人と自然　Humans and Nature 19: 71–88 (2008)

Report

Recruitment efficiency of waggle dances performed by a worker honeybee and the influence on her dance performance by recruited foragers

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Abstract

A worker honeybee, W151 (43-56 days old), went to and from a feeder located 180 m from the hive entrance and performed 188.5 waggle dances in an observation hive on Nov. 2, 2007. On the next day, W151 started to recruit 4 foragers, who did not perform waggle dances, and whose presence appeared to decrease the number of waggle dances performed by W151. Other dance performances of W151 observed within the observation hive were *shaking*, *tremble dancing*, *round dancing*, and *transition dancing*. We report on the dance performance of W151 on other days and also when the recruits were experimentally caged and released. We also discuss the genetic background of the bee brain. We observed a time lag of recruitment, starting and ending difficulties in dance performance, and the influence on dance performance of recruited foragers. We interpret these results as evidence that the dance performances of honeybees possess physiological aspects which are inconsistent with the "dance language" hypothesis.

Key words: shaking, tremble dance, round dance, transition dance, waggle dance, delayed recruitment, physiological aspect

Introduction

Recently Riley *et al*. (2005) reported that the flight courses of recruited foragers advanced directly towards the feeding station by the technique of harmonic radar. These results were accepted as what has been confirmed as the dance-language hypothesis, because the direct flight course is very different from the zigzag flight seen in scent-searching behavior (cf. Yushima, 1977; Carde, 1984). However, Riley *et al*. (2005) did not report on the experience of recruited foragers with long aerials, for example, whether they fly about near the feeder.

Some researchers who supported the dance-language hypothesis praised the mechanical model of Michelsen *et al*. (1992); however, "live dancing bees recruit 5-10 times more bees than does the model" (Michelsen *et al*., 1992). The reasons for this low efficiency of recruitment by the model remain unidentified.

The efficiency of dance recruitment has been the subject of some study. Tautz (1996) reported that dancers on empty combs recruited 3 times as many foragers to the feeder as dancers on capped brood combs. The high efficiency of dancers on empty combs was interpreted "to mean either that recruits are motivated more strongly or that they understand the signals better from dances on open cells" (Tautz, 1996). However, it is well known that younger

Figure 1. A picture of the forager W151 performing *self-cleaning*. Her number plate was underlined with a pink marker in order to identify her more easily among many numbered nestmates

workers are apt to gather in the central warmer combs while older ones tend to scatter over the peripheral colder combs (Free, 1960; Brückner, 1976; Harrison, 1987; Ohtani, 1992). Thus there is a strong possibility that experienced foragers are more likely to be on outer empty combs while younger hivekeepers are more likely to be on capped brood combs. The higher efficiency could thus be interpreted as an increase in the number of experienced foragers.

Here we describe a concrete case of dance recruitment by a specific individual. We strive for a neutral and detailed description which is also useful to those with opposing hypotheses.

Materials and Methods

1. General

Honeybees: Impure Italian subspecies (*Apis mellifera ligustica* Spinola, 1806)

Marking: On the mesosoma with numbered disks (cf. Fig.1)

Observation hive: One comb type (60 × 30 × 30 cm) on a metal vessel filled with water, whose temperature was controlled by an electric heater

Colony condition: A purchased queen and *ca.* 30 numbered workers (almost everyday) were introduced into the observation hive, which was a queenless colony, because the queen was missed a week after the introduction.

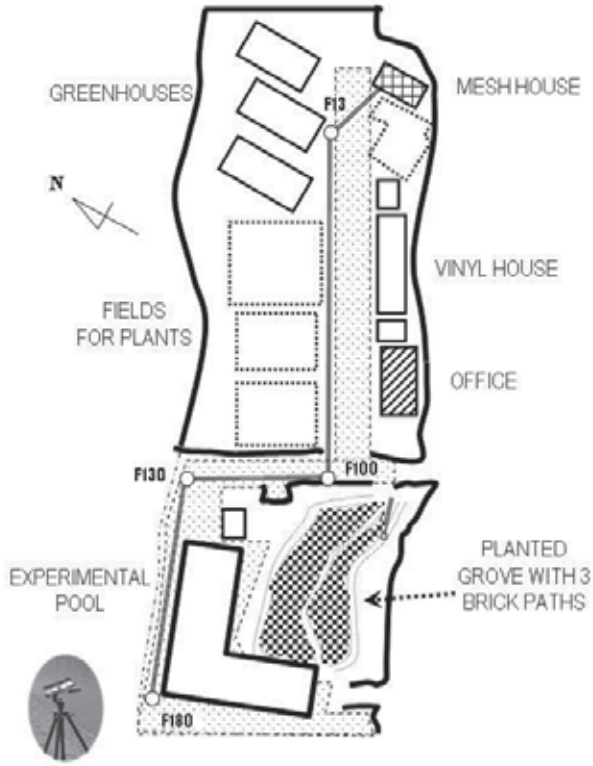

Figure 2. The map of our experimental field and the track of movable feeders (F13 to F180) at the Gene Farm at the Museum of Nature and Human Activities, Hyogo. The dotted area is a surface paved with concrete. The heavy line denotes a hedge of *Hotinea serratifolia* (Rosaceae). The last feeding station, F180 (180 m from the observation hive), is located at the side of the experimental pool. In the figures drawn in Ohtani (2002) and Ohtani *et al.* (2005), the north (N) of the Gene Farm (just above) was mistaken. The direction of this figure is correct.

Table 1. The dance performance of a forager, W151 (43 days old) after visiting the movable feeder at distances from 0.4 to 1.3 m on Oct. 27, 2007 (cloudy & light rain, 17.5-17.6°C). The double circle with the numeral denotes the observed case and the number of dance performances, and the blank or cross mark denotes a non-observed case.

BEHAVIOR	shaking	tremble dancing	round dancing	transition dancing					waggle dancing	FLIGHT TIME		FEEDING PLACE	
CODE	Sh	$Td^r \leftarrow TD \rightarrow Td^w$	Da^r	Da^{t0}	Da^{t1}	Da^{t2}	Da^{t3}	Da^{t4}	Da^w	HIVE ↓ FEEDER	FEEDER ↓ HIVE	DISTANCE FROM HIVE	
TRIP												POINT	(m)
1[1]	◎1		×	×	×	×	×	×	×	20	30	D[2]	0.4
2			×	×	×	×	×	×	×	15+10	55	D	0.4
3			×	×	×	×	×	×	×	35	35	E	0.5
4	◎2		×	×	×	×	×	×	×	10	15	F	0.6
4'			×	×	×	×	×	×	×	—	—	G[3]	0.7
5			×	×	×	×	×	×	×	35+15	10	G	0.7
6			×	×	×	×	×	×	×	15+10	10	H	0.8
7			×	×	×	×	×	×	×	5+10	10	I	0.9
7'			×	×	×	×	×	×	×	—	—	J[4]	1.0
8			×	×	×	×	×	×	×	20	20	J	1.0
9			×	×	×	×	×	×	×	15+20	15	K	1.1
10	◎2	◎2	×	×	×	×	×	×	×	15+10	5	L	1.2
11	◎3		×	×	×	×	×	×	×	20+10	10+15	M	1.3
12[5]	—	—	—	—	—	—	—	—	—	40	20	M	1.3

[1] W151 started the feeding on D-feeder at 13:44:35 on Oct. 27.
[2] W151 was feeding on the feeder of A- (3 cm), B- (6 cm), C- (30 cm) and D- (40 cm) points on Oct. 25, and D-point on Oct. 26.
[3] W151 approached on but did not land on the G-point.
[4] W151 landed on the J-point, but did not feed.
[5] The last feeding finished at 16:20:00 on Oct. 27.

