Report

A preliminary report on the dance performance of honeybees at very near distance from the hive

Takeshi OHTANI

Division of Ecology, Institute of Natural and Environmental Sciences, Himeji Institute of Technology / Museum of Nature and Human Activities, Hyogo, Yayoigaoka 6, Sanda, 669-1546 Japan

Abstract

Some dance performances (round, transition and waggle dances; shaking dance; tremble dance) were observed at the fixed or movable feeders of 0-14 m distance from the hive entrance in Sapporo and Sanda. After the dance performances were described by the original description system, the waggle dances in 1978 and 1999 were reported with different implications and interests: the former seemed to be related to the stability of the bee flight, and the latter was performed by the past remembrance of another feeding place. As the former was an isolated and very anomalous data, it remained dormant in my register papers for 22 years. The observations in 1996 and 1999 were planned in order to observe this behavior again, but the waggle dance at very near distance could not be observed. The "failure" in 1999 is detailed and discussed in relation to the function of dance performances, which seemed to be based on human-level explanations. It comprised 2 waggle dances, 6 round dances, 43 transition dances, 10 tremble dances, 10 shaking dances and 50 no dance that could be observed when 4 workers went on 94 trips.

Key words: waggle dance, round dance, transition dances, tremble dance, shaking dance, flight course

Introduction

Some affirmative results, if they should be uncommon, are preferential and described emphatically, while some negative results are neglected and often discarded, even if they should be common phenomena and/or important events that oppose an old hypothesis or theory. An exciting book, *Anatomy of a Controversy* (Wenner and Wells, 1990), reminds me of such a general tendency among many researchers.

I observed some extraordinary waggle dances at 14 m on October 3, 1978. According to Boch (1957), *Apis mellifera ligustica* Spinola should not perform waggle dances at nearer distance than 35 m. Consequently, this observation confused me, and it was difficult to continue the following observation. This anomalous observation was almost crushed by the vast amount of investigations on the dance language hypothesis, and remained dormant for 15 years within my PhD thesis (Ohtani, 1985b) and for 22 years within 3 sheets of my register paper (cf. Fig.2).

The encouragement by Wenner and Wells (1990) was connected with the trials in 1996 (omitted in this report, but touched on later) and 1999, but the waggle dance at very near distance could not be observed again to date (exceptional Wp12 described later; cf. Fig.3).

Here a "normal" researcher must have discarded one case of anomalous data. If "learning" should be the source of anomalies (cf. Ch.7 of Wenner and Wells, 1990), however, the process of "failure" may be worth describing. Thus reconsideration is the starting point of this report.

Materials and Methods

Honeybees: Unpure Italian colonies (*Apis mellifera ligustica*), as usually kept in Japan (purchased from API Company Limited), were used in all observations.

Observation sites and dates: 1) The campus of Hokkaido University in Sapporo City (Hokkaido) on

October 3, 1978. 2) The side of the Museum of Nature and Human Activities, Hyogo in Sanda City (Hyogo Pref.) on November 10-25, 1999.

Procedures: 1) Some workers were carried several times on a feeding place fixed at 14 m from the hive entrance (Fig.1a), and the behavior of a worker was observed since the worker began to go to and from the feeder. 2) Several workers were carried to a movable or fixed feeding plate at 0.3-12.0 m (Fig.1b, c), and then a few workers were observed soon after they began to attend the feeder.

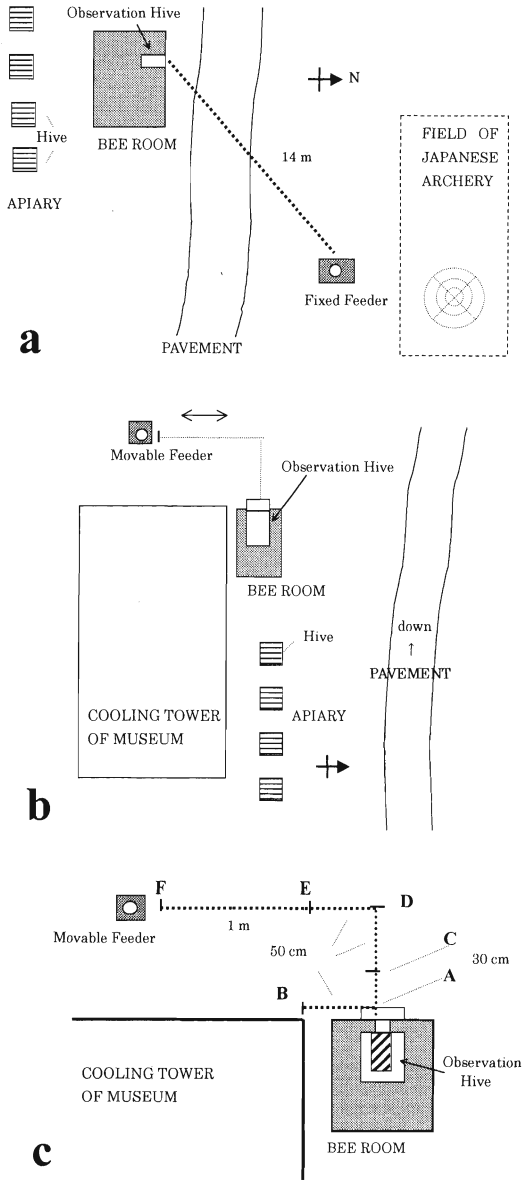


Fig. 1. The arrangement for observing the dance performance. **a**, An apiary and a bee room (a wooden house, ca. 50 m^2) were located on the campus of Hokkaido University (Sapporo City, 1978). A fixed feeder was placed at 14 m from the entrance of an observation hive for 4 Langstroth's combs. **b**, Another apiary and another bee room (a ready-made barn, ca. 10 m^2) were located beside the cooling tower nearby the Museum of Nature and Human Activities, Hyogo in Sanda City (1999). A movable feeder was placed at each distance from the entrance of an observation hive for 1 comb. **c**, Enlarged detail map from b. Each mark A-F denotes the temporary position of a movable feeder (referred to sometimes in the text).

