Tolman and Tryon

Early Research on the Inheritance of the Ability to Learn

Nancy K. Innis   *University of Western Ontario, London, Ontario, Canada*

Few psychologists today are aware of the seminal role played by learning theorist Edward C. Tolman in the early development of the field of behavior genetics. Tolman was the first to publish a study of selective breeding for maze-learning ability in rats. He continued to foster research in this field by supporting the work of his students, particularly Robert C. Tryon. Tryon carried out the first major long-term study of maze-bright *and* maze-dull *rats. This article focuses on Tolman's early years at Berkeley and the events culminating in the inheritance project, as well as on the evolution of this research under Tryon's direction.*

Psychology and biology have at least one thing in common—the enormous debt owed to Charles Darwin, whose theory of evolution by natural selection is considered by many to be the most important milestone in the history of both fields. The evolution of behavior, therefore, has concerned both biologists and psychologists for some time. Research in what now is called *behavior genetics* began shortly after the turn of the century, when the rediscovery of Mendel's work on genetic transmission in garden peas provided a mechanism for natural selection (see Bateson, 1909/1930, for a contemporary discussion).

Hirsch and McGuire (1982) briefly discussed the history of behavior genetics in the introduction to a volume that reprinted benchmark papers in the area. The early history of the field spanned the entire first half of the century, ending in 1951, when Calvin Hall introduced the term *psychogenetics* to describe what he believed was a new interdisciplinary science, with psychologists and geneticists working together on problems in the genetics of behavior. The name did not catch on, but the field of behavior genetics continued to develop and attract an ardent band of dedicated researchers. The early 1960s were, no doubt, the most exciting years, as research flourished and the discipline finally achieved recognition. Enough had been accomplished for reviews of developments in the field to appear (see, especially, Fuller & Thompson, 1960; McClearn, 1962) and for the organization of two important conferences on behavior genetics, held in 1961 and 1962 (see Hirsch, 1967).

Nevertheless, enthusiasm must have been just as strong during the early decades of this century when the very first studies of the inheritance of behavior were conducted. Two approaches were evident in this early work; one utilized the inbred animals of the pure strains being developed at the time (e.g., by the Wistar Institute), the other involved selective breeding for a particular trait or ability. It is not surprising that the inheritance of the ability to learn was one of the first to be examined. Interest in learning was high at the time, particularly among psychologists. John B. Watson (1913, 1914) was promoting what would become a new school of psychology, *behaviorism,* in which the importance of learning was emphasized. The nature–nurture controversy would soon become full-blown, as those who championed instincts (e.g., William McDougall) were challenged on several fronts.

One of the earliest studies of the inheritance of learning ability was Ada Yerkes's (1916) comparison of maze learning in inbred albino rats (*Mus Norvegicus albinus*) obtained from the Wistar Institute and rats from the local stock. As well as comparing errors and trial times in different mazes, Yerkes obtained measures of the brain weights for each group. A report by Basset (1914) had shown that inbred Wistar rats with lower than average brain weights showed deficits in habit formation. Yerkes's results were inconclusive because of the small number of subjects involved, although there was a tendency for the stock rats to learn more rapidly. Brain weight to body length ratios were slightly lower in the inbred rats. The behavioral differences were ascribed to differences in temperament—the inbred rats were more timid. This finding confirmed the suspicion of Ada's husband, Robert Yerkes (who previously had studied the inheritance of savageness in rats; R. Yerkes, 1913), that differences in emotionality were responsible for the differences in habit formation reported by Basset.

Few psychologists are aware of the seminal role played by learning theorist Edward C. Tolman in selection studies of maze-learning ability, the other (and what would become the more popular) approach to the study of the inheritance of behavior. This article examines Tolman's early concern with the innate determinants of animal behavior and his part in initiating research involving the selective breeding of rats for maze-learning ability. More-

Material related to this article was presented at the meeting of the Canadian Psychological Association, June 1989, and at the meeting of the International Society for Comparative Psychology, August 1990.

