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Continuous Spontaneous Alternation and Turn Alternation in *Artemia sp.*

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Free-running spontaneous alternation refers to the animal's tendency to prefer the least recently visited locations in successive spatial choices, which is attributed to the animals' choice between stimuli based on prior experience. *Turn alternation*, which is observed in directional choices preceded by a forced turn in one direction, also reflects the animals' tendency to alternate between directional choices but this tendency has been assumed to rely on other cues (e.g., proprioceptive cues) derived from the prior responses (e.g., forced turn in one direction). Based on previous studies, the turn alternation appears to rely on more primitive (lower-form) information features and to be a more frequently observed empirical phenomenon than the spontaneous alternation. We investigated these two behavioral alternation tendencies in *Artemia sp.* Experiment 1 tested the continuous spontaneous alternation (cSAB) performance of *Artemia sp.* in two different mazes: t-maze (three options) and plus maze (four options). Experiment 2 tested the turn alternation performance of *Artemia sp.* counter-balancing the direction of initial forced-turn between subjects. Our results showed that *Artemia sp.* had nearly chance level spontaneous alternation performance in the t-maze and plus maze whereas a higher than chance level turn alternation performance. These results support the ubiquity of turn alternation tendency across species and point at the lack of spontaneous alternation in *Artemia sp.*

Many species of animals exhibit a tendency to alternate between different locations and prefer the least recently visited place even in the absence of differential reinforcement of this pattern of responding (Balcı, Ramey-Balcı, & Ruamps, 2014; Ramey, Teichman, Oleksiak, & Balcı, 2009; Still, 1966; Schultz, 1964; Wayner & Zellner, 1958). This behavioral policy is referred to as *spontaneous alternation behavior* (SAB), and it is assumed to be adaptive for the organisms in their natural environments in terms of exploration, foraging, and avoidance of predators (Hughes, 1990; Richman, Dember, & Kim, 1986). For instance, SAB has been claimed to reduce environmental uncertainty, which would prove beneficial in cases of significant perturbations in the distribution of biologically critical variables such as resource allocation and predation risk (e.g., Inglis, Langton, Forkman, & Lazarus, 2001; Ramey et al., 2009). The results of two separate experimental studies indeed suggested the possible behavioral contribution of SAB to the range expansion of an invasive crustacean species, *Carcinus Maenas*. The continuous SAB (cSAB) performance in a plus maze (four locations) was shown to be higher (above chance level alternation performance) in this invasive compared to native species (i.e., *Callinectes Sapidus* and *Uca Pugnax*, chance level alternation performance) of marine crabs (Balcı et al., 2014; Ramey et al., 2009). These researchers suggested that the stronger alternation tendency of *C. Maenas* might contribute to their dispersion by reducing the adaptation period of this species to the new environment. A similar alternation tendency, referred to as *turn alternation*, is observed in directional choices preceded by a forced turn in one direction. For instance, if the animals were forced to turn left at an earlier choice point, when provided with two

choices (left vs. right) at the next choice point, they tended to turn right. Interestingly, if the animals were forced to turn in the same direction multiple times, the turn alternation tendency is strengthened, whereas the alternation tendency is weakened as a function of distance travelled since the forced turn (Wilson & Fowler, 1976; for review see Iwahara, 1963).

Hughes (1989) offered a conceptual differentiation between these two behavioral instantiations of the alternation tendency. According to his conceptualization, SAB is the result of active choices between exogenous stimuli based on the differential familiarity of the organism with these stimuli based on its prior experience. The turn alternation, on the other hand, was claimed to rely primarily on the proprioceptive cues gathered from previous responses of the organism (Hughes, 1985). From an information processing perspective, the implementation of SAB might require more complex mechanisms, and thus SAB might be relatively less likely to be observed in animals with simpler nervous systems. It is possible that tactile input that emerges from the interaction of the organism with the physical environment (e.g., thigmotaxis) also contributes to the directional choice behavior. For instance, Hughes (1990) showed that when available tunneling mud-crab relied more on tactile (i.e., contact with the vertical surface in the maze) than proprioceptive cues in guiding their directional choice behavior. Hughes (1989) also argued that the importance of tactile stimulus varies between different invertebrate species, and when present thigmotactic input can overpower the use of other endogenous cues (e.g., reactive inhibition).

