use of this test, the role of sex hormones in the acquisition of the capacity to reason and thereby to discover the effect of gonadal maturation on post-natal neural maturation. It is well known that instinctive behaviour (e.g. sexual responses) can be induced by hormonal conditioning, and it has also recently been shown that performance of a learned response can be altered by hormonal conditioning (Douglas, Hanson & Zuckerman, 1948). The problems set in the present study were therefore, first, to confirm Maier's (1932*a*) conclusion that young rats do not solve the three-table problem as well as adults; and then to find how a premature puberty, induced and maintained from 22 days of age onwards by injection of a gonadotrophin, affects the capacity of pre-pubertal animals to solve the problem.

Since Maier's (1929, 1932*a*, *b*, *c*) early investigations on reasoning in rats, the three-table test has been used to investigate both the dependent and independent variables of the process of reasoning. One salient fact that is immediately obvious when one compares investigations on the effect of cerebral injury (Maier 1932*b*, *c*), diet (Wentworth, 1936), genetic stock (Loevinger, 1938), bromides (Hamilton & Harned, 1944), and glutamic acid (Hamilton & Maher, 1947), on reasoning, and on the relation of reasoning to learning (Campbell, 1935; Vaughn, 1937; Wolfe & Spragg, 1934), is that the success of animals has varied greatly in different investigations. Any satisfactory account of the three-table test should therefore indicate a basis for these wide variations. Suggestions that they are due to inherent differences in the reasoning capacity of animals of different genetic stock (e.g. Maier, 1935; Hamilton & Maher, 1947) only beg the question. The results of the present study lead to more specific answers to the question.

MATERIALS AND METHODS

Apparatus

The apparatus used in the three-table test for reasoning, which has been described in detail by Maier and other workers, consists essentially of three tables of different shapes. They are equidistant from and connected to a centre point by 1½ in. wide and 3 ft. 6 in. long elevated wooden runways. Each table surface is of a different texture, and food placed on a table cannot be seen from the centre point, because a wooden shield is placed along the centrally directed edge of the table. Two such apparatuses, housed in adjacent rooms, were used in the present investigation. Since the results at no time differed significantly for comparable groups, the group results were pooled as if all the animals were performing on the same apparatus.

Subjects

One hundred albino rats (forty-eight males, fifty-two females) from eighteen litters were used. They were bred by the experimenter so that the exact age was known. After weaning, they were divided into groups of similar ages, as shown in Table 1. Each group contained the litter-mates of one sex from two or three litters, and comparable groups of litter-mates of each sex were used side by side on the test, so that the performance of the sexes could be compared. All except groups

VII and VIII, which are considered below, were fed in their cages until 7 days before the beginning of the test.

Vaginal smears were taken daily during the test period from group VI.

Table 1. *Composition of groups of experimental animals and sequence of experiments*

Series	Group no.	Age at test (days)	Cage no.	Sex	Injection	No. of animals		Dates of test
						In cage	In group	
1	I	30–50	H_1	Male	—	7	10	1. xii. 47–15. xii. 47
			H_2			3		
	II	30–50	J_1	Female	—	6	11	1. xii. 47–15. xii. 47
			J_2			5		
	III	50–70	B	Male	—	3	14	14. xi. 47–29. xi. 47
			D			9		7. xii. 47–21. xii. 47
			E			2		10. i. 48–24. i. 48
	IV	50–70	A	Female	—	5	19	14. xi. 47–29. xi. 47
			C			3		7. xii. 47–21. xii. 47
			M			11		10. i. 48–24. i. 48
	V	70–90	K	Male	—	6	12	14. i. 48–29. i. 48
			L			6		30. i. 48–12. ii. 48
	VI	70–90	N_1	Female	—	9	10	14. i. 48–28. i. 48
			N_2			1		30. i. 48–12. ii. 48
2	VII	30–50	O_1	Male	Gonadotrophin	6	12	13. ii. 48–28. ii. 48
			P_1	Male	Saline	6		
	VIII	30–50	O_2	Female	Gonadotrophin	6	12	13. ii. 48–28. ii. 48
			P_2	Female	Saline	6		

Hormonal treatment

Groups VII and VIII were taken from two large litters (containing fourteen and ten animals) which were born on the same day, and in which there were twelve males and twelve females. These litters were divided into males and females after weaning at 22 days of age. Six males (cage O_1) and six females (cage O_2) were then injected daily with 10 i.u. of pregnant-mare serum ('Antostab') in 0·1 c.c. saline. Their litter-mates (cages P_1, P_2) were injected with 0·1 c.c. saline only. The vaginae of the gonadotrophin-injected females opened 3–5 days after the first injection. The injections were continued daily until after the experiment was finished.