I thank the Social Sciences and Humanities Research Council of Canada for support, and D. Dewsbury, J. Higa, and J. Mortenson for helpful comments on previous versions of the article.

Correspondence concerning this article should be addressed to Nancy K. Innis, Department of Psychology, University of Western Ontario, London, Ontario, Canada N6A 5C2.

Vol. 47, No. 2, 190–197

over, even after he turned his attention to more theoretical issues, Tolman continued to promote the inheritance research through his support of Robert Tryon, his student and later his colleague at the University of California.

Edward Chace Tolman: Early Years at the University of California (1918–1923)

In 1918, Edward Tolman accepted the position of instructor at the University of California and arrived in Berkeley in September of that year. After earning his doctorate at Harvard under the supervision of Hugo Münsterberg in studies of human memory (Tolman, 1915), Tolman had continued this line of research while on the faculty at Northwestern University. His move to California involved far more than relocating on the other side of the country; it resulted in a major change in the emphasis of Tolman's research, from human to animal psychology.

Tolman had agreed to teach a course in animal psychology when he accepted the Berkeley position, but circumstances delayed this venture. Because of the war, the course was not offered as scheduled in the fall of 1918. He taught army recruits instead. In fact, it was not until the following summer that Tolman acquired his first animals—six white rats, obtained from and housed in the Anatomy Department. Like many rat runners, his first impression was not entirely positive. "I have begun with my rats. At present I am merely playing with them every day. I have six to begin with. I don't like them. They make me feel creepy" (Tolman, July 1919a). His feelings, however, did not deter him; he built cages and by October had 50 rats, two students in his animal behavior course working on projects, and his own research under way (Tolman, October 1919b).

On November 17, 1919, Tolman's application for funding to the Board of Research at the University of California was approved, and he received a grant of $105 "For study of inheritance of unusual ability in learning as exhibited by lower mammals." This was a relatively substantial sum for the time; for example, Tolman's salary his first year in Berkeley was only $1,500. In a footnote to the article reporting the results of the inheritance study, Tolman (1924) credited his colleague, Warner Brown, with the "original impetus which started the problem" (p. 1). Exactly how this came about is not recorded; however, one may speculate that the nature–nurture issue, very topical at the time, was the subject of more than one lively discussion, as psychology faculty and students met each afternoon for tea. Students from that time fondly remember the very positive atmosphere in the department and the free interchange and openness to all ideas, no matter how divergent, that prevailed.

Warner Brown, who had obtained his PhD (with Robert Woodworth) at Columbia during a period when interest in individual differences was strong among James McKeen Cattell's group, had returned to Berkeley to complete a major work on individual differences in suggestibility (Brown, 1916). In general, at that time, concern with individual differences in behavior was of growing importance to psychologists, and individual differences in animal behavior were not to be ignored. Tolman, who had been at Harvard when Ada Yerkes was carrying out her study of the genetics of maze learning, may well have recalled this work in taking the next step—attempting to determine whether individual differences in maze-learning ability could be enhanced by selective breeding, and then attempting to discover the genetic basis of this ability.

The issue of inheritance versus environment was likely an important topic in Tolman's advanced psychology course in the fall of 1920. Among the 12 students in the course was a precocious undergraduate, Zing Yang Kuo, who kept Tolman's interest in the topic of instinct alive over the next few years. Many readers will recognize Kuo as the champion of environmental explanations of behavioral control and recall his work in developmental psychology. At the time, Kuo had barely turned 20 and had been in the United States for only two years. Nevertheless, he was stimulated to respond to those supporting the importance of instinct in psychology and did so by publishing an article denouncing instinct in the *Journal of Philosophy*, early in 1921. In the fall of that year, Tolman held a "voluntary seminar on Instinct" at his home each Thursday evening with a group of hand-picked students, including Kuo, who by now was enrolled as Tolman's graduate student (Tolman, 1921). What lively debates must have occurred at those meetings. Kuo's article denouncing instinct resulted in an extended exchange between Tolman and Kuo in the literature (Kuo, 1921, 1922, 1924; Tolman, 1922a, 1923) and played a key role in the broad-based attack on instinct, initiated by Dunlap (1919), that continued throughout the early 1920s. Many psychologists joined in this assault, which soon resulted in the demise of instinct as a useful construct in explaining behavior.

