

UCLA

International Journal of Comparative Psychology

Title

Decision-Making and Turn Alternation in Pill Bugs (*Armadillidium Vulgare*)

Permalink

<https://escholarship.org/uc/item/1wn9s57r>

Journal

International Journal of Comparative Psychology, 12(3)

ISSN

0889-3667

Author

Moriyama, Tohru

Publication Date

1999

License

<https://creativecommons.org/licenses/by/3.0/> 4.0

Peer reviewed

DECISION-MAKING AND TURN ALTERNATION IN PILL BUGS (*ARMADILLIDIUM VULGARE*)

Tohru Moriyama
Future University-Hakodate, JAPAN

ABSTRACT: Twelve pill bugs (*Armadillidium vulgare*, Isopoda, Crustacean) were examined in 200 successive T-mazes. When obstacles are present, *A. vulgare* tend to move by means of turn alternation, which is generally considered an innate adaptive behavior. With a decrease in air moisture, the bugs have a tendency to increase their turn alternation rate. However, in such long successive T-mazes as in this study, continued turn alternation should actually accelerate the bugs' desiccation. This fact implies that turn alternation cannot always work adaptively. In this trade-off situation, while three individuals kept turn alternation at a high rate (1) and four at a low rate, (2), the other five spontaneously increased the rate of turn alternation and then decreased it (3). This instability of turn alternation in group (3) is interpreted as resulting not from stochastic factors but rather from the bugs' own decision-making, and seems to be an escape behavior used to get out of the experimental apparatus. In order to verify the decision-making hypothesis, all animals were subsequently tested in another successive T-maze apparatus, where the ends of the chosen alleys were shut, i.e., with 50 successive blind alleys. In this situation, while individuals of groups (1) and (2) continued to wander inside the apparatus, those of group (3) found a vertical rough wall, climbed it, and escaped from the apparatus in the middle of the experiment. Most of the unexercised individuals in the control experiment did not show climbing behavior.

Generally, a cornerstone of ethological theory is the understanding that behavior of animals comes in modal action patterns (MAP) (Barlow, 1977). MAP was introduced to soften the concept of fixed action patterns (FAP) (Thorpe, 1951) and is considered to explain the variability among individuals when performing a particular sequence of action patterns. It means that a MAP consists of a main adaptive stereotyped pattern resulting from a species-characteristic stable mechanism, and minor nonadaptive variant patterns resulting from individual-characteristic genetic variation. However, sometimes we encounter individuals for which the MAP cannot be identified, because

Address correspondence to Tohru Moriyama, Department of Complex Systems, School of Systems Information Science, Future University-Hakodate, 116-2, Kamedanakano-cho, Hakodate, 041-8655 Japan. e-mail; moriyama@fun.ac.jp

the frequency of variant patterns is higher than or almost the same as that of the stereotyped pattern. For these individuals, we cannot discard the idea that such variant patterns may imply autonomous behavior resulting, not from innate genetic variation, but from decision-making. If so, in contrast to commonly accepted ideas, we can experimentally observe that such individuals spontaneously increase the variant patterns for adaptation. In this paper, by testing the movements of *A. vulgare*, the generation of variant patterns implying adaptability is demonstrated.

In an open field, *A. vulgare* move forward in a straight line (Iwata & Watanabe, 1957a). It is said that in natural settings, a linear path of movement is the most efficient adaptive strategy when the animal lacks precise information about environmental resources or hazards (Jander, 1975). When obstacles are encountered, a number of invertebrate species use turn alternation, i.e., a left turn followed by a right turn (or vice versa), to correct the deviations from linear movement (Hughes, 1989a). Such behavior has also been investigated in *A. vulgare* (Watanabe & Iwata, 1956; Iwata & Watanabe, 1957a, b; Kupferman, 1966).

It is suggested for terrestrial isopods that the mechanism underlying turn alternation is based mainly on proprioceptive information about the previous turn which arises in the process of turning from bilaterally asymmetrical leg movements (BALM) on the two sides of the body (Hughes, 1985, 1987, 1989b). The adaptive function of turn alternation has also been interpreted as an 'escaping' one ensuring efficient motion away from biologically unfavorable conditions, since it is intensified by desiccation or contact with a predator (Hughes, 1967; Carbines, *et al.*, 1992). Overall, when performing a sequence of action patterns, keeping turn alternations at a high rate constitutes an 'escape behavior' and can be considered as MAP. The stereotyped pattern in such a setup is each turn alternation, i.e., a pair of successive turns in opposite directions, based on a stable BALM mechanism. The variant patterns are those such as successive turns in the same direction, backtracking, and so on, based on individual genetic variation.

In extant studies, escape behavior was studied in only three or four successive T-mazes (e.g., Watanabe & Iwata, 1956; Hughes, 1967; Carbins *et al.*, 1992). In such short-path situations turn alternation may seem to work efficiently. In the present experiments, each individual experienced 100 successive T-mazes in each of two successive days (Experiment 1). In such long-path situations, continued turn alternation would result in water deficit in the body. Since, as described above, there is a tendency to increase turn alternation in response to desiccation, it can be seen that in this trade-off situation turn alternation

no longer works adaptively. This situation seems to present an unsolvable problem if one believes the MAP concept, i.e., that an intrinsic mechanism underlying turn alternation, BALM, is stable. But on the contrary, since the pill bugs are free from any observer's MAP concepts, it can be expected that they solve it by spontaneously discarding turn alternation, i.e., by increasing variant patterns after the spontaneous stabilization of turn alternation.

