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Human and Rat Behavioral Variability in the Dashiell Maze: A Comparative Analysis

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To assess their orientation in mazes, Dashiell (1930) developed a procedure allowing rats to reach the goal by utilizing paths of equal distance from the starting point. The main finding was the variety of new pathways that the subjects took to reach the goal. Given the need for a task that might evaluate behavioral variability in humans, a simulation of the Dashiell procedure was developed: a virtual maze for human participants. With the goal of validating an animal model task for assessing human behavior variability, this study presents an experiment comparing rat and human performance when traversing a Dashiell maze. Results showed that rats in their maze and humans in the virtual version had similar path variability for reaching the goal, although humans showed higher dispersion from the mean. We conclude that the adaptive function of route variability in rats is similar to that in humans; thus, the virtual Dashiell maze could become a reliable and straightforward task for assessing human behavior variability. Our study encourages the use of virtual mazes to compare behavioral variability between humans and other species.

Keywords: Dashiell maze, humans, rat, route, spatial, variability

Based on research and theoretical reflection, some authors have argued that animals in their habitats do not act in an unvarying manner. Instead, variation and flexibility are basic features of behavior (Gibson, 1994; Pisula, 2009; Reed, 1982, 1996). Novel responses have been linked to the adaptive value of variation in species selection (Neuringer, 2009; Skinner, 1985), creative processes, and novel behaviors (Pryor et al., 1969; Stahlman et al., 2013), as well as in the phenomenon of response induction through reinforcement (Keller & Schoenfeld, 1950; Lee et al., 2007). Page and Neuringer (1985) have emphasized the operant nature of behavioral variability and its modifiability and sensitivity to contingencies of reinforcement (for a critical review, see Machado & Tonneau, 2012), but other processes, such as reward expectation value and associative processes (Stahlman et al., 2010), have been involved.

Because behavioral variability may include very diverse topographies and modes of action, it is crucial to define which behavioral property to consider the appropriate dependent variable (see Moreno & Leite-Hunziker, 2008). In the case of rats as experimental subjects, most procedures involve a comparison between sequences of right and left responses to a lever (Neuringer, 1993; Neuringer et al., 2000), with variability defined operationally as changes in sequences of responding, according to a lag-*n* schedule of reinforcement. That is, in order to obtain a reinforcer, subjects must emit responses in a different sequence than the *n* preceding sequences. For example, a lag-1 schedule shows repetition of the previous sequence as an error, or a schedule lag-2 indicates that subjects have to emit at least two different successive sequences to obtain a reinforcer. When no changes in the behavioral sequences are observed, the behavior is considered stereotyped (Rodríguez & Thompson, 2015; Zepeda, 2017). The nature of sequences might be as instrumental responses or, with human participants, may entail more arbitrary relations such as conditional discrimination tasks (Zepeda & Martínez, 2015) and verbal responses (Heldt & Schlinger, 2012; Lee et al., 2002).

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Other procedures have shown that factors influencing behavioral variability are generalizable to different domains. With laterality of forepaw use in a food-reaching task in rats, for example, variation in using the dominant left or right foreleg increases when the food becomes unreachable (Cabrera & Ortega, 2017). Rats' lever pressing topography (Stokes, 1995), force (Notterman & Mintz, 1965), and duration (Gharib et al., 2004) are modified when reward probability is lowered or suppressed. In a spatial domain, the variability of navigation strategies as animals search for food is a function of reward expectation (Blaisdell et al., 2016; Griffith et al., 2015; Stahlman & Blaisdell, 2011). That is, changes in environmental layout and reward contingencies influence behavioral variability.

