The Effect of Breakfast on Social Behavior and Brain Amine Metabolism in Vervet Monkeys[1]

A. STEVENS BOAL,*† SIMON N. YOUNG,‡[2] MICHAEL SUTHERLAND,§
FRANK R. ERVIN†‡ AND RAYMOND COPPINGER*

*Hampshire College, Amherst, MA
†Behavioral Science Foundation, P.O. Box 428, St. Kitts, Eastern Caribbean
‡Department of Psychiatry, McGill University, 1033 Pine Avenue West, Montreal, Canada H3A 1A1
and §Department of Mathematics and Statistics, University of Massachusetts, Amherst, MA

BOAL, A. S., S. N. YOUNG, M. SUTHERLAND, F. R. ERVIN AND R. COPPINGER. *The effect of breakfast on social behavior and brain amine metabolism in vervet monkeys.* PHARMACOL BIOCHEM BEHAV 29(1) 115–123, 1988.—Two groups of vervet monkeys were fed, on alternate days, either before or after a morning observation period. This enabled us to determine changes in behavior when the animals were fed a nutritionally balanced breakfast of monkey chow. Feeding did not alter the proportion of behaviors that were social or non-social, but had a marked effect on individual behaviors. Feeding increased active behaviors among the adult animals except for the vervets who were lowest in the social hierarchy in each cage. For some of the individual behaviors that were altered by feeding, the changes were most marked early on in the observation period, when the animals were still feeding. Other behavioral changes were seen only later in the observation period, a time course consistent with a food-mediated change in brain biochemistry. A parallel biochemical experiment showed that feeding decreased the levels of tryptophan and 5-hydroxyindoleacetic acid in the CSF. Our data indicate that feeding can influence both brain biochemistry and behavior. The behavioral changes may be influenced by social and psychological factors as well as changes in brain biochemistry.

Breakfast   Food   Vervet   Monkeys   Behavior   Cerebrospinal fluid   Biogenic amines
5-Hydroxyindoleacetic acid   Tryptophan

ALTHOUGH changes in mood and behavior are a common experience after food ingestion, study of the behavioral effects of normal food intake in humans is a relatively neglected area of research. Because food-related changes in behavior in humans would presumably be related to psychological, social and cultural factors as well as to biochemical changes, the work that has been done has focussed on a limited range of behaviors in controlled settings. The beneficial effects of breakfast on school performance in children has been reported, although not universally [6, 7, 13]. In adults, Spring *et al.* [19] demonstrated differences in mood and performance after consumption of carbohydrate or protein meals. Biochemical studies in experimental animals suggest that a variety of neurotransmitter precursors (tryptophan, phenylalanine, tyrosine, histidine and choline) may be affected acutely by food ingestion, and that this in turn could influence the synthesis and possibly the function of several neurotransmitters [5-hydroxytryptamine (5HT),

dopamine, noradrenaline, histamine, acetylcholine] [23]. In the only report on the effect of food ingestion on CNS metabolism in humans, a balanced meal caused a significant lowering of the levels of the 5HT precursor, tryptophan, and the 5HT metabolite, 5-hydroxyindoleacetic acid (5HIAA) in cerebrospinal fluid (CSF) [12].

To study dietary influence on the brain adequately, measurements of both individual and social behaviors, as well as some index of alterations in brain metabolism would be desirable. These requirements preclude for the most part integrated biochemical-behavioral studies on humans, but this type of investigation could be carried out on non-human primates. Behavioral studies on the effects of food in primates have, in general, been concerned with malnutrition. For example, drastic food shortage decreases both affiliative and agonistic behaviors in rhesus monkeys *(Macaca mulatta)* in the wild [10] and in captivity [18]. As part of a program to study the biochemical and behavioral effects of normal food

TABLE 1

BEHAVIORS SCORED

Social		Non-Social	
Behavior	Sub-Category	Behavior	Sub-Category
Active Behaviors			
Threat			
Displace			
Sex		Masturbate	
Play	1. Rough and tumble	Solitary	
	2. Tease or chase	play	
Join		Locomotion	
Groom		Self-clean	
		Drink	
		Arousal	1. Threat out of
		state	enclosure
			2. Vigilant
Passive Behaviors			
Huddle			3. Look out
Sit near			4. Restful wake

The behaviors are given in order of rank. When more than one social or non-social behavior occurred together only the higher ranking behavior was used in the data analysis. Thus, if an animal was grooming and huddling, only groom would be counted. One non-social behavior not included above was eating. Eating was recorded under two categories (1. chow and 2. insects or grass) in addition to other social or non-social behaviors occurring at the time.

intake, we have now looked at the effects of early morning feeding on brain biochemistry and social and non-social behaviors in vervet monkeys *(Cercopithecus aethiops)*.

METHOD

Experimental Plan

The experiment was performed on 20 vervets, some of which had been born in captivity, and some of which were feral reared, but had been in captivity for at least eight months. The animals were held in two adjacent outdoor enclosures measuring 12×6×6 ft, with a 6-ft unobstructed space between them which allowed the animals in the two enclosures to see each other. Enclosure 1 held nine animals and Enclosure 2 eleven animals. The numbers were unequal because two animals in Enclosure 1 died during the six months between the time the social groupings were formed and the behavioral observations were started. Enclosure 1 contained one adult male (6.6 kg), four adult females (3.9–4.3 kg), three juvenile males (2.1–4.1 kg) and one juvenile female (2.9 kg). Enclosure 2 contained one adult male (6.1 kg), five adult females (3.5–4.7 kg), three juvenile males (2.6–2.7 kg) and two juvenile females (1.4 and 2.5 kg). The juveniles were defined as animals whose canines had not yet begun to elongate. Observations were made from a point eight feet away from a point midway between the two cages. To control for the influence of the observer and the adjacent group on behavior, the perches, feeders and water bottles in the two cages were set up as mirror images of one another. At the start of the study all animals were familiar with the observer from 206 hours of observation in a previous study, and the

vervets paid little attention to him. It should be noted that although the groups were similar in structure and history, they were not identical in social structure or leadership styles. The general level of social integration differed between groups as it does in groups observed in the wild.

