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Neurophysiological and Behavioral Studies of Chimpanzees

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The chimpanzee program in the Space Biology Laboratory, initiated in 1961, was first established as a colony of animals suitably implanted and trained for space flight experiments. At that time this animal was considered to be the ideal experimental subject for sophisticated physiological studies in space because of its similarity to man in central nervous and motor functions. In the course of these early studies, it became apparent that this animal could also be a most important experimental subject for research in the basic neurophysiological correlates of learning, behavior and other physiological and psychological states. Although the basic neurophysiological patterns are studied in order to establish baseline data for use in evaluating flight data, the scope of a basic neurophysiological study using the chimpanzee is inappropriately restricted if the study is oriented entirely toward a flight program. Therefore, we are proposing to divide future studies in two directions: one a basic neurophysiologic study using the chimpanzee, and the other, a flight study. Support for these programs has been requested.

The following is a report on work done in the last 6 months on this study as a whole.

A. Acquisition and Training of Chimpanzees.

Four new chimpanzees in the 12-15 pound range were acquired, and are now being housed in the new NASA campus Space Sciences Center. The animals are receiving basic discipline training, and are being familiarized with objects that will be required aspects of their environment in future experiments, as for example, the space suit.

B. Data Analysis

1. Computer analysis of EEG data.

Although the electrical activity of the brain has been studied for many years and a large amount of knowledge accumulated about EEG wave processes, many fundamental questions still remain to be investigated. New methods are only now being developed which permit more than a purely, observational assessment of the wave processes, their system interrelations, and their possible causal relation to transaction and storage of information in the brain. The study of EEG wave processes for detailed patterns has long been a major effort in this laboratory, using high speed digital computing techniques. We have completed studies which elucidated patterns of relationships, both linear and non-linear, between brain areas, and which developed new parameters for estimating states of the subject. This latter technique, called discriminant analysis, has been applied by Dr. D. O. Walter and Dr. J. Hanley to data from chimpanzee performance on the tic-tac-toe procedure described in previous reports. This analysis appears at the end of this report, beginning on page 7 (RESULTS OF COMPUTER ANALYSIS OF PERFORMANCE DATA IN THE CHIMPANZEE).

2. Combining mathematical analysis of EEG data and impedance data
to study of learning and behavior in the chimpanzee.

It is proposed to extend the spectral analysis and pattern recognition
methods for EEG data developed in this laboratory to specific study of modes
of information transaction in functionally organized systems. Our early
studies with these techniques in man and in chronically implanted monkeys
and cats during learned task performance have shown that consistent wave
patterns can be detected during these behavioral performances both between
cortical regions, as well as in cortico-subcortical systems. These wave
relations have been shown to be very susceptible to peripheral sensory
influences, as revealed, for example, in our studies during whole body
vibration. In other studies of learning and the effects of drugs, we have
also shown that, with the appropriate computer techniques, wave relationships
may be extracted which otherwise are not seen, and which appear to relate
to aspects of information transaction in the tissue.

The extension of these methods to the chimpanzee in a highly sophisti-
cated learning paradigm is expected to be much more revealing of the processes
of information transaction in the complexly organized brain. For this
purpose, we have developed a task involving progressively shifting symbol
sequences, presented under computer control. We also plan further develop-
ment of computer programs required for pattern recognition in elucidation
of EEG wave patterns temporally related to a particular behavioral event.
This approach appears justifiable since our studies have already indicated
strong consistency of wave patterns in repetition of identical behavioral
performances. The implications of this finding are that consistent wave
patterns can be elicited from EEG wave data for even short epochs, in strict
temporal relation to particular behavioral states.

Impedance studies in animals and man have indicated that this method
permits the observation of on-going processes not revealed in the EEG, in-
cluding new observations during learning. Of particular importance is the
implication that the minute measuring currents are sensing processes occur-
ring at the cellular level and particularly as the tissue undergoes meta-
bolic transitions. Electro physiological studies have hitherto been confined
to the evaluation of the brain's own electrical activity. Our impedance
studies in smaller mammals have recently indicated not only regional dif-
ferences in occurrence of impedance responses to alerting, orienting and
discriminative stimuli, but have shown their dependence on levels of learn-
ing of the imposition of cue reversal. For these reasons, we are initiating
similar impedance studies in the implanted chimpanzee. With the impedance
techniques, it is believed that it will be possible to study functional
changes due to shifts in the ionic milieu surrounding brain cells, both
neural and glial.

It is planned to perform mathematical analysis of EEG and impedance
data, in studies of mechanisms of learning and discriminative behavior in
the chimpanzee. These studies will be done in conjunction with an experimen-
tal paradigm which provides incremental learning opportunities, as well as
testing short term memory. This is the "Matching to Successive Sample Device"

(MSSD) described in the previous report. The animal will be required to manually extinguish lighted symbols which are presented sequentially under computer control. A short delay follows the extinguishing of the last symbol, after which the previously presented symbols are displayed again, along with several others. The animal is then required to select the sample symbols in the order in which they were previously presented. This paradigm has been tested with humans and has been shown to be effective for up to twelve symbols; it also extends those previously used by us in studies of chimpanzee learning. Because of the complex and adjustable nature of this behavioral task, it is expected that much information will be obtained in the temporal relationships of the performance behavior of the animals. In order to properly acquire and retain this complex data in processable form, we will apply our newly developed on-line time-sharing console system, attached to a medium-sized high-speed digital computer. This console allows the investigator to define performance criteria, set up analog-digital conversion programs, and prepare the entire strategy of the experiment, from pre-programmed modules or with as much flexibility for change as he desires; to pass control to his automated system and reacquire control whenever desired for modification, delay, or other intervention. Performance criteria will be defined by the experimenter, using the computer to measure, record and compare individual response times and report these back to the experimenter in tabular form, in relation to EEG variables simultaneously derived.

The construction of the MSSD is complete, and will soon be tested with the SDS 930 computer.

C. Developments in Bioinstrumentation.

1. Packaging and miniaturization of a multi-channel biotelemetry system

The biotelemetry system previously described in the last report has been further miniaturized so that both amplifier and transmitter are packaged in one container, reducing the volume by about one-half. The once package also contains the voltage controlled oscillators, the multiplexer and all batteries. It is considered that the package may be further reduced in size. The system has been used successfully with a high quality communications receiver and standard IRIG sub-carrier FM demodulators.

The telemetry systems have been used in a broad range of experiments, from the study of sleep patterns in the chimpanzee in the unrestrained state, to 24 hour recordings from patients with chronically implanted electrodes.

A smaller two channel telemetry has been developed and can be mounted on the electrode connector in the animal's head. This transmitter provides the animal much greater range of movement since no cable is required between him and the transmitting device.

Work is also continuing on devising a rechargeable power source for the biotelemetry system for long-term ecological studies and space flight experiments.

2. Development of DC blood flow transducing devices.

In addition to central and peripheral nervous system monitoring, work is being done on the possibility of implanting a biotelemetry system in the heart to do cardiac monitoring of blood flow and cardiac output.

This device has been shown to have sufficient output signal resulting from flow at the root of the aorta to be able to drive a biotelemetry transmitter. The problems of chronically implanting this device at the aorta without producing vessel rupture have not been completely solved. However, the advantages offered by a large signal device which could drive an implantable biotelemetry transmitter, will result in a reliable cardiovascular measure which has been almost impossible to obtain in the past.

Although this device is AC coupled into the recording system, the flow curve obtained at the root of the aorta has been shown to provide an accurate measure of the rate of blood flow in systole. Since there is no flow at this location of the vascular tree during diastole, it appears that AC coupling will be adequate. The flow measurement requires a sufficiently broad band, that it results in EKG interference. This interference is primarily from the P-wave which appears to produce a laterally oriented vector component in the lumen of the probe. Since the component sensed by the electrodes is a derivative of the lead 1 P-wave, it would appear that the artifact observed in the flow measurement is due to a vector arising from the conduction through the AV node. The QRS complex occurs prior to ventricular ejection and therefore produces an artifact which precedes the flow signal. There is no indication of interference resulting from the T-wave in the flow signal; however, the difficulty of clearly differentiating between the flow signal and the T-wave has prevented a more definitive testing for this interference. The various cardiovascular phases have been clearly demonstrable by this technique, including the sharp reversal of flow at the end of diastole at the root of the aorta.

The nature of this probe appears to make it eminently suitable for use in the study of cardiovascular function in the inspace flight.

D. Apollo Applications: Chimpanzee Experiment

In this project, we are currently developing the bioinstrumentation and doing feasibility studies which will form the basis of the following experiments proposed for the Apollo Applications program.

It is proposed to utilize baseline information on central nervous, cardiovascular and autonomic functions in the chimpanzee, already available from our previous studies, in the development of a flight experiment for two chimpanzees, one substantially restrained, and the other essentially free-moving for the duration of the flight. Physiological monitoring and behavioral testing would be planned for a flight of 60 to 90 days. It is anticipated that detailed physiological monitoring will provide unique information on the long-term effects of weightlessness on physiological

functions, and that this information will be vitally important in extrapo-
lation to planned manned flights. Bioinstrumentation necessary for data
acquisition in this experiment will involve direct transducing from deep
brain structures and the cardiovascular system.

This proposal takes account of recent developments in our laboratory
resources: 1) The availability of new and substantially larger chimpanzee
housing and test facilities in the Space Sciences Building, recently com-
pleted with NASA support. 2) The development of computer-controlled beha-
vioral testing methods for the chimpanzee, which, in further development,
are anticipated to provide the basis for light hardware for sophisticated
and flexible behavioral testing. 3) Experience in feeding techniques,
waste management and environmental support in our current preparations
for 30 day primate flight in NASA Biosatellite D have provided a highly
important background for the development of a longer primate flight experiment.

1. Development of suitable environmental chambers for a two chimpanzee experiment.

Our experience has indicated that conventional couch restraint techni-
ques are unsuitable for periods much in excess of 30 days. Nevertheless, the
nature of certain CNS instrumentation requires limitation of some limb
movements, and probably also on the degree of bodily displacement. For these
reasons, it is proposed to test the effects of prolonged weightlessness on
central nervous and behavioral functions in one subject undergoing physical
restraints to insure reliability of cardiovascular monitors, and to compare
these results with another enjoying virtually unimpeded movement. The second
subject would have full central nervous monitoring, and also those cardio-
vascular sensors compatible with his unrestrained condition.

2. Physiological instrumentation.

Implantation of surface and deep brain structures will be performed in
both animals according to stereotaxic techniques established in this labro-
ratory. Structures yielding the most sensitive data on states of focused
attention, drowsiness, fatigue and sleep will be monitored; electrooculo-
graphic, neck and trunk electromyograms, and galvanic skin responses will
be recorded. In the unrestrained subject, these signals will be transmitted
by local telemetry to the capsule data acquisition system. In the res-
trained subject, attention will be directed to development of a physiological
"back-pack", and the incorporation into it of signal conditioners or local
telemetry transmitters. Connection between transducers in brain and heart
and the signal conditioning system will be by hard wire or implanted tele-
metric transducers.

3. Waste management.

In any experiment exceeding 30 days, urinary management will not allow
use of catheterization procedures. Thus, it is proposed to investigate the

use of various other methods, including the use of absorbent material, eva-
poration by airblast and/or radiant energy, low residue diets, and, in the
restrained animal, collection through an external perineal attachment,
propelling urine to a collector for in-flight or post-flight analysis.

4. Data analysis methods.

It is proposed to extend our methods of spectral analysis and pattern
recognition techniques to provide summary statements of levels of awareness
and focused attention throughout the simulated flight procedures. It is
considered that the techniques which we have so far developed (and success-
fully applied to recognition of EEG patterns accompanying discriminative
performances in the chimpanzee as discussed in the last section of this
report) will lead to development of a flight computer capable of these
recognitions for man and chimpanzee.

5. Significance of this research.

Evidence from a manned space flight up to 14 days long has emphasize the
need to secure detailed information on the interrelations of central nervous
and cardiovascular factors in the total picture of changed physiological
functions induced by prolonged exposure to weightlessness. Since there is
evidence that the combined effects of confinement and weightlessness may be
greater than either alone, it is proposed to compare these effects on
unrestrained and partially restrained subjects. Careful evaluation will be
made of the possible contributions of vestibular influences to sustained
skilled motor performances, and the cues by which an artificial horizon can
be established in the weightless state. Attention will also be directed to
the effects of the space environment on sleep wakefulness cycles, and of the
effects of manipulation of these cycles by imposed environmental constraints.
Cardiovascular monitoring will be used to assess the relative deconditioning
of the unrestrained and partially restrained individuals.

As mentioned above, many of these proposed experiments are in the stage
where bioinstrumentation is being developed, and feasibility studies are
being run on the techniques and apparatus involved.