Results and Short Comments

1. Description of some dance performances

The combination with the positions and movements of insect body parts is so effective to the objective description that I adopted the drone (Ohtani, 1974) and the queen behaviors (Ohtani, 1994), and the butterfly ones (Ohtani, 1985a). As the first step of this report, some dance performances are described here, as a harbinger of worker repertoire (in preparation) based on my many observations during 1972 to 1978 (cf. Ohtani, 1974,1994). Behavioral code system (e.g. ***DA***, ***Da^w***, w***Sh***/w, etc.), and movements and positions with asterisks of movable body parts (e.g. Lm4*, Wp3*, etc.) are defined and explained in Ohtani (1994).

1) ***Dancing (DA)*:** Locomotion (Lm4*) with drawing a circle, and/or often mid- and hindlegs swinging in walking (Lm4+10*); metasoma disposed variously (Tp1-4*), wings spread obliquely (Wp3*), and head disposed properly (Hp1*); whole body trembling (Genm1*).

First 2 types of ***DA*** were reported and studied in detail by von Frisch and his colleagues (cf. von Frisch 1967).

1a) *Round dancing (Da^r)*: "With swift, tripping steps the forager bee runs in a circle, of such small diameter that for the most part only a single cell lies within it; she runs about over the six adjacent cells, suddenly reversing direction and then turning again to her original course, and so on" (von Frisch, 1967:29).

1b) *Waggle dancing (Da^w)*: "The bee runs straight ahead for a short distance, returns in a semicircle to the starting point, again runs through the straight stretch, describes a semicircle in the opposite direction, and so on in regular alternation; the straight part of the run is given particular emphasis by a vigorous wagging of the body; this results from rapid rhythmic sidewise deflections of the whole body that are greatest at the tip of the abdomen and least at the head;" "The movement to and fro is repeated 13-15 times a second" (von Frisch, 1967:57).

Da^w has also been called the tail-wagging dance or figure-eight dance (Winston, 1987:154).

1c) *Transition dancing (Da^t)*: "The transition from round dance to tail-wagging dance is a gradual one, that takes place via either a figure eight or a sickle-shaped pattern" (von Frisch, 1967:63).

Based on the Fig. 56 of von Frisch (1967), ***Da^t*** is divided into 4 subtypes (cf. Table 1): ***Da^{t0}*** is the movements involved no tail wagging, ***Da^{t1}*** involve 1 or 1.5 tail wagging, ***Da^{t2}*** involve 2 or 2.5 tail wagging and ***Da^{t3}*** involve over 3 times of tail wagging but 2 ways of waggling run do not coincide with each other.

2) *Tremble dancing (TD)*: Locomotion (Lm4*) with drawing an irregular line, and rarely swinging mid- and hindlegs short in walking or running (Lm4+10*); whole body ardently trembling and/or twitching (Genm1,2*) with frequent changing body axis during locomotion; metasoma disposed variously (Tp1-4*), wings spread obliquely (Wp3*), and head disposed properly (Hp1*).

Perhaps ***TD*** is the same as 'Zittertanze' by von Frisch (1923), its translated term 'trembling dance' (von Frisch, 1967:282), and 'tremble dance' by Seeley (1992), Nieh (1993), Kirchner and Lindauer (1994) and Seeley (1995).

TD is provisionally divided into the following 2 subtypes that were distinguishable in our observations.

***2a) Tremble walking (Td^w)*:** "This complex activity can be analyzed in terms of its three components of motion: (1) vibrational - the strong side-to-side, and sometimes front-to-back, shaking of the body, (2) rotational - the constant changing of direction of the body axis, and (3) translational - the slow walking forward across the comb." (Seeley, 1992:377)

2b) Tremble running (Td^r)*:** (1) vibrational - the weak side-to-side, and sometimes front-to-back, shaking of the body, (2) rotational - the sometimes changing of direction of the body axis, and (3) translational - the fast walking or running forward across the comb with intermediate speed (1-2 cm/s) between excited running (Er***) and wandering (***Wa***)(cf. Ohtani, 1974, 1994).

3) *Shaking* (w***Sh***/w; ***Sh***/w and ***Sh*** in abbreviating)**:** Vibrating (Lm11 = dorso-ventral movements of abdomen) of all legs after grasping a bee by its forelegs (or rarely on cells) for ca. 1 sec., and walking (Lm4*) till finding out another bee; long repeat one set, vibrating and walking.

Since having been described by Haydak (1929), this behavior has been often reported and termed variously: 'Schuttelbewegung' (Sakagami, 1953), 'Rutten' (Schick, 1953), 'D-VAV' (= dorso-ventral abdominal vibration by Milum, 1955), 'Zitterbewegung' (Hammann, 1957), 'shaking' (Allen, 1958; Ohtani, 1994), 'jerking dance' (von Frisch, 1967), 'vibratory dance' (Fletcher, 1978), 'vibration dance' (Schneider et al., 1986a,b), 'shaking dance' (Gahl, 1975) and 'shaking signal' (Seeley, 1995).

2.Waggle dancing at 14 m in Sapporo

When von Frisch and his colleague set up an artificial feeding place, they used to move a watch glass filled with sugar solution farther at gradual increments (cf. von Frisch, 1967:17-20). This procedure involves both the gradual increase of distance and the number of visits by a training worker. As both are never separated, there is a possibility that users of the procedure had obtained the experience of a bee rather than the distance of a feeding place.

Because our feeding place was fixed at 14 m from the hive entrance, the experience and the distance were separated from the start line: only the former is a variable.

Our observations started at 10:00. When some worker bees mounted a small comb (ca. 5 cm^2) with honey and began to suck the honey, they were quietly carried to the feeder at 14 m. The filled workers returned the observation hive with 4 Langthsroth's combs (cf. Ohtani, 1985b), but almost all did not return to the feeding place, where my helper watched the feeder and observed the feeding behavior of the visitors.

After many vain trials, only one worker (D6, unknown age) came again to the feeding place. D6 repeated 35 times a successful trip (Table 1 and Fig. 2). On returning from the trip, D6 sometimes performed *tremble dancing* (***TD***), *round dancing* (***Da^r***), *transition dancing* (***Da^t***), and at last *waggle dancing* (***Da^w***).

We should remember many cases of no dance after successful returns (cf. ×-marks in Table 1). Von Frisch (1967:243) also observed cases of no dance: "Even with a high concentration of sugar, as a rule dancing does not occur after the day's first foraging flights." "The same is observed when foraging is resumed after a long interruption in feeding."