Mesh House: A greenhouse (7.7 × 11.6 m) with no glass but meshed walls and roof (cf. Ohtani, 2002)

Feeding station: The feeder on a tripod was moved from 0 to 180 m and filled with diluted honey (cf. Ohtani, 2002). Fig.2 shows the 180-m-feeder and its leading root in the Gene Farm.

Usually two observers were assigned to the feeding station and the observation hive in the small room of the Mesh House. The observers communicated with each other via their transceivers.

The single-individual trailing method (cf. Ohtani, 1974) was adopted for the main observations. To observe the behavior of insects with short lives, it is necessary to trail single individuals for as long as possible.

Table 2. The dance performance of W151 (44 days old) after visiting the movable feeder from 1.3 to 80 m on Oct. 28, 2007 (sunny, 17.2-23.7°C). The double or closed circle with the numeral denotes the observed case and the number of dance performances, and the blank or cross mark denotes the non-observed case.

BEHAVIOR / CODE / TRIP	*shaking*	*tremble dancing*	*round dancing*	*transition dancing*					*waggle dancing*	FLIGHT TIME		FEEDING PLACE	
	Sh	*Td*′ ←*TD*→ *Td*″	*Da*′	*Da*^{t0}	*Da*^{t1}	*Da*^{t2}	*Da*^{t3}	*Da*^{t4}	*Da*″	HIVE ↓ FEEDER	FEEDER ↓ HIVE	DISTANCE FROM HIVE POINT	(m)
1[1]			×	×	×	×	×	×	×	10	40	M	1.3
2			×	×	×	×	×	×	×	40	25	M	1.3
3		◎1	×	×	×	×	×	×	×	15	40	N	1.5
4			×	×	×	×	×	×	×	20	—	O	2.0
5			×	×	×	×	×	×	×	15	15	P	2.5
6			×	×	×	×	×	×	×	—	—	P	2.5
7			●2							—	10	Q	3.0
8			×	×	×	×	×	×	×	10+20	10	Q	3.0
9			×	×	×	×	×	×	×	—	15	R	3.5
10			×	×	×	×	×	×	×	10	15	S	4.0
11			×	×	×	×	×	×	×	85	15	T	4.5
12			×	×	×	×	×	×	×	15	10	U	5.0
13		◎1	×	×	×	×	×	×	×	10+40	10	V	6.0
14			×	×	×	×	×	×	×	45	—	W	7.0
15			×	×	×	×	×	×	×	30	20	X	8.0
16			×	×	×	×	×	×	×	30	10	Y	9.0
17			×	×	×	×	×	×	×	10	10	Z	10
18			×	×	×	×	×	×	×	—	10	ZA	11
19			×	×	×	×	×	×	×	—	10	ZB	12
20	◎2		×	×	×	×	×	×	×	15	10	ZC	13
21			×	×	×	×	×	×	×	25	10	ZD	14
22			×	×	×	×	×	×	×	35	10	ZE	16
23			×	×	×	×	×	×	×	—	15	ZF	18
24			×	×	×	×	×	×	×	10+35	10	ZG	20
25			×	×	×	×	×	×	×	80	10	ZH	22
26			×	×	×	×	×	×	×	15	10	ZI	24
27			×	×	×	×	×	×	×	—	—	ZJ	26
28			×	×	×	×	×	×	×	—	10	ZK	28
29			×	×	×	×	×	×	×	30	10	ZL	30
30	◎1		×	×	×	×	×	×	×	55	10	ZM	35
30′			×	×	×	×	×	×	×	×[2]	×	Zm	40
30″			×	×	×	×	×	×	×	×[2]	×	Zm	40
31			×	×	×	×	×	×	×	—	20	ZN	38
32			×	×	×	×	×	×	×	20	10	ZO	41
33			×	×	×	×	×	×	×	35	10	ZP	44
34			×	×	×	×	×	×	×	—	35	ZQ	47
35			●1.5							25	15	ZR	50
36				●●9						—	15	ZR	50
37			×	×	×	×	×	×	×	10+40	15	ZS	53
38	◎1		×	×	×	×	×	×	×	30	10	ZT	56
39	◎1		×	×	×	×	×	×	×	—	20	ZU	59
40				●3						—	15	ZV	62
41			●1							35	15	ZW	65
42	◎1		●2							25	10	ZX	68
43	◎1		×	×	×	×	×	×	×	25	135	ZY	71
44	◎◎7		×	×	×	×	×	×	×	85	20	ZZ	74
45	◎◎◎◎17		×	×	×	×	×	×	×	25	15	YA	77
46[3]			×	×	×	×	×	×	×	—	15	YB	80

[1] The feeder opened at 10:00, but the first visit started at 12:37:05 on Oct. 28.
[2] W151 twice failed to reach the feeder at 40 m.
[3] The last trip finished at 16:57:10.

2. A dictionary of abbreviations

A description of dance performances were made in my preceding report (Ohtani, 2000), and my behavioral code system was defined and explained in Ohtani (1994). Consequently, many abbreviations without explanation are used in this report. Therefore, I supply here a dictionary of all abbreviations for readers who may not have access to Ohtani (1994, 2000).

DA: *Dancing*. ***DA*=*Da*^{r}+*Da*^{t}+*Da*^{w}.**

***Da*^{r}**: *Round dancing*. Performing round dances.

dAr: the dance appearance rate (=number of dance performances / the number of flights).

***Da*^{t}**: *Transition dancing*, divided into 5 subtypes, ***Da*^{t0}-*Da*^{t4}**.

***Da*^{t0}**: *Transition dancing* without tail wagging.

***Da*^{t1}**: *Transition dancing* with 1 or 1.5 tail-waggings.

***Da*^{t2}**: *Transition dancing* with 2 or 2.5 tail-waggings.

***Da*^{t3}**: *Transition dancing* with 3 or 3.5 tail-waggings.

***Da*^{t4}**: *Transition dancing* with more than 4 vigorous tail-waggings.

***Da*^{w}**: *Waggle dancing*. Performing waggle dances, or figure-8 dances.

d.o.: days old.

F180: The feeder located 180 m from the observation hive. Numerical variation means variable distance, *e.g*. F13 refers to the feeder located 13 m from the observation hive.

Pi: *Worker piping* resembling queen piping.

Sh: *Shaking*. D-VAV(=dorso-ventral abdominal vibration) as described by Milum (1955).

TD: *Trembling dancing*. ***TD*=*Td*^{w}+*Td*^{r}**

***Td*^{r}**: *Trembling running*.

***Td*^{w}**: *Trembling walking*.

W151: The worker with the number plate of 151 (cf. Fig.1). W means worker.

W301: The worker with the number plate of 301.

Table 3. The dance performance of W151 (45 days old) after visiting the movable feeder at distances from 80 to 97 m on Oct. 29, 2007 (sunny, 20.3-24.8°C).