Recently, the generation of variant patterns has been observed as resulting in autonomous transformation of MAP in a trade-off situation, and was interpreted as 'behavioral plasticity' (Gunji, 1996; Migita & Gunji, 1996). In the experiment of rout-formation in pheromone-dependent ants, an excessive generation of pheromone-independent behavior triggered the transformation of the established route. Although such generation of variant patterns is usually considered as resulting from innate genetic variations, it was attributed to 'decision-making of the ant itself' (Kitabayashi & Gunji, 1997). Moreover, in a maze experiment, octopuses spontaneously increased variant patterns and used them for novel solutions in a maze with a trade-off condition (Moriyama & Gunji, 1997). If the increase of variant patterns of *A. vulgare* results not from innate genetic variations but rather from decision-making, which implies manifestation of their autonomous choice of action patterns, we should be able to observe the behavior's novelty and adaptability. In order to verify this hypothesis, a second experiment was performed (Experiment 2).

METHODS

Subjects

One hundred and fifty individuals of *A. vulgare* as a group were caught on a woodland path at the south foot of Mt. Rokko, Kobe, Japan (34°43' N, 135°14' E, 400 ft in altitude) in July for main stock and were kept in a plastic container (20 cm in diameter, with soil to a depth of 2 cm and an opaque thick paper lid) in the laboratory. They were fed with slices of carrot (Heeley, 1941). A moist atmosphere was maintained by wetting the soil every day. The lid was closed and illumination was off except for feeding and wetting (once in the morning). The temperature of the laboratory was kept at 23-25; the humidity was 30-40%.

In the experimental phase, some individuals, each of which was 8-9 mm in length and 4-5 mm in width, were selected from the main stock and placed one by one into petri dishes (8 cm in diameter, with a thin

layer of soil). Their ability to move actively on the horizontal floor and vertical wood wall (i.e., rough-surface wall) was also examined. Each individual was isolated and fed on a small piece of sliced carrot for 2 days prior to conducting the experiments. The condition of atmosphere and illumination were the same as in the main container.

General Procedure

On the third day, experiments were conducted. At first, each individual was placed into another petri dish without lid and soil and exposed to light for ten minutes. This sudden bright and dry condition provided the stimulus for motion. A 15-watt fluorescent light that had an intensity of 200 Lx at a distance of 100 cm from the floor of the dish was used as the light source. White paper pasted on the floor of the dishes removed the soil from their legs while they were moving around. Then each individual was placed into the experimental apparatus under the same brightness condition. Each experiment lasted for not more than 30 minutes ensuring no alternation in their behavior due to dehydration (Warburg, 1964). It was stopped when an individual stayed stationary for more than two minutes or escaped by getting over the wall of the apparatus. After each experiment, individuals were returned to their previous petri dishes with lid and soil. The behavior was recorded by CCD camera connected to a video recorder.

EXPERIMENT 1

Procedure

In order to construct long successive T-mazes, the apparatus shown in Fig.1 was devised. White paper was pasted on the runways to make the individuals move quickly (Hughes, 1992). Twenty individuals were selected and each one was safely lowered into the start alley of a T-maze. As soon as they passed the first T-junction, the corresponding turntable was rotated to lead them through the connection path to another T-maze. In this way, they were forced to continue moving from one junction to another. Locomotion from one junction to another was defined as one trial, and each individual was examined for 100 trials in the wooden wall maze (Fig.1) on the first day (Experiment 1A). In order to investigate that juxtaposition of rough and smooth walls does not cause climbing behavior on rough ones, the same individuals were also examined in the Teflon and partial wooden wall maze (Fig.2) for 100 trials on the next day (Experiment 1B).