Observations were made on 36 days over a 53-day period. Each day, 15 minutes before the start of the main behavioral observations, just after sunrise, Purina High Protein Monkey Chow (Ralston Purina Co., St. Louis, MO) was placed in one of the feed boxes of one cage. Two feed boxes could be attached to the cage, one at each end. The feed boxes were attached to the outside of the cage. Monkeys could take chow from the boxes through a 4×4 inch hole in the cage. Only one animal could take chow at any one time. Animals would take several pellets of chow at one time and then move away from the food box to eat them, thus allowing other animals to feed. The observer kept a record of the order in which the animals took their first pellet of chow in order to delineate the social hierarchies within the groups. By the end of 10 minutes all the animals had started feeding. The second feed box in the same enclosure was filled 10 minutes after the first and the behavioral ratings started. On any morning, only one group of vervets had access to food before and during the observation period. The other group was fed after the morning observation was completed. The amount of food received by each group was the same and was enough to last throughout most of the day. Feed boxes were empty at dusk. The group fed before observations alternated on roughly a daily basis. Thus, it was possible to compare behavior in the same animal with and without breakfast.

TABLE 2
DESCRIPTIONS OF BEHAVIORS

Behavior	Description
Threat	Antagonistic interaction between two animals, involving any of the following behaviors: slapping or biting another animal, lunging, charging, barking or gaping at another animal. Also barking or gaping at the observer.
Displace	Movement of one animal away from another approaching animal.
Sex	Mounting, pelvic thrusting or genitally inspecting another animal.
Play	Rough and tumble or tease and chase.
Join	Moving within 0.5 m of another animal and remaining stationary that close for at least 5 sec.
Groom	Picking through the fur of another animal with the forepaws.
Huddle	Sustained body contact with another animal for 10 sec or more.
Sit near	Remaining stationary closer than 1 m from the nearest other animal for 10 sec continuously.
Masturbate	Physical manipulation of own genitalia.
Solitary play	Playing with an inanimate object or performing solitary acrobatics.
Locomotion	Movement for more than 1.0 m.
Self-clean	Picking through own fur with forepaws.
Drink	Ingesting water.
Arousal State	
1. Threat out of enclosure	Barking or gaping at anything outside the enclosure except for the observer.
2. Vigilant	Looking outside the cage while in a tense, erect posture.
3. Look out	Looking outside the cage with relaxed muscle tone.
4. Restful wake	Relaxed muscle tone and not engaged in any activity.

Behavioral Observations

Instantaneous samples of behavior were collected as described by Altmann [1]. Every 20 seconds the observer located the next subject and recorded the subject's activities at that precise moment. Animals were always sampled in the same sequence. At the end of one cycle the observer rested for 80 seconds, so each animal's behavior was sampled every eight minutes. The observation period lasted 128 minutes, approximately 2 hours, so each animal was observed 16 times every day. When external factors, such as rain showers, or work in the adjacent sugar cane fields, influenced the animals' behavior, animals which would normally have been sampled were skipped, so that every observation period finished 128 minutes after it started. By the conclusion of the study close to 450 observations had been recorded for each monkey. Roughly half of these observations were with food and roughly half without.

The social and non-social behaviors recorded are listed in Table 1 and brief descriptions of the behaviors are given in Table 2. These behaviors represent a condensation of those described by Struhsaker [20]. Threat to observer is included among the social behaviors because the human observer is inevitably a participant by virtue of his presence in the milieu. Although he is partially concealed, regular as to time and physical appearance, and has habituated the animals to his presence over a 2–4 week period, he continues to receive threats, invitations to play, and occasional sexual solicitations. We consider these to be social behaviors and scored them as such. When two or more social or non-social behaviors occurred simultaneously, all were recorded. Eating was recorded separately from other non-social behaviors.

Biochemical Measurements

Biochemical measurements were carried out on different animals from the behavioral observations. Cisternal CSF was taken from adult vervets under Ketamine anesthesia two hours after food presentation and, either one week earlier or later, at the same time of day, from the same animals in the fasted condition. Food was given at the same time of day as in the behavioral part of the study. The animals used for the biochemical measurements, like the animals used for the behavioral measurements, were in two adjacent cages. On the two days when CSF was taken, one cage was fed, while the other was not. Thus, the animals who were not fed before the biochemical measures had exactly the same exposure to food as the animals who were not fed before the behavioral measures. In both cases they were able to observe other animals eating chow but were not able to eat themselves. Tryptophan, tyrosine, 5HIAA, homovanillic acid (HVA) and 3-methoxy-4-hydroxyphenylethylene glycol (MHPG) were measured in the CSF samples by high performance liquid chromatography with fluorometric and electrochemical detection [2,3].