RESULTS OF COMPUTER ANALYSIS OF
PERFORMANCE DATA IN THE CHIMPANZEE

Electroencephalographic recording were obtained from stereotaxically implanted chimpanzees playing an electronic game of tic-tac-toe. This data was then submitted to comprehensive computer analysis in an attempt to ascertain bioelectric characteristics which may identify the different situations in which they were recorded.

Four illustrations of a discrimination between two situations are offered. The two situations are a) not performing - the animal is attend-into to the game, awaiting his opponents move; and b) performing - the animal is responding to the opponents move.

The experiment comprised the following four cases:
Case 1. EEG recordings during the game were obtained from electrodes in the left amygdala, left hippocampus, right hippocampus, fronto-central cortex, and temporo-occipital cortex. Sixteen samples were submitted, eight of each situation; all samples obtained on the same day, and all responses correct.
Case 2. This study involved a second animal. Tracings were obtained from the left amygdala, left hippocampus, right centre-median, left midbrain reticular formation, frontotemporal cortex, and parieto-occipital cortex. All samples were obtained on the same day and all were correct.
Case 3. The animal in Case 2 was used again. Fifty samples were used covering runs on different days, and two of the responses were incorrect.
Case 4. A third chimpanzee was used. Recordings were obtained from the left hippocampus, left amygdala, right hippocampus, midbrain reticular formation, fronto-polar/frontal lead, and parieto-occipital/occipital lead. There were 60 samples collected on different days, and one response was incorrect.

Methods

The various complex operations performed on the data fall into two general categories: 1) those which generate variables for the discrimination program, and 2) the discriminant analysis.

In the first set of operations, the generation of variables for the discrimination program, the activity in each of the channels was separated into different frequency bands. In Cases 1 and 2 these bands were:

