

Mental Maze Solving

David A. Crowe, Bruno B. Averbeck, and Matthew V. Chafee

Veterans Affairs Medical Center and University of Minnesota

John H. Anderson

University of Minnesota

Apostolos P. Georgopoulos

Veterans Affairs Medical Center and University of Minnesota

Abstract

■ We sought to determine how a visual maze is mentally solved. Human subjects ($N = 13$) viewed mazes with orthogonal, unbranched paths; each subject solved 200–600 mazes in any specific experiment below. There were four to six openings at the perimeter of the maze, of which four were labeled: one was the entry point and the remainder were potential exits marked by Arabic numerals. Starting at the entry point, in some mazes the path exited, whereas in others it terminated within the maze. Subjects were required to type the number corresponding to the true exit (if the path exited) or type zero (if the path did not exit). In all cases, the only required hand movement was a key press, and thus the hand never physically traveled through the maze. Response times (RT) were recorded and analyzed using a multiple linear regression model. RT increased as a function of key parameters of the maze, namely the length of the main path, the number of turns in the path, the direct distance from entry to termination, and the presence of an exit. The dependence of RT on the number of turns was present even when the path length was fixed in a separate experiment ($N = 10$ subjects). In a different experiment, subjects solved large and small mazes ($N = 3$ subjects). The former was the same as the latter but was scaled up by 1.77 times. Thus both kinds of mazes contained the same number of squares but each square subtended 1.77° of visual angle (DVA) in the large maze, as compared to 1 DVA in the small one. We found that the average RT was practically the same in both cases. A multiple regression analysis revealed that the processing coefficients related to maze distance (i.e., path length and direct distance) were reduced by approximately one-half when solving large mazes, as compared to solving small mazes. This means that the efficiency in processing distance-related information almost doubled for scaled-up mazes. In contrast, the processing coefficients for number of turns and exit status were practically the same in the two cases. Finally, the eye movements of three subjects were recorded during maze solution. They consisted of sequences

of saccades and fixations. The number of fixations in a trial increased as a linear function of the path length and number of turns. With respect to the fixations themselves, eyes tended to fixate on the main path and to follow it along its course, such that fixations occurring later in time were positioned at progressively longer distances from the entry point. Furthermore, the time the eyes spent at each fixation point increased as a linear function of the length and number of turns in the path segment between the current and the upcoming fixation points. These findings suggest that the maze segment from the current fixation spot to the next is being processed during the fixation time (FT), and that a significant aspect of this processing relates to the length and turns in that segment. We interpreted these relations to mean that the maze was mentally traversed. We then estimated the distance and endpoint of the path mentally traversed within a specific FT; we also hypothesized that the next portion of the main path would be traversed during the ensuing FT, and so on for the whole path. A prediction of this hypothesis is that the upcoming saccade would land the eyes at or near the locus on the path where the mental traversing ended, so that “the eyes would pick up where the mental traversal left off.” In this way, a portion of the path would be traversed during a fixation and successive such portions would be strung together closely along the main path to complete the processing of the whole path. We tested this prediction by analyzing the relations between the path distance of mental traverse and the distance along the path between the current and the next fixation spot. Indeed, we found that these distances were practically the same and that the endpoint of the hypothesized mental path traversing was very close to the point where the eye landed by the saccade to initiate a new mental traversing. This forward progression of fixation points along the maze path, coupled with the ongoing analysis of the path between successive fixation points, would constitute an algorithm for the routine solution of a maze. ■

INTRODUCTION

For millennia, mazes have played a part in the rituals and folklore of a variety of civilizations. Early cultures in the British Isles used mazes in fertility rituals, courts of medieval castles contained hedge mazes for the aristocracy's amusement, and, of course, Theseus of Athens slew the half-bull half-man Minotaur in the labyrinth of Crete. Today, mazes persist mainly as children's games and as a tool of scientists. Humans, rats, monkeys, and even grain beetle larvae (Sheimann, Khutzian, & Ignatovitch, 1980) have all traversed the winding paths of labyrinths, to a variety of ends: testing of intelligence, detection of aberrant psychosocial traits (Porteus, 1965), and, to a large degree, the study of learning and memory. Whereas much research has been done on the use of mazes for human intelligence and personality evaluation, and even more on the learning of mazes, little has been done to determine the underlying brain processes involved in the solution of mazes, specifically the top-down-viewed and fully visible mazes of the kind normally administered to human subjects or patients.

In its simplest (and historically most ancient) form, a maze is an unbranched path, with one beginning and one end. The ability to follow such paths is at the heart of maze traversal, and can itself be studied outside of a maze context. Monkeys with lesions of the inferior parietal lobule or the superior temporal sulcus showed deficits in solving simple path-following tasks (Petrides & Iversen, 1979). These monkeys, while showing no obvious motor deficits, were unable to remove a ring-shaped candy from a wire bent into a convoluted path. Comparable brain damage to humans can result in a neurological disorder known as constructional apraxia (Gainotti, 1985; De Renzi, 1982; Kleist, 1934) in which patients with no obvious perceptual or movement deficits have difficulty to perform complex, goal-directed actions such as copying objects, constructing objects from component parts, or traversing a path through a maze. In fact, deficits in performing these tasks are positively correlated in people with constructional apraxia (Angelini, Frasca, & Grossi, 1992).

A different question concerns whether eye movements participate in the solution of visual mazes. In addition to their general orienting role, saccadic eye movements can be intimately linked to an ongoing cognitive process. Thus scanning eye movements selectively sample parts of the visual field where additional information is required to progress toward a particular cognitive goal (Ballard, Hayhoe, & Pelz, 1995; Yarbus, 1967). Perhaps due to the complexity of this process, several cortical eye fields have evolved in the cerebral cortex of the nonhuman primate (Andersen, Essick, & Siegel, 1987; Schlag & Schlag-Rey, 1987; Bruce & Goldberg, 1985; Bruce, Goldberg, Bushnell, & Stanton,

1985), and it is interesting that the behavioral effects of lesions of these cortical eye fields are most severe when purposive saccades are required under complex cognitive conditions such as imposed by memory-guided or antisaccade tasks (Dias & Segraves, 1999; Funahashi, Chafee, & Goldman-Rakic, 1993; Sawaguchi & Goldman-Rakic, 1991). Indeed, the activity of single neurons in the prefrontal cortex, including the frontal eye fields has been found to increase during antisaccades (Funahashi, Bruce, & Goldman-Rakic, 1993), whereas neurons in the superior colliculus, in contrast, are less active during antisaccades than prosaccades (Everling, Dorris, Klein, & Munoz, 1999). These data suggest a heterogeneity of oculomotor behaviors that variously depend on cortical and subcortical structures. It seems that the cortical eye movement network is particularly important when the cognitive process underlying the eye movement is complex. For example, neuronal activity in the frontal eye fields has been shown to encode target selection in several contexts, when a rule is employed to choose one stimulus from many (Schall, Morel, King, & Bullier, 1995), or when features of complex natural images such as the face of another primate are selectively scanned (Burman & Segraves, 1994). The present experiments explore further the interface between spatial cognitive and oculomotor processes, extending the study of human scanning eye movements made in a comparatively unconstrained, goal-directed context, while seeking to elucidate the spatial cognitive operations that may underlie them.

The goals of this study therefore were two-fold: first to determine what parameters are important for solving a maze task, and second, to assess the manner in which eye movements may be integral to the solution. For that purpose we presented subjects with a rectangular-maze stimulus on a video display, instructing them to indicate with a key press which of several possible exits from the maze were continuous with a specified entrance. This task is very different from other, commonly used maze tasks that require the traversal of the route by the hand or body: in our task, no such physical traversal was required, but it is reasonable to suppose that the correct decision would be arrived at by a corresponding mental traversal, taking place perhaps in parallel with a sequence of eye movements. This hypothesis would predict that the response time (RT) of a correct decision would depend on characteristics of the exiting route, such as its length and turns. This prediction is in accord with findings of other studies in which a close correspondence has been found between actual and imagined movements (Decety & Jeannerod, 1995). Indeed, we found that the RT increased as a linear function of the total path length and the number of turns in it. We also found that subjects executed a sequence of saccades tracking the course of the path through the maze.

Evidence supporting the existence of a time-consuming mental analysis of the maze stimulus independent from saccade execution was also obtained. We found that the fixation time (FT) depended on the length and number of turns in the upcoming section of the path. Such a dependence suggests that a covert forward-looking analysis of the path occurs in advance of subsequent saccades.

RESULTS

Performance

Subjects were highly successful in solving the mazes, scoring between 96 and 100% correct. Postexperimental subject interviews revealed that most errors resulted from an accidental press of an incorrect key rather than an error in judging the correct exit.

Random Path Length and Number of Turns (Experiment 1)

Every subject solved the same 400 mazes. Each maze was composed of a 30×20 array of square cells; the side of the square was the “maze path unit” (MPU), and each MPU subtended approximately 1 DVA. Two typical mazes are shown in Figure 1, with (Figure 1A) and without (Figure 1B) an exit. We quantified the following three parameters of the main path, namely path length (med-

ian = 35 MPU, range = 5–115, $N = 393$ mazes with valid data), number of turns (median = 7, range = 0–36, $N = 393$), and direct distance from entry to exit (“direct distance,” median = 11.66, range = 1–31 MPU, $N = 393$).