Analysis of Data

When two or more social or non-social behaviors were scored together only the highest ranking behavior in each category was used in the analysis of data. Behaviors were ranked because some behaviors are implicit in others. The higher ranking behavior of two behaviors occurring together is the more specialized of the two. Thus, aggression will often involve displacement, but only the aggression would be used in the analysis. Similarly grooming will always involve

TABLE 3
SOCIAL BEHAVIOR AS PERCENTAGE OF TOTAL BEHAVIORS

	Not Fed		Fed		
	Total Observations	Social Behavior %	Total Observations	Social Behavior %	Significance of Difference for Fed and Not Fed
Both cages					
All	6253	36.03 ± 0.61	6195	35.51 ± 0.61	NS
Adults	3410	34.43 ± 0.81	3382	34.39 ± 0.82	NS
Juveniles	2843	37.95 ± 0.91	2813	36.86 ± 0.91	NS
Enclosure 1					
All	2928	35.08 ± 0.88	2533	31.70 ± 0.92	NS
Adults	1621	33.62 ± 1.17	1380	29.93 ± 1.23	NS
Juveniles	1307	36.88 ± 1.33	1153	33.82 ± 1.39	NS
Enclosure 2					
All	3325	36.87 ± 0.84	3662	38.15 ± 0.80	NS
Adults	1789	35.16 ± 1.13	2002	37.46 ± 1.08	NS
Juveniles	1536	38.87 ± 1.24	1660	38.98 ± 1.20	NS

Values are given for the total number of observations in each category and the percentage of the observations that were social behaviors ±SD. The totals include all the behavioral incidents observed except for eating. NS=not significant ($p > 0.05$).

huddling, but only the grooming would be counted. The two lowest ranking social and non-social behaviors, namely, huddle, sit near, look out and restful wake, were defined as passive behaviors. All other behaviors (except for eat) were included in the category active behavior in the analysis. Eating behavior was analyzed separately since eating occurred simultaneously with other activities, and only one group had access to food each observation period.

The data were essentially simple frequency counts of behavior. We considered two groups of behaviors, social and non-social. We also considered various groups of animals defined by age or enclosure. Within the context of social and non-social behaviors we calculated simple proportions based on total social or non-social behaviors, for each behavior type observed. It is these proportions (p) which are given in Tables 3–8 along with their estimated SD. These SDs were calculated in the classical manner as

$$\left[\frac{p(1-p)}{n} \right]^{1/2}$$

where n is the total social or non-social behaviors observed, depending on which type is under discussion. Comparing the various behaviors either at individual animal or at some aggregate level depending on age and cage consists essentially of looking for differences in the observed proportions between the fed and not fed states. This was done in the classical manner. For example, if there was no overlap between two SDs from the mean of two quantities then they were significantly different at $p < 0.05$.

RESULTS

Table 3 gives the total numbers of behaviors observed (excluding eating) and the percentage of them that were social for animals in the fed and not fed states. These results are given not only for each enclosure's adults and juveniles but also for the aggregate totals across both enclosures.

There was no significant difference between the proportion of social behaviors in the fed and unfed states for any of the subgroupings.

Table 4 gives the relative proportions of individual behaviors for all animals, and for adults and juveniles, in the fed and not fed states. Differences between adults and juveniles in the not fed state are what might be expected. Thus, adults show a higher incidence of agonism (threat plus displace) and threats out of the enclosure, while the juveniles show more play. Among the other behaviors, taking all the animals together, feeding causes significant increases in groom, drink and look out, significant decreases in huddle, self-clean and restful wake, and no significant alteration in vigilant. For these behaviors similar changes were seen in adults and juveniles, although for the smaller groups the changes in behavior on feeding were not always statistically significant. The only behavior, seen at an appreciable incidence in both adults and juveniles, that showed a different pattern of change on feeding was sit near. This showed a significant increase in the juveniles and a non-significant decline in the adults.

Table 5 shows the percent breakdown of social and non-social behaviors in the fed and not fed adult animals, with the results given separately for the two enclosures. Table 6 is a similar compilation of data for the juvenile animals. Behaviors with a low incidence are omitted from these tables. A comparison of the two enclosures in the not fed state reveals definite difference in behaviors between the two enclosures. For example, the adults in Enclosure 2 show more than twice as much grooming as those in Enclosure 1, although for the juveniles in Enclosure 2 only half as much grooming is seen as in Enclosure 1. On the other hand, the juveniles in Enclosure 2 played more than twice as much as those in Enclosure 1. In spite of these differences in baseline (i.e., not fed) behaviors between the two enclosures, the changes seen on feeding are for the most part similar. For example, although there is a large difference in play levels between the

