MOTIVATION DEPENDENCE OF BRAIN SELF-STIMULATION IN THE PIGEON

JUAN D DELIUS*, ALAN S WILLIAMS** and ROBERT J WOOTTON***

Department of Psychology, Durham University (Great Britain)

ABSTRACT

Delius, J D , Williams, A S and Wootton, R J , 1976 Motivation dependence of brain self stimulation in the pigeon *Behav Processes*, 1 15—27

Several brain sites in the pigeon were identified as maintaining electrical brain self-stimulation Depending on the site, stimulus currents yielding maximal responding varied from 20 to 160 μA A high proportion of the sites only yielded self-stimulation behaviour if the subjects were deprived of food, when the birds were at full weight there was only one site at which the stimulation continued to be rewarding Some, but weak, evidence of stimulus satiation was found Overt behaviour elicited by non-contingent stimulation did not correlate with the reinforcing or neutral nature of the sites tested While some positive sites were associated with structures known to be involved in the control of feeding, others were not The hypothesis that stimulation at the hunger-dependent sites might have elicited temporary satiation signals is considered

INTRODUCTION

Since the phenomenon of self-stimulation was discovered in 1954 a vast amount of information has been amassed about it However, research has been virtually restricted to mammals, or more precisely to rats There is still very little known about its occurrence and properties in non-mammalian species Initially the research reported in this paper was conceived as an exploratory study on reinforcing electrical brain stimulation in birds and, accordingly, we have also included information that does not directly bear on the title-theme

In rats it is not necessary for a suitable motivating state to be induced for operant conditioning with a brain-stimulation reinforcement to proceed (Reynolds, 1958, Olds, 1958a) Conventional rewards on the other hand usually are not effective without such treatment This contrast has been the source of some theoretical imperspicuity and indeed, ingenuity (see Gallistel, 1973,

Present addresses
* Department of Psychology, Ruhr-Universitat, Bochum (Federal Republic of Germany)
** Department of Psychology, Birkbeck College, London (Great Britain)
*** Department of Zoology, University College, Aberystwyth (Great Britain)

Lenzer, 1972, Rolls, 1975) We present data suggesting that, at least in the
pigeon (*Columba livia*), the discrepancy might not be as general as is assumed
In this species electrical stimulation of many brain sites only supports
instrumental performance if an adequate drive state has been previously
instituted

METHODS

Sixteen adult pigeons of local homing stock and undetermined sex were
anaesthetized with Equithesin (intramuscular, 0 25 ml/100 g), then implanted
with up to 8 intra-cerebral electrodes terminating in miniature sockets cemented
to the skull The uninsulated electrode tips had a surface of between 0 2 and
0 3 mm^2 (Delius, 1966) The implanting was done stereotactically according
to the Karten and Hodos (1967) pigeon brain atlas using a modified Stellar-
Johnson apparatus A 5-cm length of bare stainless steel wire placed under the
scalp served as the neutral electrode One week after the operation the animals
were deprived of food to 80% of their normal weight (350—450 g) and shaped
to peck a key for access to food in a Skinner box A pigeon box with a food
hopper that projected into the box was used for all experiments 50-Hz sine
currents of up to 200 μA r m s could be delivered with a constant current
stimulator via counterbalanced hearing-aid cables to a miniature connector plug
On occasions, ballrace swivel contacts were used to take up cable torsion The
stimulus currents were monitored (as a voltage drop across a series resistor)
with an oscilloscope throughout the experiments The contingencies and the
timing of the events in the Skinner box were programmed with conventional
relay equipment The animals' responses were registered with a cumulative
recorder and electromagnetic counters Further procedural details will be given
below The stimulation sites are identified by a three-digit number, where the
first two digits specify the subject and the third the electrode