Despite all the time that has transpired since its first use in experimental psychology (Dashiell, 1925), the open-alley multiple-choice maze, or Dashiell maze, remains a novel procedure to evaluate variability for rats in the spatial domain (see Griffith et al., 2015). Motivated to assess rats' orientation in mazes, Dashiell developed a procedure that allowed rats access to the goal by means of different paths that were equidistant from the starting point (see Figure 1). The main finding was that once having learned, subjects took a variety of new pathways to reach the goal (Dashiell, 1930; Tolman, 1932). Travel from the start box to the goal could occur along multiple equal-length pathways. After some trials, subjects reduced time and distance to the goal. A very important finding was that no fixed reverse routes were found; instead, different successions of turns and runs toward the exit were observed. For Dashiell (1930), the use of newly correct pathways from trial to trial was evidence of a general orientation function and not just a fixed pattern of specific turns.

Though Dashiell's open-alley multiple-choice maze has been used infrequently, a recent study by Griffith et al. (2015) employed it to assess whether ambulatory variability changes according to reward expectation. The authors compared palatable food (cereal) with a nonpreferred food (chow). They found that rats showed more path variability when the nonpreferred food (chow) was available than when the more palatable food (cereal) was used. Even though the main objective of Griffith et al. (2015) was to evaluate reward expectation between two food qualities, their general findings confirmed Dashiell's (1930) original results: once the rats have learned to traverse the maze, they do not fixate on a particular route but take a variety of different correct paths.

Although the Dashiell maze has been used almost exclusively with rats, Dashiell's striking findings regarding path variability inspired a plan to adapt the maze with alternative tasks to assess behavioral variability in humans. The similarity between it and the urban grid plan, wherein streets run at right angles to each other, raises the question as to whether humans, like rats in Dashiell mazes, take different routes when the same place can be reached by several equidistant pathways. Given the difficulty of creating a real setting for evaluating locomotion in humans and wanting to promote translational research into human path selection variability, we used a virtual environment that simulated the Dashiell maze.

Spatial research in humans has shown that using virtual environments obtains reliable results (Baumann & Mattingley, 2010; Riecke et al., 2010; Riecke et al., 2002; Wartenberg et al., 1998). For example, Mallot et al. (1998) simulated a 3-D hexagonal village named *Hexatown* (see Mallot & Gillner, 2000), where the authors evaluated route navigation and the role of information about the maze's map in participants' errors and planning during excursions, returns, and novel routes. Another virtual environmental procedure that simulated urban areas is *Squareland* (Hamburger & Knauff, 2011; Hinterecker et al., 2014), which is more similar to the Dashiell maze given its structure of squares resembling the layout of urban areas. Nevertheless, the main emphasis in these virtual procedures is the relevance of landmarks to navigation; however, the variability of participants moving through the maze to arrive at the same goal has not yet been analyzed. Thus, the objective of the present experiment was to assess whether humans' behavioral variability of turns and runs in a virtual environment simulating the open-alley multiple-choice maze is comparable to rats' performance in the Dashiell maze. Our findings would provide evidence to justify using the virtual Dashiell maze as a parallel human task for analyzing behavior variability and related processes.

Method

Subjects and Participants

Human Participants

Twenty-three undergraduate psychology students (15 females and 8 males) between 18 and 20 years old volunteered to participate in the experiment in exchange for extra class credits equivalent to 3.00% of the total grade. Each participant signed a consent form and all treatment was conducted in accordance with the University Ethics Committee guidelines for human participation in experimental procedures.