TABLE 4
THE OCCURRENCE OF BEHAVIORS IN THE FED AND UNFED STATES

	All animals			Adults only			Juveniles only		
	Not Fed	Fed	p	Not Fed	Fed	p	Not Fed	Fed	p
Social Behaviors									
Threat	0.44 ± 0.14	0.95 ± 0.21	NS	0.51 ± 0.21	1.38 ± 0.34	NS			
Play (rough and tumble)	3.86 ± 0.41	1.91 ± 0.29	<0.05				7.97 ± 0.82	3.57 ± 0.58	<0.01
Play (tease or chase)	1.38 ± 0.25	0.59 ± 0.16	NS				2.87 ± 0.51	1.25 ± 0.35	NS
Play (total)	5.24 ± 0.47	2.50 ± 0.33	<0.01				10.84 ± 0.95	4.82 ± 0.67	<0.01
Displace	0.62 ± 0.17	1.41 ± 0.25	NS	0.51 ± 0.21	1.55 ± 0.36	NS			
Agonism (threat plus displace)	1.07 ± 0.22	2.36 ± 0.32	<0.05	1.02 ± 0.29	2.92 ± 0.49	<0.05			
Join	3.28 ± 0.38	4.64 ± 0.45	NS	2.90 ± 0.49	4.13 ± 0.58	NS	3.71 ± 0.57	5.21 ± 0.69	NS
Groom	9.41 ± 0.62	15.59 ± 0.77	<0.01	11.07 ± 0.92	20.72 ± 1.19	<0.01	7.60 ± 0.81	9.84 ± 0.92	NS
Huddle	33.91 ± 1.00	26.73 ± 0.94	<0.01	34.16 ± 1.38	25.80 ± 1.28	<0.01	33.64 ± 1.44	27.77 ± 1.39	<0.05
Sit near	46.74 ± 1.05	48.00 ± 1.07	NS	50.26 ± 1.46	45.92 ± 1.46	NS	42.91 ± 1.51	50.34 ± 1.55	<0.05
Non-Social Behaviors									
Drink	3.35 ± 0.28	6.48 ± 0.39	<0.01	4.43 ± 0.44	7.62 ± 0.56	<0.01	1.98 ± 0.33	5.07 ± 0.52	<0.01
Self-clean	4.22 ± 0.32	2.95 ± 0.27	<0.05	4.03 ± 0.42	3.06 ± 0.37	NS	4.48 ± 0.49	2.82 ± 0.39	NS
Threat out of of enclosure	0.47 ± 0.11	0.95 ± 0.15	NS	0.85 ± 0.19	1.67 ± 0.27	NS			
Vigilant	4.05 ± 0.31	3.45 ± 0.29	NS	2.28 ± 0.32	2.61 ± 0.34	NS	6.29 ± 0.58	4.50 ± 0.49	NS
Look out	33.10 ± 0.74	37.42 ± 0.77	<0.05	26.97 ± 0.94	31.10 ± 0.98	<0.05	40.87 ± 1.17	45.33 ± 1.18	NS
Restful wake	54.25 ± 0.79	48.24 ± 0.79	<0.01	61.27 ± 1.03	53.67 ± 1.06	<0.01	45.35 ± 1.18	41.44 ± 1.17	NS

The occurrence of different behaviors is expressed as percentages of total social or non-social behaviors ±SD. The total numbers of observations made are given in Table 3. Data are omitted when less than 20 observations were made of a particular behavior in both the fed and unfed states.

TABLE 5
OCCURRENCE OF BEHAVIORS FOR FED AND NOT FED ADULT ANIMALS IN THE TWO ENCLOSURES

	Enclosure 1			Enclosure 2		
	Not Fed	Fed	p	Not Fed	Fed	p
Social Behaviors						
Join	3.30 ± 0.77	2.91 ± 0.83	NS	2.54 ± 0.63	4.80 ± 0.78	NS
Groom	6.42 ± 1.05	12.59 ± 1.63	<0.05	15.10 ± 1.43	25.20 ± 1.59	<0.01
Huddle	34.86 ± 2.04	26.63 ± 2.18	<0.05	33.55 ± 1.88	25.33 ± 1.59	<0.05
Sit near	53.76 ± 2.14	54.48 ± 2.45	NS	47.22 ± 1.99	41.20 ± 1.80	NS
Non-Social Behaviors						
Drink	2.42 ± 0.47	11.38 ± 1.02	<0.01	6.29 ± 0.71	4.71 ± 0.60	NS
Self-clean	3.53 ± 0.56	3.00 ± 0.55	NS	4.48 ± 0.61	3.12 ± 0.49	NS
Vigilant	2.60 ± 0.49	2.79 ± 0.53	NS	1.98 ± 0.41	2.48 ± 0.44	NS
Look-out	28.44 ± 1.38	32.99 ± 1.51	NS	25.60 ± 1.28	29.63 ± 1.29	NS
Restful wake	62.08 ± 1.48	47.78 ± 1.61	<0.01	60.52 ± 1.44	58.23 ± 1.39	NS

The occurrence of different behaviors is expressed as percentages of total social or non-social behaviors ±SD. The total numbers of observations made are given in Table 3.

enclosures in the not fed state, feeding causes play to decline by somewhat more than one half in both enclosures. In general, if there is a significant change on feeding for a particular behavior in one enclosure, the other enclosure exhibits a similar change in the same direction, although sometimes not statistically significant. However, there are exceptions to this pattern. Adults in Enclosure 1 show a significant increase in drinking when fed, but in Enclosure 2 there is a

TABLE 6

OCCURRENCE OF BEHAVIORS FOR FED AND NOT FED JUVENILE ANIMALS IN THE TWO ENCLOSURES

	Enclosure 1			Enclosure 2		
	Not Fed	Fed	*p*	Not Fed	Fed	*p*
Social Behaviors						
Play (rough and tumble)	3.94 ± 0.89	1.79 ± 0.67	NS	11.22 ± 1.29	4.64 ± 0.83	<0.01
Play (tease or chase)	2.70 ± 0.74	0.51 ± 0.36	NS	3.02 ± 0.70	1.70 ± 0.51	NS
Play (total)	6.64 ± 1.13	2.31 ± 0.76	<0.05	14.24 ± 1.43	6.34 ± 0.96	<0.01
Join	2.49 ± 0.71	4.62 ± 1.07	NS	4.69 ± 0.87	5.56 ± 0.90	NS
Groom	10.79 ± 1.41	16.92 ± 1.90	NS	5.03 ± 0.89	5.56 ± 0.90	NS
Huddle	31.95 ± 2.12	20.51 ± 2.04	<0.05	35.01 ± 1.95	32.15 ± 1.84	NS
Sit near	47.10 ± 2.27	53.35 ± 2.53	NS	39.53 ± 2.00	48.53 ± 1.96	<0.05
Non-Social Behaviors						
Drink	1.45 ± 0.42	6.29 ± 0.88	<0.01	2.45 ± 0.51	4.15 ± 0.63	NS
Self-clean	2.67 ± 0.56	3.41 ± 0.66	NS	6.07 ± 0.78	2.37 ± 0.48	<0.05
Vigilant	3.76 ± 0.66	4.19 ± 0.73	NS	8.52 ± 0.91	4.74 ± 0.67	<0.05
Look out	38.79 ± 1.70	42.73 ± 1.79	NS	42.71 ± 1.61	47.29 ± 1.57	NS
Restful wake	52.97 ± 1.74	42.73 ± 1.79	<0.05	38.66 ± 1.59	40.47 ± 1.54	NS