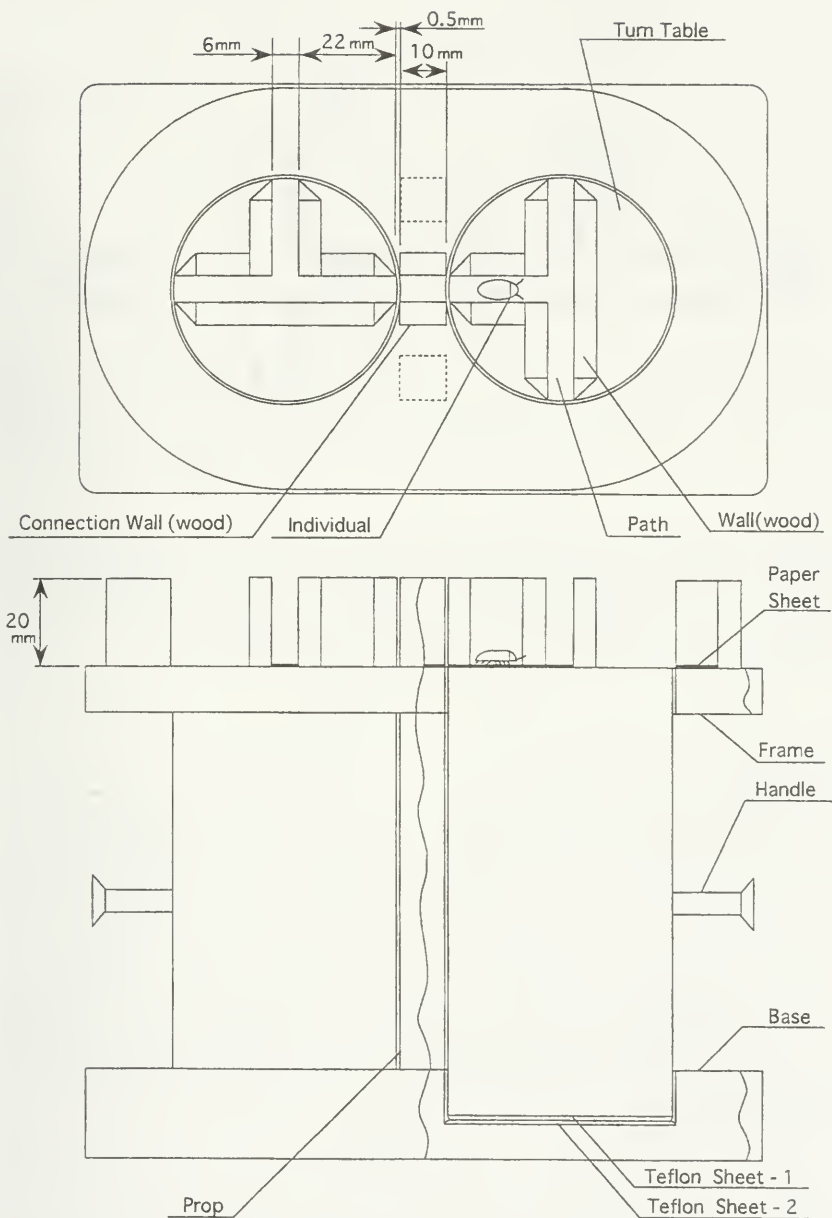


Figure 1. Apparatus implementing long successive T-maze with wooden walls. Each turntable mounts a T-maze, and has a handle to be turned manually. An observer can make each individual experience successive T-mazes by turning the turntables. As a result, each alley of the maze becomes 54 mm.

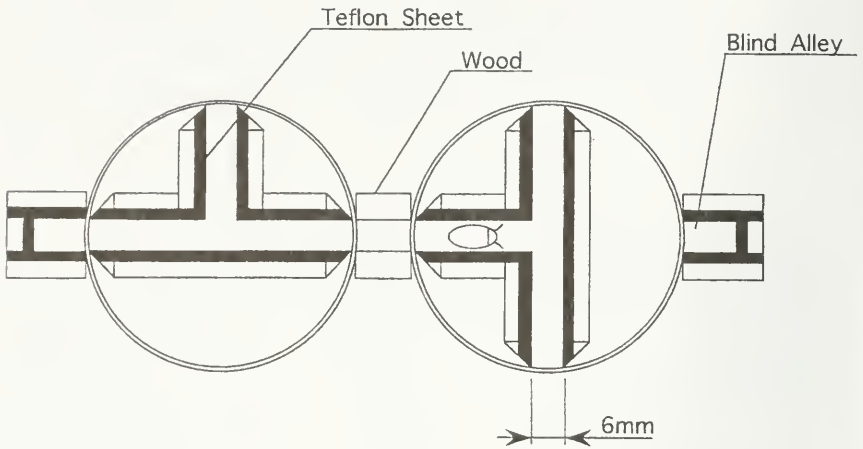


Figure 2. Apparatus implementing long successive T-maze with Teflon walls. All the walls except for the connection wall are covered with Teflon sheets. Notice that blind alleys with Teflon walls are used only for Experiment 2A and 2B, not for Experiment 1B. Other details are the same as in Fig. 1.

RESULTS - EXPERIMENT 1

A sequential action pattern of '2-3-4' in Fig.3 was defined as 'L-1', and '4-5-6' as 'R-1'. In this way, the second turn in an action pattern becomes the first turn of the next one. These turn alternations are the stereotyped patterns. The other patterns (6 patterns, R-2~R-4 and L-2~L-4), illustrated in Fig.4 were also observed. These constitute the variant patterns. The patterns R-3, R-4, L-3 and L-4, in which the individual begins to turn in one direction, and then reverses its choice and completes the turn in the opposite direction are distinguishable in this framework.

First, for the analysis of occurrence of L-1 and R-1, the total number of each pattern for each individual in each experiment was counted. Individual No.3 escaped after three trials in both Experiments 1A and 1B. Nos.8 and 10 stayed stationary for more than two minutes from the start in both experiments Nos. 9 and 15 started in motion, but in the middle of the trials (No.9, 10th trial in Experiment 1A, 23rd trial in 1B; No.15, 48th trial in 1A, 15th trial in 1B) stayed stationary for more than two minutes. As for Nos.6, 14 and 16, though they moved in all the 100 trials in Experiment 1B, they stayed put in the middle of

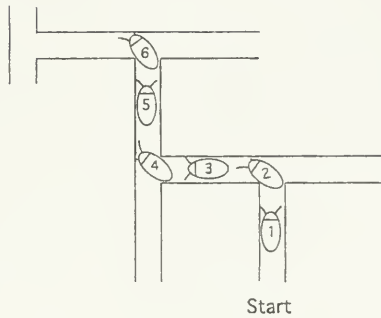


Figure 3. Illustration of turn alternation. The numbers indicate successive position as an individual moves. The individual is turning to alternating directions. '2→3→4' is defined as 'L-1'. '4→5→6,' 'R-1'.