Since the alternation tendency has not been widely studied in invertebrates, our knowledge regarding the ubiquity of this behavioral policy and the mechanisms that underlay it in invertebrates is rather limited. The majority of the studies conducted with invertebrate species point at the lack of alternation tendency in this group of animals (except in several earthwork species, centipede species, crab species, cockroaches; Hughes, 1989). When this situation is coupled with the bias against publishing negative results (Brunner et al., 2010), the alternation tendency might be even less prominent than it first appears to be in invertebrates (Hughes, 1989). However, one should exercise caution about these generalizations since the peculiar behavioral/environmental challenges faced by individual species might be an important factor in shaping directional choice patterns (e.g., type of foraging activities).

In this study, we investigated the continuous spontaneous alternation (cSAB) and the turn alternation performance of another crustacean species, *Artemia sp.* (Schlösser, 1756; Kuenen & Baas-Becking 1938). *Artemia spp.* live in inland hyper-saline lakes distributed virtually all over the world. These salt lakes constitute very distinct ecological niches for these organisms (Lenz & Browne, 1991; Persoone & Sorgeloos, 1980; Van Stappen, 2002). For instance, these harsh habitats contain few to no predators or competitors for these passive, non-selective filter-feeders. These distinct ecological characteristics motivated us to investigate the SAB performance of *Artemia sp.* since lower predation and competition pressures coupled with their relatively passive foraging behaviors might nullify the adaptive function of this behavioral tendency. Since turn alternation is considered to be a more frequently observed and possibly a more primitive and locally determined behavioral tendency (e.g., Iwahara, 1963; Wilson & Fowler, 1976), we also investigated the alternation behavior of *Artemia sp.* within a turn alternation-based experimental setting. The cSAB performance was tested in two different settings with different degrees of complexity (four arm maze,

three arm maze). The turn alternation was tested after a single forced leftward or rightward turn. We expected close to chance level spontaneous alternation performance in Experiment 1 and higher than chance level turn alternation performance in Experiment 2. Our study was not designed to test the mechanisms that underlay the alternation tendency of *Artemia sp.* We instead aimed to test the generalizability and the comparison of two different forms of alternation tendency in a Genus that has a different mode of movement (e.g., compared to isopods), live in a peculiar habitat (e.g., low competition and predation), and that was not studied before in this particular experimental setting.

Method

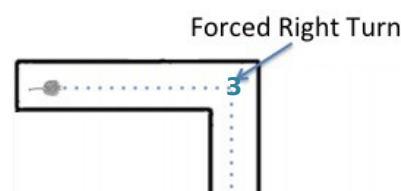
Subjects

Artemia sp. were purchased from a local pet shop in adult form and were kept in a aquarium (height 24.7 cm- width 25 cm- length 25 cm) in water at room temperature and with 53 ppt salinity. *Artemia sp.* were fed every twelve hours with five drops of *JBL Artemio Fluid®* or *Phyto-A*. The water in the tank was changed every ten days. Each subject was picked randomly from the housing aquarium (females with eggs were not included in the study). Each subject was tested in the same room where the aquarium was kept. The water used in the maze during testing in both experiments was sampled from the aquarium that housed the *Artemia sp.* in order to prevent any acclimation problems. There was no specific acclimation period provided to the subjects. No systematic effect on the behavior of animals was observed upon placing them in the maze (except for few subjects that exhibited circling behavior upon placement in the maze).

In Experiment 1, only those subjects that made more than 10 entries were included in the analysis. In T-maze 64.66% of the subjects (resultant $N = 42$) met this criterion and 70% of the subjects met this criterion (resultant $N = 45$) in the plus maze. This criterion for including subjects was used to be able to estimate the probabilities with sufficient precision (see also Balci et al., 2014; Ramey et al., 2009). In Experiment 2, within 78 subjects, if a subject did not make a turn during the first 10 min of testing, it was excluded from the study (resultant $N = 62$, 21% excluded).