The occurrence of different behaviors is expressed as percentages of total social or non-social behaviors ±SD. The total number of observations made are given in Table 3. Data are omitted when less than 20 observations were made for a particular behavior in both the fed and unfed states.

non-significant decrease. Also, after feeding the juveniles in Enclosure 2 show significant decreases in self-cleaning and vigilance, although non-significant increases in both these behaviors were seen in Enclosure 1.

When considering individual animals, the number of incidents of individual behaviors that were observed is small. Therefore, total active behavior, which is based on a larger sample, and is therefore more accurate, was calculated as a percentage of total behaviors observed for each animal. The change in percent active behaviors after feeding is given in Fig. 1. For the adults, all the animals except one from each cage showed an increase in activity after feeding. In both cages, the animal that showed the decrease in activity was the lowest in the social hierarchy (the last animal to start feeding). In Enclosure 1 all the juveniles showed an increase in activity, while in Enclosure 2 all except one showed a decrease in activity after food. This interaction of age status and enclosure is more fully explored in the discussion section.

Behaviors were also examined for time-dependent changes. Table 7 shows the percent change in eating over time for adult and juvenile groups. We analysed the data for the 128 minute observation period in four 32 minute (or approximately half hour) intervals. As might be expected, in the first half hour of observation, which started only 15 minutes after the animals were given food, eating was relatively frequent. However, eating declined with time, and was only a minor activity in the last half hour period.

Figure 2 shows changes in percent active behaviors over time for the two groups in the fed and not fed state. When not fed, both adults and juveniles showed a slow but steady decline in activity over time. When fed, both groups showed a time-dependent increase in activity, which peaked in the third half hour period. Individual behaviors showed distinct patterns of change with time (Table 8). For some behaviors,

TABLE 7

CHANGE IN EATING WITH TIME

	Half-Hour Intervals of Observation			
	1	2	3	4
Eat Chow				
Adults	43.3	22.6	8.8	7.2
Juveniles	43.3	26.6	14.5	7.0
Eat Other				
Adults	1.1	0.6	0.7	1.5
Juveniles	10.7	10.4	5.8	5.6

Results are expressed as number of observations of eating as a percentage of the total other behaviors (excluding eating) during the appropriate time interval.

such as the decrease in play on feeding in the juvenile, the increase in agonism in the adults, and the increase in look out for both groups, the largest change between fed and not fed animals is seen in the first half hour period. For these behaviors the effect of feeding has, to a large extent, disappeared by the end of the observation period. For other behaviors, such as grooming, feeding seems to cause little change early on, but substantial changes are seen in the last hour of observation. With other behaviors, such as huddling, the food-mediated decrement is seen in each time period, but the trend for increase is parallel in the two groups.

Figure 3 shows the CSF data. Feeding caused significant declines in CSF tryptophan and 5HIAA while no consistent change was seen in tyrosine, HVA and MHPG.

DISCUSSION

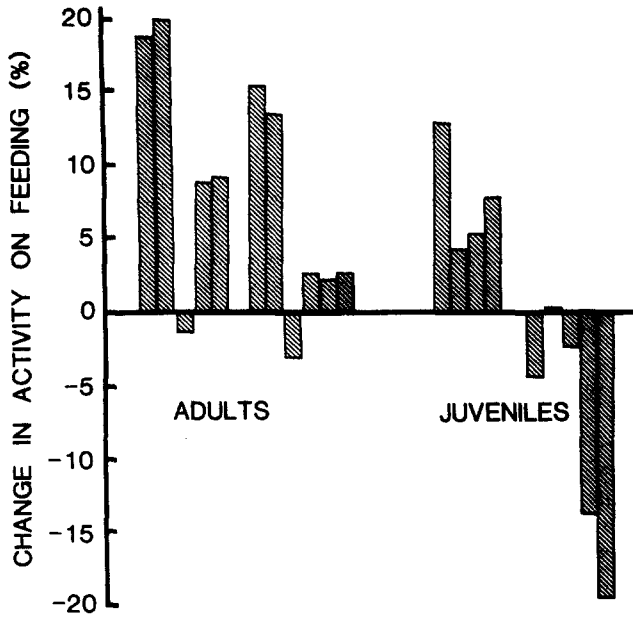The most important finding of this study is that acute