At 11:53, D6 was firstly transported from the hive entrance to the feeding place. A few minutes after returning to the hive, D6 came back the feeder. After this 1st trip, D6 attended the feeder. Our registration was started at 12:15 from the 3rd trip (Table 1). Detailed behavioral data was registered at 13:28 from the 8th trip (Fig. 2). After the 5th trip, D6 performed *shaking* (***Sh***), and never afterward. After the 6th trip, D6 performed *tremble walking* (***Td^w***). And after the 7th trip, *round*

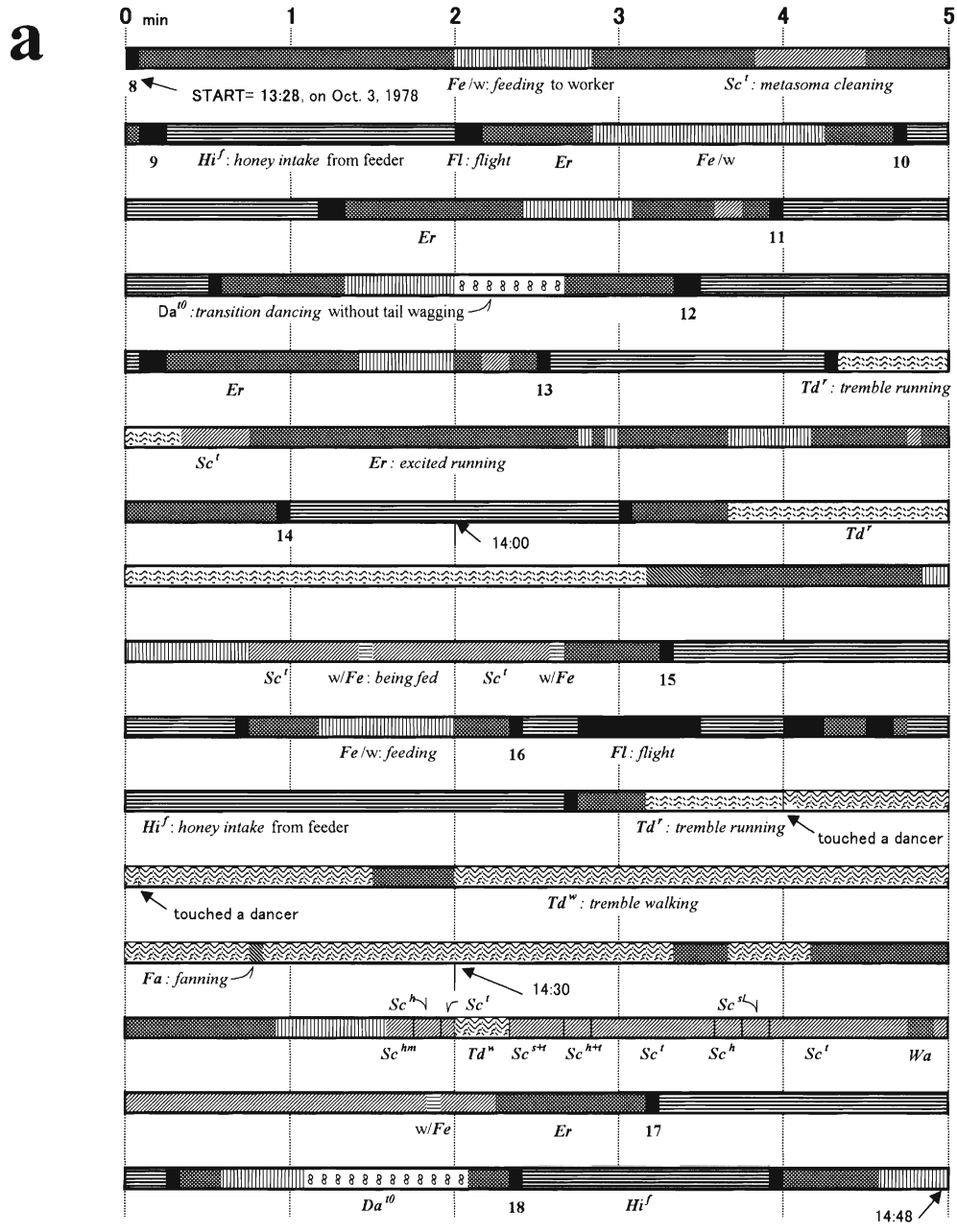
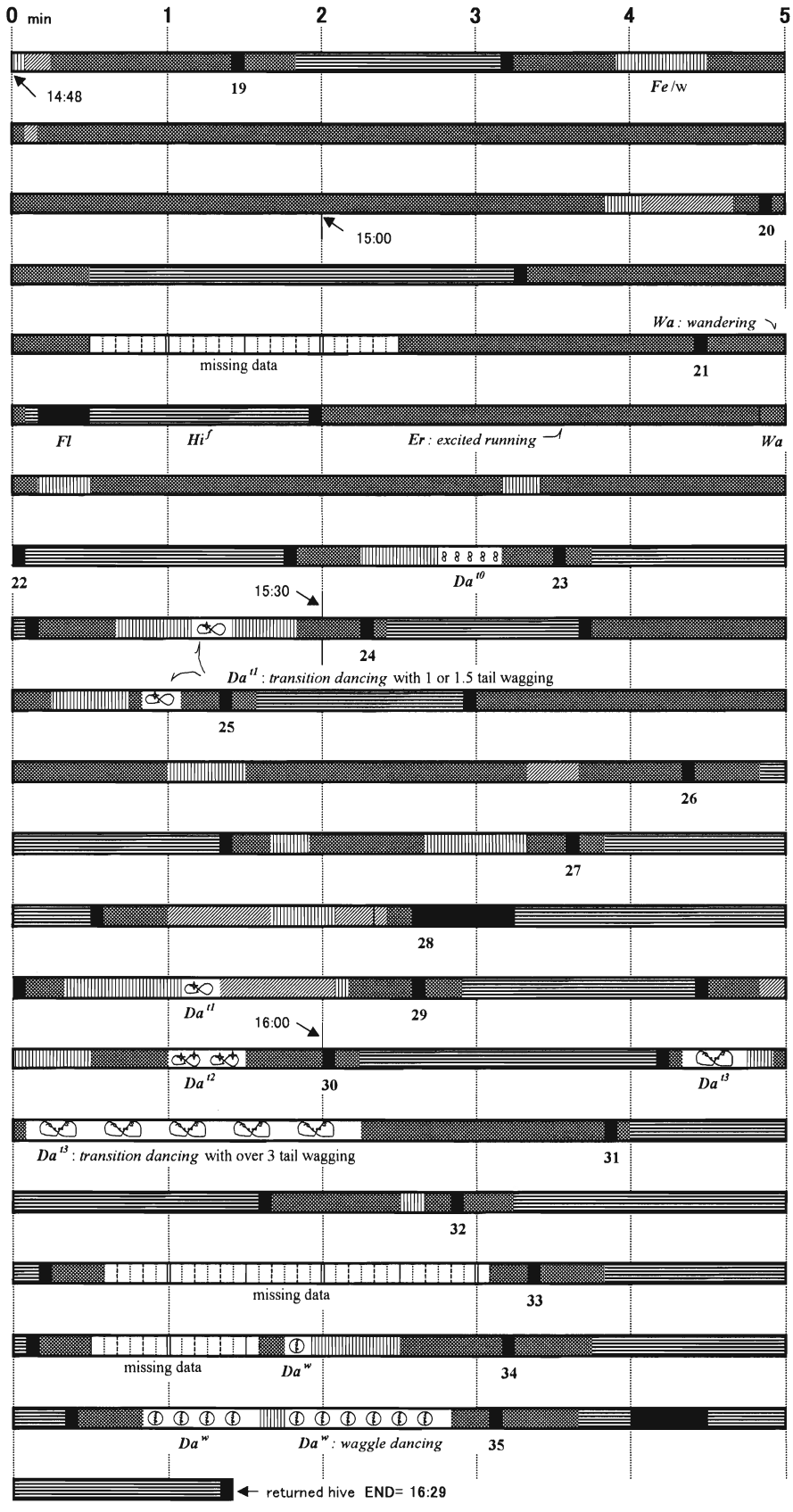