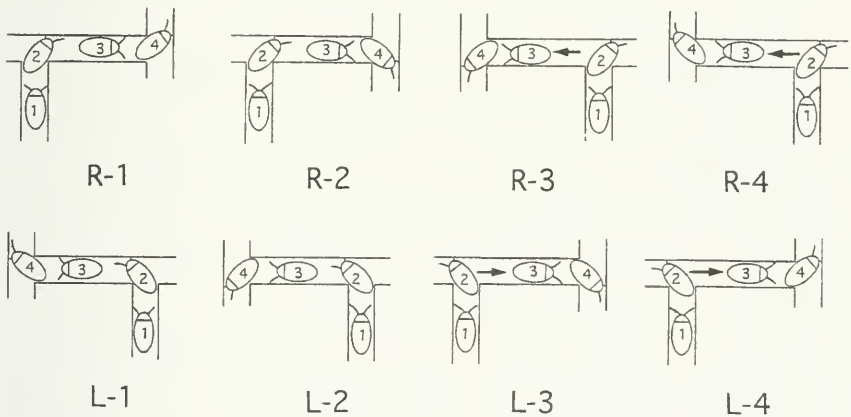


Figure 4. Variant patterns (L-2, 3, 4 and R-2, 3, 4), and stereotyped patterns (L-1 and R-1). The numbers show the time sequence for the locomotion of individuals. In L-3 (R-3) and L-4 (R-4), individuals begin turning to the left (right) at the choice point, but change direction before reaching the next turning point.

Experiment 1A (No.6, 35th trial; No.14, 21st trial; No.16, 8th trial). In order to perform a consistent analysis, the data corresponding to these eight individuals were discarded and the remaining twelve data were investigated (Tables 1 and 2). The juxtaposition of rough and smooth walls of the apparatus in Experiment 1B did not elicit climbing behavior. Since the total number of L-1 and R-1 in each experiment (the

Table 1. Number of Action Patterns in Experiment 1A. G-scores (resulting from log-likelihood ratio Goodness of Fit test) of 3.84 correspond to the threshold significance of P-value 0.05 (df = 1). Values in the tables larger than 3.84 mean that the number of L-1 or R-1 is significantly larger than 50% of the total number of 'left action patterns (L-1,2,3,4)' or 'right action patterns (R-1,2,3,4)'. ns, not significantly larger than 50%.

	No. 1	No. 2	No. 4	No. 5	No. 7	No. 11	No. 12	No. 13	No. 17	No. 18	No. 19	No. 20	Total
L-1	30	32	39	32	33	28	29	30	37	38	38	33	399
L-2	10	13	11	5	12	26	22	3	9	3	6	4	124
L-3	1	1	1	2	2	2	2	1	0	0	0	2	14
L-4	4	12	2	0	1	6	15	0	1	1	3	0	45
Total	45	58	53	39	48	62	68	34	47	42	47	39	582
G-score	5.1	ns	12.27	17.36	6.92	ns	ns	22.5	16.5	31.81	19.25	20.58	82.1
R-1	24	32	39	32	34	30	29	31	36	38	37	36	398
R-2	15	6	4	23	12	4	1	25	15	20	12	24	161
R-3	5	3	1	1	0	0	1	0	0	0	0	0	11
R-4	9	0	2	5	5	2	0	10	1	0	3	0	37
Total	53	41	46	61	51	36	31	66	52	58	52	60	607
G-score	ns	13.68	25.54	ns	5.78	17.47	28.14	ns	7.89	5.68	9.61	ns	59.8

Table 2. Number of Action Patterns in Experiment 1B. G-scores (resulting from log-likelihood ratio Goodness of Fit test) of 3.84 correspond to the threshold significance of P-value 0.05 (df = 1). Values in the tables larger than 3.84 mean that the number of L-1 or R-1 is significantly larger than 50% of the total number of 'left action patterns (L-1,2,3,4)' or 'right action patterns (R-1,2,3,4)'. ns, not significantly larger than 50%.

	No. 1	No. 2	No. 4	No. 5	No. 7	No. 11	No. 12	No. 13	No. 17	No. 18	No. 19	No. 20	Total
L-1	29	33	34	30	34	40	34	38	38	37	40	26	413
L-2	7	16	31	3	13	15	6	10	9	4	5	5	124
L-3	0	1	0	1	0	1	1	0	0	3	0	1	8
L-4	2	13	1	0	3	1	0	3	0	2	0	1	26
Total	38	63	66	34	50	57	41	51	47	46	45	33	571
G-score	11.08	ns	ns	22.5	6.63	9.55	19.36	12.8	19.25	18.29	30.99	34.03	118
R-1	28	32	33	31	32	40	35	39	38	39	40	26	413
R-2	31	6	1	30	15	4	21	9	15	14	15	36	197
R-3	0	0	1	0	1	1	0	0	1	0	1	0	5
R-4	5	0	0	5	3	0	4	1	0	1	0	6	25
Total	64	38	35	66	51	45	60	49	54	54	56	68	640
G-score	ns	19.53	33.19	ns	ns	30.99	ns	18.34	9.23	11.05	10.63	ns	54.8

right hand marginal column in each table) is statistically significant, MAP, i.e., escape behavior constituted by keeping turn alternations at high rate, can be observed. However, on an individual level, only three individuals (Nos.17, 18 and 19) maintained high frequency of stereotyped patterns in both experiments. This result indicates that turn alternation is not always stable over time.