FIG. 1. Change in activity level on feeding for individual animals. Values show percentage alterations in total active behaviors on feeding with non-fed values as the baseline. Each bar represents one animal. For both adults and juveniles the contiguous sets of bars on the left are the animals in Enclosure 1 and those on the right, the animals in Enclosure 2.
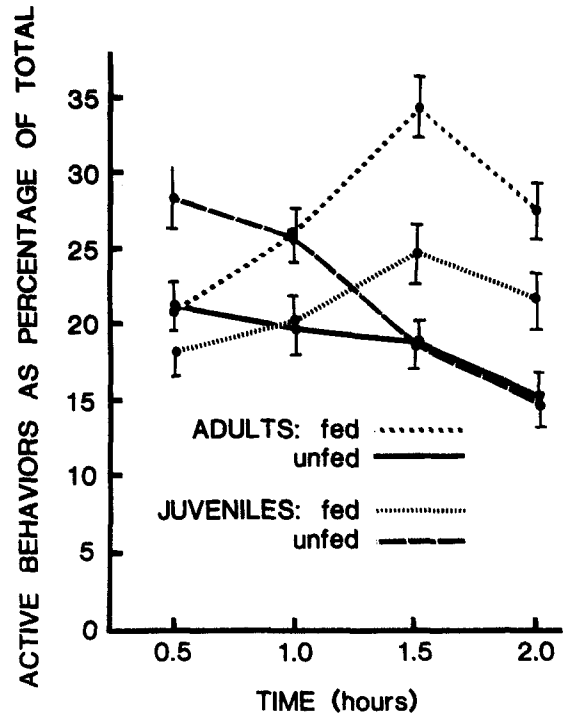

FIG. 2. Alterations in total active behaviors over time. Active behaviors are given as a percentage of total behaviors for the groups of animals shown. Points are mean±SD. Each point represents values for one half hour period of the two hour observation session.

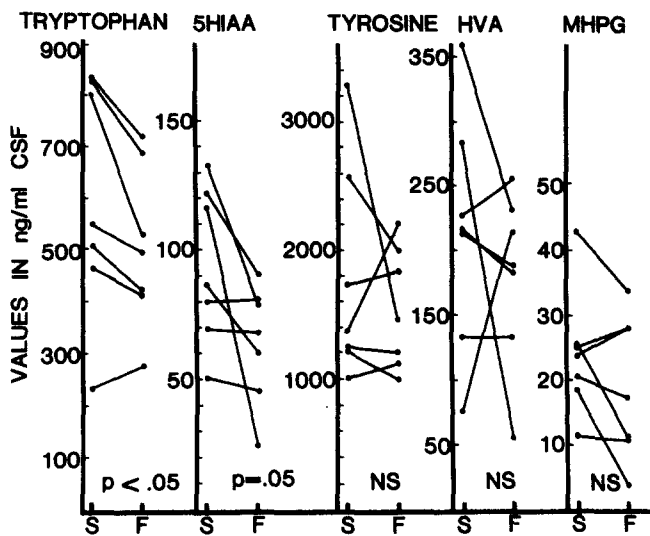## THE EFFECT OF STARVATION (S) OR FEEDING (F) ON VERVET CSF

FIG. 3. CSF amine related compounds in vervets that were either starved overnight or fed, using the same schedules as for the behavioral testing. When CSF was taken from the fed animals, it was taken 2 hr after food was given. When it was taken from the fasted animals, it was taken at the same time of day. Joined points are from the same animal.

intake of food has a marked effect on behavior in a primate. The behavioral frequency data were analyzed at various levels of aggregation and for various grouping of the animals, where the divisions were made on the basis of enclosure and

age. In spite of several differences between the baseline (not fed) behaviors for the different subgroups the changes on feeding were reasonably consistent across groups. In no situation did feeding cause significant changes in different directions in different groupings, with the exception of the differences in active behaviors for the individual animals which are discussed below. Thus, the changes in behavior that we observed on feeding seem to reflect the overall type of change that occurs in vervets held in small social groups.

Although feeding produced definite changes in various specific behaviors there was no change in the proportion of behaviors that was social or non-social (Table 3). Thus, food influenced the specific type of interaction between animals but not the extent to which they interacted. This somewhat surprising finding may reflect some basic aspect of vervet social functioning, either in a general sense, or in the confined space the animals occupied.

In general the changes in specific behaviors after feeding (Table 4) show an increase in active behaviors. When the data were analyzed for individual animals variability in the response was seen (Fig. 1). Among the adult animals the majority showed more active behaviors when fed. However, in each cage one adult animal became less active. In both cages this animal was the adult animal lowest in the social hierarchy. We suggest that in this situation social factors are modifying the response to food.

Among the juveniles, all four in one cage increased active behaviors after feeding, while four out of five in the other cage showed a decline in activity. This difference seems to be due mainly to differences in baseline levels of behaviors in the two cages. Juveniles in Enclosure 2 showed more than twice as much play as those in Enclosure 1 when not fed. In

TABLE 8
CHANGE IN BEHAVIORS WITH TIME

Behavior	Animals	Fed/Not Fed	Half-Hour Intervals of Observation			
			1	2	3	4
Social Behaviors						
Play	Juveniles	Not Fed	15.9	16.7	8.6	2.8
		Fed	0.8	6.4	7.1	4.7
Agonism	Adults	Not Fed	1.3	1.0	0.7	1.0
		Fed	6.9	3.3	1.9	0.3
Groom	Adults	Not Fed	7.0	12.0	13.1	12.2
		Fed	4.2	11.6	31.6	31.6
	Juveniles	Not Fed	4.0	12.7	7.1	7.1
		Fed	3.7	8.4	15.2	11.3
Huddle	Adults	Not Fed	28.8	32.3	35.4	40.4
		Fed	19.1	26.9	25.9	30.3
	Juveniles	Not Fed	24.2	23.8	39.4	46.3
		Fed	21.2	15.7	29.4	43.1
Non-Social Behaviors						
Look out	Adults	Not Fed	37.3	26.5	21.3	22.5
		Fed	46.1	33.0	22.0	23.0
	Juveniles	Not Fed	53.0	46.6	33.9	29.5
		Fed	61.2	47.8	38.2	33.2
Restful wake	Adults	Not Fed	47.3	61.0	67.9	69.4
		Fed	36.2	48.7	62.3	68.1
	Juveniles	Not Fed	26.3	38.9	55.5	61.4
		Fed	23.6	39.2	48.1	45.9