The methods of training and testing were similar to those used by Maier, Campbell, Loevinger and others.

Training

Groups of animals of the same age (± 2 days) were taken 7 days before the beginning of the test, and allowed to explore the apparatus for 1 hr. daily, after which each was given a large piece of bread soaked in milk in a separate cage, and was allowed to feed for 30 min. In their home cages they were allowed water *ad lib.* only. On one day each week neither training nor testing took place, and animals were fed in their home cages. 10 g. rat cake per animal was placed in each cage on this day. Within 6 days all animals had learned to run freely over the apparatus.

Testing

Fifteen tests were given, the first three of which are not included in the results. Testing was begun so that the tests on which scoring was based took place between 35 (±2) and 50, 55 (±2) and 70, and 75 (±2) and 90 days of age.

For the test, each animal was placed with a piece of bread soaked in milk on a table (food table) and allowed to nibble for 30 sec. The rat was then lifted from the table and placed directly on one of the other two tables (start table). If the animal returned directly to the table on which food was placed, the test was recorded as correctly solved. After feeding for 30 sec. on the food table, each animal was placed in a separate cage and allowed to feed for 30 min. In their home cages the animals were allowed water *ad lib.* only for the duration of the tests.

The two non-contiguous experiences thought by Maier to be combined in the solution of the problem of where the food lay were (*a*) knowledge of the apparatus acquired during training, and (*b*) knowledge of the table carrying food on the day of the test. Each day different start and food tables were used. Rotas were devised in which the six possible combinations of start and food tables were used in order. Each animal was on one of four different rotas, so that on any one day only a quarter of the animals was required to make the same response. This ensured that no olfactory trail was established.

Criterion of performance

A run was correct if the animal did not go more than half-way to the incorrect table. It was otherwise regarded as incorrect. The number of equivocal responses was very small.

RESULTS

The pooled results for each age group, in terms of right (+) and wrong (−) responses, are given in Table 2. The results are also scored in Maier's notation, so that comparison may be made with other workers' results. Maier expressed results as a percentage of right—wrong/total responses. According to his index the score that would result if the direction at the choice point were determined by chance only (i.e. 50 % correct responses), is marked as 0 %. Comparisons between groups of different

Table 2. *Pooled scores in the Maier test, in terms of right (+) and wrong (−) responses, of rats of comparable ages*

Groups	Age (days)	No. of animals	Score		Total trials	Success Maier index (%)
			+	−		
I and II	30–50	21	174	78	252	38·1
III and IV	50–70	33	274	122	396	38·5
V and VI	70–90	22	210	54	264	50·1
VII and VIII	30–50	24	249	39	288	72·9

age and sex were made by means of the χ^2 test, and results and comparisons are presented in Tables 3–6. In all comparisons there is only one degree of freedom.

The results show that in the first series of tests (groups I–VI) there is a gradient of acquisition of the ability to solve this problem (Table 2). Groups III and IV were not significantly more successful than groups I and II, whereas groups V and VI were significantly more so than either groups I and II or groups III and IV (Table 3). Comparison of the performance of males and females shows that between 70 and 90 days the males were significantly more successful than the females (Table 5). The females were also less successful than the males between 30 and 50 days and between 50 and 70 days of age. The differences at these ages are not statistically significant.

Table 3. *Comparisons of differences in performance of groups of rats of different ages*

Groups	Compared with groups	χ^2	P
I and II	III and IV	0·0015	>0·95
	V and VI	7·40	<0·01
	VII and VIII	23·97	<0·001
III and IV	V and VI	8·68	<0·01
	VII and VIII	27·68	<0·001
V and VI	VII and VIII	4·68	<0·05

Table 4. *Scores of each group of animals*

Group	Age (days)	Sex	No.	Score		Success Maier index (%)
				+	−	
I	30–50	Male	10	85	35	41·6
II	30–50	Female	11	89	43	34·8
III	50–70	Male	14	124	44	47·6
IV	50–70	Female	19	150	78	31·6
V	70–90	Male	12	120	24	66·7
VI	70–90	Female	10	90	30	50·0
VII E*	30–50	Male	6	63	9	75·0
VII C†	30–50	Male	6	64	8	77·8
VIII E*	30–50	Female	6	58	14	61·1
VIII C†	30–50	Female	6	64	8	77·8

* E = Experimental group. † C = Control group.