RESULTS

Identification of rewarding sites

An experiment of a design similar to that used by Goodman and Brown
(1966) was used to identify electrodes whose stimulation had reinforcing
properties The rate of key-pecking was measured while the birds were at
80% of their normal weight for each of the electrodes under three conditions
(a) when each peck led to 4 s access to food (food reward condition), (b) when
a peck yielded a 1 s (early experiments) or 0 4 s (later experiments) current train
of 120 μA (self-stimulation condition), and (c) when a peck had no sequel
(extinction condition) Each condition was tested 6 times in randomized blocks
consisting of three 10-min sessions Each block was separated by approximately
24 hours Of the 68 sites examined, 17 gave an average of at least 3 times more
responses during the self-stimulation condition than during the extinction

condition and were classified as rewarding In fact these sites could be recognized easily on the basis of the cumulative records While the response scores varied from block to block depending on the order of the conditions, the cumulative records of such sites regularly climbed with a steady, if sometimes shallow, slope during the self-stimulation condition In the extinction condition the records invariably showed the characteristic, progressively decreasing slope (Fig 1)

Two electrodes gave on average one third or fewer responses during the self-stimulation condition than during the extinction condition, and were tentatively classified as aversive The experiment however, was not favourable for the detection of aversive sites because the low response rate during extinction hardly allowed the recognition of a further response depression during self-stimulation (see also Macphail, 1967, Goodman and Brown, 1966)

Stimulation current

For 14 of the rewarding electrodes we determined the current level that yielded maximum response rates The pigeons continued at 80% of their normal weight but received no food reinforcement Five different current
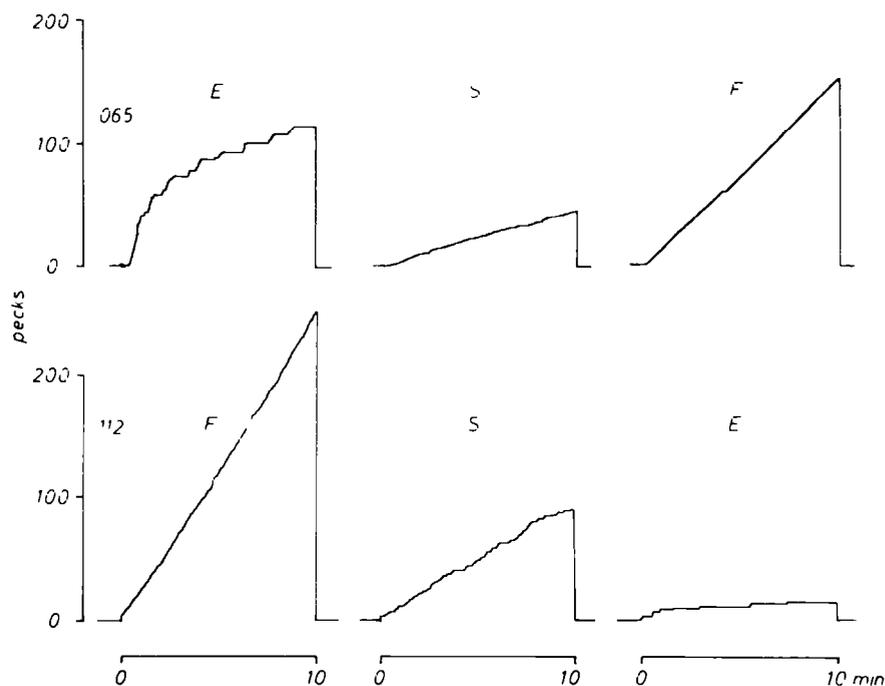

Fig 1 Sample cumulative records of two sessions (sites 065 and 112) from the identification experiment described in the text E = extinction, S = stimulus reward, F = food reward In the session shown for electrode 065 the total number of responses in the S condition is less than the E condition, but the shape of the records is clearly different

levels ranging between 0 and 200 μA were tested in twenty-five 15-min sessions in a random sequence A block of 5 sessions was given each day

The intensity of the stimulation current eliciting the highest rate of response ranged between 20 and 160 μA for the various sites These "best" currents are comparable with those reported in several self-stimulation studies on birds (Goodman and Brown, 1966, Macphail, 1967, Andrew, 1967, Davis et al , 1972) except that Webster and Beale (1970) and Hollard and Davison (1971) report current intensities that are unusually high We found that currents of 400 μA invariably led to convulsions