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0.5 - 3.5 c/sec  (delta)
3.5 - 7.5 c/sec  (theta)
7.5 - 12.5 c/sec (alpha)
12.5 - 25.5 c/sec (beta)
```

In Cases 3 and 4 the bandwidth was extended and the divisions slightly different:

        1.0 - 3.0 c/sec
        4.0 - 7.0 c/sec
        8.0 - 12.0 c/sec
       13.0 - 18.0 c/sec (beta-1)
       19.0 - 25.0 c/sec (beta-2)
       26.0 - 29.0 c/sec (beta-3)

(In the initial analysis, the frequency resolution was 1 c/sec.)

These bands were then subjected to spectral analysis, a novel mathematical approach to the EEG pioneered at the Space Biology Laboratory, UCLA, by D.O. Walter (Walter, 1963; Walter and Adey, 1963). This method incorporates frequency analysis and also preserves fundamental relationships such as phase angle between wave phenomena. In each band, four parameters were measured:

1. Sum of spectra, which is proportional to the mean square of the intensity.
2. Mean frequency within the band (this will be close to the dominant frequency, if there is one).
3. Bandwidth within the band (this expresses the invariability of the dominant frequency).
4. Coherence: analogous to the correlation coefficient of classical statistics; a quantity which expresses the strength of linear relationship between two traces.

The next operation begins the discriminant analysis procedure. The above spectral estimators, which have a chi-square degrees-of-freedom distribution (Blackman and Turkey, 1959), were used as input data for a stepwise discriminant analysis program. In this program, a hybrid offspring of pattern recognition and classical discriminant analysis (Dixon, 1965; Anderson, 1958), the computer considers all the measurements of each of many EEG segments and selects that parameter which best discriminates between traces recorded in the different situations. After the selection of the first variable, the program reexamines the remaining data and chooses that parameter expected to add most to the power of the initial selection. The process continues until further selection cannot provide enough improvement in categorization to justify inclusion.

Results of Discriminant Analysis

Case 1

In this case, the computer required only three variables to perfectly assign the 16 samples to the situations in which they were recorded. The parameters chosen, in order of selection, were:

1) The sum of spectra (related to the mean square of the intensity) from the fronto-central channel in the beta band (12.5 - 25 c/sec).
   Direction: values increased with performance.
2) Mean frequency in the theta band (3.5 - 7.5 c/sec) from the left amygdala.
   Direction: mean frequency slowed with performance.
3) Mean frequency in the theta band (3.5 - 7.5 c/sec) in the left hippocampus.
   Direction: mean frequency slowed with performance.

The actual values of these spectral estimators appear in Appendix I in tabular form. Tables of the individual parameter and an overall table appear in Appendix II. Also included is a schematic of the space occupied by the derived discriminant values which illustrates the 'distance' between the two groups (see Appendix III).

Case 2

Five steps were required to completely separate the 26 samples of the two situations. The first selection correctly classified them with higher than 90% accuracy. The five parameters chosen were:

1. Sum of spectra from the left hippocampus in the delta band (1-3 c/sec).
   Direction: values decreased with performance.
2. Mean frequency from fronto-temporal cortex in the alpha band (8-13 c/sec).
   Direction: mean frequency slowed with performance.
3. Sum of spectra from the left amygdala in the theta band (3.5 - 7.5 c/sec).
   Direction: values decreased with performance.
4. Bandwidth in the alph band (8-13 c/sec) from the left hippocampus.
   Direction: bandwidth narrowed with performance.
5. Mean frequency from the right centre-median in the alpha band (8-13 c/sec).
   Direction: mean frequency increased with performance.

Case 3

Although it took 19 steps to discriminate perfectly between the 50 samples in this Case, a separation with 90% accuracy was obtained after a selection of only two variables. The first five parameters are offered as illustration, in order of selection:

1. Sum of spectra from the temporo-occipital channel in the beta band (25-29 c/sec).
   Direction: values increased with performance.

2. Left midbrain reticular formation/left hippocampus coherence in the theta band (4-7 c/sec).
   Direction: coherence decreased with performance
3. Sum of spectra from left hippocampus in beta band 1 (13-19 c/sec).
   Direction: values decreased with performance.
4. Left midbrain reticular formation/left hippocampus coherences in beta band 1 (13-19 c/sec).
   Direction: values decreased with performance.
5. Left amygdala/temporo-occipital coherence in the delta band (1-3 c/sec).
   Direction: values increased with performance.

Case 4

Again, 19 steps were required to completely discriminate the samples into the non-performing and performing groups. Over 80% of the samples were correctly assigned after four selections. Five parameters in the order chosen are listed:

1. Mean frequency in the fronto-polar/frontal channel in the delta band (1-3 c/sec).
   Direction: mean frequency slowed with performance.
2. Sum of spectra from parieto-occipital/occipital channel in the delta band (1-3 c/sec).
   Direction: values increased with performance.
3. Mean frequency in fronto-polar/frontal channel in beta band 3 (26-29 c/sec).
   Direction: mean frequency slowed with performance.
4. Right amygdala/left hippocampus coherence in beta band 1 (13-18 c/sec).
   Direction: coherence decreased with performance.
5. Midbrain reticular formation bandwidth in beta band 3 (26-29 c/sec).
   Direction: bandwidth widened with performance.

Discussion

The results obtained here would appear to emphasize characteristics not readily discernible by the ordinary visual examination of the EEG. The sum of spectra, and its increase with performance as in Case 1, is scarcely visually obvious in the low-amplitude, higher frequencies; yet it discriminated 87% correctly in the non-performing group and 63% in the performing group. Indeed, the beta band rarely comes to attention with the exception of specific situations such as the spindling of stage II sleep, and in activity influenced by barbiturates. This parameter in this band, chosen first again in Case 3, despite the added variables of more leads and different days, discriminated 88% of the performing segments and 64% of the non-performing. Though the channels were different in each case (fronto - central in Case 1, temporo-occipital in Case 2) it is worthy of note that both are cortical leads. The sum of spectra was selected a second time in

Case 3, as third choice; this time, however, the activity decreased in a subcortical lead, the left hippocampus.

Although Walter and co-workers (1966) have shown that the characterization of individuals is more accurate than that of a group, it is still interesting to note that in Cases 2 and 4, the sum of spectra was again selected. In Case 2, it was chosen first and third: the sum of spectra in the delta band from the left hippocampus, and also in the theta band from the left amygdala, and its <u>decrease</u> in activity separated the performing and non-performing segments with better than 90% success. In Case 4, this parameter in the delta band of the parieto-occipital cortex was selected second, and here the activity increased. Thus, it can be seen that in the cortical leads the sum of spectra values increased, and in the subcortical leads the values decreased (based on group means). This parameter was the only one included in all four cases in the first five selections.

The intriguing selection of theta band mean frequencies in the amygdala and hippocampus in Case 1 brings to mind extensive earlier work which revealed the importance of these structures and their role in the acquisition of a learned discriminatory task (Adey and Walter, 1963; Walter and Adey, 1963). In Case 4, mean frequency in the adjacent delta band in the fronto-polar/frontal linkage was selected first and corrrectly assigned 74% of the samples from the non-performing segments and 70% of the performing ones. In Case 2, where another cortical lead, the fronto-temporal derivation, was selected the mean frequency again slowed, though this time the alpha band was the frequency represented. The mean frequency slowed on the average five out of the six times it was selected as being significant: in man it has been observed that theta band frequency slowed in scalp vertex recordings during the performance of two stressful visual discrimination tasks (Walter, Rhodes, and Adey, 1966).

Coherence, a quantity first discovered to have electroencephalographic significance by Walter, <u>et al.</u> (1966) appears as second, fourth, and fifth choice in Case 3. It must be recalled that the left midbrain reticular formation lead was not obtained in Case 1; on its inclusion, its coherence with the left hippocampus in both theta and beta-1 band was included in the selection. Walter noted an increase in theta band coherence between the left parieto-occipital derivation and the vertex in the scalp EEG from man when the speed of a visual discriminatory task was increased from 1 every 3 seconds to 1 per second. Here, subcortical structure coherence <u>decreased</u>, as it did in Case 4 when selected (left amygdala/left hippocampus), both in the beta-1 band. Cortical-subcortical coherence (tempero-occipital/left amygdala) however increased in Case 3.

Other phases of chimpanzee performance during this task are being investigated. Analyses of correct and incorrect decisions at various performance levels during the acquisition of the learned task, comparisons across an ensemble of animals, and the possible changes of important parameters at different times are being pursued.

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APPENDIX I.

Tables of the Values of the Spectral Estimators

CASE 1

TABLE I

Sum of spectra F-C channel, beta-band.

Sample	Not performing	Performing
1	24.62	30.21
2	25.59	41.50
3	37.76	49.53
4	27.68	40.28
5	19.13	27.01
6	27.16	22.53
7	22.22	34.21
8	20.29	39.58

Group means

25.55578	35.60543

Standard deviation

5.81930	8.80003

TABLE II

Mean frequency in the theta band from the left amygdala

Sample	Not performing	Performing
1	5.20	4.71
2	4.73	4.64
3	5.39	5.04
4	5.33	5.41
5	5.45	5.10
6	5.48	5.11
7	5.17	4.68
8	5.42	5.08

Group means

5.27296	4.97144

CASE 1, TABLE II (Cont'd.)

Not performing   Performing

Standard deviation

0.24844   0.26796

TABLE III

Mean frequency in the theta band of the Right Hippocampus

Sample	Not performing	Performing
1	4.79	4.96
2	5.39	5.04
3	5.06	5.10
4	5.25	4.90
5	5.28	4.72
6	5.09	4.82
7	5.31	4.79
8	4.83	4.53

Group means

5.12535   4.85698

Standard deviation

0.22323   0.18383

CASE 2

TABLE I

Sum of spectra from the left hippocampus in the delta band (1-3 c/sec)

Sample	Not performing	Performing
1	955.86	461.53
2	1397.40	457.27
3	861.54	826.02
4	1142.89	785.07
5	1129.24	313.81
6	567.84	1329.30
7	1130.95	635.96
8	949.04	661.44
9	1070.59	702.32
10	893.84	463.21
11	969.14	627.80
12	1022.51	568.78
13	1442.86	537.79

Group means

1041.05530   643.86898

Standard deviation

226.31287   250.58386

TABLE II

Mean frequency from the fronto-temporal alpha band (8-13 c/sec)

Sample	Not performing	Performing
1	10.53	9.45
2	9.49	9.57
3	9.30	9.44
4	9.72	9.41
5	9.24	9.70
6	10.33	9.00
7	9.73	8.80
8	9.59	9.92
9	9.44	9.86
10	10.10	9.38
11	9.27	9.37
12	9.84	9.21
13	9.53	9.81

CASE 2, TABLE II (Cont'd.)

	Not performing	Performing
Group means	9.69987	9.45639
Standard deviation	0.40646	0.32856

TABLE III

Sum of spectra from left amygdala in the theta band (4-7 c/sec).

Sample	Not performing	Performing
1	307.66	438.95
2	210.11	164.89
3	494.91	269.48
4	90.75	258.06
5	668.85	193.38
6	477.67	100.21
7	152.71	218.57
8	165.77	149.39
9	390.76	454.46
10	249.81	388.50
11	676.57	221.91
12	318.14	210.18
13	527.93	256.39

	Not performing	Performing
Group means	363.97323	255.72136
Standard deviation	193.40861	109.21013

TABLE IV

Bandwidth in the left hippocampus alpha band (8-13 c/sec).

Sample	Not performing	Performing
1	2.83	3.61
2	2.75	2.34

CASE 2, TABLE IV (Cont'd.)

Sample	Not performing	Performing
3	3.84	1.58
4	3.24	2.15
5	3.98	2.53
6	2.76	2.37
7	4.02	3.06
8	2.88	2.38
9	3.12	3.25
10	4.24	4.02
11	2.30	3.14
12	3.16	3.16
13	2.48	3.00

Group means

3.19922   2.84944

Standard deviation

0.62832   0.69366

TABLE V

Mean frequency in the right centre-median in the alpha band.

Sample	Not performing	Performing
1	9.74	9.88
2	9.50	10.45
3	10.40	9.63
4	10.07	10.06
5	9.74	10.37
6	10.28	9.87
7	9.33	9.83
8	10.53	10.43
9	10.03	9.56
10	10.07	9.48
11	9.76	9.56
12	9.45	10.15
13	9.53	9.68

Group means

9.88053   9.91918

Standard deviation

0.38131   0.34449

CASE 3

TABLE I

Sum of Spectra in the Temporo-Occipital Beta Band 6 (26-29 c/sec).

Sample	Not performing	Performing
1	66.30	188.18
2	76.66	124.10
3	93.94	94.93
4	46.82	84.56
5	16.80	63.85
6	23.24	117.92
7	25.68	59.22
8	27.00	71.42
9	64.85	66.26
10	31.73	85.17
11	25.61	107.10
12	68.69	218.12
13	40.81	137.05
14	56.90	200.59
15	56.90	200.59
16	66.70	78.13
17	105.20	112.91
18	126.63	169.38
19	83.99	153.94
20	50.20	66.78
21	68.70	84.72
22	47.41	120.37
23	41.24	32.59
24	54.25	76.05
25	53.31	72.41

Group means

56.78188	111.45272

Standard deviation

26.7088	50.99847

TABLE II

Left Midbrain Reticular Formation / Left Hippocampus Coherence in the Theta Band

Sample	Not performing	Performing
1	0.05	0.10
2	0.31	0.15
3	0.27	0.05

CASE 3, TABLE II (Cont'd.)

Sample	Not performing	Performing
4	0.09	0.05
5	0.00	0.01
6	0.01	0.04
7	0.13	0.06
8	0.03	0.04
9	0.04	0.00
10	0.05	0.04
11	0.11	0.04
12	0.11	0.08
13	0.01	0.06
14	0.04	0.09
15	0.04	0.09
16	0.06	0.07
17	0.09	0.10
18	0.04	0.01
19	0.19	0.07
20	0.05	0.01
21	0.25	0.00
22	0.17	0.08
23	0.01	0.00
24	0.23	0.01
25	0.05	0.01

Group means

0.09817	0.05174

Standard deviation

0.08962	0.03882

TABLE III

Sum of Spectra in Left Hippocampus in Beta-Band 1 (13-18 c/sec).

Sample	Not performing	Performing
1	242.96	214.08
2	195.79	273.13
3	207.71	161.91
4	238.59	169.11
5	235.39	132.20
6	176.39	201.22
7	144.56	170.51
8	141.59	147.90
9	144.64	197.17
10	154.54	119.77

CASE 3, TABLE III (Cont'd.)

Sample	Not performing	Performing
11	281.60	300.41
12	440.26	353.86
13	369.98	277.58
14	400.27	198.39
15	400.27	198.39
16	621.09	264.48
17	272.79	355.68
18	278.05	145.17
19	179.61	255.47
20	181.37	207.23
21	205.01	186.65
22	299.81	105.91
23	176.20	96.08
24	271.13	131.47
25	200.80	164.27

Group means

| 258.41692 | 201.12226 |

Standard deviation

| 113.67025 | 71.48930 |

TABLE IV

Left Hippocampus / Left Midbrain Reticular Formation Coherence in Beta-Band 1 (13-19 c/sec).

Sample	Not performing	Performing
1	0.13	0.01
2	0.06	0.02
3	0.00	0.00
4	0.00	0.05
5	0.00	0.02
6	0.01	0.08
7	0.08	0.01
8	0.07	0.01
9	0.02	0.05
10	0.02	0.06
11	0.04	0.00
12	0.08	0.00
13	0.05	0.07
14	0.05	0.01
15	0.05	0.01
16	0.24	0.03

CASE 3, TABLE IV (Cont'd.)

Sample	Not performing	Performing
17	0.05	0.01
18	0.05	0.016
19	0.05	0.00
20	0.04	0.05
21	0.04	0.01
22	0.03	0.03
23	0.06	0.02
24	0.05	0.03

Group means

0.05053	0.031919

Standard Deviation

0.04814	0.03539

TABLE V

Left Amygdala / Temporo-Occipital Coherence in Delta Band (1-3 c/sec).

Sample	Not performing	Performing
1	0.02	0.10
2	0.10	0.36
3	0.07	0.14
4	0.20	0.02
5	0.16	0.10
6	0.07	0.12
7	0.02	0.32
8	0.09	0.20
9	0.10	0.11
10	0.04	0.10
11	0.03	0.14
12	0.11	0.51
13	0.16	0.02
14	0.37	0.67
15	0.37	0.67
16	0.06	0.15
17	0.37	0.00
18	0.32	0.01
19	0.06	0.01
20	0.11	0.03

Case 3, Table V (Cont'd.)

Sample	Not performing	Performing
21	0.21	0.13
22	0.23	0.09
23	0.04	0.05
24	0.13	0.03
25	0.11	0.29

Group means

0.14235	0.15014

Standard Deviation

0.11.192	0.19795

CASE 4

TABLE I

Mean Frequency in Fronto-Polar / Frontal Lead in Delta Band (1-3 c/sec).

Sample	Not performing	Performing
1	1.64	1.36
2	2.35	1.85
3	1.84	1.56
4	1.78	1.88
5	1.70	1.35
6	1.81	1.26
7	1.29	1.72
8	1.75	1.36
9	1.59	1.25
10	1.51	1.13
11	1.73	1.09
12	1.80	1.09
13	2.17	1.37
14	1.32	1.23
15	1.64	1.30
16	1.34	1.18
17	1.96	1.59
18	1.33	1.37
19	2.13	1.69
20	1.81	1.42
21	1.92	1.57
22	1.92	1.96
23	1.93	1.55
24	1.77	1.90
25	1.81	1.64
26	1.76	1.57
27	1.62	1.42
28	2.06	1.78
29	1.60	1.49
30	1.66	1.86

Group Means

1.75695	1.49242

Standard Deviation

0.24858	0.25564

CASE 4

TABLE II

Sum of Spectra from Parieto-Occipital / Occipital Channel in the Delta Band (1-3 c/sec).

Sample	Not performing	Performing
1	5469.02	13149.14
2	6246.78	10500.80
3	8589.03	16028.80
4	7745.14	15667.26
5	5694.27	10898.71
6	4013.86	4999.89
7	6060.84	6337.50
8	9461.76	9471.88
9	2368.34	3097.17
10	1806.84	1301.44
11	1856.26	1283.67
12	1971.76	1891.50
13	409.08	2963.19
14	1337.57	1788.47
15	768.29	2321.87
16	738.34	2185.13
17	1456.13	2125.04
18	3210.24	2429.57
19	2086.68	2272.94
20	1998.24	1505.83
21	7328.32	7785.76
22	7328.32	11731.97
23	2513.48	1933.12
24	5395.48	5029.44
25	3455.04	5342.75
26	3658.59	12023.97
27	2476.57	3304.97
28	5032.27	5360.11
29	2090.79	6943.05
30	3912.31	11558.23

Group Means

3965.09656   6127.74554

Standard Deviation

2522.62463   4615.92578

CASE 4

TABLE III

Mean Frequency in Fronto-Polar /Frontal Channel in Beta Band 3 (26-29 c/sec).

Sample	Not performing	Performing
1	27.93	27.28
2	27.40	27.48
3	27.75	27.60
4	27.53	27.35
5	27.97	27.46
6	27.44	27.60
7	27.87	27.36
8	27.54	25.87
9	27.19	27.26
10	27.63	27.12
11	27.85	27.34
12	27.26	27.63
13	27.59	27.08
14	27.35	27.47
15	27.65	27.19
16	27.07	27.47
17	27.58	27.07
18	27.30	27.40
19	27.31	27.03
20	27.74	27.31
21	27.98	27.40
22	27.98	27.13
23	27.57	27.47
24	27.78	27.74
25	27.45	27.55
26	27.57	27.62
27	26.53	27.61
28	27.16	27.15
29	27.28	27.40
30	27.31	27.29

Group Means

27.54385   27.37505

Standard Deviation

0.26092   0.22767

CASE 4

TABLE IV

Right Amygdala / Left Hippocampus Coherence in Beta Band 1 (13-18 c/sec).

Sample	Not performing	Performing
1	0.04	0.12
2	0.02	0.01
3	0.06	0.04
4	0.03	0.04
5	0.04	0.03
6	0.02	0.02
7	0.05	0.03
8	0.01	0.14
9	0.09	0.00
10	0.04	0.03
11	0.00	0.00
12	0.08	0.03
13	0.06	0.00
14	0.02	0.02
15	0.01	0.01
16	0.02	0.06
17	0.01	0.02
18	0.08	0.07
19	0.03	0.00
20	0.01	0.06
21	0.03	0.05
22	0.03	0.05
23	0.04	0.02
24	0.01	0.05
25	0.02	0.03
26	0.02	0.01
27	0.02	0.01
28	0.01	0.04
29	0.06	0.02
30	0.19	0.01

Group Means

0.03922   0.3339

Standard Deviation

0.03740   0.03181

CASE 4

TABLE V

Midbrain Reticular Formation Bandwidth in Beta Band 3 (26-29 c/sec).

Sample	Not performing	Performing
1	2.52	3.29
2	2.59	3.34
3	2.29	2.46
4	1.82	2.40
5	2.79	3.07
6	1.57	2.59
7	3.48	3.30
8	1.86	2.74
9	2.08	2.37
10	2.83	2.99
11	2.85	2.37
12	2.77	3.21
13	2.92	3.03
14	2.91	2.13
15	2.92	3.23
16	2.29	3.04
17	3.06	2.47
18	2.10	2.92
19	2.14	2.61
20	2.65	2.13
21	2.25	2.71
22	2.25	3.30
23	1.89	2.83
24	2.84	3.10
25	2.83	3.27
26	2.42	2.86
27	3.58	2.41
28	1.66	2.07
29	2.31	3.26
30	2.77	2.26

Group Means

2.52330   2.79257

Standard Deviation

0.49906   0.40962

APPENDIX II

Tables of the Individual Parameters

PARAMETER: SUM OF SPECTRA

Case	Choice	Band	Channel	Direction on Performance
1	1	Beta	F-C	↑
3	1	Beta 3	T-O	↑
4	2	Delta	P-O	↑
2	1	Delta	L HIPP	↓
2	3	Theta	L AMYG	↓
3	3	Beta 1	L HIPP	↓

PARAMETER: MEAN FREQUENCY

Case	Choice	Band	Channel	Direction on Performance
4	1	Delta	FP-F	↓
1	2	Theta	L AMYG	↓
1	3	Theta	R HIPP	↓
2	2	Alpha	F-T	↓
4	3	Beta 3	FP-F	↓
2	5	Alpha	RCM	↑

PARAMETER: COHERENCE

Case	Choice	Band	Channel	Direction on Performance
3	2	Theta	LMBRF/LHIPP	↓
3	4	Beta 1	LMBRF/LHIPP	↓
4	4	Beta 1	LAMYG/LHIPP	↓
3	5	Delta	LAMYG/T-O	↑

PARAMETER: BANDWIDTH

Case	Choice	Band	Channel	Direction on Performance
2	4	Alpha		↓
4	5	Beta 3		↑

Overall Table

CASE	CHOICE	PARAMETER	BAND	STRUCTURE	DIRECTION ON PERFORMANCE (Based on group means)
1	1	SS	Beta	F-C	↑
3	1	SS	Beta 3	T-O	↑
4	2	SS	Delta	P-O	↑
2	1	SS	Delta	L HIPP	↓
2	3	SS	Theta	L AMYG	↓
3	3	SS	Beta 1	L HIPP	↓
4	1	$\overline{F}$	Delta	FP-F	↓
1	2	$\overline{F}$	Theta	L AMYG	↓
1	3	$\overline{F}$	Theta	R HIPP	↓
2	2	$\overline{F}$	Alpha	F-T	↓
4	3	$\overline{F}$	Beta 3	FP-F	↓
2	5	$\overline{F}$	Alpha	RCM	↑
3	2	COH	Theta	LMBRF/LHIPP	↓
3	4	COH	Beta 1	LMBRF/LHIPP	↓
4	4	COH	Beta 1	LAMYG/LHIPP	↓
3	5	COH	Delta	LAMYG/TO	↑
2	4	BW	Alpha	L HIPP	↓
4	5	BW	Beta 3	L MBRF	↑