Table 5. *Comparisons of differences in performance of male and female rats in comparable age groups*

Males in group	Compared with females in group	χ^2	P	Pooled results	
				χ^2	P
I	II	0·34	0·50		
III	IV	2·93	0·05	5·559	<0·02
V	VI	9·589	0·01		
VII E	VIII E	1·34	0·20		
VII C	VIII C	0·07	0·70	0·74	>0·30

These results appear to confirm Maier's findings (1932*a*). The conclusion that young animals are unable to equal the reasoning ability of adults, drawn from the results of this test, was not, however, confirmed by the performance of the group receiving gonadotrophin and their control group. The pooled results from both sexes, and the results from both experimental and control groups independently, show that the performance of all groups in this later series was significantly more successful than that of any of the previous groups, and was as good as the most successful results reported in the literature (Tables 3, 4). There was no significant difference between the performance of experimental and control groups, or males and females, in groups VII and VIII (Tables 5, 6).

The results of all groups were also analysed to discover whether there was evidence of improvement in group performance during the course of the test. None was found in any group.

Table 6. *Comparison of performance of experimental and control animals in groups VII and VIII, together with comparison of difference in performance*

Groups		Scores		Total group score		Comparison of difference	
		+	−	+	−	χ^2	*P*
Experimental	VII	63	9	121	23	1·30	>0·20
VII E and VIII E	VIII	58	14				
Control	VII	64	8	128	16		
VII C and VIII C	VIII	64	8				

DISCUSSION

The wide variation in success of apparently comparable groups is thus similar to the variation found when the results of previous investigators are compared. The present results, however, are the work of one experimenter, and it is therefore possible to analyse what difference in the treatment of groups I–VI, on the one hand, and the control animals (which had been injected with saline only) in groups VII and VIII on the other, resulted in the greater ability of the latter to solve the problem.

There were two main differences in the treatment of the two sets of animals. Groups VII and VIII were handled extensively while receiving the injections of gonadotrophin and saline between 22 days of age and the end of the test period, and also, since they were tested last in the series, the experimenter had acquired greater experience and ability in conducting the tests. It is generally acknowledged that daily hypodermic injection of animals produces in time a marked adjustment in their somatic and autonomic responses to handling, and hence in the 'emotional' adjustment to other procedures. That 'emotional' adjustment may be a factor governing the success of rats on the three-table test has also been suggested in a postcript to Loevinger's analysis of reasoning in maze-bright and maze-dull rats (1938).

In the present experiment the rapidity with which the control animals in groups

VII and VIII became adjusted to the apparatus during training, and with which they responded during the tests, was in marked contrast to the slower time in adjustment and performance shown by earlier groups. No direct measurement of the former impression was made, but the time taken by groups VII and VIII to reach the food table after being placed on the start table was less than that taken by groups of animals tested earlier in the course of the experiment. Since the times for all animals were not recorded, these figures are not given.

Adequate 'emotional' adjustment is obviously not the only requirement for successful solution of the problem, but it is one that must be present before the factors in the situation upon which success depends can be utilized by the animal during the response. The results presented here show that 'emotional' adjustment may be the major variable on which success in solving the problem depends. The information that is given or implied in earlier reports confirms this conclusion, in so far as the most successful results recorded are those of Maier, who probably gained considerable experience in training animals while designing the apparatus. Many of his rats that had suffered cortical destruction were able to solve the problem with more success than intact animals at the hands of other workers. Similarly, Vaughn (1937) reports scores better than those that chance would determine, although his animals were required to solve a more difficult problem in which four tables were used. He also had handled these animals extensively in the course of earlier investigations. Wolfe & Spragg (1934), who present results showing evidence of improvement in group performance during the course of a test, suggest that previous training in similar situations may be necessary for successful performance. These authors are, however, considering specifically adjustment to the three-table test, and not adjustment to experimental procedures in general.

The present data also answers the question whether the better performance shown at 70–90 days of age compared to that at 50–70 days is entirely due to the fact that the older animals were tested later, when greater experience in the conduction of the test had been gained.

Although most of the tests on animals between 30 and 70 days of age were concluded before those on animals 70–90 days of age were begun, Table 2 shows that the animals in cages E and M, and K and N_1 (50–70 and 70–90 days of age respectively) were all tested between 10 and 29 January 1948. Since the handling of these animals was standardized, it is thought that the difference in age of the groups could be the only variable involved if a difference in their performance were found. A comparison between these groups shows that the group between 50 and 70 days of age performed less successfully than the group 70–90 days of age. The difference is highly significant (Table 7). Since, however, the sexes are unevenly balanced in these groups, and since it has been shown (Table 5) that females perform significantly less successfully than males, a comparison of the females only in each group is also given (Table 7). This shows that the older females were more successful, and that the probability that the difference is due to chance is between one in twenty and one in fifty. It may be noted that the female rats used were from a strain in which vaginal opening appeared most commonly between 45 and 55 days

of age. This indicates the possibility that the better performance of the older animals is due to their more adequate adjustment to the changes in external and internal environment that result from increased activity of sex hormones after puberty.