The shape of the current—response functions varied considerably from site to site This probably relates to the widely scattered anatomical location of our sites (compare Hollard and Davison, 1971, and Davis et al , 1972) At the best current settings the response rates were in each case higher than at the 0 μA current level (t-tests, $p < 0.01$) This confirmed the rewarding nature of stimulation at these sites From now onwards each electrode was stimulated with the corresponding best current intensity

We did not explore systematically the influence of the stimulus train duration but some early, informal experimentation suggested that shorter, 0 4 s trains were more effective than longer, 1 s trains This led to the adoption of the briefer stimulation trains as standard in the later experiments

Hunger dependence

Incidental observations suggested that the rewarding property of the stimulation depended on the food-deprived state of the animal during the preceding experiments Ten of the reinforcing sites were tested systematically in this regard The subjects had five 10-min self-stimulation sessions while at 80% of normal bodyweight and then a further 5 sessions when they had regained full weight 5 days later Table I summarizes the results In the case of 9 of the

TABLE I

Mean responses in 10 min sessions at normal weight and at 80% bodyweight

Electrode	Mean responses/10 min		Significance of difference p
	80% weight	Full weight	
091	385	19	< 0.01
093	86	0	< 0.01
111	293	322	n s
112	124	10	< 0.01
121	114	3	< 0.01
122	159	11	< 0.01
123	411	17	< 0.01
124	133	0	< 0.01
126	208	10	< 0.01
134	65	0	< 0.01

10 sites tested the self-stimulation behaviour extinguished during the sessions at full weight (t-tests, $p < 0.01$) For the remaining site this was not so, the response rate was not affected by the weight manipulation Fig 2 shows typical cumulative records from this experiment for both a deprivation-dependent site and the non-dependent site Five of the 9 sites were tested for their reinforcing property during five 10-min sessions after birds had been deprived of food again to 80% of their weight after a period of between 2 and 5 weeks at full weight Without exception response was resumed in the absence of any priming or retraining with food reinforcement, and maintained throughout the sessions
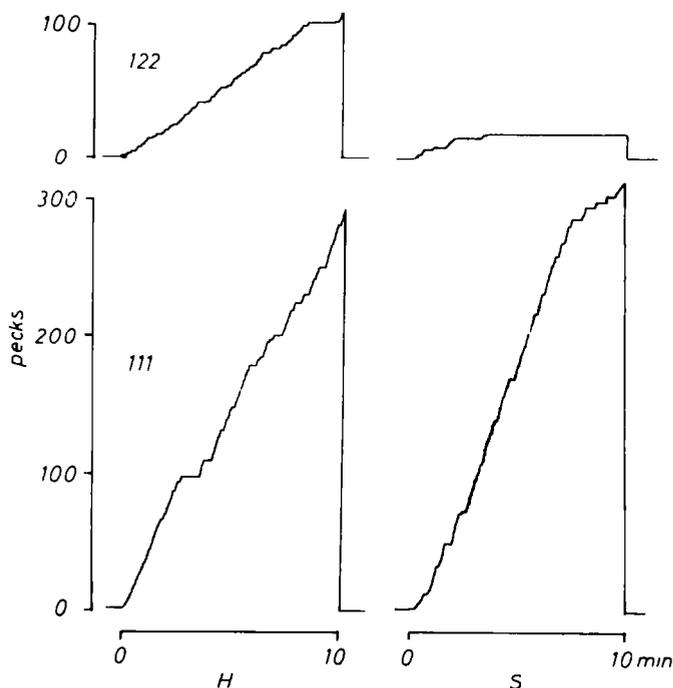

Fig 2 The effect of food deprivation on the self-stimulation rates with two electrodes in pigeons In the hungry condition (H) the animals were at 80% of their normal weight, and in the satiated condition (S) at their normal weight and fully fed