Fig. 2. The behavior sequence of D6 (a worker honeybee) who attended the feeder at 14 m from the hive entrance. This is redrawn from the register paper with 5-s-scale. One long bar denotes the sequence of 300 s or 5 min. From the 8th outward trip to the end of observation (cf. Table 1), the 16-bar block (**a**) and the 21-bar block (**b**) involve all behaviors observed. Black quadrilaterals denote the outward or homeward flight of D6, and those with numerals denote the number of outward trips (from the entrance to the feeder). Behavioral codes are explained in the figure, except the following behaviors. ***Sc^h***: *head cleaning*; ***Sc^hm***: *mouthparts cleaning*; ***Sc^h+t***: *self-cleaning* performed at same time *head cleaning* and *metasoma cleaning*; ***Sc^s+t***: *self-cleaning* performed at same time *mesosoma* and *metasoma cleaning*; ***Sc^sl***: *legs cleaning*. Because *honey intake* from cell is coded as ***Hi***, it is coded ***Hi^c*** in the discrimination from ***Hi^f*** (*honey intake* from feeder).

b


0 min
1
2
3
4
5
14:48
19
Fe/w
15:00
20
Wa : wandering
missing data
21
Fl
Hi^f
Er : excited running
Wa
22
Da^t0
23
15:30
24
Da^t1 : transition dancing with 1 or 1.5 tail wagging
25
26
27
28
Da^t1
16:00
29
Da^t2
30
Da^t3
Da^t3 : transition dancing with over 3 tail wagging
31
32
missing data
33
missing data
Da^w
34
Da^w
Da^w : waggle dancing
35
returned hive END= 16:29

dancing (***Da***^{r}) was firstly observed. Afterward, however, no dance and longer flight times were observed in 3 successive trips.

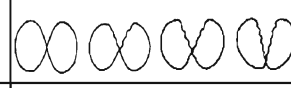
After the 11th trip, *transition dancing* without tail wagging (***Da***^{t0}) was observed. ***Da***^{t0} was performed after the 17th and 22nd trips. During 2 ***Da***^{t0}, 3 *tremble running* (***Td***^{r}) and 1 *tremble walking* (***Td***^{w}) were observed. As ***Td***^{r} seemed an intermediate type ***Td***^{w} and *excited running* (***Er***), there is a possibility that ***TD*** and ***Er*** are related.

After the 23rd, 24th and 27th trips, D6 performed *transition dancing* with 1 tail wagging (***Da***^{t1}). The flight time of the 27th trip was abnormally long (40 s), but its reason and influence were unknown.

After the 29th and 30th trips, ***Da***^{t2} and ***Da***^{t3} were observed, respectively. After the 31st and 32nd trips, no dances were observed, but *waggle dancing* (***Da***^{w}) was observed after the 33rd and 34th trips (Fig. 2b). As the duration of ***Da***^{w} after the 33rd trip was short (10 s), the observer thought that something was wrong with his own eyes. The duration of ***Da***^{w} after the 34th trip was sufficient to trust one's own eyes. The ***Da***^{w} after 33rd and 34th trips were completely the same as many dances previously observed.

It was the "My God!" reaction (Bruner and Postman, 1949; Kuhn, 1970:62-64; Wenner and Wells, 1990:119-

Table 1. Some dance performances of a forager (D6, unknown age) attending a feeding place fixed at 14 m from the hive entrance in the campus of Hokkaido Univ. (Sapporo City) on Oct. 3, 1978. All behaviors were observed in an observation hive. See Fig. 2 on the relationship with other behaviors.