Next, in order to analyze temporal stability of turn alternation, the frequency of occurrence of each stereotyped pattern for each individual was investigated. A set of ten successive action patterns was taken in time order and called a 'session.' The frequency of L-1 and R-1 in a session were calculated as:

$$\text{freq. of } L-1 = \frac{\text{Number of } L-1}{\text{Number } (L-1 + L-2 + L-3 + L-4)}$$

$$\text{freq. of } R-1 = \frac{\text{Number of } R-1}{\text{Number } (R-1 + R-2 + R-3 + R-4)}$$

For example, if an observed time series in a session is:

→(R-1)→(L-1)→(R-1)→(L-1)→(R-2)→(R-1)→(L-1)→(R-3)→(L-3)→(R-1)→
then, the frequency of L-1 = 0.75 and the frequency of R-1 = 0.67.

Frequency values were then plotted as shown in Figs.5, 6 and 7. Though the two experiments were conducted on different days, an interesting behavior appears in the plots of individuals No.1, 2, 5, 11 and 12 if we take the effect of their past experience into account and regard the two experiments as continuum (Fig.5). The time series of L-1 frequencies for Nos.2, 11, and 12, and those of R-1 for Nos.1 and 5 illustrate this behavior. In these plots, in spite of the very low initial values (under 0.5, except for No. 2 (0.6)), the frequencies reach even lower values (the first minimum values). After this, the frequencies gradually increase and reach the first value of '1' (the first maximum value). In this time interval, i.e., from the initial value to the first maximum value, each of these individuals' frequencies significantly increases (See the results of Spearman's rank correlation test for each graph in the caption of Fig.5).

This kind of spontaneous increase of turn alternation, which is characterized by the overall increase in frequency of stereotyped patterns with a local minimum (first minimum value), was found only for these five individuals. Especially for Nos.1, 11 and 12, one can see

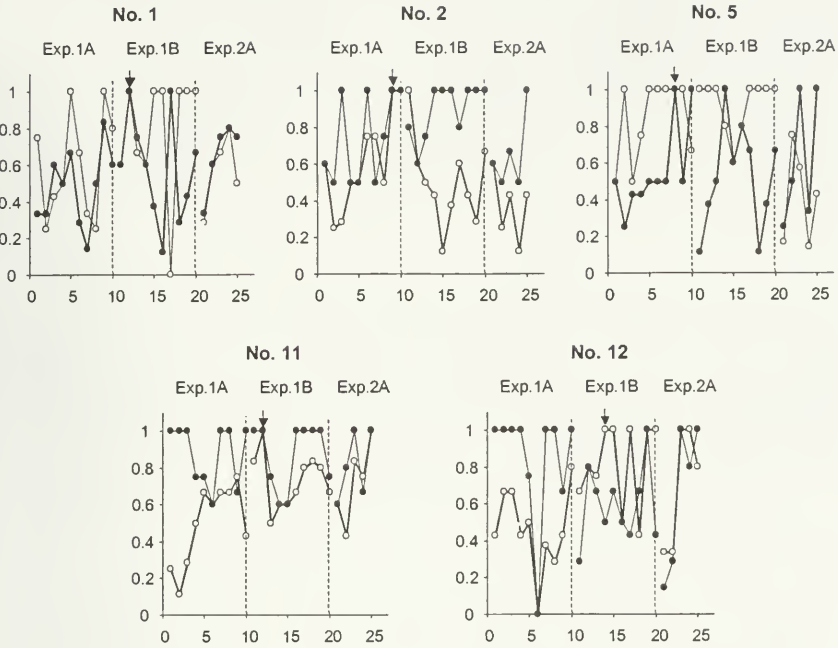


Figure 5. Time series of frequency of L-1 (unfilled circles) and R-1 (filled circles) in the generative variation group (Nos.1, 2, 5, 11 and 12). Vertical axis represents 'frequency'. Horizontal axis represents 'session'. Individual subject number is shown at the top of each graph. The first maximum value (the first value of '1') is indicated by the arrow. The behaviors of action patterns which show the tendency of spontaneous increase are emphasized by bold lines. The values of Spearman rank correlation coefficient (r_s), sample size (n) and significance level (p) are (individual subject number (r_s , n , p)); No.1 (0.5244, 12, <0.05), No.2 (0.6125, 9, <0.05), No.5 (0.6845, 8, <0.05), No.11 (0.8252, 12, <0.01), No.12 (0.5308, 14, <0.05).

that the values continue increasing from Experiment 1A to 1B despite different days, and reach '1' in Experiment 1B. Importantly, just after this process, the frequency of each stereotyped pattern abruptly decreases again, i.e., the frequency of variant patterns increases, and reaches a value below 0.5. In this paper, these five individuals are called 'generative variation group.' Nos.17, 18 and 19, which maintained a high frequency of stereotyped patterns in both experiments, are called the 'stereotype group, (Fig.6)' and the other four individuals, the 'error group (Fig.7).'