Tolman credited Brown with getting him started on the inheritance research; however, Tolman's theoretical work at the time indicates that he was very interested in the role of instinct and innate factors in determining behavior (Tolman, 1920). Moreover, although influenced by Watson's behaviorism, Tolman was unwilling to go as far as Watson in rejecting the traditional constructs of psychology, including purpose and cognition. Thus, he began to devise a "new formula for behaviorism" (Tolman, 1922b) that would be both objective and purposive. In the fall of 1919, when he was requesting funds from the Board of Research for his inheritance study, Tolman was also preparing an address for the Berkeley Philosophical Union, which he delivered that December. His topic was "Instinct and Sensitivity," and shortly after the talk, he submitted a related article, "Instinct and Purpose," to the *Psychological Review* (Tolman, 1920). This was the second in what would be a long series of theoretical papers in which Tolman attempted to define objectively the terms of psychology.

Instinct and Purpose

Tolman (1920) used the idea of instinct to show how a purposive psychology could be objective. He presented a "two-level theory of instinct" (p. 233) involving "determining adjustment" and "subordinate acts." Subordinate acts included "all the things we do, not as separate and independent reflexes [e.g., unconditioned responses], but as parts of bigger groups of activity" (p. 220). A determining adjustment "set in readiness the subordinate acts" (p. 220). Depending on the prevailing determining adjustment, a certain random, albeit limited, set of responses (subordinate acts) was activated. Thus, a particular stimulus produced a determining adjustment, which then released a set of relatively random responses that continued until that stimulus was removed (the familiar "persistence until" characteristic of purposive behavior). For Tolman, the "determining adjustment . . . [provided a] theory of instinct," and so purpose, comprising the "interaction of determining adjustment and subordinate acts" (p. 233), involved a completely deterministic mechanism.

The key feature of Tolman's (1920) conceptualization that distinguished it from similar contemporary positions, such as Woodworth's (1918) notion of drive and mechanism, was his emphasis on "the *variability* among the subordinate acts" (p. 223). Although Tolman did not relate the idea of response variability, as he conceptualized it in his theory, to the possibility of selection for particular subordinate acts, the implications are obvious. For Tolman, the relationship between the determining adjustment and the particular set of subordinate acts it released was innate, although the importance of learning was not ignored. In selectively breeding rats for maze-learning ability, one could be selecting for differences in the kinds of subordinate acts that were more likely to be set in readiness by the determining adjustment activated in the maze situation.

Although various maze-learning studies were carried out by Tolman and his students between the summer of 1919 (when he encountered his first white rats) and the summer of 1923 (when he left the University of California at Berkeley for a six-month sabbatical leave in Europe), the inheritance study was by far the most extensive project. With much of his teaching and theoretical efforts during this period centered on innate determinants of behavior, it is easy to understand why the work on the inheritance of maze-learning ability intrigued Tolman. Moreover, he had debates with Zing Yang Kuo to keep his interest in instinct alive; a diligent research assistant, Frederick Adams, to carry out much of the extensive data collection; and another competent student, Barbara Burks (who would later continue to work on the nature–nurture problem with humans; e.g., Burks, 1928), to supervise the computations. (The tedium and time consumption involved in calculating the numerous correlation coefficients necessary for analyzing these data are difficult to imagine by a generation raised with computers.) Tolman also continued to receive financial support from the Board of Research at the University of California ($150 in 1921 and $180 for the construction of mazes in 1922), and in January 1922 the attic of the Psychology Building was remodeled to provide new housing for his growing colony of rats.