BEHAVIOR	*shaking*[1]	*tremble dancing*[2]	*round dancing*	*transition dancing*[3]				*waggle d.*	FLIGHT TIME[4]		NO. OF RECRUITED WORKERS	
CODE	***Sh***	***Td***^{r} ←***TD***→***Td***^{w}	***Da***^{r}	***Da***^{t0}	***Da***^{t1}	***Da***^{t2}	***Da***^{t3}	***Da***^{w}	ENTRANCE ↓ FEEDER	FEEDER ↓ ENTRANCE	NEW	OLD
TRIP												
1	—	—	—	—	—	—	—	—	—	—		
2	—	—	—	—	—	—	—	—	—	—		
3[5]			×	×	×	×	×	×	170"	30"		
4			×	×	×	×	×	×	27"	18"		
5	◎		×	×	×	×	×	×	15"	5"		
6		◎	×	×	×	×	×	×	24"	10"		
7		observed	●						5"	5"		
8			×	×	×	×	×	×	8"	8"		
9			×	×	×	×	×	×	12"	5"	1	
10			×	×	×	×	×	×	5"	7"	1	
11				●					6"	5"		
12			×	×	×	×	×	×	5"	4"		
13		◎	×	×	×	×	×	×	6"	4"	2	
14		◎	×	×	×	×	×	×	5"	6"		
15			×	×	×	×	×	×	6"	4"		1
16		◎ ◎	×	×	×	×	×	×	4"	4"	1	1
17				●					4"	6"		
18			×	×	×	×	×	×	4"	4"		
19			×	×	×	×	×	×	4"	3"		
20			×	×	×	×	×	×	5"	6"		
21			×	×	×	×	×	×	3"	4"		
22				●					5"	3"		
23					●				4"	3"		
24					●				5"	5"		
25			×	×	×	×	×	×	5"	6"		
26			×	×	×	×	×	×	4"	4"		
27			×	×	×	×	×	×	4"	4"		
28					●				40"	3"		
29						●			5"	6"		
30							●		6"	6"	1	2
31			×	×	×	×	×	×	4"	4"	2	
32			×	×	×	×	×	×	5"	6"		
33								●	5"	4"		
34								●	6"	5"		
35[6]	—	—	—	—	—	—	—	—	4"	5"		

[1] Fletcher (1978) used *vibratory dance*, Seeley (1995) did *shaking signal*, and Hammann (1957)'s figure cited below.
[2] Seeley (1992) used *tremble dance* with its figure cited below. [3] Von Frisch (1967) divided 4 types with their figures cited below.
[4] Rough measurement by a wrist watch. [5] The observations started at 12:15. [6] The finish time was 16:29.

120). I could not continue to observe.

During the 33 trips of D6, 8 new (unmarked) workers were recruited to the feeder without waggle dances, and 4 workers were come again (last right column of Table 1). We had lost our chance to observe the salient recruit after waggle dances as the Fig.2 of Seeley and Visscher (1988).

3. Observations of dancing in Sanda

In order to observe again the waggle dance at very near distance, I started our observations in Sanda City on June and November of 1999, but in early summer, almost all workers did not pay attention to our feeding place. As a matter of fact, the observations having the same goal in Kashihara City (Nara Pref.) on May of 1996 were "failure", too: no workers attended a feeding place at 10 m. The result of an "unsuccessful" experiment is not regarded as precious data. All of the data were discarded without exception. Then, regrettably, it was impossible to report in more detail than that the experiments in spring did not go well, in the same way as von Frisch (1967:247) recorded: "In the spring, at the time of abundant flowering and a good supply of food, it is often impossible even with 1-2M sucrose to induce the bee to dance."

1) Transition dancing of a worker, W1110

When October of 1999 set in, many Japanese giant hornets (*Vespa mandarinia japonica*) made frequent attacks on our apiary. On Oct. 30, Colony M110 was introduced into the observation hive for one Langstroth's comb, as the number of workers in M110 had been reduced to fewer than 500 because of the hornets' attack.

The honeybees seemed frightened of the Japanese giant hornet. They had a low activity rate and avoided some strange scents such as the old honey and the vanilla essence.

After the failure of attendance to a feeding place on Nov. 5 and 6, and on the morning of Nov. 10, a worker (W1110, unknown age) began to attend the feeding place (A of Fig.1c) at 13:49. W1110 performed 3 *round dancing* (***Da***^{r}) during 6 round trips (Table 2). Afterward the feeder was moved 50 cm southward (B of Fig.1c). W1110 did not come to the new feeding place in the 7th and 8th trips. Then, the feeder was moved 30 cm from the entrance westward (C of Fig.1c) and W1110 visited. Afterward W1110 performed 1 *transition dancing* (***Da***^{t0}). No *shaking* and no *tremble dancing* were observed during 14 trips (Table 2). As the activity of W1110 became low, our observation was finished at 15:50 and we hoped to resume the next day (Nov. 11). However, it was rainy day and the following day (Nov. 12) was rainy, too.

2) Transition and waggle dancing of a worker, Wp12

On Nov. 14, our observations started again, but W1110 had disappeared from the observation hive. The position of the feeder was 30 cm westward (C of Fig.1c). Four workers were invited several times to the feeder, but no workers attended there. At 13:00, the feeder was

Table 2. Some behaviors of a forager (W1110, unkown age) attending 3 feeding places (A-C) at very near distance (within 0.5 m) from the hive entrance of an observation hive in the Museum apiary (Sanda City) on Nov. 10, 1999.

BEHAVIOR CODE→	*shaking*	*tremble dancing*	*round d.*	*transition dancing*				*waggle d.*	Related behavior[1]	FEEDING PLACE[2]
TRIP ↓	***Sh***	***Td***^{r} ***Td***^{w}	***Da***^{r}	***Da***^{t0}	***Da***^{t1}	***Da***^{t2}	***Da***^{t3}	***Da***^{w}		
1[3]	—	—	—	—	—	—	—	—	—	A
2			×	×	×	×	×	×	Er	A
3		observed →	●						Er	A
4			×	×	×	×	×	×	Er	A
5			●						Er	A
6			●						Er	A
7[4]			×	×	×	×	×	×	Er	B
8[4]			×	×	×	×	×	×	Ru	B
9			×	×	×	×	×	×	Ru	C
10			×	×	×	×	×	×	Er	C
11				●					Er	C
12			×	×	×	×	×	×	Er	C
13			×	×	×	×	×	×	Er	C
14			×	×	×	×	×	×	Ru	C
15[5]			×	×	×	×	×	×	Wa	C

[1] Observed before flight: Er = *excited running*, Wa = *wandering*, Ru = *sheer running*, cf. Ohtani (1974). [2] See A-C of Fig.1c.
[3] The start time was 13:49. [4] W1110 could not come to the feeding place (B). [5] The finish time was 15:50.

moved to 0 cm from the hive entrance (A of Fig.1c). The 4 workers were invited again to the nearest feeder.

After several vain invitations for about 1 hour, one of 4 workers (Wp12, unknown age) began to attend the feeder. Wp12 took 14 trips and performed 4 *shaking* (***Sh***), 3 *tremble walking* (***Td***^{w}) and 8 *transition dancing* (***Da***^{t}) till 17:20 (Table 3). It was very interesting that the ***Da***^{t} once proceeded from ***Da***^{t0} to ***Da***^{t2}, but it returned to ***Da***^{t0} when the feeder was moved farther (C → D of Fig.1c). The dance performance may be related with the instability of flight course in seeking the new feeding place in comparison with the fixed feeding place (Table 1). It was also interesting that *shaking* (***Sh***) and *tremble dancing* (***TD***) appeared in the latter half with a movable feeder. There is a possibility that they are also related to the unstable flight course.