Results are expressed as percentages of total social or non-social behaviors for the appropriate time period, state of feeding and age group.

both cages play declined by more than half on feeding (Table 6). In absolute terms this change was much larger for Enclosure 2 than for Enclosure 1. This difference accounts, in part, for the differential response of the two cages in total active behaviors. However, significant declines were also seen in self clean and vigilant in Enclosure 2 but not Enclosure 1. Although these are behaviors with a lower frequency than play, they obviously also contributed to the decline in total active behaviors among juveniles in Enclosure 2. It is interesting that both of these two behaviors showed much higher frequencies in the not fed state in Enclosure 2 than in Enclosure 1, but the reason for their differential response to feeding in the two cages is not known.

The time courses for active behaviors over the two hour observation periods show the most interesting differences between fed and unfed animals (Fig. 1). In the unfed state, activity shows a steady decline over time for both adults and juveniles. This is presumably due to the increased ambient temperature, which soon after the end of the observation period reduces activity to very low levels until the late afternoon and evening. In the fed animals, this decline in activity is seen only in the last half hour of observation. Up to that time there is a steady increase in active behaviors. The maximal increase in activity occurs at a time when feeding has

declined to low levels (Table 7). The time course of changes in activity is consistent with the time course of changes in aromatic amino acid levels [4]. Thus, the alteration in active behaviors is more likely to be mediated by the biochemical changes that occur after food ingestion, rather than by a direct effect of the presence of food on behavior, i.e., it is mediated by biochemical rather than by psychological factors. In this context, the time courses of individual behaviors show instructive differences (Table 8). For example, the food-mediated increase in grooming among adults is not seen in the first two half hour observation periods, but is substantial in the last two half hour periods. This time course, like the increase in total active behaviors, is consistent with a biochemically-mediated mechanism. On the other hand, some behavior changes, such as the food-mediated decline in play in the juveniles and the increase in agonism in the adults, occur only in the initial two half hour intervals of observation and are not seen at later times. As these alterations in behavior occur mainly at a time when the animals are eating, they may be mediated directly by the presentation of food, i.e., a social-psychological mechanism. An increase in aggression as the animals compete for the food, even if it were not, as in the present study, given in limited amount, seems intuitively reasonable. Our results differ from those of Wasserman and Cruikshank [22] who studied aggression in a small captive group of hamadryas baboons. They found that aggression was higher in the three hour period preceding a 1:00 p.m. feeding than in the three hours from 1:00 p.m. However, in their study they did not control for diurnal variations in behavior by looking at aggression during the second time period when the animals were not fed. The reason why the presence of food should decrease play in juveniles is not clear. The post-prandial alterations in some behaviors, such as huddle, occur across the entire two hour observation periods, thus making any speculation on the mechanism mediating these changes difficult.

Our results show that food can have a marked effect on behavior in a primate. Our interpretation of the data indicates that several mechanisms may mediate these changes. Some behaviors may be altered by psychological factors (the presence of food) and some by food-mediated changes in brain biochemistry. Social factors are at work modulating how food can influence behavior. The interaction of these factors is complex and considerably more work will be needed to unravel the various mechanisms at work. Even as far as the biochemistry is concerned several different systems may be involved. Food intake is known to influence the neurotransmitter precursors tryptophan, tyrosine, phenylalanine and histidine in rodent brains [8,23]. The decline in CSF tryptophan and 5HIAA that we found after food ingestion (Fig. 4) is consistent with the data from rodents and from humans [12]. However, the profile of alteration of behavior after food is not the same as that seen when brain 5HT is lowered pharmacologically with parachlorophenylalanine [14] or with a tryptophan deficient amino acid mixture [5] in vervets. This does not mean that altered 5HT plays no role in food-mediated behavioral effects, only that its effects do not predominate. We found no alteration in catecholamine metabolites. However, the variability in these measurements may have obscured a small change in the catecholamine metabolites. We did not obtain indices of brain histidine or histamine or of changes in the various satiety hormones.

The effects of food on CSF tryptophan and 5HIAA are mediated by ingestion and absorption of food. However, animals secrete a variety of hormones in anticipation of food.

In our experiments animals in the two cages could see each other. Therefore, the animals who were not fed until after the observation period on any particular morning were exposed to food, in so far as they were able to observe the other animals being given food and eating. Thus, those differences in behavior between the two groups which were mediated by changes in biochemistry were probably the result of food ingestion, not exposure to food.