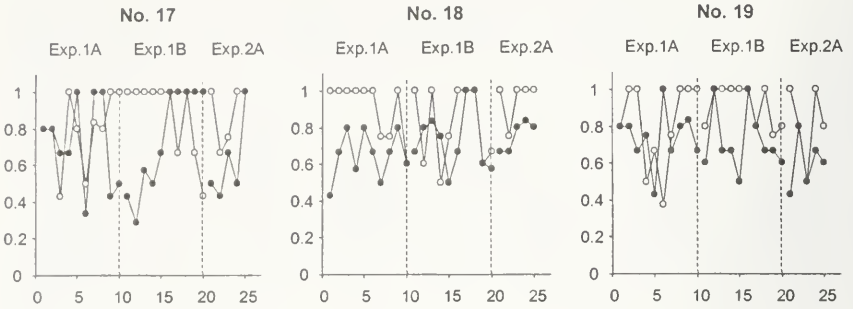


Figure 6. Time series of frequency of L-1 (unfilled circles) and R-1 (filled circles) in the stereotype group (Nos. 17, 18 and 19). Vertical axis represents 'frequency'. Horizontal axis represents 'session'. Individual subject number is shown at the top of each graph.

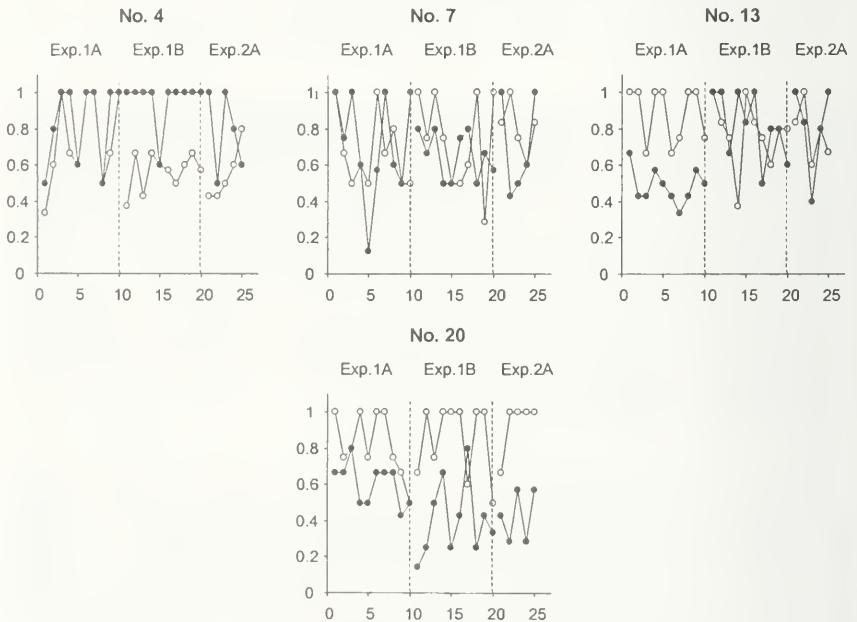


Figure 7. Time series of frequency of L-1 (unfilled circles) and R-1 (filled circles) in the error group (Nos. 4, 7, 13 and 20). Vertical axis represents 'frequency'. Horizontal axis represents 'session'. Individual subject number is shown at the top of each graph.

In order to verify whether such an increase of variant patterns in the generative variation group results not from innate genetic variations but rather from decision-making, i.e., to verify the novelty and adaptability of the increase of variant patterns, a second experiment was performed.

EXPERIMENT 2

Procedure

The day after Experiment 1B, the same twelve individuals were examined in the same maze again. In this case, after passing the fifty-first T-junction, they were led to the blind alley situated at the end of the selected arm (Fig.2). Teflon sheets were also pasted on the walls of the blind alleys, because pill bugs climb walls at corners as a result of excess movement of forward-going-tendency, as do centipedes (Shafer, 1976). Then they were expected to backtrack and move to the next T-maze on the other turntable. After turning at the next junction, they were led to the opposite blind alley. In this manner, they were led into blind alleys successively for fifty trials (Experiment 2A). Moving around in this apparatus would only result in water deficit in their body. In this experiment, since two successive turns were precluded by the blind alley, individuals could not constitute escape behavior based on turn alternation or on variant patterns shown by the generative variation group in Experiment 1. In this situation, another novel escape pattern was required for survival.

Another twenty unexercised individuals were selected from the main stock and examined in a control experiment with the same apparatus under the same conditions. This experiment was implemented to investigate that the Experiment 1 with trade-off situation essentially effects on the generation of the novel behavior. These individuals were led to the blind alley from the first trial and ran into the blind alleys for fifty trials (Experiment 2B).

RESULTS - EXPERIMENT 2

As shown in Table 3, in Experiment 2A all individuals from the generative variation group noticed the wood wall in the connection section and climbed it in the middle of the trials (No.1, at 5th trial; No.2, 14th; No.5, 11th, No.11, 13th; No.12, 6th). The other individuals, except for No.7, did not climb the wall and continued moving around

the apparatus. No.7 escaped at the 7th trial. Generally, woodlice climb vertical walls for transpiration only in the case of saturated air conditions, as the higher location has lower humidity (Den Boer, 1961). In experiment 2B, sixteen of eighteen unexercised individuals continued moving around. The remaining two climbed the connection wall (also Table 3).