The mean \pm SEM RT was 2449 ± 20.6 msec ($N = 5,012$ trials). The relations between the RT and maze parameters, gender, and age were investigated using a multiple regression analysis and a forward stepping procedure (see Methods). The results of this analysis showed that the model was a good fit to the data. The coefficient of determination R^2 (i.e., percent of variance explained) was .691 ($F(5, 5006) = 2240, p < 10^{-7}, N = 5,012$). The derived equation was:

$$RT(\text{msec}) = 321 + 72.7T + 32.9P + 13.2D + 208E - 180G \quad (1)$$

where T is the number of turns in main path, P is the main path length (in DVA), D is the direct distance of main path (in DVA; see Methods), E is the exit status (exit = 1, no exit = 0), and G is the gender (women = 0, men = 1). The coefficient of the age of subjects was not statistically significant.

The level of statistical significance varied substantially among the different variables, the highest being for the path length (t value for the regression coefficient = 31.6, $df = 5006$) and the lowest for the exit status ($t = 6.9$, $df = 5006$). A more relevant evaluation is the rank order of the standardized regression coefficients that provides a measure of the relative importance of each variable as an explanatory factor in the regression model. This was as follows, from highest to lowest: path length, number of turns in the path, exit status, direct distance, and gender.

The regression coefficients above provide estimates of the contribution of each one of these factors to the RT, as follows. (a) Path length: 32.9 msec/DVA. (b) Number of turns: 72.7 msec/turn. (c) Direct distance: 13.2 msec/DVA. (d) Exit status: The regression coefficient for this binary factor was 208 msec, which means that the RT would be 208 msec shorter when an exit was absent than when it was present. (e) Gender: Men performed faster than women as reflected in the gender regression coefficient of 180 msec. Finally, all tolerance values (see Methods) were quite high, ranging from .22 to .96. Specifically, the tolerance values for path length and number of turns were .22 and .23, respectively, and were much higher than the default tolerance threshold of .01. This means that, although these two variables were correlated ($r = .85$), their effects on RT were independent.

The regression analysis above was performed on the raw data. Since the distributions of the RT, path length, and number of turns were skewed (data not shown), we also ran the same analysis after these variables were log-transformed to normalize their distribution. The results obtained were practically identical to those above in that the regression model was highly significant, the same

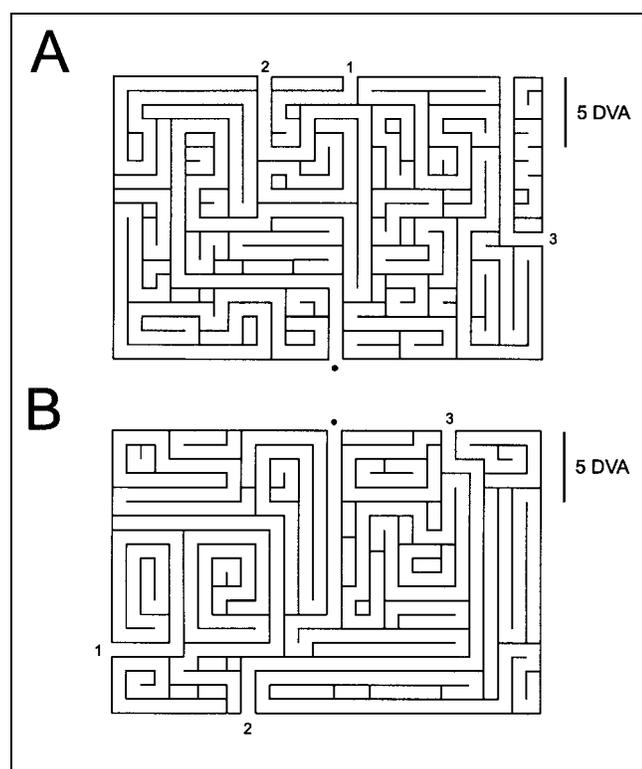


Figure 1. (1) Examples of mazes with (A) and without exit (B). Filled circles indicate entry points.

variables as above had a statistically significant effect, and their rank order was very similar. Specifically, the coefficient of determination R^2 (i.e., percent of variance explained) was .759 ($F(5, 5006) = 3162, p < 10^{-7}, N = 5,012$). The rank order of the standardized regression coefficients was very similar to that above (from highest to lowest): path length, number of turns in the path, direct distance, exit status, and gender. (Age did not have a statistically significant effect in this analysis, either.)

Fixed Path Length, Random Number of Turns (Experiment 2)

In spite of the measures above supporting the statistical validity of the assessment of the effects of path length and number of turns on RT as separate, independent variables, we ran an additional experiment in which the path length was kept fixed at three levels (25, 45, and 65 MPUs) while the number of turns varied randomly within each level. The range of the number of turns was 1–14 for the path length of 25 MPUs, 2–20 for the path length of 45 MPUs, and 4–28 for the path length of 65 MPUs.

The RT increased overall with path length (Figure 2). Three separate regressions were done on RT, one for each path length. We found that for all three regressions, the number of turns was the most important explanatory variable (based on the value of the standardized coefficient), followed by exit status, and for path lengths of 45 and 65, gender. The direct distance had a significant effect only for the case of

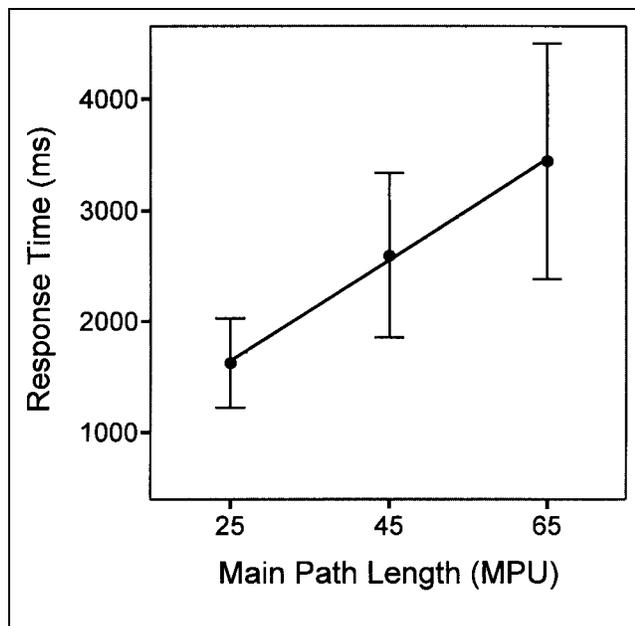


Figure 2. Mean \pm SD RT is plotted against path length. Data are from correct responses during trials with fixed path length. ($N = 1,774, 1,753, 1,759$ trials for path length of 25, 45, and 65 MPU, respectively.)

longest path length (65 MPU). All significant variables were significant to $p < .0001$. The regression coefficients for the number of turns were 54.0, 57.8, and 66.4 msec/turn for path lengths of 25, 45, and 65 MPU, respectively.

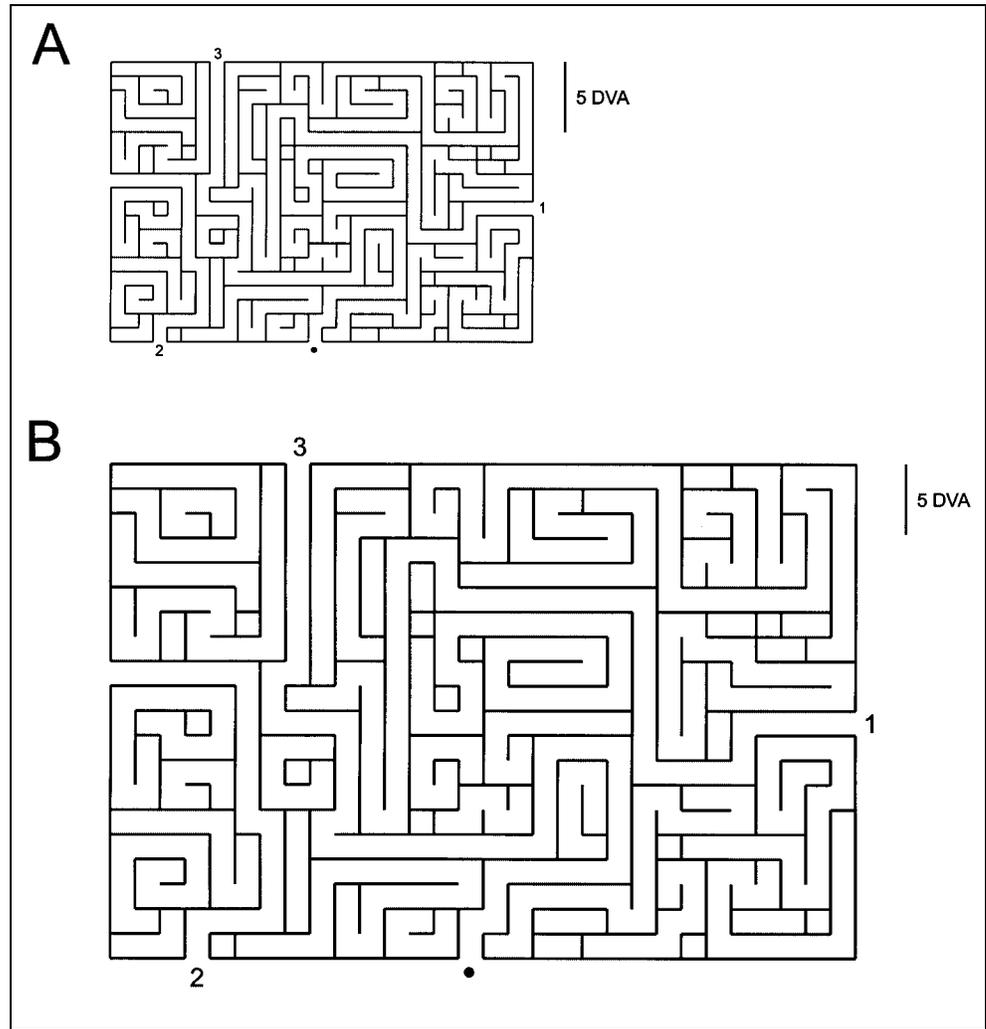
Processing of Large versus Small Mazes (Experiment 3)