Inheritance of Maze-Learning Ability in Rats

Tolman's study was the first experiment to examine the genetic basis of maze learning by breeding distinct lineages of rats selected for their maze performance. The data were reported in 1924 in the *Journal of Comparative Psychology* in an article entitled "The Inheritance of Maze-Learning Ability in Rats," completed just before Tolman began his sabbatical.

Tolman (1924) began the article with a discussion of the implications of this kind of research in general and acknowledged that the study was merely a first report of an extensive, ongoing research program.

> The problem of this investigation might appear to be a matter of concern primarily for the geneticist. None the less, it is also one of very great interest to the psychologist. For could we, as geneticists, discover the complete genetic mechanism of a character such as maze-learning ability—i.e. how many genes it involves, how these segregate, what their linkages are, etc.—we would necessarily, at the same time, be discovering what psychologically, or behavioristically, maze-learning ability may be said to be made up of, what component abilities it contains, whether these vary independently of one another, what their relations are to other measurable abilities, as, say, sensory discrimination, nervousness, etc. The answers to the genetic problem require the answers to the psychological, while at the same time the answers to the former point the way to the latter.
>
> But as far as the present investigation is concerned it must be admitted that only the most elementary answers of either sort have yet been obtained. The preliminary problems of technique and method have proved all important. (p. 1)

The study involved the selective breeding of rats performing very well or very poorly on an enclosed maze with four choice points. Eighty-two rats (41 males and 41 females), albinos from the Anatomy Department stock, formed what Tolman (1924) labeled the "initial or P generation" (p. 2). Their performance on the maze was assessed using three measures—number of errors, perfect runs, and time to complete a trial. A composite score was used in the selection. The top-scoring males and females were mated to begin a *maze-bright* strain, and those scoring lowest were bred to start a *maze-dull* strain. The offspring of these pairs (labeled the F_1 generations) were then tested on the maze, and eight new pairs (siblings from among the highest scoring *bright* males and females and from the lowest scoring *dulls*) were selected to continue each line. The study concluded with the testing of their offspring, the F_2 generation rats.

The performance of the F_1 maze-bright rats improved in comparison with the original unselected group, whereas that of the maze-dull subjects was worse. However, the divergence between the two lineages did not continue; the F_2 maze-bright rats did not perform as well as their F_1 counterparts, whereas the F_2 maze-dull rats were about the same as theirs. Several possibilities for the decline in performance of the F_2 bright strain were considered, including age at testing, environmental conditions, nutrition, and inbreeding. All of these were taken into account in future research.

All in all, the results of the inheritance study were not as clear-cut as Tolman had hoped. In fact, the work pointed to numerous methodological problems. However, adopting the philosophy that we can learn from our mistakes, Tolman began to develop a more rigorous approach to selective breeding research.

A test of individual differences must be both reliable (providing the same result on different occasions) and valid (measuring what you claim it is measuring). Thus, considerable effort was directed toward developing a performance measure that had both high reliability and validity. In order to assess the reliability of the scores obtained, data for the initial group of 82 rats tested on the maze were subjected to a number of statistical treatments, including determining correlations of performance on different runs (e.g., first five and last five runs and odd vs. even runs). All correlations for the error measure were disappointingly low, and even a corrected measure, eliminating extreme scores, resulted in a correlation of only .509. The correlations for time were not much better, and when intercorrelations using all three measures (errors, time, and perfect runs) were computed, the effect of time turned out to be ambiguous.

The validity of the maze for assessing a general maze-learning ability was also of concern, and in a follow-up study Davis and Tolman (1924) compared the performance of white rats on two versions of a maze that was very similar to the one used in the original study (Maze A) and a second maze of a very different configuration (Maze B) and its replica. Correlations of error scores on odd and even trials for individual mazes were consistent with these same correlations for the inheritance study, whereas correlations between each maze and its twin were somewhat higher. As in the previous study, time proved to be an ambiguous measure and the least reliable in comparisons between mazes.