BEHAVIOR	*shaking*	*tremble dancing*	*round dancing*	*transition dancing*					*waggle dancing*	FLIGHT TIME		FEEDING PLACE	
CODE	*Sh*	*Td*^{r} ←*TD*→ *Td*^{w}	*Da*^{r}	*Da*^{t0}	*Da*^{t1}	*Da*^{t2}	*Da*^{t3}	*Da*^{t4}	*Da*^{w}	HIVE ↓ FEEDER	FEEDER ↓ HIVE	DISTANCE FROM HIVE	
TRIP												POINT	(m)
1[1]	◎1		×	×	×	×	×	×	×	20+85	50	YB	80
1'–(1)			×	×	×	×	×	×	×	—	—	YB	80
1'–(2)			×	×	×	×	×	×	×	—	—	YB	80
1'–(3)	◎1		×	×	×	×	×	×	×	—	—	YB	80
1'–(4)	◎1		×	×	×	×	×	×	×	—	—	YB	80
1'–(5)			×	×	×	×	×	×	×	—	—	YB	80
2[2]			×	×	×	×	×	×	×	—	25	YB	80
3			×	×	×	×	×	×	×	35	15	YB	80
4			×	×	×	×	×	×	×	—	15	YB	80
5		◎1	×	×	×	×	×	×	×	10	15	YB	80
6			×	×	×	×	×	×	×	25	—	YB	80
7			×	×	×	×	×	×	×	—	15	YB	80
8			×	×	×	×	×	×	×	20+5	15	YB	80
9	◎1		×	×	×	×	×	×	×	30	20	YB	80
10			×	×	×	×	×	×	×	—	20	YB	80
11			×	×	×	×	×	×	×	—	30	YB	80
12		◎1	×	×	×	×	×	×	×	20	—	YB	80
13			×	×	×	×	×	×	×	—	—	YB	80
14			×	×	×	×	×	×	×	—	15	YB	80
15	◎2		×	×	×	×	×	×	×	15+10	15	YB	80
16			×	×	×	×	×	×	×	30	15	YC	83
17			×	×	×	×	×	×	×	20	15	YD	86
18			×	×	×	×	×	×	×	35+15	—	YE	90
19			×	×	×	×	×	×	×	90+20	20	YF	93
20[3]		◎2	×	×	×	×	×	×	×	25+50	20	YG	95
20'			×	×	×	×	×	×	×	—	—	YH	97
20''			×	×	×	×	×	×	×	—	—	YH	97

[1] The first visit started at 10:53:25 on Oct. 29.

[2] The second visit started at 14:12:55, after W151 failed 5 times to reach the feeder at 80 m.

[3] The last visit finished at 16:24:20, thereafter W151 flew out and twice failed to reach the feeder at 97 m.

Results with Short Comments

1. Dance performances by W151 (43-48 days old) at the movable feeder

Most papers and reports on the honeybee dance omit the procedures for moving the feeder and the dance performances (e.g. *transitional dancing*) which result, but Ohtani (2000), Ohtani (2002) and Ohtani *et al*. (2005) reported that these observations might contain information which could resolve the dance communication controversy (cf. Wenner & Wells, 1990).

(1) Da^{r} and Da^{t0} in twice visiting at the feeder toward 97 m

On Oct. 25, 2007, W151 began to feed at the feeder 3 cm from the hive entrance. The movable feeder then extended the distance from the entrance to 6 cm, 30 cm and 40 cm. The next day, Oct.26, was a rainy day. W151 did not go out till 14:50, After returning from the 40-cm feeder, she performed *tremble walking*

Table 4. The dance performance of W151 (46 days old) after visiting the movable feeder at distances from 95 to 100 m on Oct. 30, 2007 (from cloudy to fine weather, 18.1-19.7°C). The closed or open circle with the numeral denotes the observed case and the number of dance performances, and the blank or cross mark denotes the non-observed case. The open circle of round dancing denotes the observation of transition dancing or waggle dancing.

BEHAVIOR	shaking	tremble dancing	round dancing	transition dancing					waggle dancing	FLIGHT TIME		FEEDING PLACE		
CODE	Sh	$Td^{r} \leftarrow TD \rightarrow Td^{w}$	Da^{r}	Da^{t0}	Da^{t1}	Da^{t2}	Da^{t3}	Da^{t4}	Da^{w}	HIVE ↓ FEEDER	FEEDER ↓ HIVE	DISTANCE FROM HIVE		
TRIP												POINT	(m)	
1[1]			×	×	×	×	×	×	×	—	—	YG	95	
2			×	×	×	×	×	×	×	—	20	YG	95	
3			×	×	×	×	×	×	×	35	—	YG	95	
4			×	×	×	×	×	×	×	—	—	YG	95	
5			×	×	×	×	×	×	×	25	25	YG	95	
6			×	×	×	×	×	×	×	30	20	YG	95	
7			×	×	×	×	×	×	×	10+10	15	YG	95	
8			●2							20+10	20	YH	97	
9			×	×	×	×	×	×	×	25+110	—	YI	100	
10			×	×	×	×	×	×	×	25	20	YI	100	
11			×	×	×	×	×	×	×	85	15	YI	100	
12			●1.5							20	—	YI	100	
13			×	×	×	×	×	×	×	—	—	YI	100	
14			×	×	×	×	×	×	×	35	15	YI	100	
15			●2							20+5	15	YI	100	
16				●1.5						35	20	YI	100	
17			×	×	×	×	×	×	×	20+5	—	YI	100	
18			●2.5							25+10	20	YI	100	
19			○4	●●8.5						35	15	YI	100	
20				●1				●5		15	15	YI	100	
21								●4.5		15	15	YI	100	
22			○0.5					●●8		20+45	10	YI	100	
23								●2.5		30+x	20	YI	100	
24									●●●12	25	15	YI	100	
25									●●10	30+20	15	YI	100	
26			×	×	×	×	×	×	×	25+35	20	YI	100	
27			○2.5						●1	20+20	15	YI	100	EF[2]
28									●2	35+85	20	YI	100	EF
29			×	×	×	×	×	×	×	75	15	YI	100	EF
30			×	×	×	×	×	×	×	30+70	40	YI	100	
31			×	×	×	×	×	×	×	—	15	YI	100	
32			×	×	×	×	×	×	×	35+5	15	YI	100	
33			×	×	×	×	×	×	×	30	15	YI	100	
34			×	×	×	×	×	×	×	—	15	YI	100	EF
35			×	×	×	×	×	×	×	25	20	YI	100	EF
36			×	×	×	×	×	×	×	—	15	YI	100	
37									●?	25	—	YI	100	
38									●●9.5	50	30	YI	100	
39			×	×	×	×	×	×	×	20+15	15	YI	100	
40			×	×	×	×	×	×	×	—	20	YI	100	
41									●●●11.5	25	15	YI	100	
42			×	×	×	×	×	×	×	45	15	YI	100	
43			×	×	×	×	×	×	×	25	15	YI	100	
44			×	×	×	×	×	×	×	—	—	YI	100	
45			×	×	×	×	×	×	×	—	15	YI	100	
46			×	×	×	×	×	×	×	—	20	YI	100	
47[3]			×	×	×	×	×	×	×	15	15	YI	100	

[1] The feeder opened at 10:00, but the first visit started at 11:58:10 on Oct. 30.
[2] An electric fan was turned on.
[3] The last trip finished at 15:58:45.

(***Td***^{w}), and she was marked with a paint-marker to distinguish her from other numbered nestmates. W151 flew out elsewhere once, but did not do for bad weather after performing tremble walking (***Td***^{w}).