Three subjects performed 200 mazes each, while their eye movements were recorded (see below). The mazes in this experiment subtended a larger area of the visual field than in previous experiments (53×35 DVA vs. 30×20 DVA) (Figure 3). However, RT remained similar. In fact, the average RT for this experiment was the same as the average RT of the same three subjects during the original experiment (2150 and 2160 msec, respectively). This means that the larger mazes in this case were processed as fast as the smaller ones in the experiments above. This, in turn, implies that some aspect(s) of the maze were processed faster. The most crucial maze parameters include the number of turns, path length, direct distance, and exit status. In order to find out which one of these factors might have been processed faster when the mazes were larger, we carried out two multiple regression analyses on the data obtained from these three particular subjects, one on the original data with smaller mazes and another on the second set of data with larger mazes. The regression coefficients obtained for the maze parameters in the two cases are shown in Table 1. It can be seen that there was a clear dissociation between the effects of two sets of parameters. One set (number of turns, exit status) did not relate to distance, and they remained invariant when larger mazes were processed. In contrast, the other set (path length, direct distance) showed major changes in that their coefficients were reduced to approximately one-half when processing large mazes, as compared to small mazes. This means that the processing of these distance-related parameters was sped up by factor of ~ 2 , which indicates that the efficiency of processing distance scaled with maze size and almost doubled for the larger mazes used. This finding, in association with the finding above that processing of number of turns and exit status remained the same, suggests that the more efficient processing of distance-related maze factors could probably account for the isochrony of solving mazes of different sizes.

Effects of Maze Parameters and Eye-Movement Measures on the RT (Experiment 3)

Recordings of the eye movements during maze solution revealed that subjects made a number of saccades in a trial and that different distances were traveled by each saccade (Figures 4 and 5). These eye-related measures could have an effect on the RT. We examined this

Figure 3. Examples of small (A) and large (B) mazes.



possibility by performing two kinds of analysis, namely a multiple linear regression and a path analysis.

Regression Analysis

In this analysis, we tested the hypothesis that the RT is influenced by both maze-related (path length, number of turns, exit status) and eye-related (number of fixations, total distance traveled by eyes—“eye distance”) factors. We evaluated the effects of these factors on RT by performing a multiple linear regression analysis in which the RT was the dependent variable and the factors

mentioned above were the independent variables. All of these factors, except eye distance, had a statistically significant effect on RT ($p < 10^{-7}$ for number of turns and number of fixations, $p < 10^{-7}$ for path length, and $p = .0015$ for exit status); the model was an excellent fit ($R^2 = .898$, $p < 10^{-7}$, F test).

Path Analysis

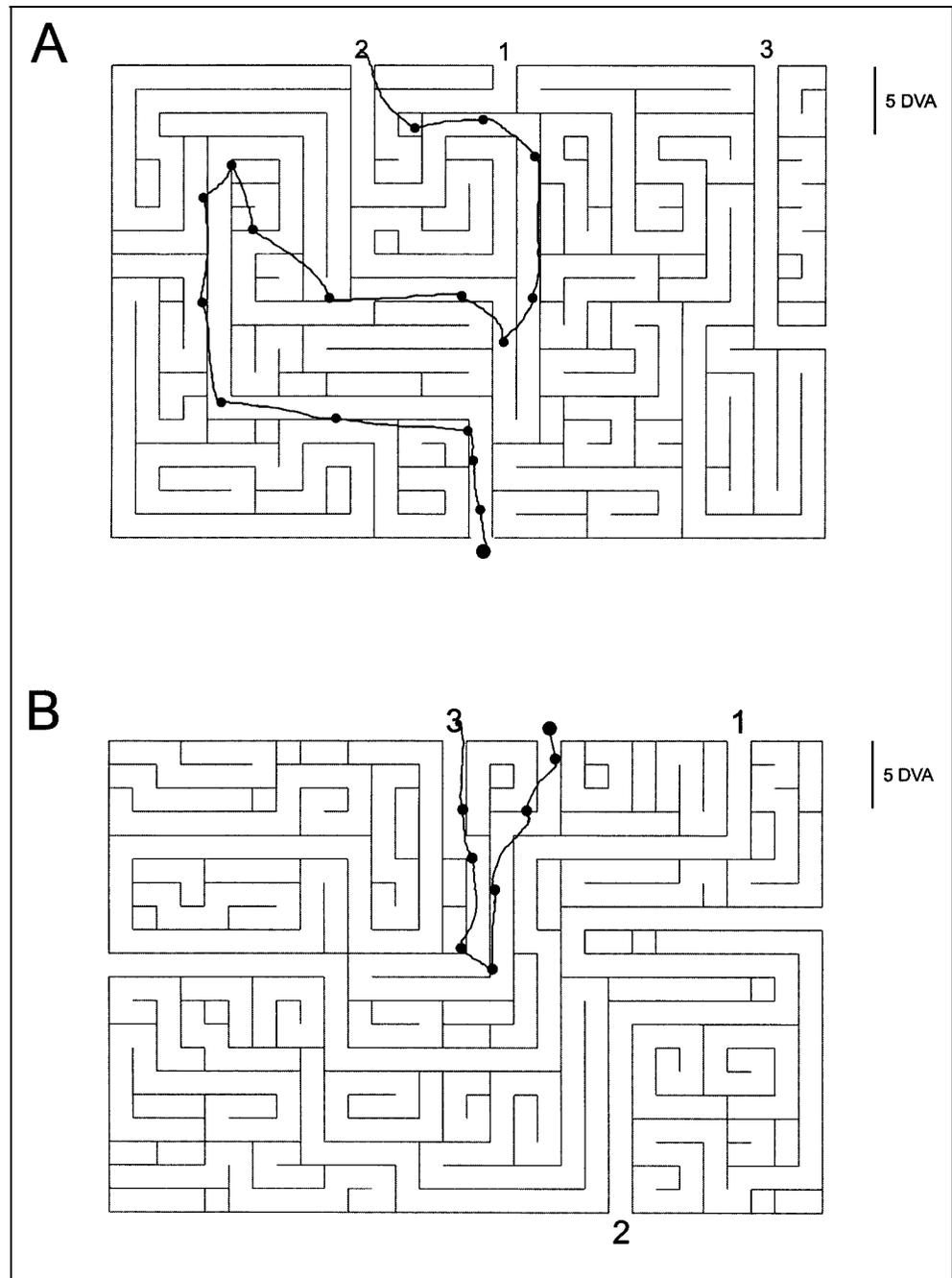
It is apparent from the results above that several variables influence the RT, and that eye movements and fixations play a role in solving the maze. In order to

Table 1. Results of Regression Analysis Between RT (Dependent Variable) and Four Independent Variables Shown

	Number of Turns (msec/turn)	Path Length (msec/DVA)	Direct Distance (msec/DVA)	Exit Status (msec)	R^2	p of F Test
Small mazes	51.4 ± 3.8	29.0 ± 1.2	10.4 ± 2.1	300.3 ± 33	.829	$p < 10^{-7}$
Large mazes	52.3 ± 4.3	$15.4 \pm .8$	4.8 ± 1.3	291.3 ± 37	.869	$p < 10^{-7}$

Regression coefficients ($\pm SE$) and associated statistics are given for solving small ($N = 1,200$) and large ($N = 600$) mazes. (See text for details. Data from the same three subjects.)