Table 7. *Comparison of groups in series* 1 *that were tested between* 10 *and* 29 *January* 1948

Cage no.	Age (days)	Sex	No.	Score		Total score		χ^2	P
				+	−	+	−		
E	50–70	Male	2	17	7				
M	50–70	Female	11	81	51	98	58	9·50	<0·01
K	70–90	Male	6	60	12				
N_1	70–90	Female	9	80	28	140	40		
M	50–70	Female	11	81	51	81	51	4·33	<0·05
N_1	70–90	Female	9	80	28	80	28		>0·02

It is therefore concluded that age may be a variable in the ability to perform this test, given that the 'emotional' adjustment of the animals is not complete. This suggests that the ease with which an animal adjusts emotionally to a situation is greater after 70 days of age than between 50 and 70 days of age, but that if adequate adjustment is made (and it can be made before 50 days of age), it is within the capacity of the pre-pubertal rat to solve the problem presented by the three-table test.

The cause of the significantly greater success of males than females also requires explanation. This sex difference is not observed in the results of groups VII and VIII, although the fact that the gonadotrophin-injected females do not appear to differ significantly from either the gonadotrophin-injected males or from the saline-injected females among their litter-mates may be attributable to the small size of the sample. The significant sex difference is not present either in the groups in series 1 of 30–50 and 50–70 days of age (groups I and II, and groups III and IV respectively), although the difference between the latter groups approaches significance. It may be noted that Maier (1935) found no difference between the performance of males and females, and that, as far as can be discovered, all other workers have used males only in this test.

The conclusion that can be drawn from Maier's results and those presented in this paper is therefore that when factors are present in the experimental situation that tend to prevent successful performance, the effects of these factors are greater on the post-pubertal female than the post-pubertal male. When, however, these factors are not sufficient to interfere markedly with performance. no sex difference is found. If it is possible to interpret 'reasoning' in terms of the effects of immediate environmental variations on the central nervous system, rather than in terms of central nervous system function divorced from immediate environmental control, the above conclusion may be restated in the following terms. If the connexion between stimulus and response is sufficiently strong, either because motivation is high or because no inhibiting factors are present, the factors tending to weaken the

response that are present only (or to a greater extent) in the post-pubertal female will be subthreshold. Such factors may, however, reach a threshold value if the strength of the connexion between stimulus and response is lessened.

Since Douglas *et al.* (1948) have reached a similar conclusion in an investigation on the effects of female sex hormone on learning, it seems possible that the processes involved in solving the three-table problem may be subject to the same modification as are these involved in learning, and that the difference between the sexes may be due to the effects of oestrogens on the female.

However, although the vaginal smears of group VI were taken daily during the test period, no significant difference could be found between percentage of success of animals in vaginal oestrus and of those in vaginal dioestrus. Thus, if there is a relationship between vaginal oestrus and lack of success in solving the problem, the relationship is not a direct one.

The results reported here thus suggest that the ability of rats to solve the problem presented by the Maier three-table test depends to a large extent on the adaptation of the animals to the situation, and that, given adequate adaptation, there are enough cues, either present at the moment of response or derived from the past experience of an animal, to enable a group of rats between 30 and 50 days of age to solve the problem in as high a proportion of trials as that recorded by adult rats in Maier's previous experiments.

If, however, adaptation to the experimental procedure is incomplete, both age and sex may be variables upon which the success of the response depends. Since it is possible for young females to solve the problem as successfully as adult males, the effects of age and sex must therefore be primarily on the adaptation of the animals, and not primarily on their capacity to 'reason'. Animals 50–70 days of age adapt less well to the apparatus than do animals 70–90 days of age, and post-pubertal females adapt less well than post-pubertal males. It is not certain what causes the physiological variations that underlie each of these differences, but it is possible that both are due to the effects of sex hormones on the nervous system.

SUMMARY

The effect of age, sex, and a prematurely induced puberty on the solving of Maier's three-table test by rats has been investigated.

It is found that rats 70–90 days of age are able to solve the problem more successfully than rats 30–70 days of age, unless the animals are fully adjusted to the experimental procedure. When fully adjusted, rats 30–50 days of age can solve the problem more successfully than animals 50–90 days of age, and just as successfully as the adults previously investigated by Maier.

Post-pubertal females have been found to be less successful in problem solving than post-pubertal males. The cause of this difference appears to lie in difference in the adjustment of animals to experimental procedure, and not primarily to differences in 'reasoning' ability.