On the next day, Oct.27, the distance to the feeder was increased from 0.4 to 1.3 m. W151 performed shaking (***Sh***) and tremble walking (***Td***^{w}) during 12 trips in cloudy and light-rainy weather (Table 1).

On the next sunny day, Oct. 28, W151 flew 46 feeding trips from 12:37 to 16:57, only 16 of which were followed by dance performances (***Sh***, ***Td***^{w}, round dancing (***Da***^{r}) and transition dancing (***Da***^{t0})). The dance appearance rate (Ohtani *et al*., 2005) was 0.3478 (Table 2). The feeder was then speedily moved from 1.3 m to 80 m. In general the feeder stayed at a given station for only one feeding trip. When the feeder could not be moved after W151 visited (2.5m and 50m), she performed ***Da***^{r} (2.5m) and ***Da***^{t0}(50m). Many ***Sh*** were observed toward the end of the observation period.

On Oct. 29, a sunny day, W151 reached the 80-m feeder at 10:53, but did not land on it in spite of passing close to it on 5 successive flights. In all 20 trips on this day, on her return W151 performed only *shaking* (***Sh***) or *tremble walking* (***Td***^{w}) (Table 3). Finally the feeder reached 97 m, but their was no ***DA***,

Table 5. The dance performance of W151 (47 days old) after visiting the movable feeder at distances from 100 to 173 m on Oct. 31, 2007 (sunny, 17.3-21.9°C).

BEHAVIOR	*shaking*	*tremble dancing*	*round dancing*	*transition dancing*					*waggle dancing*	FLIGHT TIME		FEEDING PLACE		
CODE	*Sh*	*Td*^{r} ←*TD*→ *Td*^{w}	*Da*^{r}	*Da*^{t0}	*Da*^{t1}	*Da*^{t2}	*Da*^{t3}	*Da*^{t4}	*Da*^{w}	HIVE ↓ FEEDER	FEEDER ↓ HIVE	DISTANCE FROM HIVE POINT	(m)	
TRIP														
1[1]			×	×	×	×	×	×	×	—	—	YI	100	
2			×	×	×	×	×	×	×	—	—	YI	100	
3			×	×	×	×	×	×	×	—	—	YI	100	
4			×	×	×	×	×	×	×	—	—	YI	100	
5			×	×	×	×	×	×	×	—	—	YI	100	
6			×	×	×	×	×	×	×	—	—	YI	100	
7			×	×	×	×	×	×	×	—	—	YI	100	
8			×	×	×	×	×	×	×	—	15	YI	100	
9		◎1	×	×	×	×	×	×	×	35	20	YJ	103	
10			×	×	×	×	×	×	×	30	20	YK	106	R1[2]
11			×	×	×	×	×	×	×	25+40	15	YK	106	
12			×	×	×	×	×	×	×	—	20	YL	109	
13	◎1		×	×	×	×	×	×	×	90+10	25	YM	112	
14	◎◎8		×	×	×	×	×	×	×	180	15	YN	115	
15			●1							—	20	YO	118	
16			×	×	×	×	×	×	×	75	—	YP	121	F1[3]
17			×	×	×	×	×	×	×	70	15	YQ	124	
18			×	×	×	×	×	×	×	—	15	YR	127	F2[4]
19			×	×	×	×	×	×	×	35	15	YR	127	
20			×	×	×	×	×	×	×	40	20	YS	130	
21			×	×	×	×	×	×	×	35	25	YS	130	
22			×	×	×	×	×	×	×	—	15	YT	134	
23			×	×	×	×	×	×	×	—	20	YT	134	F2
24			×	×	×	×	×	×	×	35	20	YT	134	
25			×	×	×	×	×	×	×	—	15	YT	134	
26			×	×	×	×	×	×	×	65	20	YU	137	
27			×	×	×	×	×	×	×	50	30	YV	140	
28			×	×	×	×	×	×	×	95	35	YW	143	
29			●1							40	—	YX	146	
30			×	×	×	×	×	×	×	45	—	YY	149	
31			●1							80	15	YZ	152	
32			×	×	×	×	×	×	×	205	—	XA	155	
33			×	×	×	×	×	×	×	—	25	XB	158	F2
34			×	×	×	×	×	×	×	—	20	XC	161	
35			●0.5							—	15	XD	164	
36			×	×	×	×	×	×	×	—	20	XE	167	
37			×	×	×	×	×	×	×	—	—	XF	170	
38			×	×	×	×	×	×	×	—	—	XG	173	
39									●3.5	—	—	XG	173	
40			×	×	×	×	×	×	×	15	—	XG	173	
41			○2.5						●0.5	—	20	XG	173	
42									●●●13.5	20	25	XG	173	
43[5]			×	×	×	×	×	×	×	15	40	XG	173	

[1] The feeder opened at 10:00, but the first visit started at 10:37:20 on Oct. 31.
[2] W151 returned once to the feeder.
[3] W151 failed once to reach the feeder.
[4] W151 failed twice to reach the feeder.
[5] The last trip finished at 16:55:45.

for unknown reasons. We note that the entrance to the office was near this feeder position (cf. Fig.2), and that there was frequent foot traffic near the feeder due to many persons visiting the office.

(2) Disturbance by the electric fan and twice 90° change at the feeder from 95 m to 180 m

On Oct. 30, a partly cloudy day, the feeder started at 95 m. On the 8th trip, the feeder was set at 97 m, and *round dancing* was observed (Table 4). After the 10th trip, the feeder was fixed at 100 m. *Waggle dancing* (***Da***^{w}) via *transition dancing* (***Da***^{t}) was observed (Table 4), but the dance appearance rate (dAr) was low (0.3830) over the 47 trips. No ***Sh*** or ***TD*** were observed. An electric fan was used to disturb the flight course (Table 4: EF). It did not seem to be effective as a mechanical disturbance, but the dAr from the 25th to the 35th trip was low (2/11=0.1818). We conjecture that the observer's behavior on the arrangement of electric fan caused the decrease in dAr between the 25th and 35th trip.

On the sunny day Oct. 31, the feeder was moved from 100 m to 173 m. W151 flew out 43 times, but only 9 dance performances were observed (dAr=0.2093). ***Da***^{w} was observed only after the 3 trips toward the end of the observation (Table 5). These dances seemed to relate that the direction of the feeder was changed twice: 90° northwest at 100 m and 90° southwest at 140 m (cf. Fig. 2).

On Nov. 1, a cloudy day, the air temperature was low (16.2-16.3°C). W151 started to fly at 13:45, but flew out 16 times with only 2 ***Sh*** (dAr=0.1250). The feeder was moved from 173 m to 180 m (Table 6).

2. Waggle dances of W151 (49-53 days old) at the 180-m-feeder and influence of recruited foragers

(1) Many bouts of *waggle dancing* by W151 and by 4 recruits on the next day

On Nov 2, a sunny day, W151 performed powerful *waggle dancing* (***Da***^{w}), but there were no recruited foragers all day long. Other performances were a few bouts of *round dancing* (***Da***^{r}) and *shaking* (***Sh***) after the last trip (Table 7). The dance appearance rate (=dAr) was 0.7826. From all of our past data, we have the impression that there is some difficulty in performing ***Da***^{w} in the starting and ending periods of a day. The lack of ***Da***^{w} following the 1st, 2nd and 4th trips is conceivably attributable to this starting difficulty, and the similar lack in the 38th, 40th, and 44th-46th trips to the ending difficulty. In the 18th and 24th trips, W151 returned once to the feeder after flying out from the feeder. Thus, abnormal flight courses were possible. After the 32nd trip, W151 returned to the hive swiftly as usual (for 25 s), but did not perform ***Da***^{w}, for unknown reasons.