```
SS      =  Sum of Spectra
F̄       =  Mean Frequency
COH     =  Coherence
BW      =  Bandwidth Within the Band
Delta   =  1 - 3 c/sec.
Theta   =  4 - 7 c/sec.
Alpha   =  8 - 13 c/sec.
Beta    =  (in cases 1 & 2) 14 - 25 c/sec.
Beta 1  =  13 - 19 c/sec.
     2  =  20 - 25 c/sec.   in cases 3 & 4
     3  =  26 - 29 c/sec.
```

```
F-C     =  Frontocentral Lead
T-O     =  Temporo-Occipital Lead
P-O     =  Parieto-Occipital Lead
L HIPP  =  Left Hippocampus Lead
L AMYG  =  Left Amygdala Lead
FP-F    =  FrontoPolar - Frontal Lead
F-T     =  Fronto-Temporal Lead
RCM     =  Right Centre-Median Lead
LMBRF   =  Left Midbrain Reticular Formation Lead
```

APPENDIX III

Schematics of Space Occupied by the Derived

Discriminant Values

These figures illustrate the planar separation of the two situations
under consideration. The boundaries enclose the space which contains
all the samples of the given situation; asterisks mark the position
of the group means, demonstrating the 'distance' between the two
groups.

CASE 1

NOT PERFORMING   PERFORMING

i6 samples: 8 in each group, all correctly assigned.

CASE 2

NOT PERFORMING   PERFORMING

26 samples: correctly sorted after 5 steps.

CASE 3

NOT PERFORMING   PERFORMING
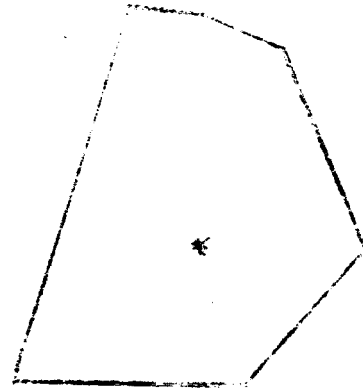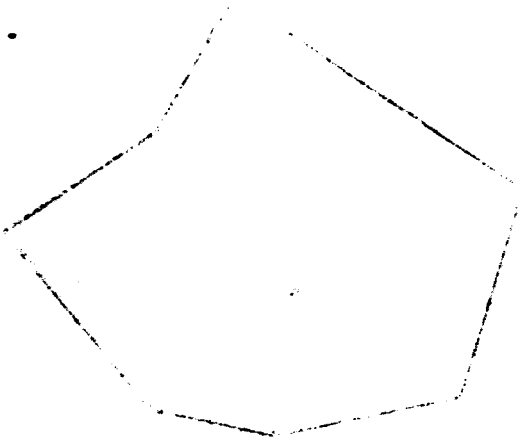
50 samples: 25 in each group, all correctly assigned.

CASE 4

NOT PERFORMING   PERFORMING
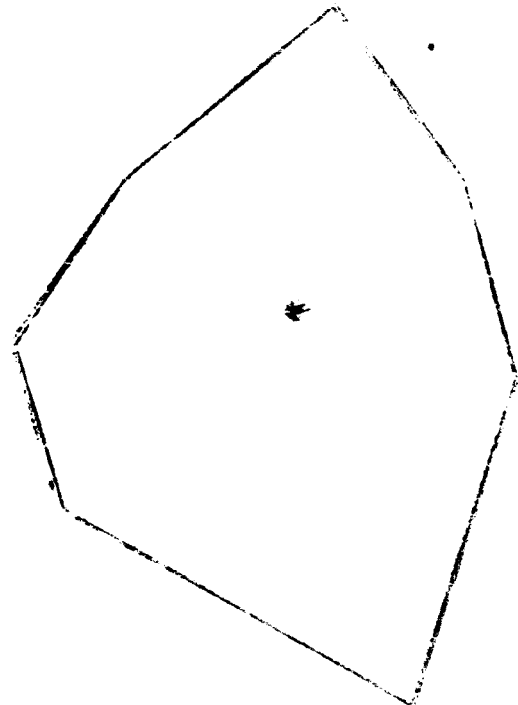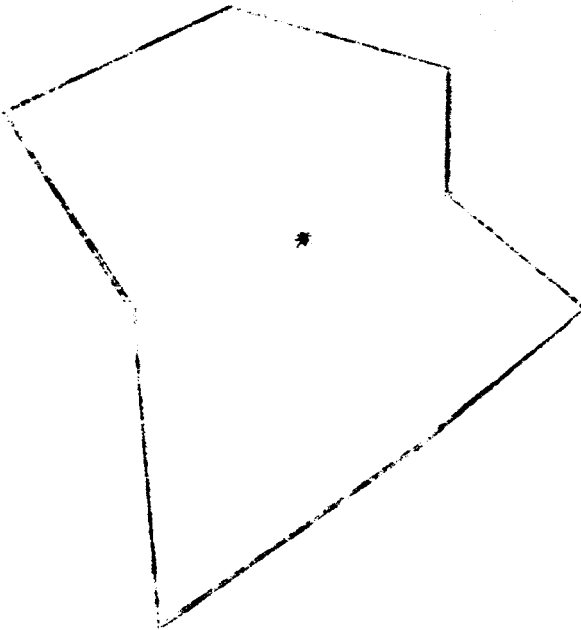
60 samples: 30 in each group, all correctly assigned.

By using these feed equivalents of changes in body mass, it is possible to correct the ad libitum feed intake, and obtain an estimate of the maintenance requirement (Table 5). When these results are compared with the time of their collection (Figure 3, for ad libitum intake; and Figure 4 for maintenance requirement), cyclic changes are evident. These appear to be related to environmental factors (principally temperature variation), rather than duration of the treatment. For example, when individual groups are examined, all show similar cycles, although some had 100 days more of centrifugation than others (Figure 1). A mean of the data from 320-500 days age covers enough of the cycle to be representative, and over this period the feed intake of the centrifuging animals can be expressed as a %-difference from that of the controls:

	$\pm \Delta$ % from gravity controls	
Treatment	Ad libitum feed intake	Maintenance feed intake
1.5 G	+ 4.3%	+ 8.7%
2.0 G	+10.2%	+14.9%

However, the direct comparison of feed intakes of centrifuging and control animals is not entirely satisfactory, since there are appreciable size differences between the groups (Table 3). The lesser body masses of centrifuging animals do not appear to result from some form of feed restriction. After a three day fast, centrifuging animals recover their body mass even more rapidly than do controls. Thus, the smaller size of the "high-G" animals is perhaps a regulated phenomena, and represents some sort of physiological adjustment to the increased accelerative force. Since body size also is known to affect energy metabolism it may be preferable to compare the feed intake of the experimental birds with that of controls of the same size. Over the range involved (1.8-2.1 kg body mass), the effect of size on maintenance requirement at normal gravity is quasi-rectilinear -- the maintenance feed decreasing 0.55 gms/kg body mass/day with each 0.1 kg increase in body mass (Brody, 1945; p. 479). On this basis, the relative effect of acceleration on the feed intake becomes (see Figure 4):

	$\pm \Delta$% from gravity controls	
Treatment	ad libitum intake	maintenance feed intake
1.5 G	+ 2.1%	+ 6.4%
2.0 G	+ 6.2%	+10.9%

These latter results are compared with the ambient accelerative force in Figure 5. It seems most likely that the acceleration effect on feed intake is rectilinear, rather than some more complex relationship (e.g., exponential). If the increased feed intake is simply a weight-related phenomenon, then it should be rectilinear, since equal increments in accelerative force produce equal increments in the weight:mass ratio. This contention is supported by the apparently rectilinear relationship between accelerative force and body mass loss rate during fasting. The maintenance requirements and fasting loss rate have a common basis, and the latter is more directly and accurately determined.

Fitting the data to a linear relationship (Figure 5), the feed intake obeys the relationship:

$$F_G = F_M + kG$$

Where: F_G is the feed intake at a given accelerative force, G, relative to the intake at normal gravity (i.e., where G = 1.0, F_G = 1.0);
F_M is the mass-determined part of the feed intake; and, k is the proportionality constant between accelerative force and weight-dependent feed intake.

For the ad libitum feed intake:

$$F_G = 0.94 + 0.06G$$

and, for the maintenance requirement:

$$F_G = 0.88 + 0.12G$$