Apparatus

A transparent Plexiglas plus maze (arm length 8 cm, arm width 2 cm, arm height 12 cm) surrounded by a white poster board (height 15 cm) was used in Experiment 1. One of the randomly picked arms of the plus maze was blocked by a transparent Plexiglass in order to convert it to and use it as a T-maze. In order to score the arm entries, a threshold was located 4 cm from the entrance of each arm. *Artemia sp.* were tested in 2 cm deep water. For Experiment 2, a Plexiglas multiple T-maze (arm length 9 cm x width 2 cm x arm height 7 cm) was used. The maze was surrounded by a white poster board (height 14 cm). After compartmentalizing it by inserting transparent Plexiglas panels to close appropriate arms (Figure 1), the multiple T-maze allowed us to induce a forced initial right or left turn. After this initial turn, the subject encountered a T-junction at the end of the alley. Subjects could make a free turn direction choice at this junction point. The threshold used to score a turn was 2 cm from the intersection. Due to positive phototactic behaviors of *Artemia spp.*, a light source (light bulb with 220-240 volt) was placed above the maze and diffused with a white sheet of paper to achieve a uniform distribution of light throughout the maze. Sessions were recorded using Sony Carl Zeiss Vario-Tessal camera, which was connected to a PC with a Dazzle DVD recorder. Videos were converted via Pinnacle software for further analysis.



Procedure

Experiment 1. Experiment 1 consisted of two test sessions; one conducted with plus maze and the other conducted with t-maze. The same subject was tested successively in two mazes and the order of testing with different mazes was randomized between subjects. Each session began with the placement of the *Artemia sp.* at the start of one of the arms (randomized between subjects) with the help of a plastic spoon. An arm entry was recorded when the subject (whole body) passed the arm entry threshold (described in the Apparatus Section). For the next arm threshold crossing to be considered as an arm entry, subjects were first required to fully exit the arm (thus entering the square zone that constituted the middle of the maze). Immediate repeated entries to the arms were defined as those threshold crossings made without fully exiting the arm since the previous threshold crossing. These entries were not counted because this behavior represents the continuation of the previous arm choice (see also Balci et al., 2014; Ramey et al., 2009 for a similar approach to scoring arm entries). Each arm entry was time-stamped and recorded. Each session lasted for 30 min.

Experiment 2. *Artemia sp.* were placed with a plastic spoon at the beginning of the alley that first led to the forced-turn. Subjects made either a right or left turn in the first choice point. After subjects made a forced turn, their next direction choice (free choice) was time-stamped and recorded. Subjects tested in Experiment 2 were different from the subjects tested in Experiment 1.

Data Analysis

The alternation scores were calculated for the plus maze as described in Balci et al. (2014) and Ramey et al. (2009). For the plus maze, we checked if four different arm entries were made within five consecutive choices (e.g., n to $n + 4$). This scoring method was chosen to be consistent with the literature (Balci et al., 2014; Ramey et al., 2009). If this criterion was met, a score of 1 was recorded, and if not, a score of 0 was recorded. This procedure was repeated for the next five consecutive choices (e.g., $n + 1$ to $n + 5$) until all choices were included in the analysis. For instance, if a subject has made the following choices: A-B-C-D-A-C-A-C-A-B, it would be considered to have made 2 alternations out of the possible 6 alternations (110000) for the plus maze. The alternation score for this subject would be $2/6 = .33$. A similar scoring regime was used for the T-maze data. In this latter case, we checked if three different arm entries were made within four consecutive choices. For example, if a subject has made the following choices A-C-A-B-A-C-A-C-A-C, it would be considered to have made 4 alternations out of the possible 7 alternations (111100) for the plus maze. The alternation score for this subject would be $4/7 = .57$. The chance level performance for the plus maze and T-maze were calculated as .44 and .75, respectively.

We only describe the calculation of the chance level performance (not allowing repeated choices) for the T-maze as the same calculation for the plus maze was reported elsewhere (e.g., Ramey et al., 2009). Since all three arms would be counted as a novel arm in the first entry, the probability of entering a new arm in the first arm choice would be 1 ($p(\text{novel}|1^{\text{st}} \text{ visit}) = 3/3$). In the second arm visit, the subject can directly choose one of the remaining two novel arms ($p(\text{novel}|2^{\text{nd}} \text{ visit}) = 2/2$) as the repeated entries (entering the previously visited arm) were not counted. The subject could complete all three arms by the third visit by choosing a new arm with the following probability at this choice point: $p(\text{novel}|3^{\text{rd}} \text{ visit}) = 1/2$. Thus, the probability of visiting three different arms through this series of choices is .5. On the other hand, the subject could follow a different series of choices by repeating one of its previous arm choices in the third arm visit. In this situation, the probability of making a repeated choice in the third visit is $p(\text{old}|3^{\text{th}} \text{ visit}) = 1/2$. In this case, the subject could still complete all three different arms within four choices by visiting a new arm on its fourth arm choice ($p(\text{novel}|4^{\text{th}} \text{ visit}) = 1/2$). Thus, the probability of completing all three different arm choices through this series of choices is .25. The chance level performance for the T-maze is equal to the sum of the abovementioned partial probabilities, $.5 + .25 = .75$.

