matters arising

Maze-learning ability of *Drosophila melanogaster*

HAY[1] reported that the probability of right–left choices by *Drosophila melanogaster* in a uniformly illuminated multiple-step maze depends on the path through the maze before reaching the choice point. Animals which had initially turned right and were subsequently forced to take five right turns, by blocking the alternatives, had a greater tendency to turn right again than to turn left and vice versa. Hay interprets these findings to demonstrate that *Drosophila* "learn that this sequence of turns enables them to proceed through the maze towards the light" and "that the flies display associative learning. With no apparent positive or negative reinforcement they associate passage through the maze towards the light with a sequence of turns or, more accurately, with a particular orientation towards the light at each choice point, . . .".

In two-step maze experiments (designed for a different purpose) with *D. melanogaster* we observed similar deviations from binomial distribution[2]. These deviations were also found, however, in dark controls and, furthermore, when none of the alternatives in the maze was blocked such that the flies could proceed to the end of the maze by either route. We therefore do not agree with Hay's interpretation but would tend to relate these observations to the correcting behaviour or reverse turning observed from several different species[3-7].

To demonstrate our point of view we have performed several experiments which we report here. Figure 1 shows a scale drawing of the Plexiglas maze[8] used for these experiments. All dimensions are large compared with the size of *D. melanogaster* except for the inner diameter of the funnels used to provide a one-way passage[2]. The collecting vessels were empty *Drosophila* culture flasks. The experimental setup was different from that of Murphey[9] in that our maze included forced turns between first and second choice points. The maze was washed and carefully cleaned before each run. Experiments were performed in complete darkness, at $22 \pm 1 °C$. Of approximately 400 flies (*Drosophila* wild type, Berlin, males plus females, age 3–10 d after eclosion) placed in the starting vessel usually 250 had completed the run after 12 h.

Table 1 shows the results of a typical experiment together with the total of 16 experiments. To eliminate the possibility that an inherent asymmetry of
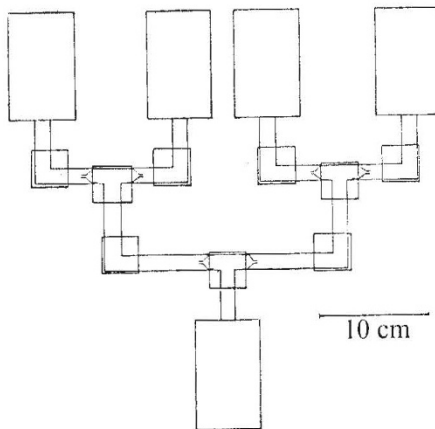

Fig. 1 Plexiglas maze used for experiments with *Drosophila*.

the maze causes the observed distribution, eight experiments were performed in orientation I (*a,b,c,d,*) and eight in orientation II (*b,a,d,c,*) by permuting the parts of the maze.

Table 1 also gives the average of the choice frequencies and the standard deviation of the mean. P_{LL} is the frequency of two subsequent left choices, P_{LR} is the frequency of a left choice and a subsequent right choice in the maze. It is obvious that $P_{LL} > P_{LR}$ and $P_{RL} < P_{RR}$. The differences are highly significant as tested with a *t*-test and a Wilcoxon rank sign test. The effect observed in our maze, however, is only about half as large as that reported by Hay[1].

Hay reported an experiment in which all passages in the evenly illuminated maze were allowed and yet a non-binomial distribution of flies was found. For our purposes we have only found it necessary to report that the effect is still observed in the dark. Thus it can hardly be associated with a successful "passage through the maze towards light". It is not intended to give an explanation[5] of this reverse turning behaviour; however, associate learning seems to be an unappropriate description.

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HAY REPLIES—I welcome the opportunity to expand the arguments in my report[1] on associative learning in *Drosophila*. There I listed and eliminated alternative explanations of the behaviour. Bicker and Spatz[2] have pointed out that one of these alternatives, namely correcting behaviour, could affect my results. Although I did not use the term 'correcting behaviour', it encompasses two of the variables I considered, namely centrifugal swing and spontaneous alternation.

The crucial experiment, however, (at the top of page 46 in my report), by which I distinguished correcting behaviour from associative learning is impossible in their case as they used only one strain of *Drosophila*. I demonstrated that, although there are strain differences in the probability of following the outer walls of a maze where all choices are available (which is what a correcting behaviour explanation would require), these strain differences are unrelated to the performance in the maze where choices are forced. That is, I accept that correct-

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Table 1 Performance of *Drosophila* in maze

	LL	LR	RL	RR
No. of flies counted in collecting vessels in a single experiment	75	45	39	69
Total of 16 experiments	1,331	903	903	1,391
Average of the choice frequencies	$P_{LL} = 0.296$ ± 0.019	$P_{LR} = 0.202$ ± 0.012	$P_{RL} = 0.196$ ± 0.015	$P_{RR} = 0.306$ ± 0.015
In Hay's notation	$P^*_{LL} = 0.602$ ± 0.021			$P^*_{RR} = 0.604$ ± 0.021