Implicit in these equations is the effect of weight per se upon feed intake. Gravity appears to be responsible for approximately 12% of the maintenance requirement -- or, conversely, 88% of it is determined by the quantity and nature of the animal's constituent matter. The equations also predict the nutritional status of an animal after adaptation to weightlessness (perhaps involving many months' exposure). In this situation, the maintenance requirement would be reduced 12% (compared to Earth gravity), but the ad libitum intake, only 6%. This and the acceleration-related changes in body size and composition measurements, indicate a considerable increase in body-mass and adiposity after prolonged exposure to weightlessness. Of course, predictability and validity are not synonamous, and the reality of these changes must be tested in orbital, or similar weightless situations.

The metabolizability of feed (i.e., % of fed dry matter retained), also appears to be influenced by the ambient accelerative force (Table 2), the relationship being inverse. These results are not very satisfactory, there being little difference between the 1.5G and 2G groups. However, if a linear relationship is assumed, it appears that one of the consequences of gravity in chickens is a 13% reduction in the metabolizability of feed.

At 516 days of age, by which time they had been exposed to the increased acceleration field for at least 325 days, the experimental birds were returned to Earth-gravity. The immediate response in feed intake and body mass to this change in environment was quite variable (see period "s", Table 1), as has been noted with other trials (e.g., trial N, Smith & Kelly, 1963). When the body mass changes of individual birds are examined, it is evident that the variation occurs principally in the first three days postcentrifugation:

previous acceleration field	(No.)	Change in body mass (gms/kg/day)		
		days 0-3	days 3-7	days 0-7
gravity controls	(8)	-1.8±2.3*	+ 2.1±1.5	+0.5±0.8
1.5 G	(11)	-6.2±7.9	+ 7.4±3.5	+3.1±3.9
2.0 G	(14)	-3.2±14.1	+13.7±7.0	+6.3±7.3

* mean ± standard deviation

In the birds previously exposed to 2G, the changes in the first 3 days tended to be the inverse of those of the next 4. Thus, a bird gaining body mass rapidly in the first few days at normal gravity, gained very little in the next few days. Similarly, those losing body mass soon after return to normal gravity made very great gains subsequently, so that after 7 days there was very little difference between individuals in the net response. In the animals released from 2G, there also appeared to be a relationship between body size and response -- larger animals tending to suffer greater losses in body substance:

$$\Delta bm = a - kW = 25.4 - 9.7W \quad (r = -0.53; \ p < o.05)$$

No similar relationship was found between body size and change in body mass $(r = 0.02)$ in the animals adapted previously to 1.5G. However, in the spontaneous changes encountered over the same period with the gravity controls, a reverse relationship (i.e., direct) was found between body mass and changes in body mass:

$$\Delta bm = a + kW = -4.4 + 2.4W \quad (r = 0.74, \ p < 0.05)$$

At the present, the basis for this growth response is obscure -- however, some importance must be attached to the significant and opposite response of control and 2G animals.

Upon return to normal gravity, the previously centrifuged animals appear to undergo a "de-adaptation" with all of the differences that had existed between them and the controls being reduced or eliminated. Generally, this de-adaptation involves increases in body mass, body fat content and feed metabolizability, and decreases in fasting loss rate and subsequent recovery rate:

Changes following return to normal gravity
($+\Delta\%$ between periods "p-r" and "u-x")

previous treatment	body mass	terminal body fat	metabolizability	fasting loss rate	recovery rate
normal gravity*	+4.4%	+ 75.6%	-0.2%	- 9.9	-15
1.5 G	+6.9%	+196.4%	+2.6%	-29.8	-35
2.0 G	+9.9%	+269.2%	+5.8%	-27.7	-29.9

*differences encountered in the gravity controls between the two periods of observation.

At normal gravity the _ad libitum_ feed intake of the previously centrifuged birds increases, becoming very much greater than that of the controls in the period 30-100 days after centrifugation (period u-x, Table 2). There are not sufficient observations to permit a regression of body mass changes on feed intake, however, the indications (body fat content, fasting loss rate, etc.) are that the same tissue-feed equivalent obtains for previously centrifuged animals as for the controls (Table 4). When the feed intake measurements are corrected for changes in body mass on this basis, and also for differences in body size, the relative effect of previous acceleration on the feed intake becomes (Fig. 4):

Previous acceleration	+Δ% from controls	
	ad libitum intake	maintenance requirement
1.5 G	+10.2%	- 2.0%
2.0 G	+22.4%	-12.2%

When these results are compared with those obtained previously under chronic acceleration (Figure 5), it appears that the deadaptation from a higher accelerative force leads to quite different results than would be expected from the indications for the weightless adapted state. In the period reasonably soon after a reduction of the ambient accelerative force, the maintenance requirement increases, and the ad libitum feed intake decreases. Consequently, under these conditions, moderate losses of body mass may be encountered. Recent experiences of astronauts, in variable periods of weightlessness, all indicate a decrease in food intake and body mass (Nantz et al., 1966).