For completeness, similar chance level calculations were also conducted for the arm entry scoring regimes that allowed for repeated arm entries. These values were .23 for plus maze and .44 for the T-maze. The alternation scores in Experiment 1 were compared to the corresponding chance levels with one-sample *t*-test. The data collected from the turn alternation experiment was compared to the data expected from random choices with one-sample chi-square test.

Results

Experiment 1

Figure 2 presents the empirical and the corresponding chance level performances for both T-maze and plus maze. *Artemia sp.* exhibited chance level alternation performance in the T-maze test, $t(41) = -1.207$, $p = 0.23$ ($M = .72$, $SEM = .025$), and significantly lower than chance level alternation performance in the plus maze test, $t(44) = -2.53$, $p < 0.05$ ($M = .38$, $SEM = .024$). There was no significant correlation between the alternation performances in the T-maze and plus maze test, $r = .05$, $p = 0.75$ (the analysis only included those subjects that had enough data points in both mazes). There was no significant effect of test order on the alternation performance in either T-maze or plus maze, $t(40) = -1.74$, $p = 0.09$ and $t(43) = 0.34$, $p = 0.74$, respectively (T-maze $M_{1stOrder} = .68$ vs. T-maze $M_{2ndOrder} = .76$; plus maze $M_{1stOrder} = .38$ vs. plus maze $M_{2ndOrder} = .39$).

For completeness, the comparisons to the chance level performances were also conducted after including the repeated arm entries (excluding immediate repeats). In these analyses, the alternation performance of *Artemia sp.* was not significantly different from the chance either in T-maze ($M = .44$, $SEM = 0.023$; $t(48) = 0.15$, $p = 0.88$) or plus maze ($M = .24$, $SEM = .024$; $t(51) = 0.298$, $p = 0.77$). Note that the number of subjects that met the minimum ten arm visit criterion was higher for this second set of analysis. Overall, these results suggest that *Artemia sp.* did not exhibit spontaneous alternation tendency.

Finally, in order to investigate if there was a difference between the average time spent prior to repeated vs. alternation trials, we conducted paired-samples t -test comparisons of these two measures separately for T-maze and plus maze tests. There was no significant difference between the average time spent prior to repeated vs. alternation choices either for T-maze, $t(48) = -0.01$, $p = 0.99$, or plus maze, $t(50) =$

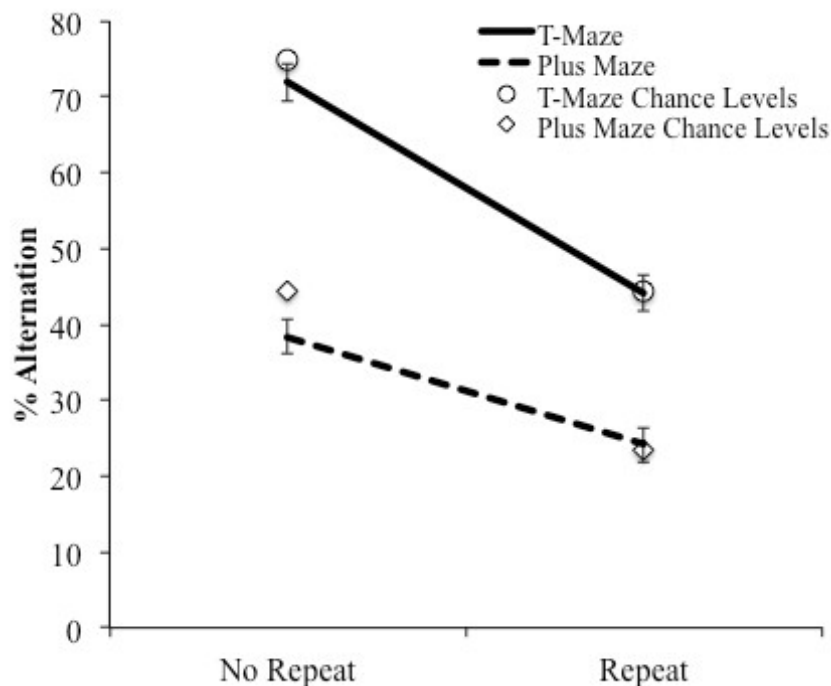


Figure 2. Percent alternation for no-repeat and repeat scoring regimes for T-maze and plus maze along

1.40, $p = 0.17$ (one subject was excluded because it did not exhibit any repeated arm visit in the plus maze).