Our observations stopped for 9 days because of our other work. As it was somewhat cold (11-12°C) in the morning on Nov. 23, our observations started from the afternoon. Wp12 was found returning to the hive entrance at 13:12. She performed no dance and *wandering* (***Wa***). As Wp12 mounted a small comb with honey when it was presented before her eyes, she was carried and released on the feeder at 30 cm from the entrance (C of Fig.1c). It was surprising that she performed *waggle dancing* (***Da***^{w}) soon after returning the comb surface. The direction and distance indicated by the waggle dance differed from that of the feeder. In fact, Wp12 flew out elsewhere other than the feeder.

After ca. 14 min, Wp12 returned to the hive but performed no dance but *tremble running* (***Td***^{r}). Then, Wp12 was again carried on a small honeycomb to the feeder, and she performed *waggle dancing* (***Da***^{w}), *shaking* (***Sh***) and *excited running* (***Er***) (Fig. 3). It was a new fact that waggle dances can be performed according to old and familiar information rather than what is new and unfixed.

The information of the waggle dance in Wp12 was maintained even till the afternoon on Nov. 24, in spite of no foraging because of rain during the morning of Nov. 24 from the afternoon of the day before. After 2 trials of the same procedure, the observation of Wp12 was deliberately stopped (cf. Fig. 3), and the following observation was newly started.

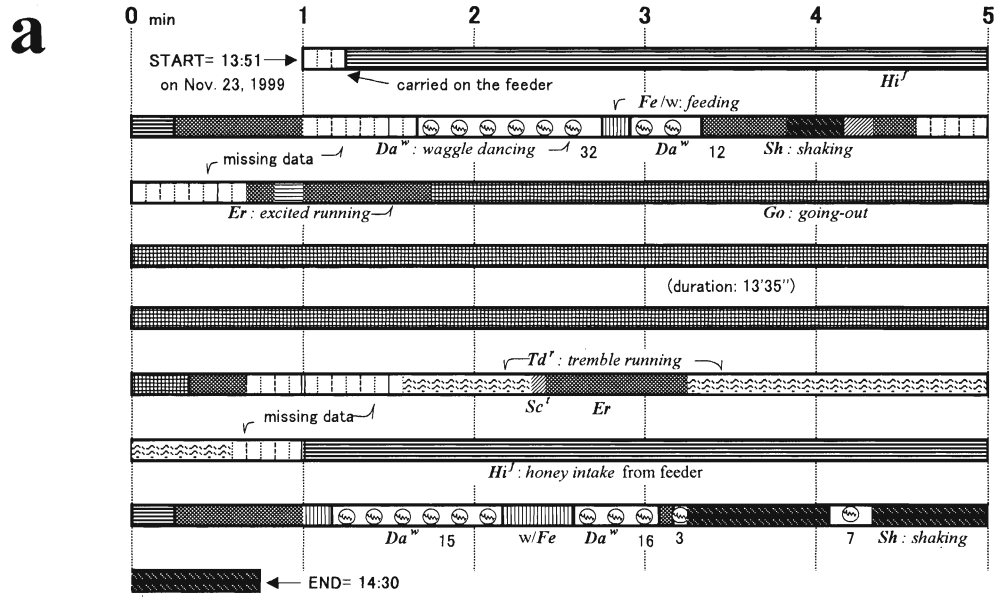


Fig. 3. Two behavior sequences of Wp12 worker who attended the feeder at 30 cm from the hive entrance. The 9-bar block (**a**) denote all behaviors on Nov. 23, and the 17-bar block (**b**) denote those on Nov. 24. The numerals nearby the quadrilateral of *waggle dancing* (***Da***^{w}) are the number of waggling runs in ***Da***^{w}. All waggling runs of ***Da***^{w} are expressed in the same direction. Being induced by the information of the ***Da***^{w}, Wp12 went out somewhere in the vicinity (flight duration: 13'35", 13'20" and 18'35"). After these trips, Wp12 performed no dance, but did ***Da***^{w} after returning to the hive with honey from the feeder where Wp12 was forcibly transported.

3) Dance performance of a worker, Wb13

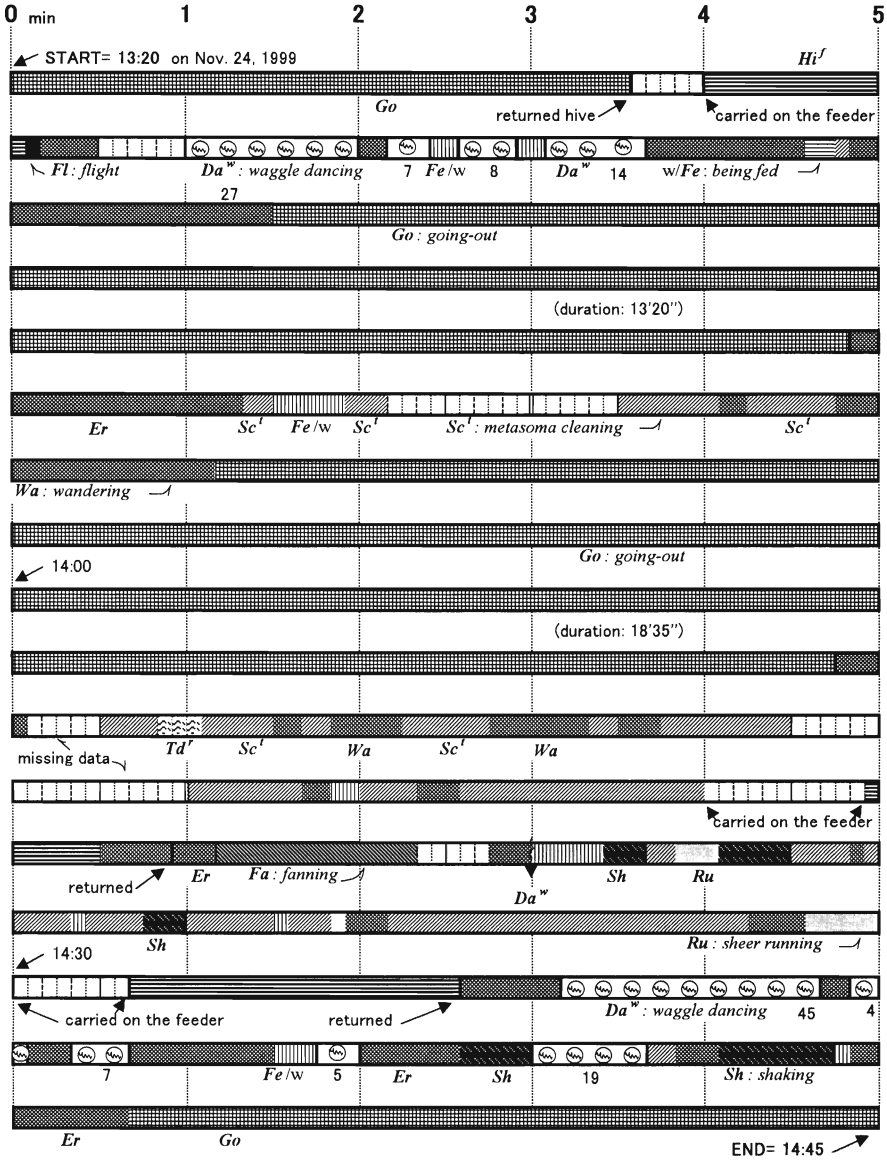
Several workers were marked with a white marker during feeding in the feeder at 30 cm on Nov. 23. When one of the workers was found again during the observation of Wp12 (unknown age), she was marked again with a blue marker and named Wb13, who soon attended the feeder 15 times during the afternoon of Nov. 14 (the upper of Table 4).