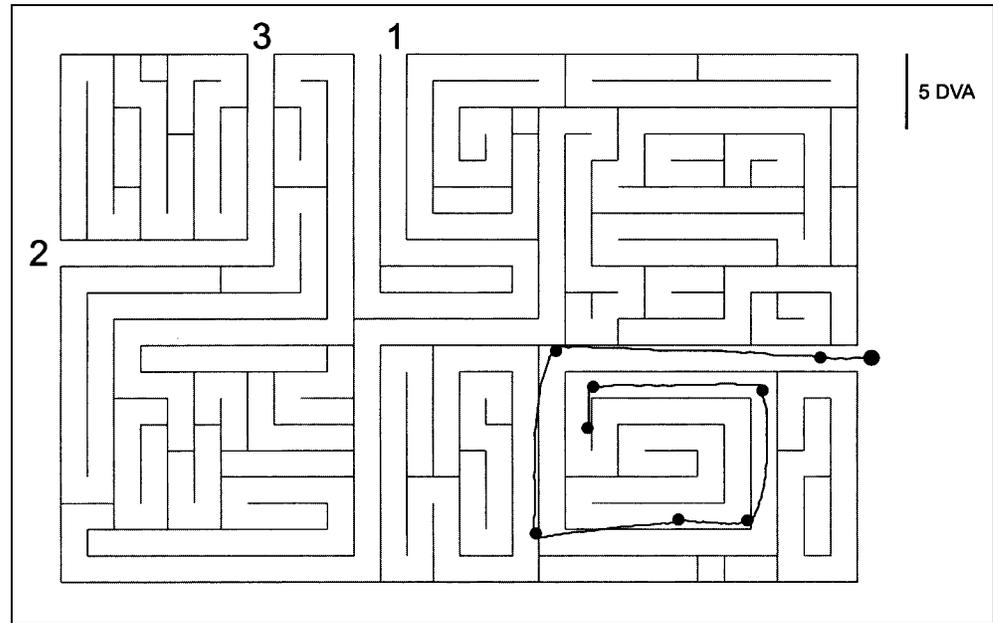
Figure 4. Examples of eye movements during maze solution for two mazes with an exit. Filled circles and interconnecting lines indicate eye fixations and intervening saccades, respectively.



derive a more general scheme of the interrelations of these various factors, we performed a path analysis the results of which are shown in Figure 6. The following should be noted with respect to the structure of this figure. (A) Boxes contain the variables entered in the analysis and are arranged in three tiers to indicate their grouping as the maze variables (path length, number of turns, exit status), eye-movement measures (total distance traveled by saccades, number of fixations), and the RT, as the performance outcome related to the solution of the maze. (B) An arrow indicates the effect of the variable from which the arrow originates (independent variable) on the variable on which the arrow terminates

(dependent variable), as shown by the directed arrow-head; multiple arrows indicate convergent effects. (C) The values are standardized path coefficients; in general, the higher the absolute value, the stronger the effect. The sign of the path coefficient indicates the direction of the effect (positive or negative). Numbers with short arrows indicate the residuals unaccounted for by the converging arrows. (D) With respect to maze parameters, there are no arrows between them because these were generated randomly by design and, therefore, they cannot be considered as having effects on each other. With respect to eye measures, there is a presumed effect of the number of fixations on the total

Figure 5. An example of eye movements during solution of a maze without an exit. Conventions as in Figure 4.



distance traveled by the saccades. This analysis revealed the following. All three maze parameters had a significant effect on eye measures and on the RT. Of these parameters, path length had the most influential effects (as indicated by the magnitude of the path coefficients), followed by the number of turns and exit status. The effect of path length was positive in all cases; that is, dependent measures (RT, number of fixations, eye distance) increased with increasing path length. The effect of the number of turns was positive on RT and number of fixations but negative on eye distance. This latter effect suggests that saccades may “cut corners” and skip over path turns. Finally, the binary variable of exit status had a positive effect on all measures.

With respect to the RT, all factors, except eye distance, had a significant and positive effect. Judging from the

magnitude of the path coefficients, the number of fixations was the most influential factor, followed by the number of turns, path length, and exit status. It seems that the variation in RT was well accounted for by the factors entered, since the residual coefficient of .1 was small. Finally, it should be noted that the effects of the maze parameters on RT are both direct and indirect, via the number of fixations. The magnitude of this indirect effect can be estimated by multiplying the relevant path coefficients. The magnitude of direct and indirect effects on the RT are shown in Table 2. The following can be seen. First, of the three maze parameters, only path length has a substantial indirect effect that, actually, is larger than its direct effect. This finding indicates that path length influences the RT both as an independent factor and through its effect on eye fixa-

Figure 6. Flow diagram and results of path analysis (see text). Numbers are statistically significant ($p < .05$) standardized path coefficients; ns = statistically not significant.

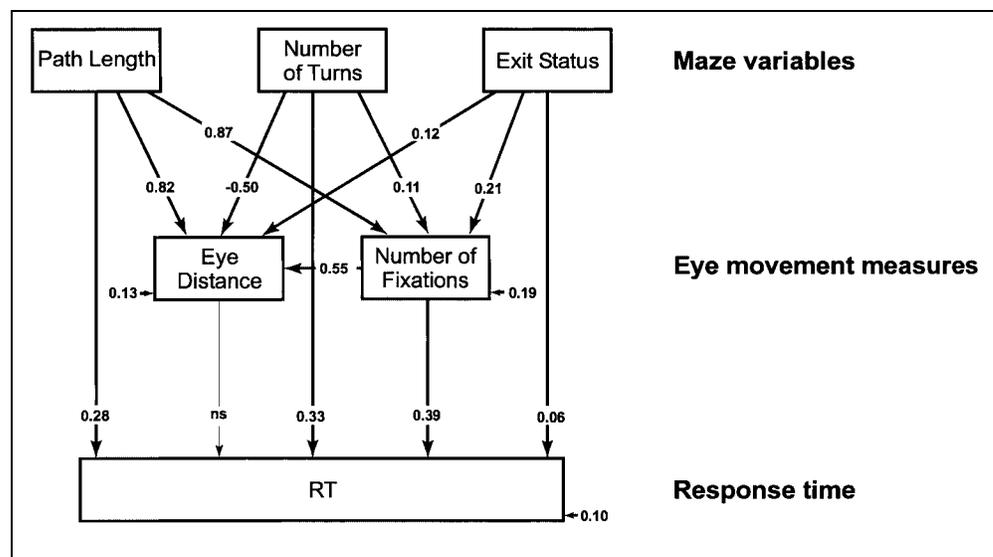


Table 2. Magnitude of Direct and Indirect Effects of Maze Parameters on RT (See text for details)

	<i>Path Length</i>	<i>Number of Turns</i>	<i>Exit Status</i>
Direct effect	.28	.33	.06
Indirect effect	.34	.04	.08

tions. And second, the indirect effects of the number of turns and the exit status are much smaller than that of the path length, although the indirect effect of the exit status is larger than its corresponding direct effect.

Strategy for Maze Solution: Path Following by the Eye

General

Eye movements made by subjects during maze solution consisted of saccades separated by eye fixations. Eye movements provided interesting information concerning some differences in the strategy employed to solve mazes with and without exit. In the first case, the last eye fixation was very near the exit of the path ($1.39 \pm .20$ MPU, mean \pm SEM, $N = 385$ trials) whereas it was rather far from the termination of the path ($7.81 \pm .68$ MPU, $N = 158$ trials) in the no-exit case; this difference was highly statistically significant ($p < 10^{-7}$, t test). These findings indicate that the eyes followed an exit main path near its end but did not go as close to the end of a no-exit path. This was probably due to the fact that no-exit paths tended to wrap around (Figure 5), and this could have provided a clue as to the nature of a specific main path.

Effects of Maze Parameters on Number of Fixations

A different issue concerns the effects of the path length and number of turns in the whole main path on the number of fixations in a trial. This relation was:

$$\text{Number of Fixations} = 1.1 + .14P + .12T \quad (2)$$

This model was statistically highly significant overall ($p < 10^{-7}$, F test; $R^2 = .791$, $N = 543$ FT) as well as for both slopes ($p < 10^{-7}$ for both P (in DVA) and T slopes). This means that the number of fixations increased with path length and number of turns.

Path Following

The eye movements routinely followed the path with little or no backtracking or straying off the path. The absolute (unsigned) error distance between the eye position at fixation points and the main path averaged .5 DVA. This indicates that the fixation points tended to be within the main path, given that the width of the main path was 1 DVA. Therefore, eye fixations were highly accurate with respect to the main path. In addi-

tion, the average error distance was very stable; specifically, it did not vary significantly among subjects (ANOVA), and was not affected statistically significantly by the main path length, number of turns in it, or exit status (multiple regression analysis).

A different question concerns the possible following of the main path by the eyes. We investigated this issue quantitatively by calculating normalized serial measures for the eye fixations and the main path (see Methods). In Figure 7 the normalized serial fixation number is plotted against the normalized serial path location. It can be seen that these two measures are positively highly correlated ($r = .999$). This means that fixations at progressively later times (corresponding to increasing serial number) tended to occur at progressively longer distances from the origin of the path. This, in turn, indicates that mazes were solved without substantial backtracking eye movements and were, instead, “traced” in a discrete fashion by a string of eye fixations. This point was also corroborated by the fact that 95% of all saccades were made to a point further along in the path than the previous fixation point. It is also of interest that the number of saccades in a trial was generally much smaller than the number of turns in the path, which suggests that the saccades “cut corners” and the eyes did not obligatorily trace the path.