DISCUSSION

Increases in feed intake and decreases in body size have been observed generally in a variety of animals (including small mammals) when exposed to chronic acceleration (Wunder, 1962; Steel, 1962; Casey, 1965; Oyama, 1965). In all liklihood, the greater feed requirements of animals in hyperdynamic environments are related to the increased work for the performance of various mechanical activities (i.e., the fields employed are much too weak to affect osmotic or thermochemical processes). If these apparent differences in energy metabolism are the direct result of the increased accelerative field, then most certainly the natural field, Earth gravity, also has a similar effect. From the data presented, it appears that gravity is responsible for approximately 12% of the feed intake of chickens. If this proportion applies equally to the energy metabolism, a 2 kg (or 1.67 $kg^{3/4}$) homoiotherm would expend about 14 kcal/day (Brody, 1945; Kleiber, 1961), or 7 kcal/kg mass/day in meeting the load of gravity. Since this energetic expenditure is determined physically, it should apply to animals generally and irrespective of body size, assuming equivalent activity. However, the intensity of energy metabolism (i.e., per kg) is inversely related to body size, so the "gravity component" would appear to become a major part of the energy metabolism of larger animals (see Table 6). The calculations for large animals do not appear reasonable -- e.g., a 1000 kg animal must perform a great amount of non-mechanical work (osmotic, chemical, etc.), and the energetics indicated as available for these processes (44% of the basal) is most certainly too small. It is commonly understood that larger animals are less active than smaller ones (Thompson, 1961), and some (like the horse) have developed "non-work requiring" systems of postural maintenance. So it is likely that gravity imposes a lesser metabolic requirement, per kilo body mass, on larger animals.

However, there are indications that metabolic phenomena are important to the processes whereby the ambient accelerative force becomes limiting for animals. For example, the lethal effects of chronic acceleration can not be anatomically related, and appear to have a metabolic basis (Burton & Smith, 1965). The rapid "selection progress" in developing the acceleration-tolerant strain (Smith & Kelly, 1961), is indicative of a metabolic basis for that tolerance. Also, the inverse relationship between body size and the maximum tolerable accelerative force, at least in small animals (Table 7), indicates a common critical metabolic limit. The cited "G-limits" are only approximations -- so far, no experiments have been conducted

specifically to determine them, nor are there any established criteria for their recognition. However, calculations of the apparent energetic requirement of the increased accelerative force (i.e., 7kcal/kg mass/G/day) at these approximate limits, compared with the probable energy metabolism, indicate that the accelerative force which accounts for about 21% of the energy metabolism is the maximum that can be tolerated (Table 7). The implication that inability to survive an increased acceleration field is a direct result of caloric insufficiency does not seem reasonable. Under these experimental conditions, the feed intake, at least for mature chickens, is much less than their feed capacity. Also, their capability of very rapidly recovering lost body mass after a brief fast indicates that they can readily and greatly increase their feed intake. Most likely, the critical factor is metabolic, and the derived energetic relationship is only one way of expressing it.

The foregoing statement for the limit of G-tolerance may not apply to animals greater than 2 kg body mass (the largest which have been exposed to chronic acceleration). However, it is possible to generalize the relationship; which appears to be hyperbolic:

$$G_T = 2.7 \ W^{-0.25}$$

Where: G_T is the maximum tolerable increased ambient accelerative force (above Earth-gravity);
W is the body mass (kg); and,
-0.25 is the proportionality constant (since it is assumed that the limit is related to metabolic intensity -- kcal/kg/day-- this is dimensionally correct, since both are proportional to the -1/4 power of body size.)

Applying these mathematics to humans (75kg), it appears that the maximum field to which we could become adapted is 1.9G.

Although some certainty can be attached to the statements regarding the physiological consequences of Earth-gravity (since that condition was within the range of observations), reservations must be applied to the predictions of the effects of weightlessness (which are based on extrapolation). It will be necessary to test these hypotheses under true weightlessness -- and such predictions should be very useful in designing the tests. If it becomes established that there is a continuity of the biological effects of accelerative forces from weightlessness to the limit of tolerance, then centrifugation experiments, such as reported herein, furnish a relatively convenient (and economic) means of developing information pertinent to bioastronautics. In this regard, it should be noted that the only observations of biological function (hemodynamic) from weightlessness through several G (Roman et al., 1962) indicate such a continuity -- but only brief exposures were involved. Differences between the predicted and actual effects of weightlessness will obtain only if there are different and discontinuous regulatory mechanisms for physiological processes in acceleration fields above and below Earth-gravity -- a very difficult situation to comprehend. In any event, the hyperdynamic information will be of great importance in rationalizing observations under weightlessness. If the biological effects of accelerative forces are known only for two conditions (weightlessness and Earth-gravity) few generalities will result.