In the 5th trip, *round dancing* (***Da^{r}***) and *transition dancing* (***Da^{t0}***) were firstly observed. In the following trip appeared the *transition dancing* with 2 or 2.5 tail wagging (***Da^{t2}***), but in 4 successive trips the *transition dancing* with 1 or 1.5 tail wagging (***Da^{t1}***) was maintained. Both the *transition dancing* without tail wagging (***Da^{t0}***) and ***Da^{t2}*** were observed at same time in the 11th trip. ***Da^{t0}*** and ***Da^{t1}*** were also observed with *shaking* (***Sh***) in the 14th trip. ***Sh***, tremble running (***Td^{r}***) and no *dancing* (***DA***) were found in the last trip on Nov. 24.

It was warm day on Nov. 25 (14.0℃ at 9:00). Wb13 began to forage soon after the feeder opened at 9:20 (the lower of Table 4), but performed no dances till the 3rd trip. In 4 successive trips, only ***Da^{t1}*** were observed. Although the feeder was not moved, Wb13 did not perform *transition dancing* with more than 1 or 1.5 tail wagging till the 18th trip.

The *transition dancing* with 2 or 2.5 tail wagging (***Da^{t2}***) were observed in the 19th and 20th trip. Very regrettably, however, our observations were abruptly stopped at 12:10. Wb13 suddenly disappeared. It may be due to an accident with relation to the hive heater, but the corpse of Wb13 was not found.

b



The observation of that warm Nov. 25 was the last chance to observe *waggle dancing* (***Da***^{w}) at very near distance in 1999.

Discussion

1. The stability of the flight course

It is too difficult to observe and/or measure the flight course of honeybees, which can fly at the speed of ca. 7.5 m/s (Wenner, 1963). Consequently, there was only the impression from our naked eyes: first several flights had unstable courses and/or repeated circular ones, and the following several flights became gradually stable, and then the last several flights had often unstable course because of the movable feeder moved, or perhaps because of the worse condition in the evening. With relation to the stability of the flight course, appeared various kinds of dance performances. Although based on poor data as yet, there seems a tendency that *dancing* (***DA***) appears with stability of bee flight, while *shaking* (***Sh***) and *tremble dancing* (***TD***), and/or no dances do in the instability of the flight course. My idea is that foragers may perform *waggle dancing* (***Da***^{w}) when the flight course have become most stable.

It is after the day's first flights and after a long interruption that von Frisch (1967:243) observed no dance. Though von Frisch interpreted the no dances as the poor security of uniform flow from the source of food, it can be explained as the instability after a long stoppage of the flights.

The above outlook is important in studying the reason why various dance performances appear from the point of view that none of the dance information is communicated among honeybees. This "rebellious" viewpoint is mostly followed about by a question: Does an energetic behavior such as ***Da***^{w} evolve meaninglessly? Here is, however, a speculation of mine: when a stable and straight flight-course decreases the flight cost, an excess energy by the cheap cost produces a sort of "imitation flight": some imitative movements by using the nervous system and some muscles for flying. My speculation is that the imitation flight is ***Da***^{w}. It would not be odd that a meaningless behavior is released by an excess energy, and it could not be discarded in evolution, because it is really released in a normal situation (that is, *flying*).

Only lately, Capaldi et al. (2000) observed the direct course of orientation flights tracked with harmonic radar. Regrettably, flight courses of infant foragers were not studied, but positive correlation was found between the number of orientation flights and 4 flight attributes (round trip distance, maximum range, covered area and average ground speed). Their foraging bees flew significantly faster, further and straighter than their orienting bees.

2. The relationship among dance performances

When all of the same behavior after one trip are regarded as one case, we counted 48 cases of *dancing* (***DA***), 14 cases of *shaking* (***Sh***) and 10 cases of *tremble dancing* (***TD***) from the data of Table 1-4 and Fig.3. In 7 cases ***DA*** and ***Sh*** were observed at the same time. In 5

Table 3. Intranidal behaviors of a forager (Wp12, unkown age) attending 5 feeding places (A-F) at near distance (within 2.5 m) from the hive entrance in the Museum apiary (Sanda City) on Nov. 14, 1999.