For 3 sites several 10-min self-stimulation sessions were intercalated into the subjects' weight recovery phase, and then again as they were deprived to 80% weight for a second time The session response rates in each case correlated negatively with the current body weight (r values between -0.53 and -0.79, p between < 0.05 and < 0.01) Fig 3 illustrates this dependence for two sites, the third site produced a comparable function

The preceding result suggested that the brain stimulation of the deprivation-dependent sites might have an effect similar to food reward through activation of central satiation mechanisms If this were so one might expect response saturation effects to become apparent in longer self-stimulation sessions Eight
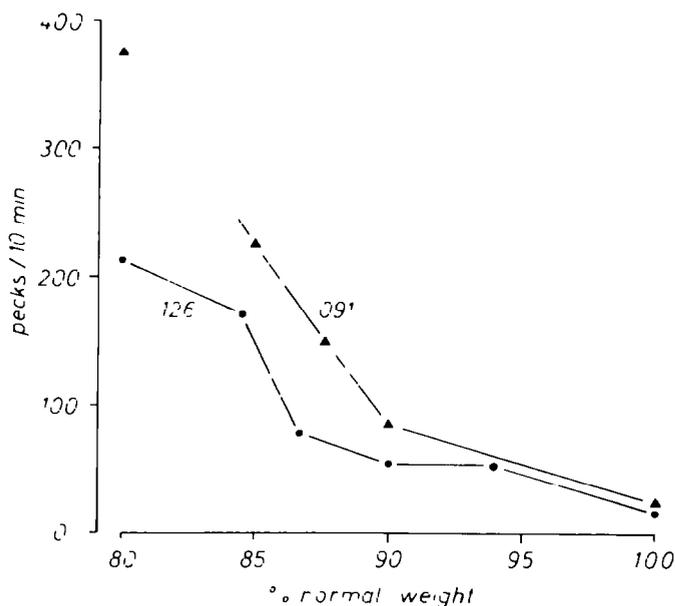
Fig 3 Food deprivation-response rate functions for two self-stimulation sites in pigeon
Each point is an average for two or three data points that were close together on the weight
scale, plotted at their mean weight Spearman correlation coefficients based on the original
data are significant at $p < 0.05$ (091) and $p < 0.01$ (126)

of the deprivation-dependent sites were tested in several sessions of at least
1 hour's duration Between 700 and 4750 key pecks per hour were emitted
depending on the site being stimulated Each electrode produced cumulative
records with a characteristic stepped pattern of its own Typical examples are
shown in Fig 4 The pauses in response that occurred with some sites (site
134 for example) could perhaps represent the result of a short-term satiation
process but the fine response pattern characterizing other sites cannot be con-
fidently interpieted in this way (compare Olds, 1958b)