Nonhuman Subjects

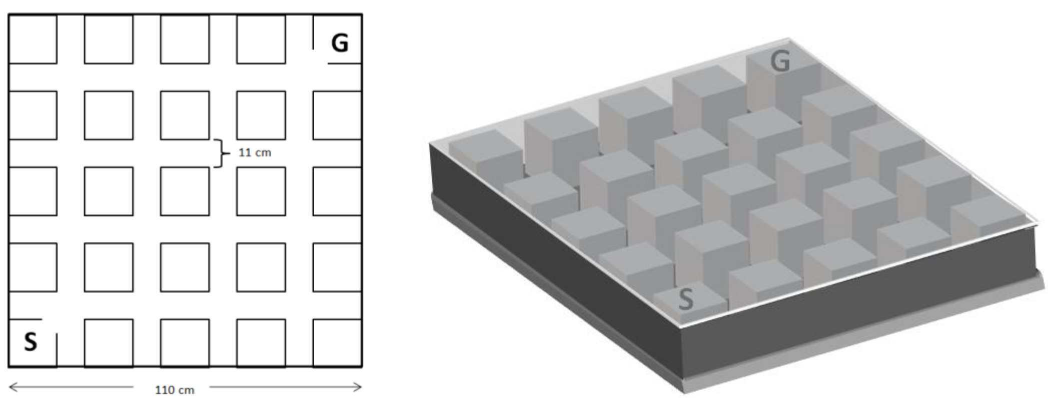
Twenty-three female albino Wistar rats (*Rattus norvegicus*) inbred at the University of Guadalajara Neuroscience Institute were used in the experiment. They were 18 months old at the beginning of the experiment and had previous experience in responding to a continuous schedule of reinforcement in a Skinner box. Rats were housed individually, maintained at 85% of their free-feeding weight (M = 189.76 g, SD = 15.91), and had free access to water. Feeding occurred within 20 min of the end of the session. Housing, food deprivation, and handling of nonhuman subjects were done following the University Ethics Committee's guidelines for animal care.

Materials and Apparatus

Materials used for the human subjects were a commercial PC computer equipped with a 10.5 in. (26.67 cm) screen, a mouse, and a keyboard. The experimental task was programmed using the software Maze Suite software (Ayaz et al., 2008). The map of the virtual maze that participants had to navigate is shown in Figure 1. The whole maze simulated brick walls (see Figure 2), and the participants advanced through the streets by pressing the keyboard arrow keys or using the mouse. The experiment was conducted individually, with each subject seated in a room with artificial illumination.

Figure 1

The Dashiell Maze

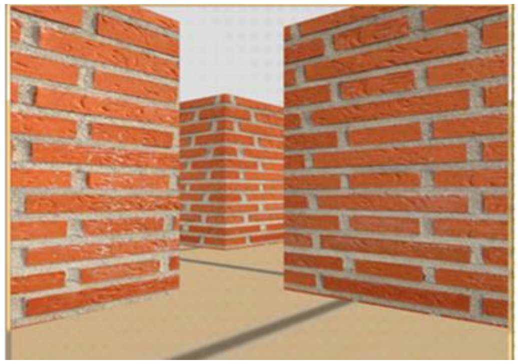


Note. Left: Overall plan of the open-alley multiple-choice maze based upon Dashiell (1925). S: Starting point, G: Goal. Right: Image of the actual apparatus with transparent roof and plastic walls.

For the rats, an open-alley multiple-choice maze was employed (see Figure 1, left). The apparatus was built of a 110 cm × 110 cm wooden floor, coated with black epoxy paint to facilitate cleaning and avoid odor marks. Twenty-five black plastic cubes (13 cm × 13 cm × 13 cm) were weighted with sand, making them too heavy to be moved by the rats. The cubes were distributed equidistantly upon the floor; five cubes on each side, with 11-cm pathways between. The perimeter was enclosed by attaching hard black plastic pieces to the outsides of cubes and floor. Transparent Plexiglas covered the entire square to prevent rats climbing and walking over the cubes (Figure 1, right). For all conditions, the start box was at the south-east corner of the apparatus, and the goal box was located in the north-west corner. The goal box contained five pieces of 45 mg food pellets (Bio-Serv®). The experimental sessions were carried out in darkness, but no attenuating noise chamber could be used. An IR Video camera (Panasonic®) suspended 90 cm over the maze and connected to a PC (HP) registered all sessions with an automated video tracker (EthoVision 7.0, Noldus®). The apparatus was located in a large room, its west side close to the wall. One metallic shelf was located 1.5 m along the north side of the maze and supported the computer, among other things. Another metallic shelf was located 1 m along the south side. Two experimenters, dressed in black, were placed beside the maze, one near the starting point (south of the apparatus) and the other on the computer, to the north of it.