Robert Choate Tryon: Early Years at California (1924–1932)

Tolman's ability to continue the selection project when he returned to Berkeley following his sabbatical in 1924 was certainly facilitated when Robert Tryon enrolled as his graduate student. Tryon, who had been an undergraduate at Berkeley, had interest and skill in both genetics and statistics—the two areas of expertise most important for work on the inheritance project—and Tolman was eager to get him involved.

During the four years from 1924 until he defended his doctoral dissertation, "Individual Differences at Successive Stages of Learning," in 1928, Tryon, along with others associated with the selection project, worked diligently to overcome the problems made obvious by the original inheritance study. These problems included (a) the reliability and validity of the measures of maze learning, which entailed consideration of both the adequacy of statistical treatments and the generality of the findings from a particular maze; (b) the nature of the initial subject population and the method of selecting mates in future generations; and (c) the control of environmental variables, such as living conditions, diet, and handling. Other concerns were the high cost of the research, both in terms of the care and maintenance of the rats in an expanding colony, and the extensive time and effort necessary for data recording and analysis. Each of the problem areas identified in the original research was addressed before Tryon initiated the decisive study in 1927, a study that would continue for more than a decade and provide data from more than 20 generations of maze-bright and maze-dull rats.

Reliability and Validity of the Behavioral Measures

The reliability coefficients obtained for data from both within and between mazes in the initial research (Davis & Tolman, 1924; Tolman, 1924) were not very large. Tolman and Nyswander (1927) assessed the necessity of obtaining high reliability coefficients in general, and concluded that

> Even though an instrument (as applied) is not precise enough, or consistent enough, to distinguish very reliably between all the separate individuals of a population (i.e., gives a low reliability coefficient), it may none the less be reliable enough to distinguish (a) between small groups at the two extremes, or (b) between the mean performances of very large groups even though the latter fall fairly near together on the scale. (p. 428)

Thus, because comparisons between maze-bright and maze-dull rats involved the extreme ends of the population distribution, they felt that the low coefficients obtained might not be a critical problem; however, it would be desirable to use a maze that resulted in higher correlations. Efforts were therefore made to find a maze that led to reliable scores. Rats were trained on seven mazes, each with a different configuration, and odd–even and split-half correlations over trials were computed for the data. Multiple T mazes proved to be the most reliable, and reliability increased with the number of T units in the maze. Turning to the problem of validity, the researchers tried to assess which measure—time, errors, retracings, or perfect runs—would be the best index of learning. Tolman and Nyswander (1927) confirmed that time was an ambiguous index and, after examining the other measures, concluded that "errors" was "the one desirable type of score for measuring learning *per se*". (p. 459)

Genetic Makeup of the Rat Population and Breeding Methods

Tryon started with a new and more heterogeneous breeding stock than the one originally used by Tolman (1924). He chose animals from a large number of litters that had been unrelated for many generations. Tolman was of the opinion that his original population (all albino rats from the Anatomy Department colony) may have been too close genetically and that the inbreeding from the brother–sister matings in his F_1 generation was responsible for the decline in performance of their maze-bright offspring. Tryon continued to use brother–sister matings, but only in alternate generations. (The issue of inbreeding has continued to be a controversial one in the field of behavior genetics; see Hall, 1951; McClearn, 1962.)

Laboratory Procedures—Data Recording, Housing, and Handling

An important concern for researchers using mazes, particularly in studies in which large numbers of animals are tested, has always been the immense amount of time and effort involved in conducting the daily trials (i.e., recording errors and choices in the maze). The most obvious solution to this problem was automation, and with the assistance of Lloyd Jeffress, a psychology student who was very good at gadgetry, Tolman began to construct a self-recording maze. The prototype maze (Tolman & Jeffress, 1925) involved multiple T units, each of which permitted a choice between a cul-de-sac and an arm that led to the next unit. Telegraph keys under treads on the floor of the maze, closed by the rat's weight, activated relays and counters that registered errors and correct choices. The researcher was required only to place the rat in the maze and return at the end of a trial to remove the animal and record the data from the counters. This type of maze was used for a number of different studies by Tolman's students.