Overt behaviour

In the same vein it was conceivable that the hunger-dependent self-stimulation
sites might yield overt feeding behaviour upon experimenter-controlled, non-
contingent stimulation (compare Goldstein et al , 1970) The behaviour
elicited by such stimulation was recorded for 58 electrodes, including 14 of
the rewarding sites, during at least 30 stimulation trials each A variety of current
levels (0 to 150 μA) and train durations (0 5 to 60 s) was used including, where
relevant, those that were rewarding Each stimulation setting was tried in not
less than 2 trials
Only one of the rewarding sites yielded food-related behaviour, a diffuse
facilitation of feeding, similar to that described by Harwood and Vowles (1966)
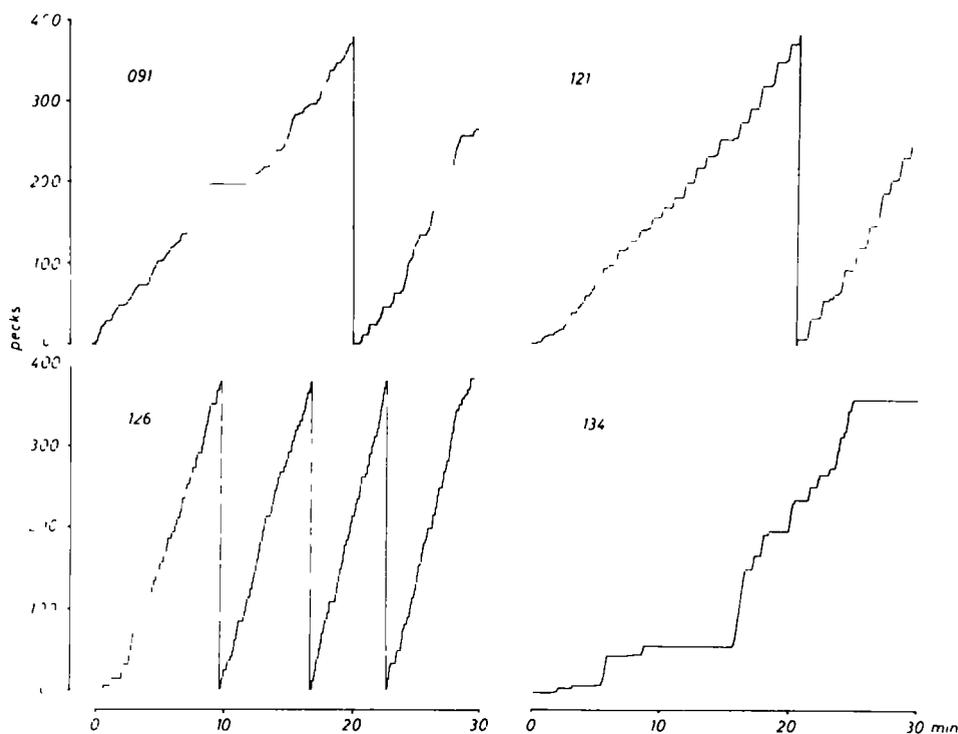
Fig 4 Sample of self-stimulation cumulative records obtained during extended sessions with four different electrodes in pigeons Note the varying stepped patterns of the records

as following stimulation of various forebrain sites in the dove (*Streptopelia risoria*) It must be remarked, however, that clear-cut stimulus-bound eating is very rarely obtained in birds (Wright, 1975) and furthermore that, differing from the self-stimulation experiments, the animals were not now deprived of food On the other hand, the association of self-stimulation and elicited feeding that unquestionably exists in rats represents somewhat of a paradox On general grounds reinforcement would be expected to be associated with the cessation rather than with the initiation of food intake (but see Hoebel, 1969)

More generally, with perhaps one exception, we could find no indication whatsoever of any consistent correspondence between the overt behaviour elicited by a given electrode and its rewarding or non-rewarding property Thus, for example, of 12 electrodes that yielded an attentive posture followed by turning during free stimulation, only 3 maintained self-stimulation Similarly one bird bore 5 electrodes that reliably elicited nearly identical bow-cooing behaviour during non-contingent stimulation, but only 2 of them yielded self-stimulation

The possible exception to this lack of correlation between overt behaviour and stimulation is perhaps the inactivity and drowsiness sometimes associated

with grooming, that we noticed during and after non-contingent, long duration stimulation (60 strains) of 3 out of 4 positively reinforcing medial neostriatum intermedium sites It is interesting to note that one of the areas mentioned in connection with a similar syndrome elicited in gulls by electrical brain stimulation was also the neostratium intermedium (Delius, 1967, 1970, and unpublished) and that Goodman (1974) also reports a few sites in this area yielding drowsiness and sleep This association between self-stimulation and dearousal needs to be confirmed before it is considered any further

Localization

To determine the location of the electrode tips the pigeons were sacrificed and their heads were perfused through the carotids and fixed in formalin After withdrawal of the electrodes the brain was removed from the skull and sectioned (25 μ) transversely in the same plane as the electrode tracks on a freezing microtome The sections were stained with cresyl violet Electrode tips were identified with the aid of a microscope and transferred onto stereotactic atlas (Karten and Hodos, 1967) drawings These are illustrated in Fig 5 The figure also includes the reinforcing sites that have been localized in pigeons by other authors, who are listed in the legend