Effects of Maze Parameters on FT

The analyses above documented the systematic variation of the fixations during maze solution but did not address

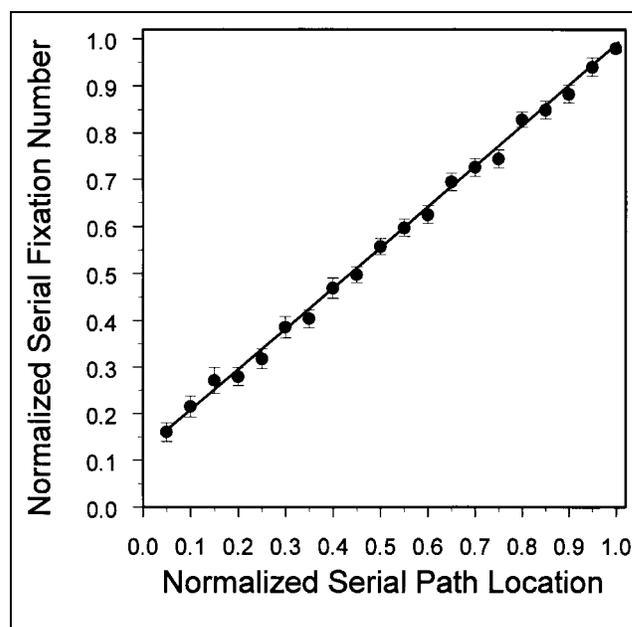
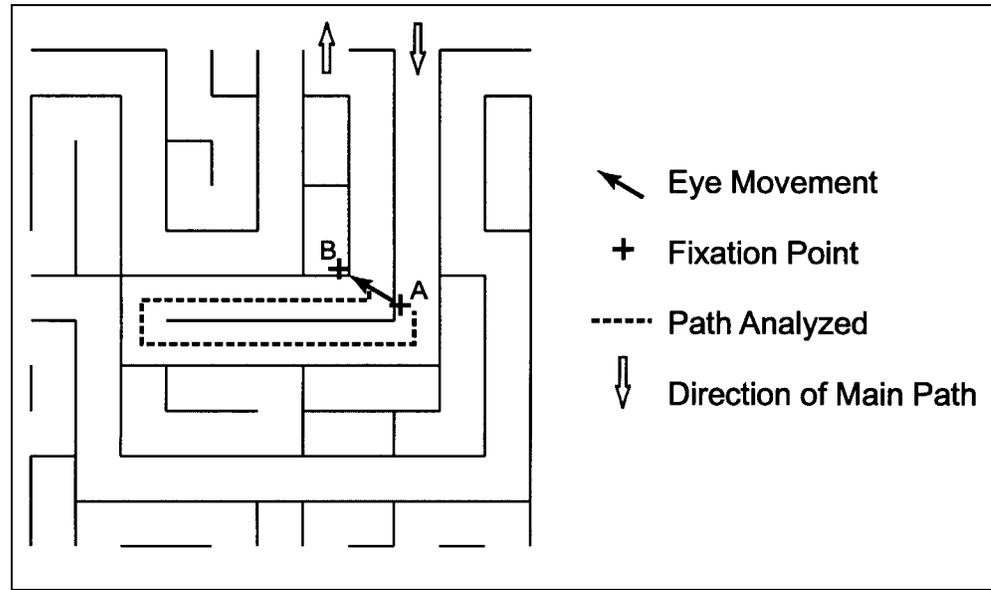


Figure 7. Normalized serial-fixation number (mean \pm 2 SEM) is plotted against normalized serial path location (see text for details). The line is the least-squares, linear regression line fitted on the means above.

Figure 8. Diagram illustrating two fixation spots (crosses A and B) and the intervening path (dashed line). The hypothesis is that the FT spent in A relates to the distance of the dashed line and the three turns contained in that path.



the issue of what might be analyzed during a fixation. Now, we hypothesized that the time spent in a fixation was, at least partly, used to analyze upcoming maze elements (Figure 8). Since FT may vary with the distance, D_s , traveled by the saccade that follows, we assessed the effect of path length and number of turns on FT after adjusting its value by removing the effect of D_s , as follows. For that purpose, we estimated, first, the effect of D_s on FT:

$$FT = a + bD_s \quad (3)$$

This relation was statistically significant ($p = .03$, $b = .01$ msec/DVA). Next, we computed

$$FT^* = FT - (bD_s) \quad (4)$$

where FT^* is the adjusted value of FT with respect to D_s . Finally, we estimated the effect of path length and number of turns on FT^* by performing a multiple linear regression between FT^* , as the dependent variable, and path length, P_F , and number of turns, T_F , interposed between the current and the next fixation spot, as the independent variables. The regression equation obtained was

$$FT^*(\text{msec}) = 164 + 4.27P_F + 27.2T_F \quad (5)$$

This model was statistically highly significant overall ($p < 10^{-7}$, F test; $R^2 = .132$, $N = 2,035$ FT) as well as for both slopes ($p = .00002$ for P_F , in msec/MPU, and $p < 10^{-7}$ for T_F , in msec/turn). These results document the effect of these maze parameters on FT independently of the effect of D_s .

The Mental Path Traversing Hypothesis

The results above indicate that the maze segment from the current fixation spot to the next (Figure 8) is being

processed during the FT, and that a significant aspect of this processing relates to the length and turns in that segment. In fact, the slopes (regression coefficients) for P_F and T_F in Equation 4 provide estimates of the time taken to process one MPU or turn. Therefore, given a particular fixation spot along the main path and the FT spent in the spot, and assuming that the forward-maze path is mentally traversed at a rate dictated by these coefficients, one could estimate the distance thus traversed within the FT and determine the (unique) locus on the path where this traversing would terminate. We estimated these measures as follows. First we notice that Equation 5 provides two rate constants for the time it would take to traverse a path unit (4.27 msec/MPU) and a turn (27.2 msec/turn). It also contains a constant that is apparently unrelated to these processes and could reflect other processes such as processing of the raw visual input, preparation and initiation of the next saccade, decision making as to whether there is an exit or not in the portion of the path analyzed, etc. Now, given a specific FT^* , we first subtracted the constant and obtained $FT' = FT^* - 164$, which is the estimated time available to mentally traverse the main path forward from the current fixation spot. (The mean \pm SEM of FT' was 75.6 ± 2.4 msec, $N = 2,035$.) We then estimated the distance of the path traversed by following the path forward at the cost of time dictated by the rate coefficients above: as traversing of the path progressed, the time available became progressively shorter, until it was exhausted, and this was the estimated endpoint of the simulated mental traversing. We postulated then that the processing of the next portion of the main path would be carried out during the ensuing FT, and so on for the whole of the path.

Now, it would be interesting to know why this mental traversing is terminated at a certain point. A plausible

hypothesis is that the path is analyzed within central vision, so that when the path being traversed comes near the edge of central vision, a new saccade is being initiated to recentralize the path. A prediction of this hypothesis is that the farthest point of the path traversed from the current fixation spot should lie near the edge of central vision. Indeed, this was the case. The mean \pm SEM of the point of the path at maximum eccentricity from the fixation spot was $9.04 \pm .077$ DVA ($N = 2,035$). This value falls at the edge of central vision, commonly assumed to be approximately 10 DVA. This means that the other points of the path analyzed are at shorter eccentricities and, therefore, well within the area of central vision.

Predicting the New Fixation Spot

Now, if the mental path traversing hypothesis were true, one would predict that the upcoming saccade would land the eyes at or near the locus on the path where the mental traversing ended, so that “the eyes would pick up where the mental traversal left off.” This prediction can be tested rigorously by analyzing the relations between the path distance of mental traverse, estimated as above, with the distance along the path between the current and the next fixation spot (Figure 8). Since this is an important point, we carried out three different kinds of analyses. First, we analyzed the difference

$$d = A - M \quad (6)$$

where A is the distance along the main path from the current fixation point to the next, and M is the distance assumed to have been mentally traversed along the same path from the current fixation point onwards, consuming all of the available FT. The hypothesis above predicts that d will not differ significantly from zero, i.e., that A and M do not differ significantly. Indeed, this was the case. The mean \pm SEM of d was $-.127 \pm .205$ MPU ($N = 2,035$), and this difference was not statistically significant ($p = .53$, paired t test). Finally, we performed two additional analyses of the relations between A and M , as follows. In one analysis we correlated the raw values of A and M calculated for each FT. The correlation coefficient $r = .224$ was highly statistically significant ($p < 10^{-7}$, $N = 2,035$ pairs). In a different analysis, we used mean levels of M to reduce the noise of the individual data and perform the analysis on the central values of A and M to detect any systematic nonlinearities in their relation. For that purpose, the range of A (4–14 MPU) provided 11 discrete 1-MPU-wide levels for each of which we then calculated the mean of M . The resulting plot of M against the 11 levels of A is shown in Figure 9. It can be seen that A and M are highly correlated ($r = .92$). Moreover, the slope (\pm SE) of the line ($.927 \pm .13$) did not differ significantly from 1 ($p = .59$, t test) and the residuals were randomly distributed about zero. Both of