Figure 2

Virtual Dashiell Maze for Humans



Note. View from starting point in maze for humans

Procedure

Human participants filled out the consent form and began by individually reading the following instructions (in Spanish):

On the screen you will see a maze, and your task is to traverse this maze. You can use the mouse or the arrow-keys to move through it. When you are ready please press the OK button.

Once participants arrived at the maze exit, the trial finished, and another trial began for a total of eight consecutive trials.

In the case of the rats, there was no previous habituation phase to the maze. From the first session, they had to find their way to the goal where five pieces of food were available. Each trial began by placing the rat at the start box: after approximately three seconds, the rat entered the maze, with the trial ending when it reached the goal or after 180 s, whichever came first. Once the rat reached the goal and ate the food, the experimenter gently retrieved it from the goal box and returned it to the home cage. Rats could see neither the goal nor the food from any location in the maze. The experiment was conducted over six consecutive days, with each session consisting of two trials.

Data Analysis

For both human participants and rats, every error-free route from the first eight trials was used in analyzing data. Error-free trials were defined as those in which subjects took any one of 20 minimum-distance routes between start and goal; that is, they reached the goal by moving only in northward or eastward directions. Any movement in the opposite directions (southward or westward travel) was considered to be a route with errors.

To measure variability for performance of correct trials, a measurement of entropy, or uncertainty (*U*-value), was calculated, which considered the different routes in the maze as the relative frequency of routes used (see Denney & Neuringer, 1998; Stokes, 1995)

$$U = -\sum_{i=1}^{n}[RF_i * log_2(RF_i)]/log_2(n).$$

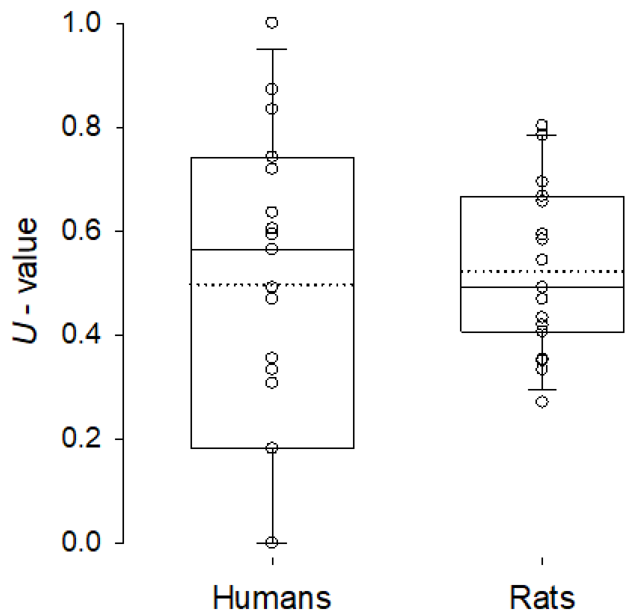
where *n* corresponds to error-free routes for reaching the goal. Although the Dashiell maze offers a total of 20 possible routes, *n* was used in the denominator as corresponding to the total correct routes for each participant. *RF* is the relative frequency of a route. The *U*-value is a measure of sequence uncertainty or randomness ranging from 0 to 1; when *U* approaches 1, this indicates more performance variability; that is, approximately how often each of the 20 possible routes occurred. When *U* approaches 0, it indicates only a few routes, meaning more stereotypical movement through the maze.

Results

Figure 3 shows the *U*-values for humans and rats in a box-plot. Open circles represent individual data for each species. Rat and human performance obtained similar average *U*-values, but there was considerably less dispersion among rats ($M = 0.52$, $SD = 0.16$) than among humans ($M = 0.49$, $SD = 0.33$). A *t*-test between groups confirmed no differences for rats as compared with humans, $t(44) = -0.33$. $p = .74$. This result indicates that both species have strong similitude in route variations on average, but human participants in the virtual maze showed slightly more dispersion in the virtual maze than rats running through the actual maze.