On Nov. 3, a fine day, W151 appeared at the 180-m feeder soon after the feeder was set at 10:00. ***Da***^{w}

Table 6. The dance performance of W151 (48 days old) after visiting the movable feeder at distances from 173 to 180 m on Nov. 01, 2007 (cloudy, 16.2-16.3°C).

BEHAVIOR	*shaking*	*tremble dancing*	*round dancing*	*transition dancing*					*waggle dancing*	FLIGHT TIME		FEEDING PLACE		
CODE	*Sh*	*Td*^{r} ←*TD*→ *Td*^{w}	*Da*^{r}	*Da*^{t0}	*Da*^{t1}	*Da*^{t2}	*Da*^{t3}	*Da*^{t4}	*Da*^{w}	HIVE ↓ FEEDER	FEEDER ↓ HIVE	DISTANCE FROM HIVE		
TRIP												POINT	(m)	
1[1]			×	×	×	×	×	×	×	—	35	XG	173	
2			×	×	×	×	×	×	×	35	25	XG	173	
3			×	×	×	×	×	×	×	30	25	XG	173	
4			×	×	×	×	×	×	×	25	20	XH	176	
5			×	×	×	×	×	×	×	155	25	XI	180	F1[2]
6			×	×	×	×	×	×	×	35	20	XI	180	
7			×	×	×	×	×	×	×	60	30	XI	180	
8	◎1		×	×	×	×	×	×	×	50	20	XI	180	
9			×	×	×	×	×	×	×	—	50	XI	180	
10			×	×	×	×	×	×	×	30	20	XI	180	
11			×	×	×	×	×	×	×	35	20	XI	180	
12			×	×	×	×	×	×	×	35	25	XI	180	
13			×	×	×	×	×	×	×	35	25	XI	180	
14			×	×	×	×	×	×	×	30	25	XI	180	
15			×	×	×	×	×	×	×	25	25	XI	180	
16[3]	◎1		×	×	×	×	×	×	×	30	30	XI	180	

[1] The feeder opened at 13:00, but the first visit started at 13:45:05 on Nov. 01.
[2] W151 failed once to reach the feeder.
[3] The last trip finished at 15:56:05.

were consistently observed after 2 initial trips with the starting difficulty. The first recruited forager, W759 (16 days old), appeared at the feeder at 11:03, and the second, W301 (40 days old) at 11:19. Other recruits were W461 (32 days old) and W792 (14 days old) who appeared at 13:16 and 13:49, respectively (Table 8).

These recruitments were very slow, given that W151 had performed ***Da***^{w} all day long on the previous day (cf. Table 7). It is unclear why action on the direction/distance information in the ***Da***^{w} was delayed to the next day if this information was communicated exactly between the worker honeybees by the dance language.

All recruits appeared hesitating at first, and then became more daring little by little. Their behavior

Table 7. Dance performance of a forager, W151 (49 days old) after visiting the feeding station located at 180 m on Nov. 2, 2007 (sunny, 16.0-18.1°C).

BEHAVIOR	shaking	tremble dancing	round dancing	transition dancing					waggle dancing	FLIGHT TIME		
CODE	*Sh*	*Td*^{r} ←*TD*→ *Td*^{w}	*Da*^{r}	*Da*^{t0}	*Da*^{t1}	*Da*^{t2}	*Da*^{t3}	*Da*^{t4}	*Da*^{w}	HIVE ↓ FEEDER	FEEDER ↓ HIVE	
TRIP												
1[1]			×	×	×	×	×	×	×	60	25	
2			×	×	×	×	×	×	×	30	30	
3									●2.5	35	25	
4			×	×	×	×	×	×	×	30	25	
5									●●●10.5	30	45	
6									●2	50	30	
7									●1	40	35	
8									●1	40	30	
9									●●6	30	40	
10									●●●11	40	25	
11									●●5.5	50	30	
12			●1.5							50	30	
13			●0.5							30	30	
14									●3	30	30	
15									●4	30	30	
16									●●●10.5	30	30	
17									●2	50	25	
18			×	×	×	×	×	×	×	40	25	R1[2]
19									●1.5	30	25	
20									●●7.5	30	25	
21									●●5.5	30	30	
22									●●10	30	25	
23									●0.5	55	20	
24			×	×	×	×	×	×	×	30	25	R1
25									●●●12	—	35	
26									●●9	30	30	
27			○1.5						●3	40	95	
28									●●6	35	30	
29			○2.5						●●9	50	20	
30									●●●11	40	25	
31									●●●12	70	25	
32			×	×	×	×	×	×	×	50	25	
33									●3.5	25	20	
34									●●5.5	40	30	
35									●●7	25	90	
36									●●●13.5	40	30	
37									●●6	150	25	
38			×	×	×	×	×	×	×	30	—	
39									●3	35	25	
40			×	×	×	×	×	×	×	40	—	
41									●2	—	30	
42									●1.5	30	30	
43									●0.5	40	30	
44			×	×	×	×	×	×	×	30	30	
45			×	×	×	×	×	×	×	25	30	
46[3]	◎4		×	×	×	×	×	×	×	—	305	

[1] The feeder opened at 10:00, but the first visit started at 10:47:45 on Nov. 01.
[2] W151 returned to the feeder once.
[3] The last trip finished at 15:39:10.

influenced the feeding of W151. When W151 perceived the recruited forager coming to the feeder, she usually stopped feeding and flew out. When she arrived at the feeder when a recruit was feeding,

Table 8. Dance performance of a forager, W151 (50 days old) after visiting the feeding station located at 180 m on Nov. 3, 2007 (sunny, 15.5-18.4°C) with 4 recruited foragers (W301, W461, W759 and W792).

BEHAVIOR	*shaking*	*tremble dancing*	*round dancing*	*transition dancing*					*waggle dancing*	FLIGHT TIME		
CODE	*Sh*	*Td*^{r} ←*TD*→ *Td*^{w}	*Da*^{r}	*Da*^{t0}	*Da*^{t1}	*Da*^{t2}	*Da*^{t3}	*Da*^{t4}	*Da*^{w}	HIVE ↓ FEEDER	FEEDER ↓ HIVE	
TRIP												
1[1]			×	×	×	×	×	×	×	—	—	
2			×	×	×	×	×	×	×	25	35	
3									●2.5	—	—	
4									●5	—	30	
5									●3	30	35	
6			×	×	×	×	×	×	×	35	35	
7									●1.5	30	—	
8									●3	30	70	
9									●2.5	35	—	
10									●●7	60	25	W759[2]
11									●●9	45+35	—	
12									●4.5	35+20	75	W301[3]
13			×	×	×	×	×	×	×	30+10	35	
13–14									●5	×	×[4]	
14			×	×	×	×	×	×	×	20+25	70	
15			×	×	×	×	×	×	×	20	90	
16			×	×	×	×	×	×	×	25	35	
17			×	×	×	×	×	×	×	20	—	
18									●●7	—	80	
19									●1.5	35	85	
20									●3.5	30	30	
21			×	×	×	×	×	×	×	25+35	—	
22									●●8.5	35	55	
23			×	×	×	×	×	×	×	20+35	40	
24									●3	30	30	
25				no observation for troublesome of Timechecker						25+5	—	
26									●●6.5	30	105	
27			×	×	×	×	×	×	×	40	—	
28									●●●10.5	30	30	
29									●4.5	20	—	
30									●4.5	30+10	30	
31									●●7.5	20	—	
32									●2.5	40+15	65	
33									●4.5	75	40	W461[5]
34									●0.5	100	40	
35									●5	20	50	
36									●1	30	95	R1[6]
37									●●9	40	—	
38			×	×	×	×	×	×	×	60	30	
39			×	×	×	×	×	×	×	25	—	W792[7]
40									●2.5	35	30	
41									●4	20	20	
42									●●8.5	20	30	
43									●●6.5	30	40	
44									●4.5	25	30	
45									●1.5	40	—	
46			×	×	×	×	×	×	×	30	—	
47			×	×	×	×	×	×	×	20	110	
48			×	×	×	×	×	×	×	25	55	
49			×	×	×	×	×	×	×	20	—	
50			×	×	×	×	×	×	×	30	30	
51									●1	35	—	
52			×	×	×	×	×	×	×	30	35	
53			×	×	×	×	×	×	×	25	55	
54			×	×	×	×	×	×	×	—	45	
55			×	×	×	×	×	×	×	40	180	
56[8]			×	×	×	×	×	×	×	30	70	