An additional factor that had not really been given much attention in the previous work was vitally important for trying to identify genetic differences. If differences in learning are to be accurately attributed to genetic factors, then great care must be taken to ensure that all environmental variables (e.g., housing, handling) are equivalent across groups. Jeffress devised a method whereby rats were housed in cages set in two tiers of shelves positioned on a large, automatic turntable. A rat entered the maze from its cage on the lower level, and when it reached the end of the maze ran into a cage on the upper level, where it received its daily ration of food. The turntable then revolved, allowing the next rat to begin its trial on the maze. When all of the animals had completed the maze, the top set of shelves was exchanged with the bottom set in preparation for the next training trial. Thus it was necessary to handle the rats only to check their body weights, essentially eliminating any experimenter bias in the treatment of the different groups of rats (Tolman, Tryon, & Jeffress, 1929).

Tryon also attempted to control for early differential experience in his selected generations by separating siblings at weaning and housing the offspring of bright and dull parents together until they were tested, at which point they lived in the individual cages on the automatic turntable.

Tryon's Study of the Genetics of Learning Ability in Rats

Tryon took advantage of all of the findings and technical advances described earlier in designing the experimental situation for his inheritance study. He constructed a 17-unit multiple T maze, incorporating the automatic delivery table for housing and running the rats. The self-recording maze units were modified by replacing the telegraph keys with mercury cup contacts under the floor treads, so that data could be recorded using a voltmeter to deflect a pen on a moving strip of paper. This permitted a continuous record of performance, rather than the total scores obtained when counters were used.

Tryon's maze had taken many years and much labor to develop, and he was extremely protective of it. Thus, when the Psychology Department was about to take up residence in the new Life Sciences Building, Tryon approached the move with some trepidation. Sensing his anxiety, some of the graduate students persuaded him to join them on a trip one weekend, and while they were absent, others undertook the move without his knowledge. All went well, and the maze was safely installed on the top floor of Life Sciences, where it would remain in service for many years to come.

Guided by Tolman and Nyswander's (1927) findings on reliability and validity, Tryon chose *errors* (entries into the blind arms of T-maze units) as his performance measure. The work reported in Tryon's (1928) dissertation was directed at assessing the validity of his measurements by comparing the performance of the parental (P) generation (his original group of rats) on the 17-unit maze and on another quite dissimilar maze in which the animals were run by hand. Correlations between performance in the two situations were always above .80, indicating "that the automatic maze differentiated the animals in some general fundamental ability which is likewise employed in learning another maze" (Tryon, 1929, p. 74).

Tryon's (1929) first published report of the inheritance work dealt with the question Tolman had addressed earlier: "To what degree are individual differences in mental ability (i.e. the ability to learn) due to hereditary factors, and to what degree due to environmental factors?" (p. 71). He also maintained that his work had a further objective: "the determination of the genetic mode of inheritance of this ability to learn" (p. 72). In this article, Tryon presented data for two generations of maze-bright and maze-dull rats, showing that the two populations were beginning to diverge.

Support for Tryon's Inheritance Project

By 1927, Tolman had essentially placed the inheritance research in Tryon's hands, and he wanted to make sure that the work would continue under Tryon's supervision after he had completed his doctorate. Funding, of course, was the major problem. In the spring of 1928, Tolman had "a colony of some thousand rats, a caretaker getting $750 and paid assistants amounting to about $800" (Tolman, March 16, 1928). He had spent about $2,700 in the past year for animals alone, some of which had come from his own pocket. Obviously, most of this expense was for the inheritance study, and this work would have to continue for a long time in order to observe enough generations to "work out the genetic laws involved" and permit use of the "bright and dull strains . . . for comparative purposes in all sorts of other problems" (Tolman, March 26, 1931).