Experiment 2

One-way chi-square test of the data in the turn alternation paradigm showed that, significantly higher than chance level proportion of subjects turned in the direction that was opposite to the forced-turn direction, $\chi^2(1, N = 120) = 14, p < 0.001$. The proportion of subjects that alternated in the forced left vs. forced right turn conditions were equal: 68% vs. 67%, respectively.

Discussion

The current study constitutes the first-time investigation of continuous spontaneous alternation and turn alternation performance in *Artemia sp.* Our results revealed that *Artemia sp.* had nearly chance level cSAB performance when tested in the T-maze, significantly lower than or chance level cSAB performance when tested in the plus maze (depending on the scoring regime), and a significantly higher than chance level turn alternation performance when forced to turn in one direction prior to the free-choice point. These results revealed differential alternation tendencies of *Artemia sp.* in free-running spontaneous alternation versus forced turn alternation paradigms. A similar dissociation between turn alternation and (discrete) spontaneous alternation performances was previously observed with *Armadillidium vulgare* (Iwahara, 1963).

These differential results suggest that the mechanisms that underlay SAB and turn alternation might indeed be different as suggested earlier by Hughes (1985, 1989). Under this rationale, *Artemia sp.* might be able to rely on internal response-dependent signals to guide their alternation tendencies, whereas their ability to rely on previous experiences of the exogenous stimuli (e.g., novelty) might not be sufficient to guide alternation behavior at least in the form of cSAB. Our results are also consistent with previous findings with rats that showed that alternation performance was stronger after forced turn compared to free-turn in the T-maze (Dember & Fowler, 1959; see also Wilson & Fowler, 1976 for a similar tendency in cockroaches). Given our observations during data scoring and the identical maze arm widths between the two experiments, it is not likely that the different levels of alternation performance (in comparison to the corresponding chance level performances) was due to the differential ability of the subjects to rely on tactile stimuli in different maze setups. If tactile stimuli guided the behavior of *Artemia sp.* in both experiments, one would not expect the observed performance differences between different maze setups. Since our experiments were not designed to directly test the cues that are utilized by *Artemia sp.* in guiding their directional choices, our results do not allow us to draw mechanistic conclusions.

Alternatively, our results can be accounted by conceptualizing the plus maze (four options), T-maze (three options), and turn alternation (two options) tasks in terms of task difficulty due to different numbers of spatial options provided in these experimental settings (Jaffard, Bontempi, & Menzaghi, 2001; Smith et al., 2014). Under this framework, information processing capabilities of *Artemia sp.* might be sufficient to manifest alternation tendencies only when they are confronted with few options. To

this end, the simplicity of the *Artemia sp.* nervous system might be the limiting factor for the computational complexity required for exhibiting adaptive behavior in more difficult (e.g., higher number of spatial options) spatial tasks.

The weak spontaneous alternation tendency of *Artemia sp.* might also be related to the peculiar ecological features that characterize the habitats of these organisms; e.g., few-to-no foraging and predation related pressures in their naturalistic environments. For instance, the relatively less important active exploratory tendencies of *Artemia spp.* in their natural environment might not have provided strong ecological pressures for the evolution of strong alternation mechanisms in the form of SAB. On the other hand, turn alternation might constitute a more primitive and locally determined (in terms prior behavioral history) behavioral tendency. Overall, our results characterize turn alternation as a more robust and ubiquitous behavioral phenomenon than spontaneous alternation (e.g., Balcı et al., 2014; Iwahara, 1963; Ramey et al., 2009; Dember & Fowler, 1959). Future studies are required to elucidate the factors that underlay these differential findings between different experimental settings. The potential cues organisms use to navigate can be varied in order to test their effects on the alternation performance. For instance, the light density projected to each arm might be changed. Another potential variable to study might be the effect physiological perturbation/stress level has on the alternation performance (e.g., decreased salinity of the water during testing).

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