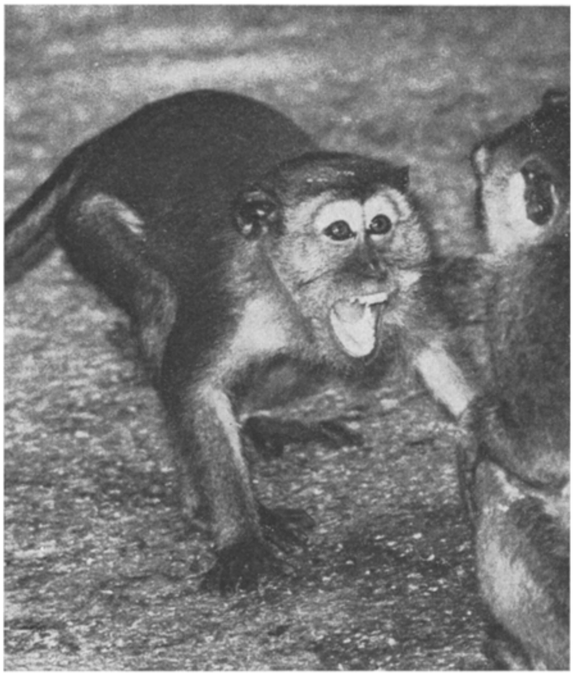

Fig. 2. Open-mouth face by adolescent female.

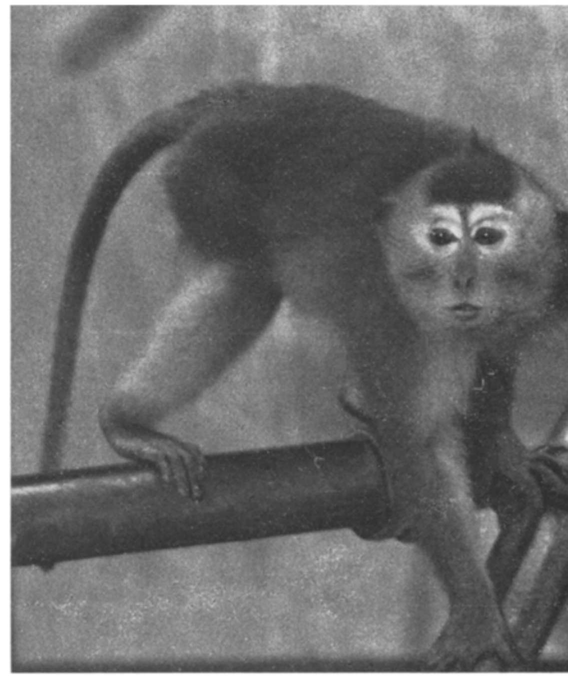

Fig. 3. Pointing face by juvenile male.

out of consideration.) Every pair of elements for which this q-value reached higher than $+2$ or lower than -2 (i.e. corresponding with a X^2-value of at least 4) received a connecting line on the positive (i.e. right) respectively negative (i.e. left) side in Figure 1. After this, the agonistic elements were arranged into subgroups in such a way as to maximize the number of positive linkages between elements belonging to the same subcategory and to minimize the number of negative linkages between these.

Results (II). This procedure resulted in 3 subcategories of agonistic behaviour: only 6 of the 101 positive linkages and all 14 negative linkages ran between elements belonging to different subcategories. The 3 clusters of elements, which have been rendered in Figure 1, clearly correspond with the subcategories previously indicated by us[4,5]: 1. straight-aggression (Figure 1, upper), 2. appeal-aggression and sub-directed behaviour (middle) and 3. fear-behaviour (lower).

It may finally be noted that the two types of aggressive behaviour which have been distinguished are easily recognizable as the facial expressions characterizing them differ strikingly: i.e. *open-mouth* (straight-aggression) and *pointing* (appeal-aggression); see Figures 2 and 3[10].

[10] Photographs made by H. VAN BEEK.

The Effect of Sulfhydryl Reagents upon the Activity of 40S Ribosomal Subunits

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Summary. p-Chloromercuribenzoate inhibited the poly (U)-dependent binding of Phe-tRNA to the 40S ribosomal subunit but displayed no inhibitory effect on the binding of poly (U) to the ribosome. Other sulfhydryl reagents tested, like *N*-ethylmaleimide and iodoacetamide, did not affect the binding of Phe-tRNA to the small ribosomal subunit.

Mammalian ribosomes have been previously shown to possess sulfhydryl (SH-) groups essential for their activities in the coded binding of AA-tRNA[3-7] and in the EF II-dependent binding of GTP[7,8]. Experiments done with *N*-ethylmaleimide (NEM) and iodoacetamide (IAA) suggested that SH-groupes required for these activities must reside on the large ribosomal subunit[6-10]. 40S ribosomal subunits appeared to be resistent to inhibition by SH-reagents on account of the results obtained with NEM[6,7]. Considering the different modes of action of different SH-reagents, we decided to study the effect of some other SH-reagents as well, before excluding the presence of SH-groupes essential for the activity of the 40S particle.

Materials and methods. Ribosomes and ribosomal subunits were prepared from human tonsillar lymphatic tissue as described[5,6]. tRNA (*E. coli*) was obtained from Schwarz Bioresearch and charged with [^{3}H] Phe as described[11]. [^{3}H] poly(U), specific activity 10,4 Ci/mole, was obtained from Schwarz/Mann, NEM from Serva (Heidelberg), IAA and *p*-chloromercuribenzoate (*p*CMB) from Merck (Darmstadt). poly(U)- dependent (non-enzymatic)