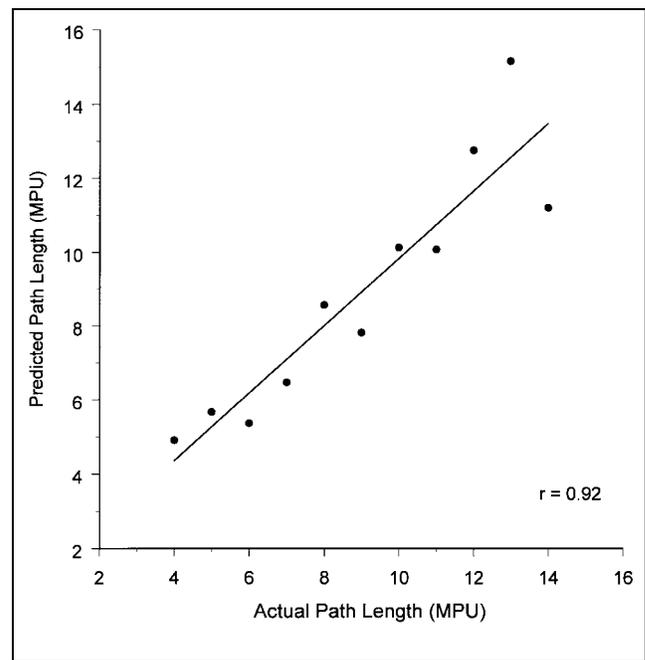


Figure 9. Predicted path length is plotted against actual path length (see text for details). The line fitted is the least-squares, linear regression line.

these analyses demonstrate that the end of the postulated mental path tracing is very close to the point of termination of the saccade and, therefore, add support to this mental tracing hypothesis.

DISCUSSION

Task Considerations

The present task involved a visual maze for which the subjects had to indicate the correct exit by pressing a key. Important characteristics of the task included the following: first, the maze could be seen all at once; second, there were no hand or body movements traversing the maze; third, there were several potential exits of which only one was correct; and fourth, the mazes were generated randomly and were composed only of unbranched paths. These characteristics distinguish the mazes we used from those used by other investigators over the years in different contexts, such as, for example, navigational mazes in which rats find a food source (e.g., O’Keefe, 1978; Tolman, 1948; Lashley & Ball, 1929; Franz & Lashley, 1917), water mazes in which rats find a platform (e.g., Morris, Garrud, Rawlins, & O’Keefe, 1982), and route-finding mazes in which the hand (e.g., Porteus, 1965) or a tool moved by the hand (e.g., van Mier, Hulstijn, & Petersen, 1993; Milner, 1965) traverse a maze in human studies. In all of these cases the maze was actually being traversed by the whole animal, the hand or a tool operated by the hand. In contrast, in our experiments the correct exit had to be selected but no hand or body traversed the maze.

Therefore, this point clearly distinguishes our study from other maze studies. Finally, it should be pointed out that our study focused on the relations among RT, eye movements, and key maze parameters, and did not investigate any aspect of maze learning, a common focus of other maze studies mentioned above. In fact, our subjects never saw the same maze twice.

The experimental design of this study placed emphasis on the selection and identification of the correct exit among three labeled possible ones in exit trials. The subject was required to press the number (1, 2, or 3) in the numerical pad of a computer keyboard that corresponded to the presumed correct exit; the number 0 was used to indicate absence of exit in the main path. Thus, there were four motor responses, and these were chosen randomly during generation of a maze. Overall, 68.4% of the paths exited (response keys 1, 2, 3) and 31.6% did not (response key 0). The no-exit mazes were included as oddball trials to ensure that subjects did not respond based on guessing. Thus the emphasis of the experimental design was not on detecting the presence or absence of an exit but on identifying which exit was the correct one, given also that some paths did not exit at all.

We had two major objectives in this study; first, we wanted to identify the factors involved in solving a maze, and, second we wanted to evaluate the role, if any, of eye movements in maze solution. Briefly, we found that the path length and the number of turns in the path were important and independent factors that influenced both the time it took to solve the maze and the number of eye movements made during a trial. Moreover, we identified the eye movement strategy used in maze solution. We discuss these results separately below.

Effects of Maze Parameters on RT: Path Length, Number of Turns, Exit Status, and Direct Distance

The length of the main path and the number of turns in the path were apparently the most influential factors in determining the duration of the RT; on the average, the former contributed 32.9 msec/DVA and the latter 72.7 msec/turn (Equation 1; Experiment 1). In terms of processing rates, these slopes correspond to 30.4 DVA/sec and 1238°/sec (given that all turns were orthogonal, i.e., of 90° angle). The effects of these two factors were independent, as evidenced from two kinds of results. First, both effects were statistically highly significant within the stepwise multiple regression model of Equation 1 in which both of them were entered as independent variables; this means that, even if they were correlated, both were retained during the stepping procedure. However, the second evidence is stronger, for it comes from a separate, additional experiment in which the length of the main path was fixed in a stratified design, but the number of turns were allowed to vary. The results of this experiment showed that the

number of turns was a highly statistically significant factor for the RT for all three levels of path length used.

At face value, the effect of path length on RT can be interpreted as an effect of a translation along a linear distance whereas the effect of the turns can be regarded as a rotation through a 90° angle. The fact that these two effects are independent implies that translation and rotation are separate processes. This conclusion is in accord with the results and conclusions of another study that showed that imagined translation and rotation are indeed distinct processes (Rieser, 1989). The general congruence of the findings of this and Rieser's (1989) study is remarkable, for they came from very different experiments; namely, in the present study, from mentally solving a maze, and, in Rieser's (1989) study, from judging self-to-object directions in a room from novel points of observation that differed from their actual point by a translation or rotation, in different trials.

In addition to path length and number of turns, two more maze parameters were also significant. One was the exit status; it would take on the average 208 msec more to solve a maze with versus without an exit. This is equivalent to stating that it would take 208 msec less to solve a no-exit maze than one with an exit. The savings in time could have come from the fact that, commonly, the no-exit main path tended to wrap around, and this would give a clue as to the nature of the path as a no-exit one, which would shorten the RT. In this view, part of the reduction in RT would reflect the earlier termination of maze processing. On the other hand, it is reasonable to assume that the main path was processed more fully when an exit was present because, in this case, the subject had to indicate which was the correct exit out of the three possible ones. We believe that both of these considerations contributed to the differences in RT observed with respect to exit status. This is supported by the behavior of eye movements during exit versus no-exit paths. In the first case, the last eye fixation was very near the exit of the path (1.39 MPU on the average) whereas it was rather far from the termination of the path (7.81 MPU on the average) in the no-exit case. In addition, there was a positive effect of the exit status on both the eye distance and the number of fixations (Figure 6) which means that there were fewer eye fixations and a smaller distance traveled by saccades in no-exit trials. Finally, another maze parameter that had a significant effect on the RT was the direct (Euclidean) distance between the entry and exit points of the main path. This probably reflected an additional process possibly searching for a shortcut to the exit.

The discussion above revolved around the effects of maze variables on RT. An additional factor to be considered concerns the eye movements made during maze solution. Saccades brought the eyes to points along the main path, and the eyes stayed at these fixation points for a variable period of time. We used two measures relating to the eye movements in a given trial, namely

the number of fixations and the total distance traveled by the eye. These eye-related variables could conceivably influence the RT and, in turn, be influenced by maze parameters. Given that these interactions can occur at various levels, we evaluated them statistically using path analysis (Figure 6). This analysis revealed the following. First, all maze parameters (i.e., path length, number of turns, and exit status) had a significant effect on both eye measures above. Second, the number of fixations but not eye distance had a significant effect on RT. Finally, all three maze parameters had a significant effect on RT independently of their effect on the eye measures. Therefore, the total effect of maze parameters on RT comprised both a direct effect and an indirect one, via the eye measures. On the other hand, the number of fixations in a trial was an important component, in addition to FT, of the strategy by which the maze was solved. This strategy is discussed in detail below.

Processing Path Length: Maze Scaling

In Experiment 3, the maze was uniformly enlarged by 1.77 times on each side while keeping the number of maze elements (i.e., MPUs) the same. Specifically, the maze was enlarged from 30×20 DVA to 53×35 DVA but contained the same number of MPUs ($N = 20 \times 30 = 600$) in both cases. This resulted in an upscaling of the path length and direct distance while keeping the number of turns the same between the two conditions. The regression analysis of the RT against maze parameters provided clear-cut and interesting results; specifically, there was a substantial reduction in the slope of RT versus path length and direct distance whereas the slopes for the number of turns and exit status remained practically the same (Table 1). The reduction of these slopes can be interpreted as an increase in the rate by which the maze size was processed. The processing rates were 34.5 and 96.15 DVA/sec for processing path length and direct distance, respectively, in the original, small mazes; these rates became 64.9 and 208.3 DVA/sec for processing path length and direct distance in the scaled-up, large mazes. Thus there was an approximately two-fold increase in the processing rate of maze size (1.88 times for path length and 2.17 times for direct distance; mean = 2.02 times). This is in accord with the results of other studies, which found that in mental tracing of curves the rate of tracing varied with the overall size of the stimulus, such that if the image of the stimulus were enlarged, higher scan rates were achieved with the net result that scan times remained relatively constant (Jolicoeur & Ingleton, 1991).