Tolman had been trying hard to find funds to pay Tryon once he received his degree. In November 1927, an attempt to get the Board of Research to provide a fellowship for Tryon had been rejected. Tolman even wrote Robert Yerkes for advice on sources of funding, and (whether or not there was a connection) early in 1928, Tryon received word that he had been awarded a National Research Council Fellowship for the coming year.

All of this became important when, in March 1928, Tolman was offered an associate professorship at Harvard. The possibility of being on the Harvard faculty resulted in considerable conflict for Tolman. A Harvard appointment was what he had most desired as a young instructor in his early years at California. Now, 10 years later, he was not so certain. He had risen through the ranks (indeed, had just been recommended for full professor) in a department with congenial colleagues; had attracted a group of productive, intelligent graduate students; and had come to love living in California. Moreover, he was getting close to completing the book in which he would present his theoretical system, and he was afraid that a move would disrupt his writing. Still, the Harvard offer was tempting.

The inheritance project played a central role in the outcome of the job offer, if not in Tolman's actual decision. He wrote to Boring:

Then there is the specific difficulty of the problem on the Inheritance of Maze-Learning Ability. We have this year got our automatic maze going and it is a humdinger. Tryon has been running it ever since last summer and gets his Ph.D. on the first generation this spring. And he has received a National Research Fellowship for next year to carry it on. . . . I hate to leave him and it behind and I hardly know if he or it would be transportable. (Tolman, March 16, 1928)

Whether Harvard would have moved the maze or built another, we will never know; Tolman decided to remain in Berkeley. Moreover, Tolman used the Harvard offer to get the administration of the University of California to permanently commit funds from the Board of Research to him for a half-time research assistant. From then on, even during the depression, when departmental funding dropped substantially, Tolman always had money for an assistant.

Tryon's work continued; his National Research Fellowship was renewed for a second year, and Tolman was trying "to pull all strings possible" (Tolman, 1931) to get a third year for him. Then in March 1931, Boring once again approached Tolman about coming to Harvard, and again Tolman used the offer to barter—this time to Tryon's decided advantage. Tolman wrote to Boring:

The deciding point seems to have been that I am just *terribly keen* to have Tryon's homogeneous "bright" and "dull" rats to do more kinds of learning experiments with, and your tentative offer was a way to wangle an assistant professorship for Tryon through the administration and through the department and hence to make possible the final completion of his inheritance problem which will take two or three years more and give me research material for the rest of my few remaining years. (Tolman, March 26, 1931)

Tryon was appointed to the Berkeley faculty in 1931, where he remained until his death in 1967.

Further Research on Selection for Maze-Learning Ability

Tryon continued to study succeeding generations of maze-bright and maze-dull rats and found that by the eighth there was virtually no overlap in performance on the multiple T maze. Although, eventually, data for more than 20 generations were collected, no further divergence between strains was observed, as indicated in Figure 1 (see Tryon, 1940, 1942, and also Hall, 1951, and McClearn, 1962, for summaries of this work).

The Berkeley group was not alone in studying the inheritance of maze learning in selected strains of maze-dull and maze-bright rats. Shortly after Tryon started his study, W. T. Heron began a similar long-term project at the University of Minnesota, even designing a similar automated apparatus (Heron, 1933). Heron was also able to establish distinct bright and dull strains of rats, confirming Tryon's work (Heron, 1935, 1941).