[1] The first visit started at 10:04:45 on Nov. 01.
[2] W759 was recruited to the 180-m-feeder for the first time (11:03).
[3] W301 was recruited to the 180-m-feeder at 11:19.
[4] W151 did not land on the feeder.
[5] W461 was recruited to the 180-m-feeder at 13:16.
[6] W151 returned once to the feeder.
[7] W792 was recruited to the 180-m-feeder at 13:49.
[8] The last trip finished at 15:19:30.

W151 often did not land and instead flew around. These behaviors seem to be related to the lack of ***Da***^{w} from the 13th to the 17th trips. W151 performed ***Da***^{w} after the 13th and 14th trips although she had returned to the hive without having landed on the feeder (Table 8). The dance appearance rate (dAr) from the 13th to 27th trips was 0.4667. The lack of ***Da***^{w} following the 38th and 39th trips seemed to be due to the influence of the behaviors of the recruited workers, W461 (33 d.o.) and W792 (15 d.o.).

(2) The influence of recruited foragers for successive 3 days

On Nov. 4, a sunny and later cloudy day, the influence of 4 recruits grew stronger: the dance appearance rate (dAr) for whole day was 0.1739 (Table 9). On the next partly cloudy day, Nov. 5, the situation was the same: dAr=0.1800 (Table 10). On Nov. 6, W151 flew out only 22 times, as it was

Table 9. Dance performance of a forager, W151 (51 days old) after visiting the feeding station at 180 m on Nov. 4, 2007 (sunny & later cloudy, 17.8-19.8°C) with 4 foragers (W759, W301, W792 and W461).

BEHAVIOR / CODE / TRIP	*shaking*	*tremble dancing*	*round dancing*	*transition dancing*					*waggle dancing*	FLIGHT TIME		
	Sh	*Td*^{r} ←*TD*→ *Td*^{w}	*Da*^{r}	*Da*^{t0}	*Da*^{t1}	*Da*^{t2}	*Da*^{t3}	*Da*^{t4}	*Da*^{w}	HIVE ↓ FEEDER	FEEDER ↓ HIVE	
1[3]			×	×	×	×	×	×	×	—	30	W301[2]
2			×	×	×	×	×	×	×	30	20	
3			×	×	×	×	×	×	×	30	30	
4			×	×	×	×	×	×	×	30	—	
5			×	×	×	×	×	×	×	35	30	
6			×	×	×	×	×	×	×	35	—	
7			×	×	×	×	×	×	×	30	30	
8			×	×	×	×	×	×	×	30	30	
9			×	×	×	×	×	×	×	25+15	35	
10			×	×	×	×	×	×	×	20	20	
11			×	×	×	×	×	×	×	30	85	
12			●2.5							25	25	
13			●0.5							20	30	
14									●2.5	25	30	
15			×	×	×	×	×	×	×	35	20	
16			●1							45	35	W792[4]
17			×	×	×	×	×	×	×	50	35	
18									●●●10.5	40	30	
19			×	×	×	×	×	×	×	50	35	W461[5]
20			×	×	×	×	×	×	×	80	40	
21			×	×	×	×	×	×	×	30	20	
22									●3.5	75	50	
23			○2.5						●3	35	40	
24			×	×	×	×	×	×	×	45	—	
25			×	×	×	×	×	×	×	45	—	
26			×	×	×	×	×	×	×	35	35	
27			×	×	×	×	×	×	×	20	20	
28			×	×	×	×	×	×	×	35	40	
29			×	×	×	×	×	×	×	40	—	
30			×	×	×	×	×	×	×	30	—	
31			×	×	×	×	×	×	×	30	35	
32			×	×	×	×	×	×	×	—	—	
33									●2.5	35	40	
34									●0.5	35	—	
35			×	×	×	×	×	×	×	35	65	
36			×	×	×	×	×	×	×	35	30	
37			×	×	×	×	×	×	×	20	35	
38			×	×	×	×	×	×	×	35	30	
39			×	×	×	×	×	×	×	40	35	
40			×	×	×	×	×	×	×	35	70	
41			×	×	×	×	×	×	×	30	60	
42			×	×	×	×	×	×	×	25	45	
43			×	×	×	×	×	×	×	35	40	
44			×	×	×	×	×	×	×	30	30	
45			×	×	×	×	×	×	×	30	60	
46[6]			×	×	×	×	×	×	×	30	20	

[1] The feeder opened at 10:00, but it was the first visit started with W759 at 10:27:30 on Nov. 04.
[2] The 2nd visit was started by W301 at 10:32:40.
[3] W151 reached the feeder for the first time at 10:37:30 following the 2nd arrival of W759.
[4] W792 joined the feeding at 12:09:05.
[5] W461 joined the feeding at 12:27:45.
[6] The last trip finished at 15:55:25.

cloudy and the air temperature was low (15.9-16.9° C), but the dAr was almost the same (0.1818; Table 11). The only difference was that W759 (20 d.o.) never appeared. It has been mentioned and discussed that the dance appearance rate is usually low in many visitors (Ohtani *et al*., 2005).

3. Waggle dances of W151 (54-56 days old) at the 180-m-feeder and influence of a caged and released forager (W301)

Table 10. Dance performance of a forager, W151 (52 days old) after visiting the feeding station at 180 m on Nov. 5, 2007 (sunny & cloudy, 17.6-19.1°C) with 4 foragers (W759, W301, W461 and W792).