In birds the quinto-frontal and the fronto-archistriatal tracts have been shown to be essential for the regulation of food intake (Zeigler, 1974) Five of the self-stimulation positive sites are in the immediate vicinity of these structures but only two were shown to be food-deprivation dependent the fifth is the one that was shown to be independent of the hunger state Since the location of the remaining 7 motivation-dependent sites cannot be related with confidence to structures definitely controlling feeding, the issue remains undecided The fact that there is still uncertainty regarding the extension of the neural substrates of feeding in birds (Wright, 1975, Delius, 1971) adds to the difficulty

A cluster of reinforcing sites in the lateral anterior hypothalamus have been reported by Davis et al (1972), and Andrew (1969) refers to active sites in the posterior hypothalamus of the chick Hypothalamic self-stimulation sites in mammals have often been related to the presence there of substrates regulating hunger and thirst (Hoebel and Teitelbaum, 1962) In birds, however, the involvement of the hypothalamus in food intake regulation is not so definite (Wright, 1975, see also Grossman, 1975) In any case, none of the sites in question appears to have been hunger-dependent

A group of positive sites is noticeable in the medial neostriatum intermedium This confirms the findings of other authors (Macphail, 1967, Webster and Beale, 1970, and possibly Andrew, 1969, he only mentions the neostriatum) We note that Harwood and Vowles (1966) obtained a diffuse facilitation of feeding (and preening) with electrical stimulation of this area in doves

Another structure that emerges as supporting self-stimulation is the paleo-striatum (similarly mentioned by Harwood and Vowles) and the lateral forebrain bundle that contains, among others, fibres efferent and afferent to the

Fig 5 The location of the rewarding (dots), aversive (triangles) and neutral (asterisks) sites found in the brain of the pigeon For one rewarding site (probably medial neostriatum intermedium) and a neutral site histology is lacking Rewarding sites from Goodman and Brown (1966), Macphail (1967), Webster and Beale (1970) and Davis et al (1972) have been entered as circles For convenience all points have been transfered to one side of the brain A = archistriatum, AL = ansa lenticularis, Bas = nucleus basalis, BO = bulbus olfactorius, CA = commissura anterior, Cb = cerebellum, CO = chiasma opticum, DS = decussatio supraoptica, E = ectostriatum, EM = nucleus ectomamilaris, HA = hyperstriatum accessorium, HD = hyperstriatum dorsalis, Hp = hippocampus, HV = hyperstriatum ventrale, Imc = nucleus isthmi magnocellularis, FA = tractus fronto-archistriaticus, FPL = fasciculus prosencephali lateralis, LPO = lobus paraolfactorius, N = neostriatum, NC = neostriatum caudale, NI = neostriatum intermedium, OM = tractus occipito-mesencephalicus, Ov = nucleus ovoidalis, PA = paleostriatum angmentatum, PMH = nucleus posteromedialis hypothalami, PP = paleostriatum primitivum, PT = nucleus pretectalis, PVM = nucleus posteroventralis medialis, QF = tractus quintofrontalis, Rt = nucleus rotundus, Ru = nucleus ruber, S = septum, SP = nucleus subpretectalis, SPC = nucleus superficialis parvocellularis, TeO = tectum opticum, ThD = thalamus dorsalis, TrO = tractus opticus, TSM = tractus septomesencephalicus, TT = tractus tecto-thalamicus

paleostriatum (Macphail, 1967, Goodman and Brown, 1966, our data)

Andrew (1967, 1969) reports sites in the tractus septomesencephalicus and the neighbouring septum of the chick as positively reinforcing Goodman and Brown (1966), Macphail (1967), Davis et al (1972) and our data, however, indicate that stimulation of the medial forebrain bundle and the septal area in pigeons is not reinforcing, though in mammals these areas support self-stimulation

Hollard and Davison (1971) and again Davis et al (1972) mention self-stimulation sites in the ectostriatum Macphail's (1967) and our few sites in this structure did not lead to self-stimulation The issue is of some interest because the ectostriatum is known to be a major visual projection area (Karten, 1969) Andrew (1969) finally mentions hippocampal positively reinforcing sites in chicks but a few sites of ours do not confirm this for the pigeon