Effects of Path Length and Number of Turns on Eye Movements

Subjects made a number of eye movements while they were solving the maze. These commonly consisted of

saccades separated by fixations. Maze parameters had a significant effect both on the number of fixations and the duration of fixation (i.e., FT). Specifically, the number of fixations in a trial increased as a function of path length and number of turns in the main path, as evidenced by the corresponding positive-path coefficients in Figure 6. The situation is somewhat different in the case of FT because the values of these maze parameters refer to, and are calculated from, that portion of the main path that intervenes between the locations of the current and subsequent fixation. Therefore, in this case the effects of path length and number of turns can be thought of as operating on a “micro” scale. Indeed, there was a strong effect of both of these parameters on FT.

Covert Maze Processing by Attention

The findings above indicate that a portion of the maze was processed within a single fixation, and that the whole path was processed by successive fixations along it. Therefore, maze solution can be regarded as consisting of a sequence of covert analyses strung together in time (i.e., RT) and space (i.e., along the main path), as evidenced by the fact that eye fixations were very near the center of the 1-MPU width main path (within .5 MPU on the average) and apparently followed the main path along its course (Figures 4 and 5). This postulated covert spatial analysis of the maze path is similar to the operation of a visual routine as proposed by Ullman (1984). Curve tracing has been proposed as an example of a visual routine that evaluates the continuity of contours present in the visual input (McCormick & Jolicoeur, 1991; Jolicoeur, Ullman, & Mackay, 1986, 1991; Jolicoeur & Ingleton, 1991). Jolicoeur et al. (1986) found that the reaction time taken to decide whether two targets lay on the same curve in a visual display depended on the length of the section of curve intervening between the targets (and not on the absolute spatial distance between the targets, which was invariant). This was true at stimulus presentation intervals that were too short (250 msec) to allow the curve to be traced with a sequence of eye movements. The result was interpreted to reflect the existence of a local operator or region of analysis that could move along the curve in the absence of eye movements. It was subsequently demonstrated that the rate of tracing was inversely related to the curvature of the traced contour (Jolicoeur et al., 1991).

We hypothesize that the covert maze processing above involves a continuous shift of attention from the fixation point forward, along the main path, so that the maze path is mentally traversed. This hypothesis is made possible by several pieces of evidence. First, it has been conclusively shown that attention can shift to a different locus from that of the fixation point and that detection of stimuli at the newly attended locus is improved (see Posner, 1980 for a review). Second, shifts of attention to

peripheral loci improves the spatial resolution of the visual system at those locations (Yeshurun & Carrasco, 1998). Third, attention can move through space in an analog fashion (Shulman, Remington, & McLean, 1979), that is, attentional shifts can be continuous. And finally, covert shifts of attention have been shown to occur during a period preceding saccadic eye movements (Posner, 1980), that is, they can occur during the FT.

In a way, solving a maze can be compared to reading a line of a text, where the main maze path would correspond to the line of text and the local features of the path (length and orientation of straight segments, turns, exit/termination points, etc.) to local features in the text. Studies of eye movements during reading (see Rayner, 1998 for a review) have identified similar strategies, namely a mostly forward progression of fixations along the line, the location of the fixation on or near the line, and the tendency to analyze during an FT a segment of text falling within central vision. However, there are also fundamental differences between solving a maze and reading; specifically, in reading, but not in maze solving, there are words separated by spaces, there is semantic content, and the text being followed lies along straight lines.

Strategy for Maze Solution: Mentally Traversing the Main Path

According to our hypothesis, then, the sequence of events would be as follows. First, the eyes are brought to fixate the entry point in the maze and then attention begins to move through the path to enable the analysis of its spatial structure. This analysis is carried out to a certain extent, and then the eyes are moved to a new point forward in the main path. It would be of interest to know what determines the timing of termination of a fixation, or, equivalently, the initiation of the saccade. Most probably, several factors are involved in this decision. First, it is reasonable to suppose that the analysis of the maze path would be done most effectively and efficiently in central vision. A traditional upper limit of central vision would be 10 DVA. The average direct (Euclidean) distance between the current fixation point and the farthest point of the forward point in the maze path analyzed during the FT was 9.04 DVA, which is at the edge of central vision; this means that the remaining points of the path analyzed would be well within central vision. Therefore, one plausible consideration is that a fixation would be terminated when the leading edge, so to speak, of the mental path tracing approaches the limits of central vision. Another factor could relate to a limit in information processing in time, in the sense of following the path and determining at times whether an exit or termination point has been encountered: after a period of path following, and if no such points have been detected, a new search would start from a new fixation point. According to this view, the termination of

the fixation would be necessitated by the saturation of a limited capacity channel processing spatial information. Although this idea is plausible, we do not have any evidence for or against it. Finally, another contributing factor could relate to a possible internal clock-type mechanism for initiating saccades at semiregular intervals, independently of considerations of information processing during the fixation. All of these factors, alone or in combination with different weights, would lead to the initiation of a saccade.

Finally, another question is, what determines the termination point of the saccade, given that there are no guiding posts to attract the eye to rest in a specific location. In fact, many times the fixation points were along straight segments of the maze and were not confined to corners in the path (Figure 4). The results of our analyses show that a saccade was directed to, and terminated on, a point within or close to the main path, in a forward pattern. In addition, this point was close to the end of the path mentally traversed during the current FT. This forward progression of fixation points along the maze path, coupled with the ongoing analysis of the path between successive fixation points constitutes an algorithm for the routine solution of a maze.

METHODS

Subjects

Thirteen human subjects (five women and eight men, age 19–39) participated in these experiments. They were healthy volunteers. The experimental protocol was approved by the Institutional Review Board.

Maze Task and Experimental Design

Three experiments were performed, as follows.

Experiment 1: Small Maze, Random Path Length, and Number of Turns, No Eye Movement Recordings

All 13 subjects performed this task in which they were shown a maze and the starting point of a path through it, and they had to determine the proper exit point, if any, of the path. Each maze was composed of a 30×20 array of square cells. When displayed on a 14-in. computer monitor, the dimensions of the maze were 25.5×17 cm (8.5 mm/MPU) and subtended approximately $30^\circ \times 20^\circ$ of visual field; one MPU subtended approximately 1 DVA. All lines were parallel to the sides of the maze, that is, there were no obliquely placed squares. Subjects sat approximately 50 cm away from the monitor and rested their hands on a computer keyboard in front of them.

Each maze contained three randomly generated unbranched paths that started from separate sides of the maze and either exited the maze at one of the walls or terminated inside the maze. A red dot indicated the

entry and the exits of the three paths were labeled “1,” “2,” and “3.” Figure 1A shows a typical maze whose path exits and Figure 1B shows a typical maze whose path terminates inside the maze. After the red starting dot appeared on the screen, the subject initiated the trial by pressing any key on the keyboard, whereupon the maze and exit labels appeared. The subject was asked to press the number on the numeric keypad corresponding to the appropriate exit if it was determined that the path exited, or to press the “0” key if it was determined that the path terminated inside the maze. Each subject completed four sessions containing 100 mazes each, and although the mazes were generated randomly, each subject saw the same set of mazes. Finally, the RT from the time that the maze was displayed to key press was recorded. In order to give a broad distribution of maze parameters, the path-generating algorithm used a probability of turning at each MPU that varied for each maze ranging from .1 to .3.

Experiment 2: Small Maze, Fixed Path Length, Random Number of Turns, No Eye Movement Recordings

Of the 13 subjects above, 10 (five men and five women) performed in this variant of the task. Given that the length of the path and the number of turns may covary, additional experiments were run such that the path length was fixed in three levels whereas the number of turns varied randomly within each level. The path lengths were 25, 45, and 65 MPUs and were incorporated in 200 mazes that were randomly mixed for a total of 600 mazes. All other experimental details were as described above for Experiment 1.

Experiment 3: Large Maze, Random Path Length, and Number of Turns, Eye Movement Recordings

Of the 13 subjects above, 3 subjects (all men) performed an additional 200 mazes while their eye movements were recorded using the magnetic search-coil technique (Robinson, 1963; CNC Engineering, Seattle, WA). An annulus was placed in the right eye of subjects, who sat with head fixed inside a magnetic field. Mazes were rear-projected onto a screen and subtended approximately 53×35 DVA. Given that a maze consisted of 30×20 MPUs, 1 MPU in this case corresponded to approximately 1.77 DVA. Eye position was recorded at a rate of 1000 Hz. All other experimental details were as described above for Experiment 1.

Data Analysis

General

Standard display and statistical analysis techniques (Snedecor & Cochran, 1980) were used to inspect and analyze the data. In all experiments, only valid (i.e., with nonmissing values) data from correct responses and

with main path length of ≥ 4 MPU were analyzed. With respect to eye movements, very short (≤ 3 MPU) and very long (≥ 15 MPU) as well as very short fixation times (≤ 50 msec) were excluded from the analyses below.