BEHAVIOR	shaking	tremble dancing	round dancing	transition dancing					waggle dancing	FLIGHT TIME		
CODE	Sh	$Td^r \leftarrow TD \rightarrow Td^w$	Da^r	Da^{t0}	Da^{t1}	Da^{t2}	Da^{t3}	Da^{t4}	Da^w	HIVE ↓ FEEDER	FEEDER ↓ HIVE	
TRIP												
1[1]			×	×	×	×	×	×	×	40	35	
2			×	×	×	×	×	×	×	25	30	
3			●1.5							25	45	
4			×	×	×	×	×	×	×	25	—	
5			×	×	×	×	×	×	×	35	50	
6			×	×	×	×	×	×	×	30	40	
7			×	×	×	×	×	×	×	25	40	
8			×	×	×	×	×	×	×	20	40	
9			×	×	×	×	×	×	×	20	25	
10			●1.5							20	35	
11			○1						●3	20	25	
12									●?	25	—	W759[2]
13			×	×	×	×	×	×	×	40	30	
14			×	×	×	×	×	×	×	20	30	W301[3]
15									●1.5	25	35	
16			×	×	×	×	×	×	×	20	—	W461[4]
17			×	×	×	×	×	×	×	25	25	
18									●3	30	20	W792[5]
19			×	×	×	×	×	×	×	30	30	
20			×	×	×	×	×	×	×	30	35	
21			○2						●4.5	25	30	
22			×	×	×	×	×	×	×	30	—	
23			×	×	×	×	×	×	×	35	35	
24			×	×	×	×	×	×	×	30	30	
25			×	×	×	×	×	×	×	30	—	
26			×	×	×	×	×	×	×	25	—	
27			×	×	×	×	×	×	×	30	30	
28			×	×	×	×	×	×	×	25	25	
29			×	×	×	×	×	×	×	25	50	
30			×	×	×	×	×	×	×	25	35	
31			×	×	×	×	×	×	×	—	55	R1[6]
32			×	×	×	×	×	×	×	35	30	
33			○1						●2.5	30	30	
34			×	×	×	×	×	×	×	25	40	
35			×	×	×	×	×	×	×	25	65	
36			×	×	×	×	×	×	×	20	35	
37			×	×	×	×	×	×	×	20	25	
38			×	×	×	×	×	×	×	25	45	
39			×	×	×	×	×	×	×	35	45	
40			×	×	×	×	×	×	×	25	20	
41									●3	30	30	
42			×	×	×	×	×	×	×	25	30	
43			×	×	×	×	×	×	×	30	25	
44			×	×	×	×	×	×	×	20	40	
45			×	×	×	×	×	×	×	20	30	
46			×	×	×	×	×	×	×	—	30	
47			×	×	×	×	×	×	×	—	30	
48			×	×	×	×	×	×	×	20	150	
49			×	×	×	×	×	×	×	—	40	
50[7]			×	×	×	×	×	×	×	30	95	

[1] The trip of W151 was begun at 10:37:30 on Nov. 05.
[2] W759 firstly visited the feeder at 11:35:20.
[3] W301 firstly visited the feeder at 11:43:50.
[4] W461 firstly visited the feeder at 11:55:20.
[5] W792 firstly visited the feeder at 12:02:00.
[6] W151 returned once to the feeder.
[7] The last trip of W151 finished at 15:21:25, just as it began to rain.

Table 11. Dance performance of a forager, W151 (53 days old) after visiting the feeding station at 180 m on Nov. 6, 2007 (cloudy, 15.9-16.917.6-19.1°C) with 3 foragers (W301, W461 & W792).

BEHAVIOR	*shaking*	*tremble dancing*	*round dancing*	*transition dancing*					*waggle dancing*	FLIGHT TIME		
CODE	***Sh***	$Td^r \leftarrow TD \rightarrow Td^w$	Da^r	Da^{t0}	Da^{t1}	Da^{t2}	Da^{t3}	Da^{t4}	Da^w	HIVE ↓	FEEDER ↓	
TRIP										FEEDER	HIVE	
1[2]			×	×	×	×	×	×	×	70	125	W461[3]
2			×	×	×	×	×	×	×	—	—	
3			×	×	×	×	×	×	×	—	40	
4			×	×	×	×	×	×	×	25	165	
5			×	×	×	×	×	×	×	30	25	
6			×	×	×	×	×	×	×	25	20	
7			○1						●1.5	30	25	W301[4]
8			●1							30	25	
9									●1.5	45	40	
10			×	×	×	×	×	×	×	65	25	
11									●3	20	50	
12			×	×	×	×	×	×	×	—	—	
13			×	×	×	×	×	×	×	50	20	
14			×	×	×	×	×	×	×	40	35	
15			×	×	×	×	×	×	×	40	—	
16			×	×	×	×	×	×	×	35	—	
17			×	×	×	×	×	×	×	30	60	
18			×	×	×	×	×	×	×	40	35	
19			×	×	×	×	×	×	×	25	45	
20			×	×	×	×	×	×	×	25	50	
21			×	×	×	×	×	×	×	40	30	
22[5]			×	×	×	×	×	×	×	35	120	

[1] W792 visited as soon as the feeder was set at 12:00:00 on Nov. 06.
[2] The trip was begun at 12:40:30.
[3] W461 firstly visited the feeder at 12:45:15.
[4] W301 firstly visited the feeder at 13:35:45.
[5] The last trip finished at 15:51:45, but the return flight time was too long (120 s) in the air temperature of 15.9°C.

An experimental manipulation was performed on Nov. 7: the three recruited foragers were caged. Interestingly, successive ***Da***^{w} by W151 were not observed till the 26th trip. We suggest that something left by the 3 recruits may inhibit ***Da***^{w} performance until the following day. After 5 successive ***Da***^{w} were observed from 26th to 30th trips, W301 was released. The other 2 recruits (W461 & W792) were found to have starved to death in the cage. The release of W301 (45 d.o.) was reflected in the dance appearance rate (dAr) of 0.3571 from the 31st to 44th trips (Table 12).

On Nov. 8, a sunny day, W151 performed worker piping (***Pi***) without the piping sound about 5 min after a *Vespa mandarinia* Radoszkowski came near the hive entrance (Table 13). Ohtani and Kamada (1980) observed ***Pi*** during the attack of another wasp, *Vespa simillima xanthoptera* Cameron. This incident may have enhanced the starting difficulty, as the first ***Da***^{w} was not observed until the 12th trip. When the dAr became 0.3000 (=6/20) after the 20th trip, W301 (46 d.o.) was caged, but the dAr did not become higher from the 21st to 29th trips (2/9=0.2222). This is conceivably explained by the remaining influence of W301.

It seemed likely that the ending difficulty began, as dAr become 0.2500 between the 42nd and 45th trips. Therefore, W301 was released in the 46th trip, which seemed to lead to performance of ***Da***^{w} 3 times during the last 6 trips (dAr=0.5000). Thus the existence of nestmates in the feeder may have excitatory as well as inhibitory effects on dance appearance.

On Nov. 9, a party cloudy day, W151 vigorously performed ***Da***^{w} (dAr=0.7538), but no recruited foragers were observed, just as on Nov. 2. The starting and ending difficulties were more clearly perceived on this day (Table 14) than on Nov. 2 (Table 7). On this day, W151 often performed ***Da***^{w} without tail waggling, which we counted as ***Da***^{r} and is represented by open circles in Table 14. The increase of the open circles may reflect the advanced age of W151 (56 d.o.).

4. Dance performances of recruited foragers

Because we had not prepared a video camera for recording the workers' movement on the whole comb, the dance performances of recruited foragers were incompletely observed. However, ***Da*^{w}** is such a distinct behavior that it is hardly ever missed. All 4 recruited foragers performed ***Sh*** and ***TD*** but did not perform ***Da*^{r}**, ***Da*^{t}** or ***Da*^{w}**.

Discussion

1. Genetic background on the honeybee brain

Based on the discussions of von Frisch (1967) and

Table 12. Dance performance of W151 (54 days old) after visiting the feeding station at 180 m on Nov. 7, 2007 (sunny, 16.4-20.5°C) with a caged and released forager (W301).