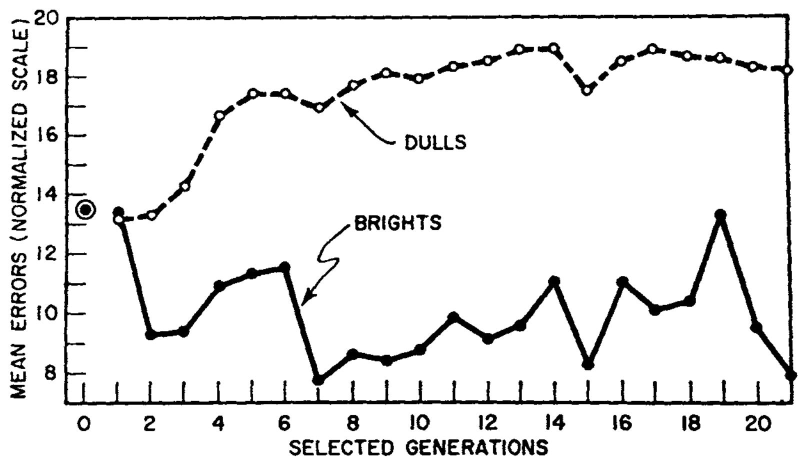
Inevitably, the question of what was being selected—a specific maze-learning ability or some more general learning ability—was addressed. One such study, carried out by another of Tolman's graduate students, I. Krechevsky (later David Krech), used rats from Tryon's colony. Krechevsky (1933) wanted to determine if rats of the bright and dull strains developed different "hypotheses" when faced with an insoluble problem. He found that rats from the maze-bright strain typically adopted spatial hypotheses, whereas those from the maze-dull strain tried nonspatial (visual) solutions. His conclusion was that the so-called bright rats were, in fact, very limited in their response repertoire as a result of their selection history.

In January 1932, Tolman's book, *Purposive Behavior in Animals and Men,* was published. Tolman dedicated the book to *Mus Norvegicus albinus,* the white rat. His attitude toward this small creature had changed markedly in the few short years since he received his first animals. Tolman spent the following academic year on sabbatical leave in Europe, and by the time he returned to Berkeley, his interest in the inheritance project seems to have waned. *Purposive Behavior in Animals and Men* had attracted a good deal of attention to Tolman's theoretical ideas, and he spent more and more time refining these. Moreover, while he was in Austria, discussions with members of the Vienna Circle, particularly Egon Brunswik (whom he helped settle in Berkeley a few years later) had stimulated him in new directions.

However, Tolman continued to maintain a role for hereditary factors in his theory of learning, incorporating them as part of the set of intervening variables represented by the acronym HATE (Heredity, Age, Training, Endocrine Conditions; see e.g., Tolman, 1938). The H stood for heredity, and Tolman had Tryon just down the hall in Life Sciences to make sure that he remembered.

Finally, even Tryon's involvement with the inheritance project began to dissipate, as he became more interested in his other area of expertise, statistics, and par-

Figure 1
Mean Errors for 21 Generations of Tryon's Maze-Bright and Maze-Dull Rats



Note. From "The Inheritance of behavior" (p. 213) by G. E. McClearn, 1962, in L. Postman, *Psychology in the Making,* New York: Knopf. Copyright 1962 by Alfred A. Knopf. Reprinted by permission.

ticularly in problems of cluster analysis (see Tryon & Bailey, 1970). However, the Berkeley legacy continued in the work of Tryon's student, Jerry Hirsch, who became a leader in the new field of behavior genetics—for which, incidentally, Hirsch and Tryon (1956) provided the name. But Hirsch abandoned the white rat for a lower organism, the fruit fly, *Drosophila,* which had the advantage of numerous offspring and a rapid turnover of generations.

Although many researchers, including Hirsch, are still active today, the field of behavior genetics seems to have passed its heyday. The excitement experienced during the early years and again with the emergence of a new discipline at the end of the 1950s is gone. Social and political pressures no doubt have played a role in this change in mood; studies of individual differences in behavior are no longer politically correct. Nevertheless, this centennial issue provides an opportunity to review the work of two pioneers—Edward C. Tolman and Robert Tryon, the first researchers to conduct successful selective-breeding studies of the inheritance of maze-learning ability. Perhaps as scientists map the genome over the next decade and interest in genetics revives, there will be another shift in attitude toward behavior genetics. For as Tolman (1924) implied when he began the inheritance project, a complete understanding of maze-learning ability will be achieved only when studies of genetic mechanisms and research on behavioral processes go on hand in hand.

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