DISCUSSION

The issue of motivational dependency requires further comment While increments in rates of self-stimulation with food deprivation do occur in rats (Olds, 1958a, Blundell and Herberg, 1968, Goldstein et al , 1970, Gallistel and Beagley, 1971, Drewett and Herberg, 1975) the dependence is not as absolute as that observed by us in pigeons where self-stimulation ceased completely when the subjects were satiated in the case of 9 sites out of 10 The situation was similar in one of two self-stimulation sites studied by Goodman and Brown (1966), and Macphail (1966) also makes reference to a deprivation dependence concerning some of the sites he dealt with

We must consider the possibility that the procedure of initially shaping key-pecking with food reward and then testing the rewarding quality of electrical stimulation by its capacity to maintain responding might have some-how been instrumental in bringing about the deprivation dependence One mechanism by which this could have occurred, namely that the electrical stimulation acquired secondary reinforcement properties through association with food reward, can be excluded since at no time during the experiment was there any short-term contingency between the two events Furthermore, apart from the initial test, the animals were exclusively reinforced with brain stimulation Several of the sites served successfully in further experiments not reported here, for example, an experiment involving responding under inter-mittent brain stimulation reward, and another involving visual pattern dis-crimination learning with the same reward, without ever receiving food other than in the home cage Any tenuous associations that might have arisen in the initial tests can surely be expected to have extinguished (see also Macphail, 1968) Nonetheless, it must be examined empirically whether brain sites can be found whose stimulation does not lead to shaping of key-pecking when the pigeons are satiated but does when they are deprived, without the operant response being initially shaped with a food reward Additionally, there is the question of the motivation specificity A preliminary experiment with one of our sites indicated that water deprivation cannot replace the food depri-

vation but this needs to be examined more thoroughly (see also Macphail, 1966) If the above finding were confirmed, could one then find sites whose reinforcing property is specifically thirst dependent? (Compare Gallistel and Beagley, 1971)

At this stage the simplest hypothesis seems to be that stimulation at the deprivation-dependent sites generates satiety signals partially equivalent to those produced by rewarding food ingestion The fact that response saturation did not occur reliably in our extended sessions could be due to the circumstance that while repeated food consumption leads to satiation signals integrating over time, electrical stimulation only generates transitory, non-cumulative signals If this difference can be overcome with longer stimulation trains it would be possible to test whether the stimulation would inhibit food consumption, as satiation signals should A preliminary experiment done with one of the hunger-dependent sites supports this equivalence hypothesis It indicated that free access to food for 5 minutes, not leading to an appreciable weight gain of the animal (short-term satiation) was effective in suppressing self-stimulation for the following 10 to 15 minutes (compare Blundell and Herberg, 1968, Hoebel, 1969)

While we only found the stimulation of one site to be rewarding independently of food deprivation, other authors (Macphail, 1966, Goodman and Brown, 1966, Andrew, 1967, 1969, Webster and Beale, 1970, Davis et al , 1972) have identified a number of sites that do not depend on the induction of an identifiable motivational state The reinforcing qualities of electrical brain stimulation do not differ in this respect from normal rewarding events It is now sufficiently plain that many natural reinforcers are capable of supporting instrumental learning in the absence of any specific motivational manipulations whereas others are only effective when gated by specified drive states

ACKNOWLEDGEMENTS

REFERENCES

Andrew R J , 1967 Intracranial self-stimulation in the chick Nature, Lond , 213 847—848
Andrew, R J , 1969 Intracranial self stimulation in the chick and the causation of emotional behaviour Ann N Y Acad Sci , 159 625—639
Blundell, J E and Herberg, L J , 1968 Relative effects of nutritional deficit and deprivation period on rates of electrical self-stimulation of the lateral hypothalamus Nature, Lond , 219 627—628

Davis, A H , Davison, M C and Webster, D M , 1972 Intracranial reinforcement in the pigeon an analysis using concurrent schedules Physiol Behav , 9 385—390