More specifically, a step-wise multiple linear regression analysis was carried out to determine the relations between the RT for correct responses and a number of maze-related and other variables. The regression model included (a) the RT as the dependent variable, and (b) the length of the exit route (“path length”), the number of turns in the path, the presence or absence of an exit (qualitative, binary factor), the direct (Euclidean) distance from entry to exit, the age, and the gender of the subjects (qualitative, binary factor). The commercially available statistical packages SPSS (SPSS, Chicago, IL, 1993) and BMDP/Dynamic (BMDP Statistical Software, Los Angeles, CA, 1992) were used for this analysis. As a safeguard against possible collinearities among the independent variables, a tolerance threshold of .01 was adopted, which is the default of the BMDP statistical package.

Analyses of Eye Movements

We wanted to know how close were eye fixations to the main path. Given that the width of the path was 1 MPU, the absolute (unsigned) error distance was calculated as the shortest distance between a fixation point and the center of the MPU along the main path. This provided information about positional accuracy of eye fixations with respect to the main path but not about a possible sequential following of the main path. To assess this issue, we determined the points along the main path that were associated with eye fixations, calculated their distance from the origin of the path, and computed their serial locations along the unity-normalized path by dividing a particular distance by the total path length. For example, consider a fixation associated with a distance of 5 MPU from the start of a path 15 MPU long; the normalized serial location of this point would be .33. Similarly, we calculated a normalized serial fixation number by dividing the serial position of a fixation by the total number of fixations; for example, this number for the third fixation in a series of six would be $3/6 = .5$. Finally, the association between these normalized measures was associated using correlation analysis.

Path Analysis

We used path analysis (Asher, 1983) to derive a general scheme of the interrelations among maze parameters, eye-related variables, and performance outcomes. For that purpose, the LISREL computer package (LISREL 8.20 and PRELIS 2.2, Scientific Software International, Chicago, IL, 1998) was used to generate correlation matrices between variables, path coefficients for specific

paths. Path coefficients are estimates of the strength of a relationship in a path.

Acknowledgments

This research was supported by USPHS grant NS17413, the Department of Veterans Affairs, and the American Legion Chair in Brain Sciences.

Reprint requests should be sent to Dr. A. P. Georgopoulos, Brain Sciences Center, Veteran Affairs Medical Center, One Veterans Drive, Minneapolis, MN 55417.

REFERENCES

- Andersen, R. A., Essick, G. K., & Siegel, R. M. (1987). Neurons of area 7 activated by both visual stimuli and oculomotor behavior. *Experimental Brain Research*, *67*, 316–322.
- Angelini, R., Frasca, R., & Grossi, D. (1992). Are patients with constructional disorders different in visuo-spatial abilities? *Acta Neurologica*, *14*, 595–604.
- Asher, H. B. (1983). *Causal modeling*. Newbury Park, California: Sage.
- Ballard, D. H., Hayhoe, M. M., & Pelz, J. B. (1995). Memory representations in natural tasks. *Journal of Cognitive Neuroscience*, *7*, 66–80.
- Bruce, C. J., & Goldberg, M. E. (1985). Primate frontal eye fields. I. Single neurons discharge before saccades. *Journal of Neurophysiology*, *53*, 603–635.
- Bruce, C. J., Goldberg, M. E., Bushnell, M. C., & Stanton, G. B. (1985). Primate frontal eye fields: II. Physiological and anatomical correlates of electrically evoked eye movements. *Journal of Neurophysiology*, *54*, 714–734.
- Burman, D. D., & Segraves, M. A. (1994). Primate frontal eye field activity during natural scanning eye movements. *Journal of Neurophysiology*, *71*, 1266–1271.
- Decety, J., & Jeannerod, M. (1995). Mentally simulated movements in virtual reality: Does Fitts's law hold in motor imagery? *Behavioural Brain Research*, *72*, 127–134.
- De Renzi, E. (1982). *Disorders of space exploration and cognition*. Baffins Lane Chichester, UK: Wiley.
- Dias, E. C., & Segraves, M. A. (1999). Muscimol-induced inactivation of monkey frontal eye field: Effects on visually and memory-guided saccades. *Journal of Neurophysiology*, *81*, 2191–2214.
- Everling, S., Dorris, M. C., Klein, R. M., & Munoz, D. P. (1999). Role of primate superior colliculus in preparation and execution of anti-saccades and pro-saccades. *Journal of Neuroscience*, *19*, 2740–2754.
- Franz, S. I., & Lashley, K. S. (1917). The retention of habits by the rat after destruction of the frontal portion of the cerebrum. *Psychobiology*, *1*, 3–18.
- Funahashi, S., Bruce, C. J., & Goldman-Rakic, P. S. (1993). Dorsolateral prefrontal lesions and oculomotor delayed-response performance: Evidence for mnemonic "scotomas". *Journal of Neuroscience*, *13*, 1479–1497.
- Funahashi, S., Chafee, M. V., & Goldman-Rakic, P. S. (1993). Prefrontal neuronal activity in rhesus monkeys performing a delayed anti-saccade task. *Nature*, *365*, 753–756.
- Gainotti, G. (1985). Constructional apraxia. In J. A. M. Frederiks (Ed.), *Handbook of clinical neurology*. Amsterdam: Elsevier, 491–506.
- Jolicoeur, P., & Ingleton, M. (1991). Size invariance in curve tracing. *Memory and Cognition*, *19*, 21–36.
- Jolicoeur, P., Ullman, S., & Mackay, M. (1986). Curve tracing: A possible basic operation in the perception of spatial relations. *Memory and Cognition*, *14*, 129–140.
- Jolicoeur, P., Ullman, S., & Mackay, M. (1991). Visual curve tracing properties. *Journal of Experimental Psychology: Human Perception and Performance*, *17*, 997–1022.
- Kleist, K. (1934). *Gehirnpathologie*. Leipzig: Barth.
- Lashley, K. S., & Ball, J. (1929). Spinal conduction and kinesthetic sensitivity in the maze habit. *Journal of Comparative Psychology*, *9*, 71–105.
- McCormick, P. A., & Jolicoeur, P. (1991). Predicting the shape of distance functions in curve tracing: evidence for a zoom lens operator. *Memory and Cognition*, *19*, 469–486.
- Milner, B. (1965). Visually-guided maze learning in man: Effects of bilateral hippocampal, bilateral frontal, and unilateral cerebral lesions. *Neuropsychologia*, *3*, 317–338.
- Morris, R. G., Garrud, P., Rawlins, J. N., & O'Keefe, J. (1982). Place navigation impaired in rats with hippocampal lesions. *Nature*, *297*, 681–683.
- O'Keefe, J. (1978). *The hippocampus as a cognitive map*. Oxford: Clarendon Press.
- Petrides, M., & Iversen, S. D. (1979). Restricted posterior parietal lesions in the rhesus monkey and performance on visuospatial tasks. *Brain Research*, *161*, 63–77.
- Porteus, S. D. (1965). *The Porteus maze test; fifty years' application*. Palo Alto, CA: Pacific Books.
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*, 3–25.
- Rayner, K. (1998) Eye movements in reading and information processing: 20 years of research. *Psychological Bulletin*, *124*, 372–422.
- Rieser, J. J. (1989) Access to knowledge of spatial structure at novel points of observation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *15*, 1157–1165.
- Robinson, D. A. (1963) A method of measuring eye movements using a scleral search coil in a magnetic field. *IEEE Transactions on Biomedical Engineering*, *10*, 137–145.
- Sawaguchi, T., & Goldman-Rakic, P. S. (1991). D1 dopamine receptors in prefrontal cortex: Involvement in working memory. *Science*, *251*, 947–950.
- Schall, J. D., Morel, A., King, D. J., & Bullier, J. (1995). Topography of visual cortex connections with frontal eye field in macaque: Convergence and segregation of processing streams. *Journal of Neuroscience*, *15*, 4464–4487.
- Schlag, J., & Schlag-Rey, M. (1987). Evidence for a supplementary eye field. *Journal of Neurophysiology*, *57*, 179–200.
- Sheimann, I. M., Khutuzian, S. S., & Ignatovitch, G. S. (1980). Periodicity in the behavior of grain beetle larvae. *Developmental Psychobiology*, *13*, 585–590.
- Shulman, G. L., Remington, R. W., & McLean, J. P. (1979). Moving attention through visual space. *Journal of Experimental Psychology: Human Perception and Performance*, *5*, 522–526.
- Snedecor, G. W., & Cochran, W. G. (1980). *Statistical methods* (7th ed.). Ames: Iowa State University Press.
- Tolman, E. C. (1948). Cognitive maps in rats and men. *The Psychological Review*, *55*, 189–208.
- Ullman, S. (1984). Visual routines. *Cognition*, *18*, 97–159.
- van Mier, H., Hulstijn, W., & Petersen, S. E. (1993). Changes in motor planning during the acquisition of movement patterns in a continuous task. *Acta Psychologica*, *82*, 291–312.
- Yarbus, A. L. (1967). *Eye movements and vision*. New York: Plenum.
- Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature*, *396*, 72–75.