Table 3. *P* values (a.- c.) from Fisher's exact probability test.

	Climbing	Wandering	<i>P</i> value
Generative variation group	5	0	a. $p = 0.0006$
Stereotype & Error group	1	6	b. $p = 0.4657$
Total	6	6	c. $p = 0.0242$
Unexercised individuals	2	16	

The number of climbing individuals in Experiment 2B is significantly smaller than that of wandering ones (bottom row of Table 3; Binomial test: $p=0.0105<0.05$). This result reflects well the fact that individuals in this experiment are not climbing the wall for transpiration. However, despite this inhibitory condition for climbing, the portion of climbing individuals was significantly larger for those which experienced Experiment 1 than for the unexercised group (statistical test (c) in Table 3). This result shows that experiencing the trade-off situation (long successive T-mazes) caused some individuals to spontaneously climb a wall. Moreover, this behavior was by individuals in the generative variation group, not by those in the stereotype and error group (statistical tests (a) and (b) in Table 3). From these results, the climbing pattern in the generative variation group can be regarded as a novel one which does not result from innate factors, and also an adaptive one which provides a chance to seek moisture outside the closed apparatus. Thus emergence of the spontaneous increase of the variant patterns in Experiment 1 apparently functioned as novel and adaptive behavior.

DISCUSSION

In experiment 1, individuals were categorized into three groups: stereotype group, error group, and generative variation group. The behavior of both the stereotype group (Fig.6) and error group (Fig.7) are predictable from the MAP concept based upon BALM and innate genetic variation among individuals. Stable BALM with minor genetic variation can be inferred from the high rate of turn alternation in the stereotype group. Excess genetic variation in BALM can be inferred from the low rate of turn alternation in the error group. In the generative variation group, a spontaneous increase and subsequent decrease of turn alternation (i.e., a subsequent increase of variant patterns) were observed (Fig.5). This behavior is unpredictable from the MAP concept. In the MAP concept, a hidden innate 'BALM-correcting mechanism' is used to explain the observed increase in the turn alternation rate. But existence of this mechanism would cause the generative variation group to maintain the high turn alternation rate, when in fact variant patterns subsequently increased – a behavior regarded here as 'spontaneous.' Experiment 1 was constituted as problematic situation which cannot be solved by turn alternation; the solution requires that the individuals spontaneously discard this pattern of turning.

As there later appears to be a 'novel escape pattern' used to get out of the experimental apparatus, the increase of variant patterns in Experiment 1 can be considered the manifestation of decision-making. This is in contrast to the view where such variant behavior is considered as resulting from a hidden mechanism, or 'noise generator.' For example, in the theory of learning machines, the continuous process of learning (parallel here to increase of the turn alternation rate) altered by generation of noise (parallel to increasing of variant patterns) is a typical way of learning for a Boltzmann Machine (Ackley, *et al.*, 1985). In these machines, the objective of learning is to decrease the energy of the system. A noise generator stochastically provides heat as a noise source for increasing the energy, while the machine searches for lower energy states. In such a stance of general computational learning theory, noise never becomes an adaptive behavior.

However, in Experiment 2A, the climbing pattern, which is considered a variant pattern in regular conditions, spontaneously appeared and became an adaptive one in the generative variation group. The fact that the appearance of this pattern correlated well with that of the increase of variant patterns in Experiment 1 strongly indicates that such variant patterns in Experiment 1 did not result stochastically from an innate 'learning-machine' mechanism, but rather were generated as novel escape patterns. Decision-making in *A. vulgare* was thus

manifested as the spontaneous increase of variant patterns in the trade-off situation. This aspect of behavior has also been observed in maze learning by octopuses, and was called 'autonomous learning' (Moriyama & Gunji, 1997). In that experiment, a novel maze solution which could not result from 'machine learning' appeared in correlation to an increase in variant patterns. While such clear adaptability was not observed in the stereotype and error groups, the difference may result from the extent of their capacity to destabilize MAP.

Other explanation could be considered for the emergence of the variant patterns in Experiment 1 and the climbing pattern in Experiment 2. For example, one could infer that, if individuals of the generative variation group have an innately higher capacity to be well hydrated, they might have been saturated while being prepared in the petri dishes. Since this would be essentially the same condition as saturated air, they would not need to perform turn alternations in Experiment 1, and so tried to climb the wall for aspiration in Experiment 2A. If such individuals existed, the same ratio of climbing individuals should appear in the control in Experiment 2B. However, as shown in Table 3, only two of eighteen unexercised individuals demonstrated climbing behavior, while six of the twelve that had experienced long successive T-mazes did so.

In this paper, decision-making in such simple animals as pill bugs has been suggested. The evidence of their decision-making can be found in their autonomous destabilization of MAP. At first glance, the idea of decision-making seems to contradict the concept of MAP itself. But the relationship between MAP and variant behavior is like the head and tail of one coin; we have individuals of the stereotype group, and, at the same time, we can verify the adaptability of variant behavior. What this paper calls into question is the assumption that there is an innate stable mechanism underlying MAP – a belief whereby a new innate stochastic genetic variation is necessarily inferred to explain any variant behavior. Once such a concept of 'stable mechanism with stochastic variation' is adopted, variant behavior, which implies spontaneous transformation of MAP, has to be considered insignificant erroneous behavior.