Delius, J D , 1966 Some techniques for the electrical brain stimulation of small un restrained animals Med Biol Eng , 4 393—397

Delius, J D , 1967 Displacement activities and arousal Nature, Lond , 214 1259—1260

Delius, J D , 1970 Irrelevant behaviour, information processing and arousal homeostasis Psychol Forsch , 33 165—188

Delius, J D , 1971 Foraging behaviour p tterns of herring gulls elicited by electrical forebrain stimulation Experientia, 27 1287—1289

Drewett, R F and Herberg, L J , 1975 Hypothalamic self-stimulation in the female rat effects of oestrus and food deprivation Physiol Behav , 14 285—289

Gallistel, C R , 1973 Self-stimulation the neurophysiology of reward and motivation In J A Deutsch (Editor), Physiological Basis of Memory Academic Press, New York, pp 175—267

Gallistel, C R and Beagley, G , 1971 Specificity of brain stimulation reward in the rat J Comp Physiol Psychol , 76 199—205

Goldstein, R S , Hill, T E and Templer, D I , 1970 Effects of food deprivation on hypo thalamic self-stimulation in stimulus bound eaters and non-eaters Physiol Behav , 5 915—918

Goodman, I J , 1974 The study of sleep in birds In I J Goodman (Editor), Birds Brain and Behavior Academic Press, New York, pp 133—164

Goodman, I J and Brown, J L , 1966 Stimulation of positively and negatively reinforcing sites in the avian brain Life Sci , 5 693—704

Grossman, S P , 1975 Role of the hypothalamus in the regulation of food and water intake Psychol Bull , 82 200—224

Harwood, D and Vowles, D M , 1966 Forebrain stimulation and feeding behaviour in the ring dove J Comp Physiol Psychol , 62 388—396

Hoebel, B G , 1969 Feeding and self-stimulation Ann N Y Acad Sci , 157 758—778

Hoebel, B G and Teitelbaum, P , 1962 Hypothalamic control of feeding and self stimulation Science, 135 375—377

Hollard, V and Davison, M C , 1971 Preference for qualitatively different reinforcers J Exp Anal Behav , 16 375—380

Karten, H J , 1969 The organization of the avian telencephalon and some speculations on the phylogeny of the amniote telencephalon Ann N Y Acad Sci , 159 625—639

Karten, H J and Hodos, W A , 1967 A Stereotaxic Atlas of the Brain of the Pigeon Johns Hopkins, Baltimore, 193 pp

Lenzer, I , 1972 Differences between behaviour reinforced by electrical stimulation of the brain and conventionally reinforced behaviour Psychol Bull , 78 103—118

Macphail, E M , 1966 Self-stimulation the problem of priming Psychon Sci , 5 7—8

Macphail, E M , 1967 Positive and negative reinforcement from intracranial stimulation in pigeons Nature, Lond , 213 947—948

Macphail, E M , 1968 Self-stimulation in pigeon tests of two alternative explanations Psychon Sci , 11 3—4

Olds, J , 1958a Effects of hunger and male sex hormone on self-stimulation of the brain J Comp Physiol Psychol , 58 320—324

Olds, J , 1958b Satiation effects in self-stimulation of the brain J Comp Physiol Psychol , 58 675—678

Reynolds, R W , 1958 The relationship between stimulation voltage and rate of hypothalamic self-stimulation in the rat J Comp Physiol Psychol , 58 193—198

Rolls, E T , 1975 The Brain and Reward Pergamon Press, Oxford, 115 pp

Webster, D M and Beale, I L , 1970 Intracranial self-stimulation in the pigeon the effect of current intensity Psychon Sci , 20 15—17

Wright, P , 1975 The neural substrate of feeding behaviour in birds In P Wright, P G

Caryl and D M Vowles (Editors), Neural and Endocrine Aspects of Behaviour in Birds Elsevier, Amsterdam, pp 319—349
Zeigler, H P , 1974 Feeding behaviour in the pigeon a neuro-behavioral analysis In I J Goodman (Editor), Birds Brain and Behaviour Academic Press, New York, pp 103—132