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Table 1. FEED INTAKE TRIALS

Ad libitum feed intake, gm/kg body mass/day; is indicated for each group.
Associated changes in body mass, as ± gm/kg body mass/day, are given in parentheses.

Period	Age (days)	Gravity Controls				1.5G				2.0G				
		1	2	3	all	4	5	6	all	7	8	9	10	all
a	192	53.7 (+2.2)*	42.9 (+1.9)	--	--	52.5 (+1.9)*	--	--	--	61.7 (+3.6)	60.1 (+2.3)	--	--	--
b	199	56.9 (-1.4)*	47.2 (+2.3)	--	--	55.3 (+2.0)*	--	--	--	51.9 (-2.4)	58.4 (+3.4)	--	--	--
c	207	--	35.0 (+0.6)	38.5 (-0.4)	--	57.7 (+2.6)	60.0 (+4.3)	--	--	52.1 (+1.1)	53.5 (-0.1)	63.9 (+0.3)	59.8 (-0.3)	--
d	214	59.1 (+2.3)	47.4 (+1.0)	49.3 (+2.4)	--	--	55.1 (+0.6)	53.3 (+0.4)	--	49.8 (+0.7)	52.0 (+1.8)	55.7 (+2.0)	54.3 (+2.0)	--
e	228	48.4 (+3.3)	45.9 (+5.9)	35.1 (-2.8)	42.5 (+1.5)	55.0 (-0.4)	56.8 (+0.2)	57.3 (-0.4)	56.2 (-0.2)	55.0 (+1.3)	56.2 (-0.2)	59.0 (-0.2)	60.8 (+0.6)	57.2 (+0.4)
f	242	35.2 (-0.5)	35.4 (-0.3)	30.3 (-1.1)	33.7 (-0.7)	53.6 (+2.2)	39.8 (-0.4)	52.9 (+2.1)	48.4 (+1.3)	43.5 (+1.5)	45.4 (+1.3)	40.9 (+0.4)	43.2 (-0.5)	43.5 (+0.8)
g	256	--	37.6 (-0.4)	36.2 (-2.7)	36.5 (-1.6)	45.9 (-2.5)	43.0 (-0.7)	47.3 (-1.2)	45.4 (-1.4)	43.5 (-2.6)	40.3 (-1.3)	45.4 (-2.0)	43.4 (-2.1)	43.0 (-2.0)
h	270	36.1 (+0.7)	--	32.7 (+1.0)	34.2 (+0.9)	51.8 (+1.7)	44.5 (+2.4)	51.8 (+1.7)	48.5 (+2.0)	43.1 (-1.3)	46.5 (-3.8)	42.6 (+1.4)	37.4 (-0.8)	42.8 (-1.5)
i	320	--	--	34.4 (-0.7)	--	39.4 (-1.5)	36.3 (-1.3)	35.0 (-2.9)	36.7 (-2.0)	--	--	--	--	--
j	334	34.5 (-0.7)	43.9 (+2.2)	37.1 (+1.0)	38.2 (+0.7)	40.6 (+1.5)	39.2 (+1.0)	34.4 (+0.8)	37.8 (+1.1)	43.8 (+4.4)	39.3 (+3.0)	41.0 (+1.0)	37.6 (0)	40.1 (+2.2)
k	358	30.4 (-2.6)	32.2 (+0.5)	30.2 (-1.6)	36.1 (-1.3)	36.1 (-0.7)	31.8 (-2.7)	29.0 (-4.0)	31.5 (-2.7)	31.9 (-7.1)	34.3 (-5.5)	38.4 (-1.0)	39.1 (0)	33.0 (-4.0)
l	362	--	--	29.2 (-3.9)	--	34.9 (-1.5)	35.4 (-4.4)	36.8 (-2.1)	34.5 (-2.7)	35.5 (-7.6)	35.2 (-10.2)	35.7 (-4.1)	33.4 (-4.5)	34.9 (-7.0)
m	392	38.0 (+1.2)	43.1 (+2.3)	34.2 (-1.7)	38.4 (+0.6)	40.9 (+1.5)	41.3 (+1.3)	43.2 (+1.3)	41.6 (+1.6)	42.6 (+2.5)	45.0 (-1.6)	39.4 (-3.6)	44.7 (+1.6)	42.9 (-0.1)
n	404	29.8 (+0.7)	50.0 (+0.8)	34.5 (0)	37.8 (+0.5)	39.6 (+1.6)	43.9 (+1.6)	--	41.6 (+0.9)	39.0 (-1.9)	41.9 (+0.1)	--	--	40.1 (-1.0)
o	413	--	40.0 (+1.9)	37.6 (+3.3)	38.7 (+4.9)	41.6 (-0.2)	41.9 (-0.9)	41.9 (+1.8)	41.7 (+0.2)	40.3 (+0.9)	38.3 (+1.0)	44.3 (+1.8)	44.8 (0)	41.4 (+0.9)

* at 2.0G during first two periods (see figure 1).

Table 1 – continued

Period	Age (days)	Gravity Controls					1.5G				2.0G			
		1	2	3	all	4	5	6	all	7	8	9	10	all
p	468	(-4.6) 29.1	(+1.2) 49.8	(-1.5) 32.6	(-2.1) 35.5	(+1.7) 46.8	(-0.2) 44.5	(-1.8) 51.8	(+0.2) 47.5	(-3.1) 46.4	(+5.2) 52.3	(+5.2) 52.4	(-0.8) 46.6	(+1.0) 48.9
q	492	(+3.2) 40.9	(+2.5) 53.4	(-0.7) 39.4	(+0.3) 43.7	--	(+2.1) 51.0	(+3.9) 55.2	(+2.9) 52.8	(-0.6) 53.0	(+2.3) 52.5	(+0.7) 55.3	(+1.8) 57.7	(+0.8) 54.1
r	499	(0) 36.8	(-0.5) 44.4	(-0.6) 35.4	(0) 38.2	(-0.5) 46.6	(+2.7) 51.1	(-1.0) 46.7	(+1.1) 48.3	(-1.5) 48.5	(+3.7) 52.2	(-0.7) 53.3	(-0.7) 53.3	(+0.9) 51.6
	516	All experimental birds returned to normal gravity; groups 1, 5, 10, sacrificed.												
s	518		--	(-1.3) 31.3	--	(-1.5) 42.9		(-5.6) 48.8	(-3.4) 45.7	(+4.2) 58.5	(-14.0) 55.5	(-11.6) 60.0		(-3.9) 58.0
t	532		--	33.1	--	(+6.6) 45.5		(-0.9) 41.2	(-1.1) 43.3	(+8.7) 47.8	(+10.8) 51.2	(+4.3) 51.7		(+8.3) 49.7
u	546		(-1.2) 34.8	(-4.6) 27.4	(-3.1) 30.8	(-1.7) 35.1		(-0.1) 37.5	(+0.1) 36.2	(+1.5) 43.6	(+2.6) 44.5	(+0.4) 45.0		(+1.6) 44.3
v	578		(+1.0) 39.9	(-0.4) 33.4	(+0.2) 36.4	(-0.9) 36.7		(+0.1) 38.7	(+0.1) 37.7	(-1.9) 38.8	(+3.0) 43.7	--		(+0.6) 41.4
w	597		(-2.8) 35.0	(-3.9) 23.8	(-3.5) 28.5	(-0.9) 35.5		(-1.1) 38.8	(-1.0) 36.8	(+1.6) 38.1	(+1.6) 40.6	--		(+1.6) 39.5
x	622		(-0.5) 36.5	(+1.9) 37.1	(+1.0) 36.7	(+0.5) 35.9		(-0.5) 34.7	(0) 36.0	(+0.2) 40.5	--	--		--
	660	All remaining birds sacrificed.												

Table 2. AD LIBITUM FEED INTAKE AND METABOLIZABILITY

Feed Intake is "gms/kg body mass/day;" Metabolizability, in parentheses,

is % of Fed Dry Matter Retained: $\dfrac{\text{Feed-excreta}}{\text{Feed}} \times 100.$

		e-h	i-1	m-o	p-r	i-r	u-x
Normal gravity controls	1	(60.4) 40.1	(62.8) 33.6	(64.9) 33.4	(62.9) 35.5	(63.3) 33.3	-- --
	2	(68.7) 38.7	(69.5) 38.3	(71.7) 45.5	(64.5) 49.1	(69.2) 43.3	(65.0) 36.5
	3	(64.9) 33.5	(75.1) 36.2	(65.8) 35.3	(63.5) 35.7	(71.2) 36.6	(62.7) 30.4
	all	(63.0) 36.8	(70.6) 35.8	67.9) 38.3	(63.6) 39.2	(68.4) 37.2	(64.9) 33.1
1.5G	4	(65.0) 50.8	(59.4) 38.0	(62.8) 40.5	(62.5) 46.7	(60.9) 39.8	(63.4) 35.7
	5	(64.5) 45.5	(57.1) 35.4	(63.2) 42.5	(62.0) 48.8	(59.8) 39.4	-- --