Moreover, even when such cognitive behavior as learning is observed, it can be considered as resulting from an innate hidden higher mechanism, and so a concept like 'learning by instinct' appears (Gould & Marler, 1987). The machine learning theory tries to explain this by regarding animals as complex machines having several innate mechanisms; and only those with a brain or complex nervous system, producing different mechanism for various circumstances, are considered as performing flexibly and autonomously. This view implies that one can never discover novel behavior in animals. In this paper, the

potential instability of the MAP concept results from the experimental demonstration of an animals' decision-making behaviour.

ACKNOWLEDGEMENTS

I am grateful to Professor K. Ito for extensive support during this research, and thank Professor Y. P. Gunji for helpful suggestions and advice. I also thank Dr. V. Ryabov and Mr. D. Rosenfeld for correcting the English text.

REFERENCES

- Ackley, D. H., Hinton, G. E. & Sejnowski, T. J. (1985). A learning algorithm for Boltzmann Machine. *Cognitive Science*, *9*, 147-169.
- Barlow, G. W. (1977). Modal action patterns. In: T. A. Sebeok (Ed.), *How animals communicate?* (pp 98-134). Indiana University Press.
- Carbines, G. D. (1992). Increased turn alternation by woodlice (*Porcellio scaber*) in response to a predatory spider, *Dysdera crocata*. *Journal of Comparative Psychology*, *5*, 138-144.
- Den Boer, P.J. (1961). The ecological significance of activity patterns in the woodlouse, *Porcellio scaber* Latr. (*Isopoda*). *Arch. Netherlands Zoology*, *14*, 283-409.
- Gould, J. L. & Marler, P. (1987). Learning by instinct. *Scientific American*, *256*, 62-73.
- Gunji, Y. P. (1996). Behavioral plasticity of hermit crabs. *Biology Forum*, *89*, 69-78.
- Heeley, W. (1941). Observations on the life-histories of some terrestrial isopods. *Proceedings of the Zoological Society of London*, *111*, 79-149.
- Hughes, R. N. (1967). Turn alternation in woodlice (*Porcellio scaber*). *Animal Behaviour*, *15*, 282-286.
- Hughes, R. N. (1985). Mechanisms for turn alternation in woodlice (*Porcellio scaber*): The role of bilaterally asymmetrical leg movements. *Animal learning and behavior*, *13*, 253-260.
- Hughes, R. N. (1987). Mechanisms for turn alternation in four invertebrate species. *Behavioural Processes*, *14*, 89-103.
- Hughes, R. N. (1989a). Phylogenetic comparisons. In: W. N. Dember & C. L. Richman (Eds.), *Spontaneous alternation behavior* (pp 39-57). New York: Springer-verlag.
- Hughes, R. N. (1989b). Tactile cues, bilaterally asymmetrical leg movements and body distortion in isopod turn alternation. *Journal of Comparative Psychology*, *2*, 231-244.
- Hughes, R. N. (1992). Effects of substrate brightness differences on isopod (*Porcellio scaber*) turning and turn alternation. *Behavioural Processes*, *27*, 95-100.
- Iwata, K. & Watanabe, M. (1957a). Alternate turning response of *Armadillium vulgare*: II. Turning and straight going tendencies. *Ann. Anim. Psychol.*, *7*, 53-57.
- Iwata, K. & Watanabe, M. (1957b). Alternate turning response of *Armadillium vulgare*: III. Effect of preceding turning response. *Ann. Anim. Psychol.*, *7*, 57-60.
- Jander, R. (1975). Ecological aspects of spatial orientation. *Annual Reviews Ecol. System*, *6*, 171-188.
- Kitabayashi, N. & Gunji, Y. P. (1997). Making decision in estimating pheromone by an ant itself, expressed as a cause-effect loop. *Biology Forum*, *90*, 393-422.
- Kupfermann, I. (1966). Turn alternation in the pill bug (*Armadillidium vulgare*). *Animal Behaviour*, *14*, 68-72.

- Migita, M. & Gunji, Y. P. (1996). Plasticity in the symbiotic behavior demonstrated by a gobiid fish (*Amblyeleotris steintzi*) associated with alpheid shrimps. *Biology Forum*, 89, 377-394.
- Moriyama, T. & Gunji, Y. P. (1997). Autonomous learning in maze solution by Octopus. *Ethology*, 103, 499-513.
- Schafer, M. W. (1976). Thigmotactic behaviour in *Lithobius forficatus* L. (*Myriapoda Chilopoda*). *Montore Zool. Ital.*, 10, 191-204.
- Thorpe, W. H. (1951). The definition of terms used in animal behaviour. *Bulletin Animal Behavior*, 9, 34-40.
- Warberg, M. R. (1964). The response of isopods towards temperature, humidity and light. *Animal Behaviour*, 12, 175-186.
- Watanabe, M. & Iwata, K. (1956). Alternative turning response of *Armadillidium vulgare*. *Ann. Animal Psychology*, 6, 75-82.