

Spontaneous alternation behavior in *Paramecium*

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Spontaneous alternating behavior (SAB), the tendency of an organism to successively turn left and right in a maze, is a standard metric of short-term memory in developmental and psychopharmacological studies. Although SAB is perhaps the most phylogenetically widespread behavior in motile lifeforms, conflicting data on SAB exist for several sets of closely related taxa. For example, previous studies provide contradictory evidence concerning the existence of spontaneous alternation behavior in the protozoan *Paramecium*. However, these studies tested different species, using very different experimental designs. Using a single, factorial design for both previously tested species, *P. multicaudatum* and *P. caudatum*, we found that, in fact, the two species do not differ in their alternation behavior; specifically, they alternate in mazes with short tracks, but not in mazes with long tracks. These results are in accord with alternation studies on other taxa, and they fully resolve the apparent contradictions in the earlier studies on *Paramecium*. They also indicate that caution should be used in interpreting variable results across species tested with different experimental designs and suggest that, in at least some taxa, SAB may not be strictly dependent on the use of short-term memory.

Spontaneous alternation behavior (SAB) is the nonrandom tendency of an organism to choose to turn in the direction opposite to that of its previous turn in the absence of reward or reinforcement (Dember & Richman, 1989). Although the underlying mechanism of SAB has been controversial over the years, most researchers agree that the ability to alternate choices requires that the organism remember its previous choice (Hughes, 2004). As a result, SAB is a standard metric of short-term memory that has been used in hundreds of psychopharmacologic and developmental studies in mice and rats (Lalonde, 2002). Recently, however, some authors have begun to question the utility of SAB and other maze-based measures of memory (Wolfer, Staglar-Bozicevic, Errington, & Lipp, 1998), noting the potential for noncognitive factors such as thigmotaxis and residual odor cues to influence subject behavior in mazes.

Perhaps the most phylogenetically general behavior of motile life forms, SAB has been reported in animals ranging from primitive flatworms (Adelman & Dawson, 1970; Shinkman & Hertzler, 1964) to mammals (Dashiell & Bayroff, 1931), in protozoans (Lepley & Rice, 1952), and even in sperm cells (Brugger, Macas, & Eblemann, 2002). It is unusual for closely related species to differ in such an apparently conservative (and fundamental) trait, and yet there are several instances in which SAB has been reported in one species but not observed in a close

relative. Some examples include paramecia (Lachman & Havlena, 1962; Lepley & Rice, 1952), planarians (Adelman & Dawson, 1970; Rice & Lawless, 1957; Shinkman & Hertzler, 1964), and chickens (Cogan, Jones, & Irons, 1979; Hayes & Warren, 1963; Hughes, 1989a). To date, little attention has been paid to this curious situation, whose interpretation is further complicated by the extreme diversity of experimental designs used to study alternation behaviors.

For example, Lepley and Rice (1952) and Lachman and Havlena (1962) used paramecia to test Hull's (1943) model of reactive inhibition. Although neither study found support for reactive inhibition, Lepley and Rice did find unambiguous evidence for SAB in *P. multimicronucleatum* (84.7% alternation, $N = 1,115$, $\chi^2 = 535.9$, $p < .001$), whereas Lachman and Havlena reported equally compelling evidence that SAB does not occur in *P. caudatum* (47% alternation in single-forced-turn trials, $N = 100$, $\chi^2 = 0.36$, $p = .55$; 48.5% alternation in multiple-forced-turn trials, $N = 800$, $\chi^2 = 0.72$, $p = .40$). Lester (1968) and Hughes (1989b) noted the conflicting evidence provided by these studies but, like Lachman and Havlena, did not comment on the basis of this discrepancy. Shinkman and Hertzler (1964) speculated that the differences might have been due to differences in the experimental design of the two studies.

It is thus unclear whether or not these species truly differ in SAB. Not only did Lepley and Rice (1952) and Lachman and Havlena (1962) use different species of *Paramecium*, but, as Shinkman and Hertzler (1964) noted, their experimental designs differed in numerous other ways as well (Table 1). Of these many parameters, only track length and, to a limited extent, runway length have been systematically tested with respect to SAB (see Figure 1 for the maze terminology used in this article). SAB

We are grateful to Bruce Schulze, Daniel Gleason, Ray Chandler, and an anonymous reviewer for providing helpful comments and advice and to Alia Allen for assistance in tracking down Jean Havlena's master's thesis. Correspondence concerning this article should be addressed to A. W. Harvey, Department of Biology, Georgia Southern University, Statesboro, GA 30460 (e-mail: aharvey@georgiasouthern.edu).

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