Figure 3

Levels of Variability, Measured by U-values for Rats and Humans

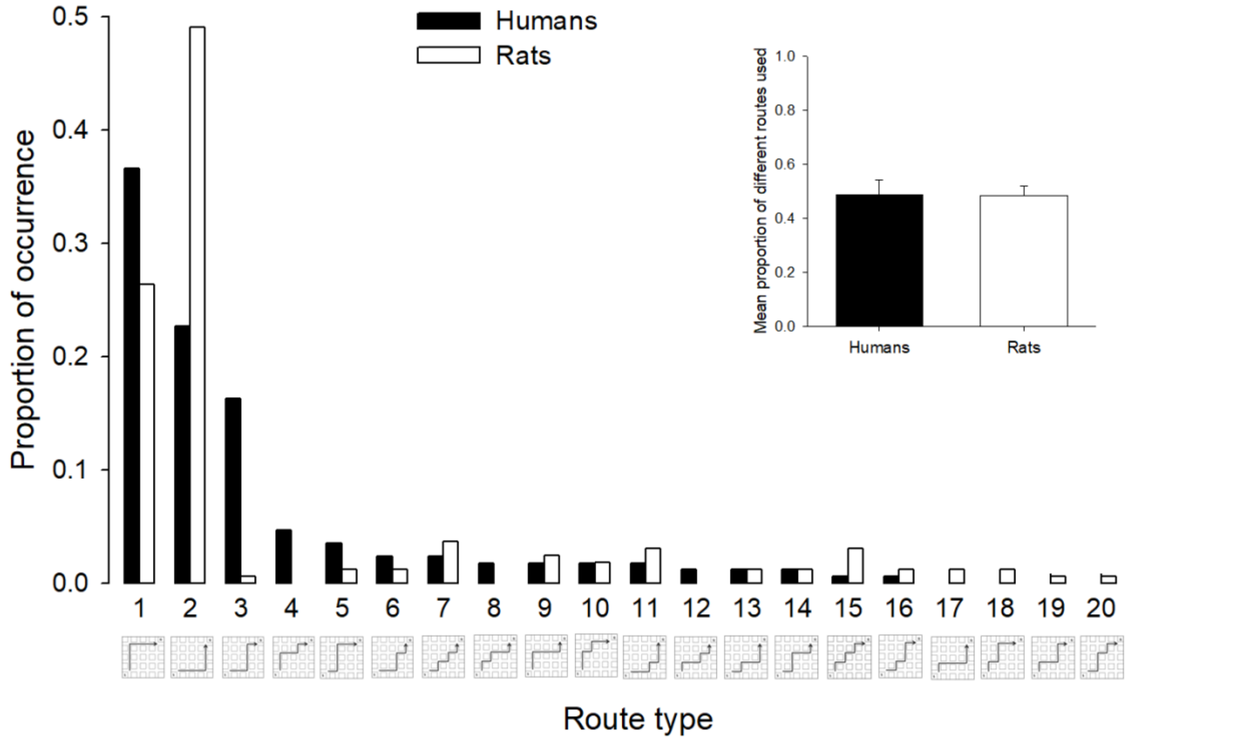


Note. Open circles represent individual data. The "error bars" indicate the range of values.

To compare the proportion of times each route occurred while subjects traversed the maze, the total frequency of a particular route was counted for each trial and divided by the number of correct routes employed. From this, the relative frequency of each route was calculated. This analysis is shown in Figure 4 for humans and rats. Filled bars represent humans, and empty bars correspond to rats. Route types were ordered from most to least used for the human group. Each route type is labeled and depicted on the x-axis. In both cases, humans and rats showed preferences for route type, $F(19, 880) = 40.30$, $p < .01$, with a particularly strong preference for routes with only one turn (right or left). While no differences were observed between species, $F(1, 880) = 0.01$, $p = .93$, routes 3, 4, and 5 were preferred more by humans than by rats, while routes 7, 11, and 15 were slightly preferred by rats. The Figure 4 inset, showing the average proportion of different routes used by humans (black bar) and rats (white bar), indicates that rats were nearly the same as humans in following different routes to the goal. A *t*-test between groups confirmed no difference, $t(44) = -0.25$. $p = .80$.