Although changes in brain neurotransmitter precursors may be among the biochemical factors involved in the behavioral effects of food, other mechanisms operate also. Elevated glucose has been reported to suppress the basal firing rate of dopamine-containing neurons in the substantia nigra [15], although this finding was denied in another study [21]. The firing rate of some neurons in the lateral hypothalamus is sensitive both to central and peripheral glucose levels. The former is mediated directly, while the latter is mediated via glucose-sensitive units in the hepatic branch of the vagal

nerve [16]. The vagus nerve also mediates the satiety effect of various peptides such as cholecystokinin, somatostatin and glucagon, which are released peripherally in response to feeding [11,17]. The vagus nerve is not limited in its effect to those areas of the brain dealing with satiety. For example, vagotomy in the rat can affect dopamine metabolism in the striatum [9]. Some satiety hormones, which are released from the gut, such as bombesin, do not act to end feeding via the vagus nerve and are presumably having a direct effect on the brain [11,17]. Any system that can influence satiety via brain mechanisms has the potential to influence other behaviors. Food can, in some ways, be regarded as a mixture of psychopharmacological agents with potential actions on many neuronal systems and potential interactions with psychological and social factors. Food undoubtedly has behavioral effects, but much careful work will be needed to elucidate the mechanisms involved.

REFERENCES

1. Altman, J. Observational study of behavior: sampling methods. *Behavior* 49: 227–267, 1974.
2. Anderson, G. M., J. G. Young and D. J. Cohen. Rapid liquid chromatographic determination of tryptophan, tyrosine, 5-hydroxyindoleacetic acid and homovanillic acid in cerebrospinal fluid. *J Chromatogr* 164: 501–505, 1979.
3. Anderson, G. M., J. G. Young, D. J. Cohen, B. A. Shaywitz and D. K. Batter. Amperometric determination of 3-methoxy-4-hydroxyphenylethyleneglycol in human cerebrospinal fluid. *J Chromatogr* 222: 112–115, 1981.
4. Ashley, D. V. and P. D. Leathwood. A high carbohydrate, protein-free meal, either at breakfast or in the evening does not alter plasma tryptophan to large neutral amino acid ratios in healthy men. In: *Progress in Tryptophan and Serotonin Research,* edited by H. G. Schlossberger, W. Kochen, B. Linzen and H. Steinhart. Berlin: Walter de Gruyter, 1984, pp. 579–582.
5. Chamberlain, B., F. R. Ervin, R. O. Pihl and S. N. Young. The effect of raising or lowering tryptophan levels on aggression in vervet monkey. *Pharmacol Biochem Behav* 28: 503–510, 1987.
6. Conners, C. K. and A. G. Blouin. Nutritional effects on behavior of children. *J Psychiatr Res* 17: 193–201, 1983.
7. Dickie, N. H. and A. E. Bender. Breakfast and performance in schoolchildren. *Br J Nutr* 48: 483, 1982.
8. Fernstrom, J. D. and D. V. Faller. Neutral amino acids in the brain: changes in response to food ingestion. *J Neurochem* 30: 1531–1538, 1978.
9. Li, E. T. S. and G. H. Anderson. A role for vagus nerve in regulation of protein and carbohydrate intake. *Am J Physiol* 247: E815–E821, 1984.
10. Loy, J. Behavioral responses of free ranging rhesus monkeys to food shortage. *Am J Phys Anthropol* 33: 263–272, 1970.
11. Morley, J. E., A. S. Levine, B. A. Gosnell and C. J. Billington. Neuropeptides and appetite: contribution of neuropharmacological modeling. *Fed Proc* 43: 2903–2907, 1984.
12. Perez-Cruet, J., T. N. Chase and D. L. Murphy. Dietary regulation of brain tryptophan metabolism by plasma ratio of free tryptophan and neutral amino acids in humans. *Nature* 248: 693–695, 1974.

13. Pollitt, E., N. L. Lewis, C. Garza and R. J. Shulman. Fasting and cognitive function. *J Psychiatr Res* 17: 169–174, 1983.
14. Raleigh, M. J., G. L. Brammer, A. Yuwiler, J. W. Flannery, M. T. McGuire and E. Geller. Serotonergic influences on the social behavior of vervet monkeys *(Cercopithecus aethiops sabaeus)*. *Exp Neurol* 68: 322–334, 1980.
15. Saller, C. F. and L. A. Chiodo. Glucose suppresses basal firing and haloperidol-induced increases in the firing rate of central dopaminergic neurons. *Science* 210: 1269–1271, 1980.
16. Shimizu, N., Y. Oomura, D. Novin, C. V. Grijalva and P. H. Cooper. Functional correlations between lateral hypothalamic glucose-sensitive neurons and hepatic portal glucose-sensitive units in rat. *Brain Res* 265: 49–54, 1983.
17. Smith, G. P. and J. Gibbs. Gut peptides and postprandial satiety. *Fed Proc* 43: 2889–2892, 1984.
18. Southwick, C. H. An experimental study of intra-group agonistic behavior in rhesus monkeys *(Macaca mulatta)*. *Behavior* 28: 182–209, 1967.
19. Spring, B., O. Maller, J. Wurtman, L. Digman and L. Cozolino. Effects of protein and carbohydrate meals on mood and performance: interactions with sex and age. *J Psychiatr Res* 17: 155–167, 1983.
20. Struhsaker, T. T. Social structure among vervet monkeys *(Cercopithecus aethiops)*. *Behavior* 29: 83–121, 1967.
21. Trulson, M. E., T. Crisp and V. M. Trulson. Dopamine-containing substantia nigra units are unresponsive to changes in plasma glucose levels induced by dietary factors, glucose infusions or insulin administration in freely moving cats. *Life Sci* 32: 2555–2564, 1983.
22. Wasserman, F. E. and W. W. Cruikshank. The relationship between time of feeding and aggression in a group of captive hamadryas baboons. *Primates* 24: 432–435, 1983.
23. Wurtman, R. J., F. Hefti and E. Melamed. Precursor control of neurotransmitter synthesis. *Pharmacol Rev* 32: 315–335, 1981.