BEHAVIOR CODE→	*shaking*	*tremble dancing*	*round d.*	*transition dancing*				*waggle d.*	Related	FEEDING
	Sh		***Da***^{r}	***Da***^{t0}	***Da***^{t1}	***Da***^{t2}	***Da***^{t3}	***Da***^{w}	behavior[1]	PLACE[2]
TRIP ↓		***Td***^{r} ***Td***^{w}								
1[3]	◎		×	×	×	×	×	×	Er	A
2			×	×	×	×	×	×	Er	A
3		↖	×	×	×	×	×	×	Er	A
4	◎			→	●				Er	A
5			*observed*			●			Er	C
6							●		Er	C
7			↙	●	●				Er	C
8				●	●				Er	D
9				●	●				Er, Ru	D
10	◎	◎			●				Er	E
11			×	×	×	×	×	×	Er	E
12	◎				●				Er	F
13	◎	◎	×	×	×	×	×	×	Er, Ru	F
14[4]	◎	◎	×	×	×	×	×	×	Er, Ru	F

[1] Er = *excited running*, Wa = *wandering*, Ru = *sheer running*. [2] See A-F of Fig. 1c. [3] The start time was 14:15.

[4] The finish time was 17:20.

cases ***TD*** and ***Sh*** were observed simultaneously. ***TD*** never appeared with ***DA***. These relationships are very interesting, but it is difficult to speculate on this because of a poor data set.

In relation to the speculation of the previous section, my rough idea is that ***TD*** may be an infant ***DA***, and ***Sh*** may be a sort of the displacement behavior. Allen (1958) and other some authors observed *shaking* to a queen (w***Sh***/q) in a royal court. Ohtani (1994) speculated that such w***Sh***/q might be displacement behavior due to a state of conflict between 2 drives, fleeing and aggression.

3. The remembrance of the feeding place

It is a new fact that honeybees can perform Da^w based on old information when stimulated with a new feeder. We have never discussed the remembrance of the feeding place. Almost all results of past experiments on dance performance may be influenced by this fact, and then have to be reconsidered. For instance, there is a possibility that it has a strong influence on the fake-information experiment by Gould (1975). Conversely, it may be usable in a fake-information experiment.

Based on the data of Capaldi et al. (2000), honeybees seem to increase their own experience by orientation flights, or to input a lot of the landmark information around vicinity of the hive. The past remembrance of bees may be gradually expanded with their experience. Anyway, the past remembrance of bees must be considered in a new experiment plan of dance performance.

Moreover, this fixed remembrance may be related to a tendency that few foragers attend an artificial feeding place in spring or early summer (touched

Table 4. Intranidal behaviors of a forager (Wb13, unkown age) attending the fixed feeding place at very near distance in the Museum apiary (Sanda City) on Nov. 24 and 25, 1999.

BEHAVIOR CODE→	*shaking* ***Sh***	*tremble dancing* Td^r Td^w	*round d.* Da^r	*transition dancing* Da^{t0}	Da^{t1}	Da^{t2}	Da^{t3}	*waggle d.* Da^w	Related behavior[1]	FEEDING PLACE[2]
TRIP ↓										
1	—	—	—	—	—	—	—	—	—	C
2[3]			×	×	×	×	×	×	Er	C
3			×	×	×	×	×	×	Er, Wa	C
4			×	×	×	×	×	×	Er	C
5			●	●					Er	C
6						●			Er	C
7					●				Er	C
8					●				Er	C
9					●				Er	C
10		*observed*			●				Er	C
11				●		●			Er	C
12					●				Er	C
13			×	×	×	×	×	×	Er	C
14	◎			●	●				Er, Wa	C
15[4]	◎	◎	×	×	×	×	×	×	Ru, Wa	C
1[5]			×	×	×	×	×	×	Er	C
2			×	×	×	×	×	×	Er	C
3			×	×	×	×	×	×	Er	C
4					●				Er	C
5					●				Er	C
6					●				Er	C
7					●				Er	C
8				●					Er	C
9			●	●					Er	C
10					●				Er	C
11	◎			●					Er	C
12					●				Er	C
13			×	×	×	×	×	×	Er,Ru,Wa	C
14			×	×	×	×	×	×	Er, Wa	C
15			×	×	×	×	×	×	Er, Wa	C
16			×	×	×	×	×	×	Er, Ru	C
17			×	×	×	×	×	×	Er,Ru,Wa	C
18					●				Er	C
19						●			Er	C
20[6]						●			Er	C

[1] Er = *excited running*, Ru = *sheer running*, Wa = *wandering*. [2] See C of Fig. 1c. [3] The start time was 14:51 on Nov. 24.
[4] The finish time was 16:45 on Nov. 24. [5] The start time was 9:22 on Nov. 25. [6] The finish time was 12:32 on Nov.

previously). Most foragers might take less interest in the feeder when their remembrance had been fixed to an abundant nectar source after they attended repeatedly there. Accordingly, the experiment during a flower season did not go well.

4. The function of dance performances

The function of *waggle dancing* (***Da***^{w}) is famous and "a fact" in the high-school text of Japan (e.g. Mizuno et al., 1996). However, it is not proved directly, but hypothesized from the various grade of correlation (cf. Ch.6 and Ch.9 of Wenner and Wells, 1990). To find out positive correlation is a different matter from establishing the relation of cause and effect (Wenner et al., 1967). The circumspect discussion by Wenner and Wells (1990) has been ignored by many researchers on social insects (e.g. Seeley, 1995; Crozier and Pamilo, 1996; Vander Meer et al., 1998). They are in the "paradigm shift" of dance language (cf. Kuhn, 1970), and each of them takes an unfair attitude.

The function of *tremble dancing* (***TD***) was studied by Seeley (1992), and that of *shaking* (***Sh***) was researched by Schneider et al. (1986a,b) and emphasized by Seeley (1995). They are firm hypotheses, which are also made being based on some correlation. 'Shaking signal' and 'tremble dance' may be had an each effect to increase the number of foragers, and the number of food-storer bees, respectively (Seeley, 1995). The schema on each function is excellent and smart, but it is constructed only by human-level explanation (in the same way as ***DA***). Honeybees must lead their life in an original "insect logic". In order to avoid the one-sided and human-level explanation, we might have to adopt direct observation such as the single-individual trailing (SIT) method (cf. Ohtani, 1994). And we can expect the direct observation on the "ontogeny" of foraging flight revealed by harmonic radar as in the investigation of Capaldi et al.(2000).

Acknowledgements

I thank the following 3 persons for their help when collecting data in 1978, 1996 and 1999: Dr. Michiya Yamamoto, Ms. Nobuko Arakawa and Mr. Taijiro Koga, respectively. And I am grateful to Dr. Hidetoshi Ikeno for stimulating discussions and valuable comments after reading through the manuscript.

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Received: February 4, 2000
Accepted: April 13, 2000