Figure 4

Proportion of Times Each Route Occurred for Humans and Rats



Note. Humans are shown by filled bars; rats, open bars. Inset graph shows the proportion of different routes used by humans and nonhuman subjects.

Overall, this experiment showed similar variability for all possible routes among rats in an actual maze compared with humans in a virtual maze. This finding contrasts with other studies in which nonhuman animals showed more variable behavior than humans in operant procedures (Maes & van der Goot, 2006).

Discussion

This study aimed to evaluate whether a virtual Dashiell maze may be reliable when comparing behavioral variability in humans with performance by nonhuman animals. Findings showed that rats in the Dashiell maze and humans in an equivalent virtual maze traversed the maze with similar path variability. The average of the uncertainty index (*U*-value) and the proportion of the different pathways used had similar values. For the rats, this result replicated Dashiell's original (1930) findings, that, instead of fixating on one pathway to the goal, the animals followed new, equally efficient routes.

Studies comparing differences in behavioral variability between humans and animals are not common (though see Stahlman, 2018). Previous studies have found results for humans and nonhuman animals to be inconsistent when reinforcing variability in sequential responses (Maes & van der Goot, 2006). However, some differences are due more to procedures than to species differences; for example, when engaged in more attractive tasks (i.e., using a computer game), humans exhibit greater variability (Hansson & Neuringer, 2018).

The advantage of rats using new paths could indicate the adaptive value of exploration and behavioral variability in animals while searching for food (Bell, 1991; Pisula, 2009). Considering that running through a maze is a niche-related behavior for a rat (Timberlake, 2002) may help explain the path variability. This assumption is supported by the fact that rats and other rodents show a *win-shift* strategy to find food; that is, they show a tendency to avoid repeating the places they obtain food, as in the cases of spontaneous alternation (Dember & Richman, 1989) and radial mazes (Timberlake & White, 1990). Furthermore, rats in radial mazes do not always use a fixed pattern to visit all the arms of the maze (Olton & Samuelson, 1976; Rojas-Leguizamón et al., 2019). Hence, the findings of the present experiments suggest that a similar win-shift strategy is used by rats to find different ways of reaching the same goal (Dashiell, 1930; Griffith et al., 2015).

The main characteristic of the Dashiell maze is successive right angles at each choice point. The high tendency for rats to use different ways could be related to the fact that "rats find it much easier to solve choice mazes when successive correct choices alternate from one side to the other" (Timberlake, 2002, p. 359), so the Dashiell maze furnishes path alternation with several correct choices.

Tying humans' niche-related behaviors to performance in the virtual Dashiell maze cannot be clearly argued, nor can ecological validity. For humans, procedures have shown high behavioral variability (Ross & Neuringer, 2002), though with some notable exceptions. In the real world outside the laboratory, the urban street grid, where streets run at right angles to each other, may be the corresponding niche-related condition. Research has shown a lack of variability in human mobility in cities, with most travel patterns having more fixed trajectories for arriving at a determined place (Song et al., 2010). Some authors (Kenett & Portugali, 2012) concluded that "routinized action, including movement in space, is thus a basic property of human behavior" (p. 11473). Much research in urban mobility coincides with the lower variability we observe in human trajectories, but several other factors, such as relative block lengths and different uses of streets, could influence lack of urban mobility (Jacobs, 1961). The absence of more information about the ecological validity of humans' niche-related behaviors into virtual environments may be the main limitation when using the virtual Dashiell maze.

Hence, a more complete description of the generative process of behavioral novelty and variability is needed, one that considers expectation and processes anticipatory to reinforcement (Griffith et al., 2015) as well as the action mode in which consequences will occur (Stahlman et al., 2013). To conclude, the environmental layout of the Dashiell maze provides an adequate setting for assessing behavioral variability, facilitating further comparative and translational research into humans and other species within the realm of variability and creativity (Stahlman, 2018; Stahlman et al., 2013).

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