	6	(65.7) 52.1	(58.6) 33.7	(63.6) 42.4	(59.8) 51.1	(59.6) 37.6	(62.1) 37.9
	all	(65.1) 49.5	(58.3) 35.4	(63.1) 41.7	(61.3) 49.0	(60.0) 38.8	(62.8) 36.7
2.0G	7	(63.3) 46.4	(61.1) 36.2	(62.2) 40.3	(61.0) 49.2	(61.4) 40.5	(63.8) 39.8
	8	(62.5) 46.6	(64.0) 36.4	(62.3) 41.5	(60.5) 52.3	(62.8) 39.7	(64.8) 43.3
	9	(63.5) 47.2	(62.1) 38.4	(63.8) 41.4	(55.9) 53.8	(61.0) 41.5	-- --
	10	(64.5) 46.0	(64.7) 36.9	(59.3) 44.8	(60.2) 53.1	(62.3) 42.3	-- --
	all	(63.3) 46.7	(62.9) 36.8	(62.0) 41.3	(59.8) 51.4	(61.9) 41.0	(64.4) 41.5

Table 3, BODY MASS, AND CHANGES IN BODY MASS DURING FEED TRIALS

Body Masses are in kg. Changes in Mass, in parentheses, are
are as ± gms/kg body mass/day.

		e-h	i-l	m-o	p-r	i-r	u-x
Normal gravity controls	1	(+1.15) 1.80	(-1.53) 2.07	(+0.95) 2.11	(-1.45) 2.01	(-1.66) 2.06	-- --
	2	(+1.26) 1.81	(+1.41) 1.94	(+2.92) 1.87	(+0.66) 1.87	(+1.77) 1.89	(-0.64) 1.97
	3	(-1.31) 1.93	(-1.18) 2.08	(+0.47) 2.10	(-0.56) 2.21	(-0.17) 2.13	(-1.76) 2.29
	all	(+0.06) 1.85	(-0.80) 2.04	(+1.43) 2.02	(-0.62) 2.03	(-0.19) 2.03	(-1.26) 2.13
1.5G	4	(+0.32) 1.73	(-0.60) 1.93	(+0.37) 1.95	(+1.15) 2.00	(-0.80) 1.95	(-0.54) 2.17
	5	(+0.37) 1.75	(-2.04 1.87	(+0.82) 1.87	(+1.55) 1.91	(-0.70) 1.88	-- --
	6	(+0.58) 1.75	(-2.11) 1.87	(+1.87) 1.85	(+0.84) 1.91	(-1.13) 1.88	(-0.36) 2.01
	all	(+0.42) 1.74	(-1.66) 1.89	(+0.86) 1.89	(+1.20) 1.94	(-0.66) 1.90	(-0.46) 2.10
2.0G	7	(-0.23) 1.68	(-4.35) 1.80	(+0.13) 1.76	(-1.75) 1.78	(-2.34) 1.78	(+0.42) 2.01
	8	(-1.00) 1.75	(-4.01) 1.78	(-0.11) 1.80	(+3.83) 1.88	(-1.70) 1.82	(+1.97) 2.01
	9	(-0.19) 1.67	(-1.03) 1.81	(-1.21) 1.80	(+2.39) 1.85	(-0.43) 1.82	-- --
	10	(-0.67) 1.68	(-1.28) 1.78	(+0.79) 1.79	(+1.29) 1.82	(-0.26) 1.80	-- --
	all	(-0.50) 1.69	(-2.88) 1.79	(-0.57) 1.79	(+0.90) 1.83	(-1.38) 1.80	(+1.18) 2.01

Table 4. LINEAR REGRESSION OF BODY MASS CHANGES ON FEED INTAKE

These calculations are based on observations of periods i-r (320-500 days age).

	Normal Gravity Controls	1.5G	2.0G
No. observation periods:	27	28	34
bird-days involved:	832	1277	1305
Δ body mass/feed intake (i.e., "slope"):	0.19	0.24	0.48
maintenance requirement [1]/	36.9	41.4	45.5

[1]/ These results are somewhat different from the pooled data", Table 5, since the regression treats all periods as equivalent.

Table 5. ESTIMATED MAINTENANCE FEED REQUIREMENT

Ad libitum data (table 2) corrected for body mass changes (table 3) and the feed-body substance ratio (table 4)

	e-h	i-l	m-o	p-r	i-r	u-x
1	34.1	41.5	28.5	43.0	41.9	--
2	32.2	31.0	30.4	45.7	34.1	39.8
3	40.3	42.3	32.9	38.6	37.5	39.5
all	36.5	39.9	30.9	42.4	38.2	39.6
4	49.5	40.5	39.0	41.9	40.1	38.5
5	44.0	43.9	39.1	42.3	42.3	--
6	49.7	42.5	34.6	47.6	42.3	39.8
all	47.7	42.3	38.1	44.0	41.5	39.1
7	46.9	45.3	40.0	52.8	45.4	37.6
8	48.7	44.8	41.7	44.3	43.2	33.1
9	47.6	40.5	43.9	48.5	42.4	--
10	47.4	39.6	43.2	50.4	42.8	--
all	47.7	42.8	42.5	49.5	43.9	35.4

Table 6. METABOLIC REQUIREMENTS OF GRAVITY AND BODY SIZE

body size (kg)	basal metabolism kcal/day		metabolic requirements of gravity	
	per animal	per kg	kcal/day	% of basal
0.01	2	200.0	0.07	3.5
0.1	13	130.0	0.7	5.4
1.0	70	70.0	7.0	10.0
10.0	394	39.4	70.0	17.8
75.0	1790	23.9	525.0	29.3
100.0	2215	22.2	700.0	31.5
1000.0	12450	12.5	7000.0	56.0

Table 7: METABOLIC STATUS AT THE LIMIT OF ACCELERATION TOLERANCE

Species	body size (gms)	estimated basal metabolism (kcal/kg/day)	limit of acceleration tolerance (G)	at G-limit		
				increased energy requirement (kcal/kg/day)	total energy metabolism kcal/kg/day	increased energy requirement (% of total)
mouse	25	174[1]	8[2]	49[5]	223[6]	22%
rat	200	105	5[3]	28	133	21%
chicken	1800	60	3[4]	14	74	19%

[1] basal metabolism at normal gravity: $kcal/d = 70W_{(kg)}^{3/4}$

[2] Wunder, 1962

[3] Oyama and Platt, 1965

[4] estimated tolerance for unselected stocks of White Leghorn chickens

[5] 7 kcal/kg body mass/G/day

[6] sum of basal and increased energy requirement
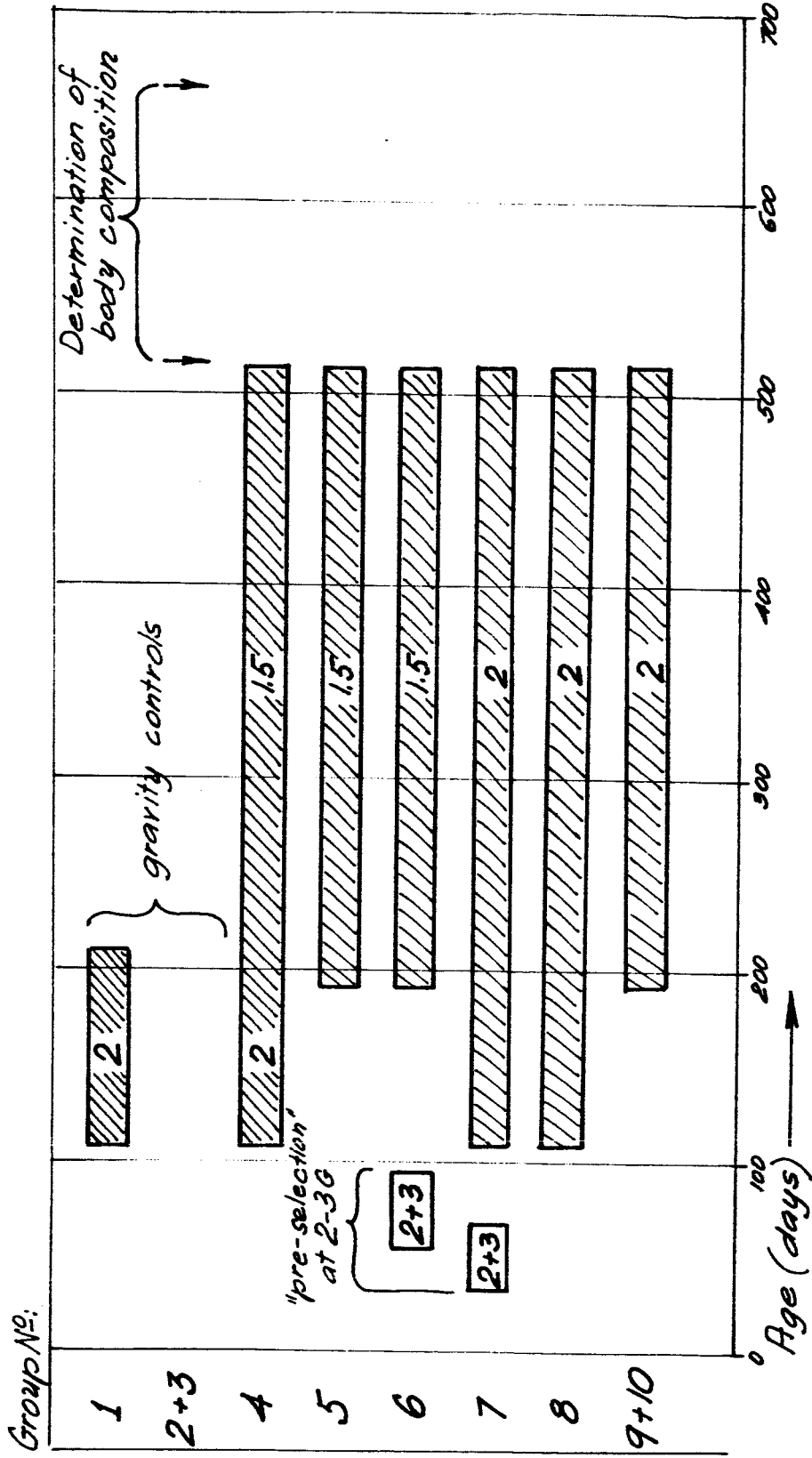
Figure 1: ACCELERATION SCHEDULE (TRIAL "T")

All birds were ♂ Leghorn (SCWL) chickens of the "acceleration selected" strain; hatched 8-26-64. Shaded bars indicate periods of exposure to increased accelerative force (i.e., duration of chronic centrifugation).
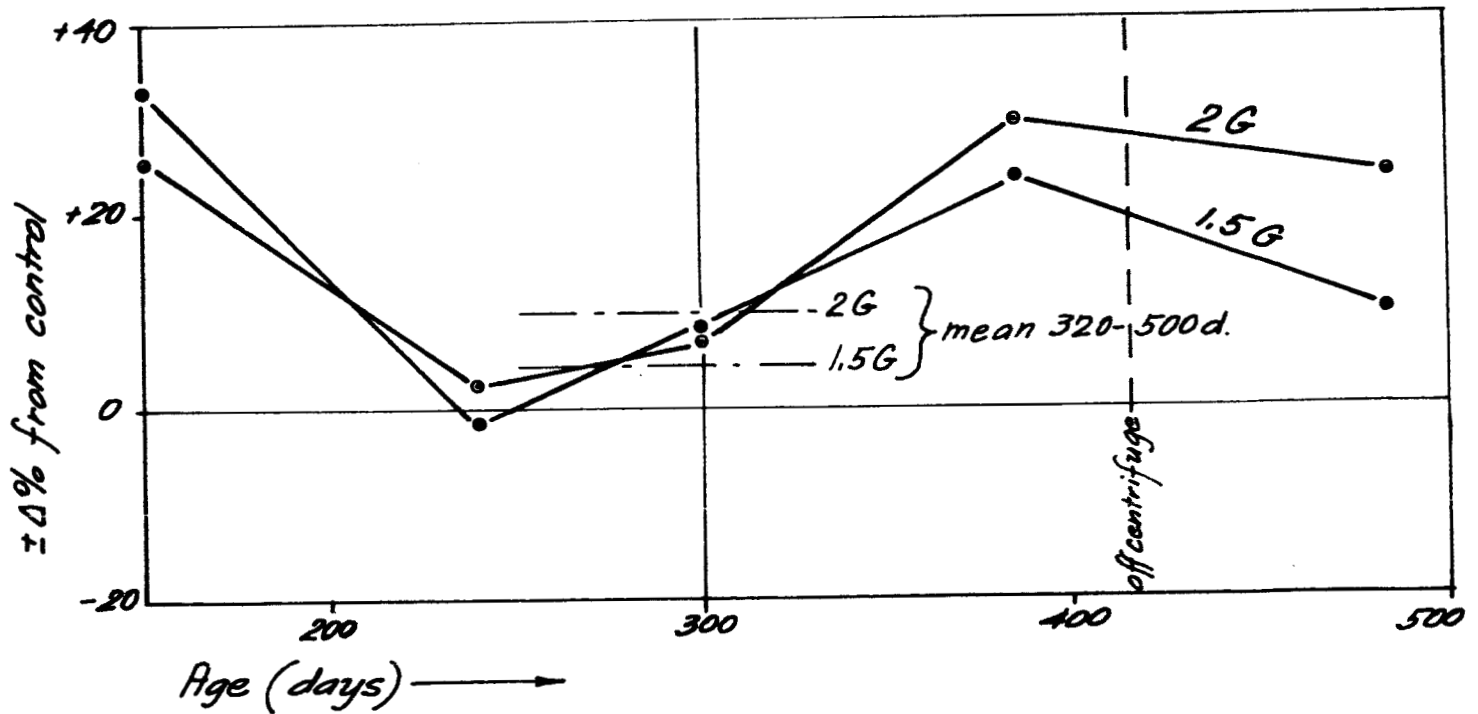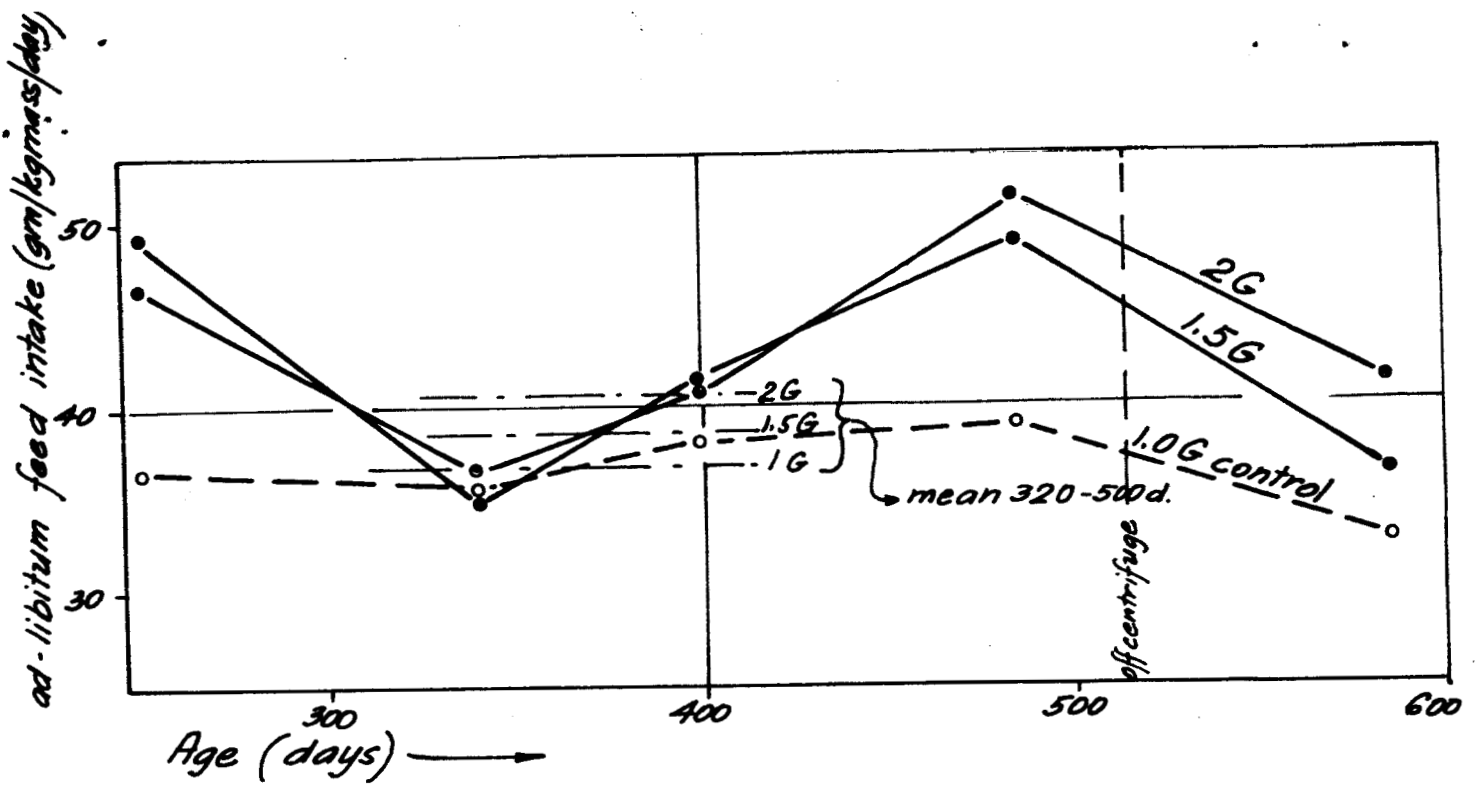
Figure 2:   AD LIBITUM   FEED INTAKE.

Observed feed intake rates of experimental and control groups are given (a):
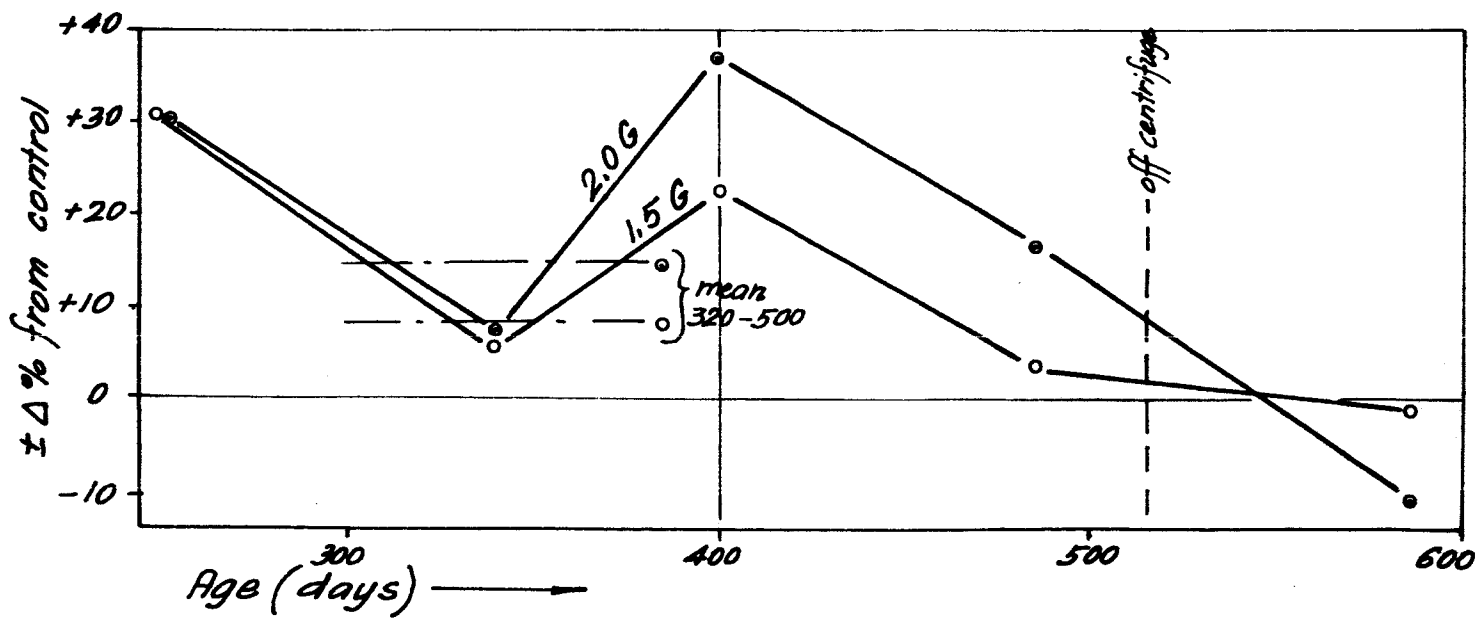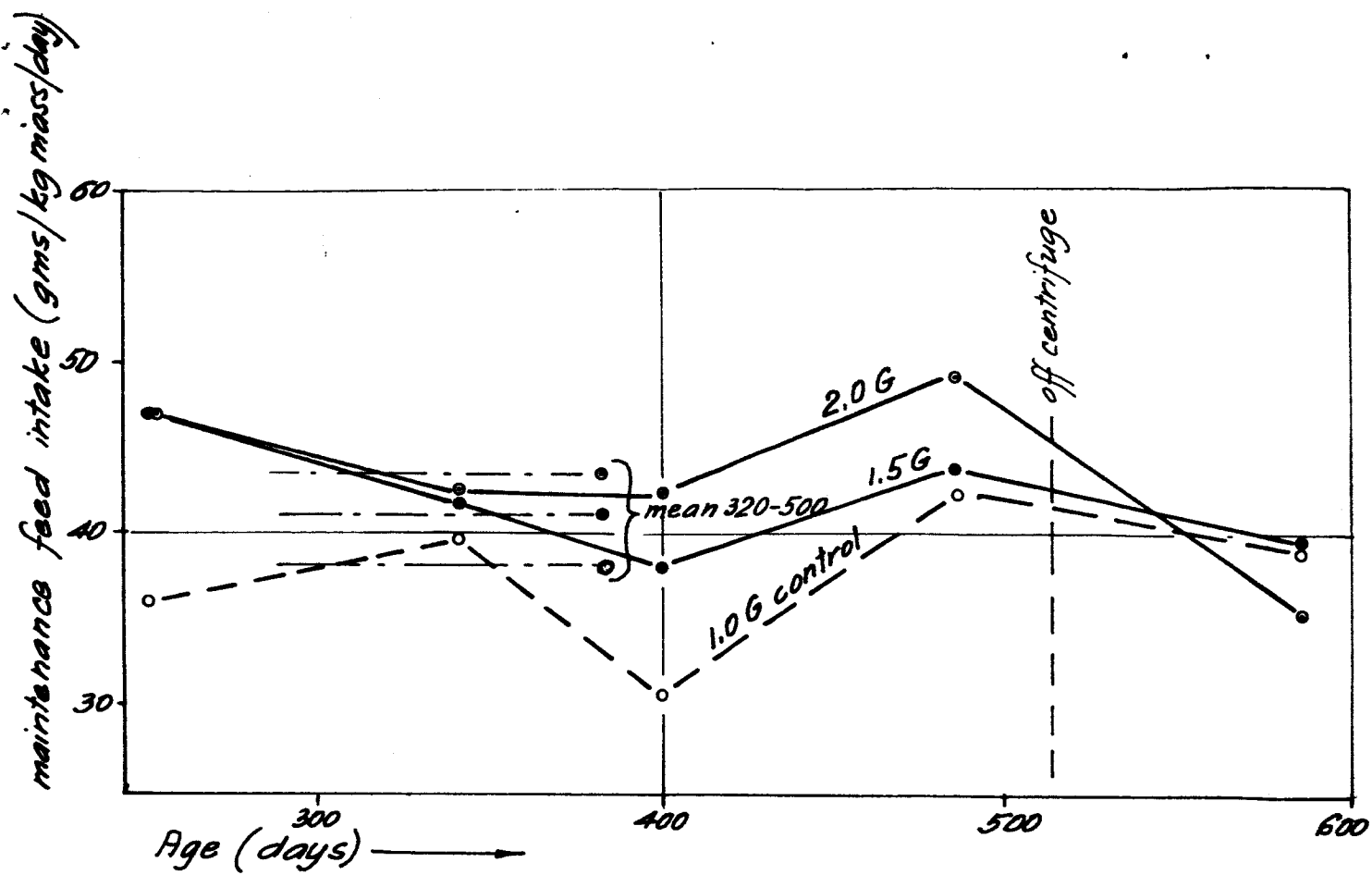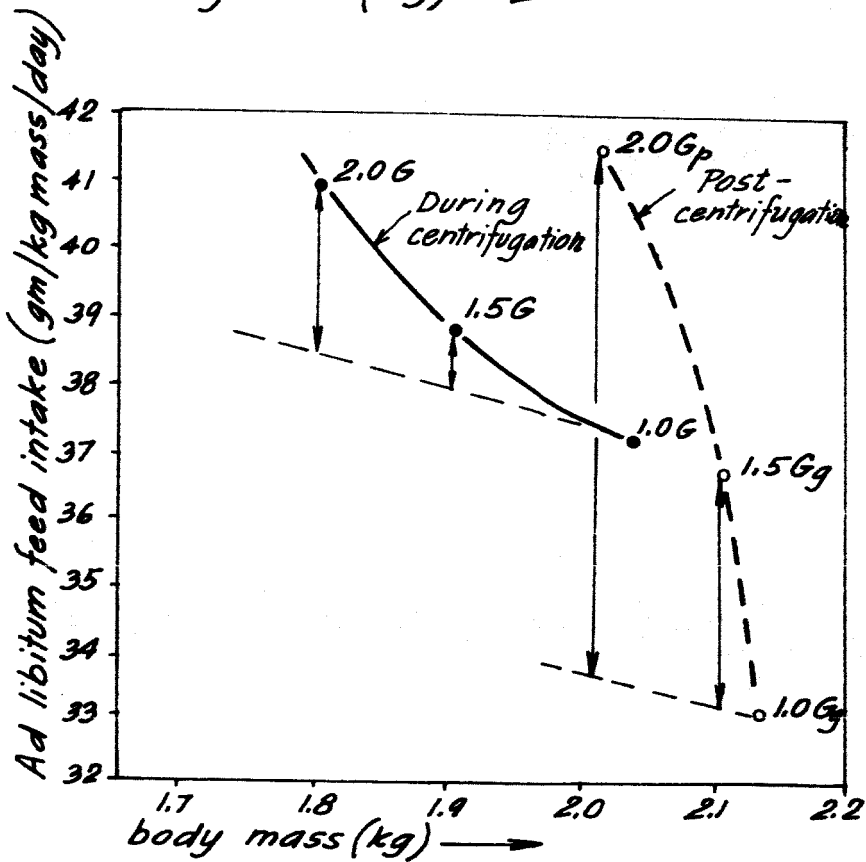in absolute units; and also (b): as ± Δ% of controls, for the experimental
animals.

Figure 3: MAINTENANCE FEED REQUIREMENT.

Calculated maintenance feed requirements for experimental and control groups
are given (a): in absolute units; and also (b) as $\pm$ Δ% of controls for the
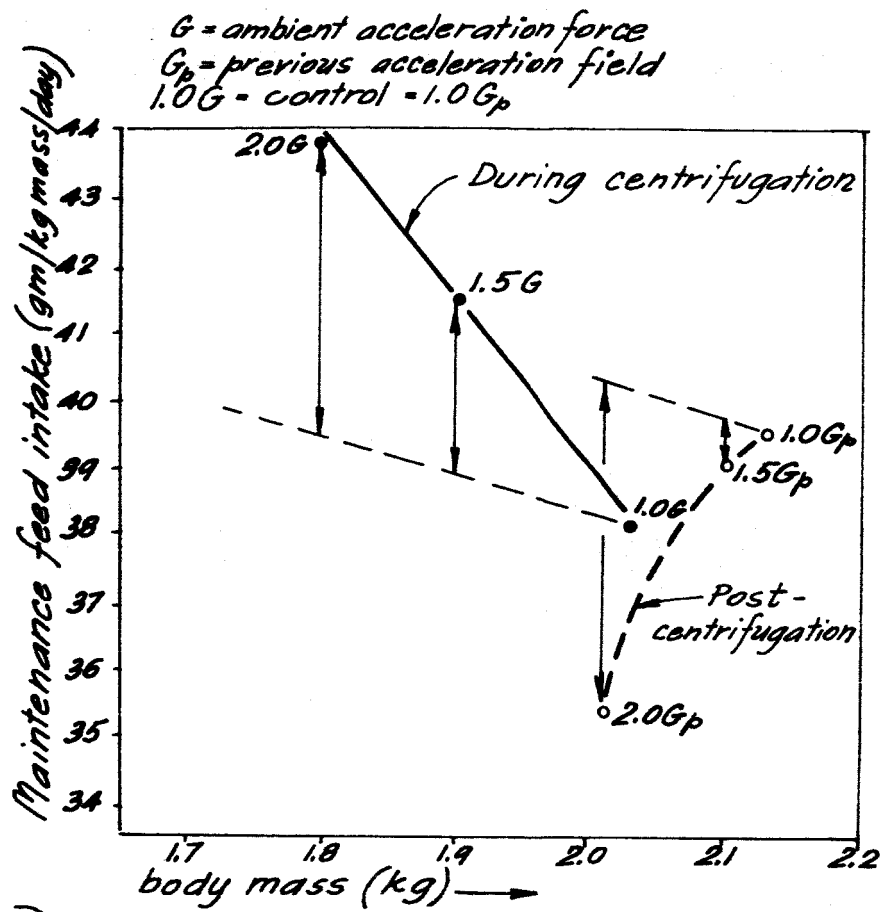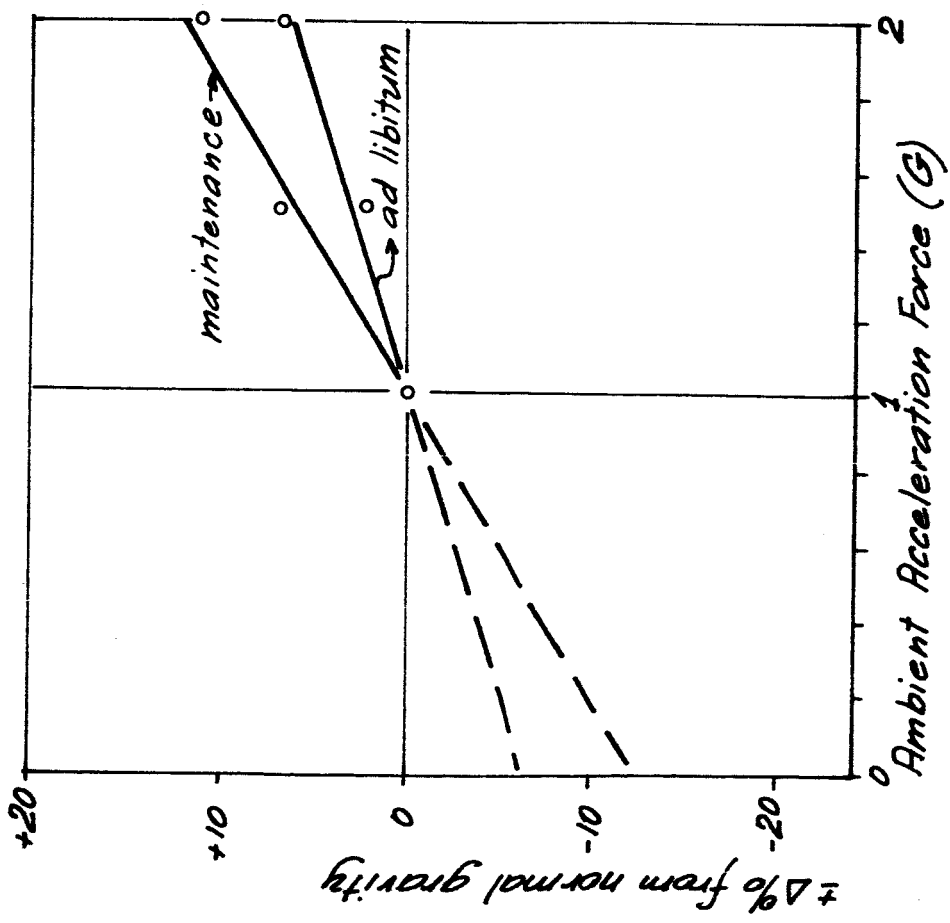experimental animals.

Figure 4: COMPARISON OF FEED INTAKE WITH BODY SIZE

Ad libitum and estimated maintenance feed intakes are given for experimental
and control animals on the basis of body size. For comparison, control values
are adjusted for size, assuming an increase of 0.55 gm/kg body mass/day with
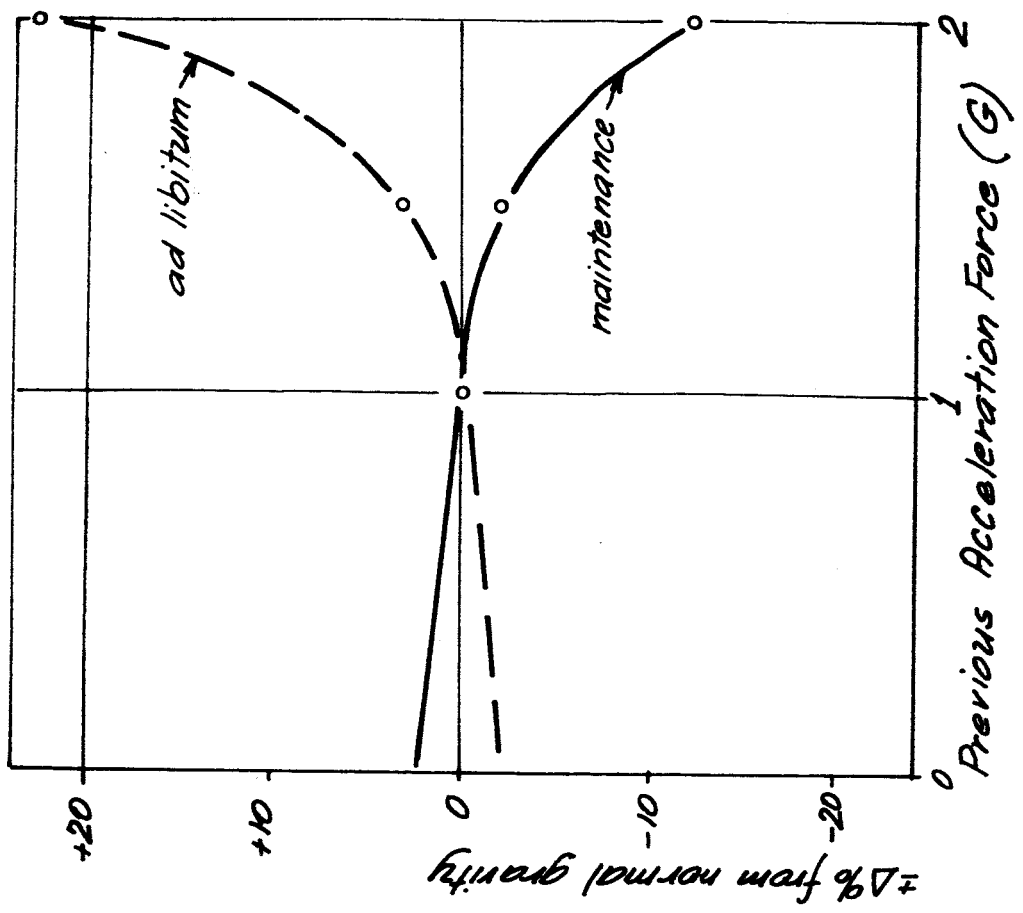each decrease in body size of 0.1 kg (Brody, 1945; p 479).

Figure 5: INFLUENCE OF ACCELERATION FIELD ON FEED INTAKE.