BEHAVIOR / CODE / TRIP	*shaking* *Sh*	*tremble dancing* *Td*^{r} ←*TD*→ *Td*^{w}	*round dancing* *Da*^{r}	*transition dancing* *Da*^{t0}	*Da*^{t1}	*Da*^{t2}	*Da*^{t3}	*Da*^{t4}	*waggle dancing* *Da*^{w}	FLIGHT TIME HIVE ↓ FEEDER	FEEDER ↓ HIVE	
1[1]			×	×	×	×	×	×	×	30	75	W301,W461 and W792 were caged.
2			×	×	×	×	×	×	×	25	35	
3			×	×	×	×	×	×	×	40	20	
4			×	×	×	×	×	×	×	40	40	
5			×	×	×	×	×	×	×	20	40	
6			×	×	×	×	×	×	×	25	40	
7			×	×	×	×	×	×	×	20	30	
8			×	×	×	×	×	×	×	25	70	
9			×	×	×	×	×	×	×	—	40	
10			×	×	×	×	×	×	×	25	35	
11			×	×	×	×	×	×	×	30	70	
12			×	×	×	×	×	×	×	30	30	
13			×	×	×	×	×	×	×	30	60	
14			×	×	×	×	×	×	×	25	35	
15									●1	30	35	
16			×	×	×	×	×	×	×	25	65	
17			×	×	×	×	×	×	×	40	75	
18			×	×	×	×	×	×	×	30	65	
19			●0.5							30	30	
20			×	×	×	×	×	×	×	25	65	
21			×	×	×	×	×	×	×	—	30	
22			×	×	×	×	×	×	×	30	65	
23			×	×	×	×	×	×	×	30	30	
24			×	×	×	×	×	×	×	25	35	
25			×	×	×	×	×	×	×	25	90	
26									●1.5	25	25	
27									●2.5	45	55	
28									●●8	25	35	
29									●2	25	50	
30									●●6.5	—	30	
31			×	×	×	×	×	×	×	25	30	W301was released[2]
32			○2						●4.5	—	30	
33			×	×	×	×	×	×	×	35	30	
34									●2	30	35	
35			×	×	×	×	×	×	×	30	40	
36			×	×	×	×	×	×	×	35	40	
37			×	×	×	×	×	×	×	30	30	
38			×	×	×	×	×	×	×	30	30	
39			×	×	×	×	×	×	×	40	35	
40									●●6	25	35	
41									●●6	25	30	
42			×	×	×	×	×	×	×	30	35	
43			●1							30	—	
44									●0.5	—	—	
45			×	×	×	×	×	×	×	—	—	
46			×	×	×	×	×	×	×	40	70	
47			×	×	×	×	×	×	×	30	70	
48										—	75	
49			×	×	×	×	×	×	×	40	30	
50[3]			×	×	×	×	×	×	×	25	100	

[1] The trip was begun at 10:20:20, after other 3 foragers (W301, W461 & W792) were removed from the observation hive and caged before the start at 10:00 on Nov. 07.

[2] Only W301 was alive, but W461 and W792 starved to death in the cage.

[3] The last trip of W151 finished at 15:16:20.

Wenner and Wells (1990), honeybees seem to have two different languages: odor and dance. What are the substrates of the odor and dance language in the central nervous system of honeybees? To approach this question we will examine the genetic background of the two languages.

The last two decades have witnessed then the *Evo Devo* (=evolutionary developmental biology) revolution. The first shot in this revolution was the discovery of many common "tool kits" of "master"

Table 13. Dance performance of W151 (55 days old) after visiting the feeding station at 180 m on Nov. 8, 2007 (sunny, 15.1-22.0°C) with a caged and released forager (W301).

BEHAVIOR	*piping*	*tremble dancing*	*round dancing*	*transition dancing*					*waggle dancing*	FLIGHT TIME		
CODE	*Pi*	$Td^r \leftarrow TD \rightarrow Td^w$	Da^r	Da^{t0}	Da^{t1}	Da^{t2}	Da^{t3}	Da^{t4}	Da^w	HIVE ↓ FEEDER	FEEDER ↓ HIVE	
TRIP												
1[1]			×	×	×	×	×	×	×	55	20	
2			×	×	×	×	×	×	×	30	—	
3	◎4[2]		×	×	×	×	×	×	×	25	30	
4			×	×	×	×	×	×	×	25	20	
5			×	×	×	×	×	×	×	—	20	
6			×	×	×	×	×	×	×	95	25	
7			×	×	×	×	×	×	×	40	60	
8			×	×	×	×	×	×	×	40	60[3]	
9			●1							35	65	
10			●0.5							35	60	
11			×	×	×	×	×	×	×	25	20	
12			○1						●1	25	25	
13			×	×	×	×	×	×	×	30	20	
14			×	×	×	×	×	×	×	25	25	
15			×	×	×	×	×	×	×	25	35	
16			×	×	×	×	×	×	×	25	—	
17									●8.5	35	30	
18									●1.5	30+30	45	
19			×	×	×	×	×	×	×	35	35	
20									●2	35	25	
21			×	×	×	×	×	×	×	30	30	W301 was caged[4]
22			×	×	×	×	×	×	×	60	25	
23									●7	—	40	
24			×	×	×	×	×	×	×	35	20	
25									●4+?	40	—	
26			×	×	×	×	×	×	×	—	25	
27			×	×	×	×	×	×	×	25	70	
28			×	×	×	×	×	×	×	30	30	
29			×	×	×	×	×	×	×	50	40	
30			○2						●2	40	20	
31			○1.5						●5	55	25	
32									●●●15	35	20	
33									●●●14.5	45	20	
34									●4.5	75	35	
35									●3.5	40	25	
36									●●6	40	20	
37									●●7	35	20	
38			○1						●●6	50	25	
39			○2						●●7	—	20	
40			○1						●●5.5	40	25	R1[5]
41			○1						●●●●16.5	40	20	
42			×	×	×	×	×	×	×	35	45	
43									●●8	30	40	
44			×	×	×	×	×	×	×	25	35	
45			×	×	×	×	×	×	×	30	40	
46			○4						●3	30	20	W301 was released[4]
47			×	×	×	×	×	×	×	35	55	
48			○1						●3	40	25	
49									●5	30	—	
50			×	×	×	×	×	×	×	—	70	
51[6]			×	×	×	×	×	×	×	30	35	

[1] The trip was begun at 11:08:00 on Nov. 08.

[2] W151 performed ***Pi*** (*worker piping*) without piping sound, about 5 min after *Vespa mandarinia* came near the hive entrance.

[3] Half of the flight time for returning was spent resting on the glass.

[4] W301 was caught on the feeder and caged at 13:04:45, and released at 15:30:30.

[5] W151 returned to the feeder once.

[6] The last trip of W151 finished at 16:12:10.

Table 14. Dance performance of W151 (56 days old) after visiting the feeding station located at 180 m on Nov. 9, 2007 (sunny & cloudy, 17.9-20.6°C).

BEHAVIOR	*piping*	*tremble dancing*	*round dancing*	*transition dancing*					*waggle dancing*	FLIGHT TIME	
CODE	*Pi*	$Td^r \leftarrow TD \rightarrow Td^w$	Da^r	Da^{t0}	Da^{t1}	Da^{t2}	Da^{t3}	Da^{t4}	Da^w	HIVE ↓ FEEDER	FEEDER ↓ HIVE
TRIP											
1[1]			×	×	×	×	×	×	×	30	20
2			×	×	×	×	×	×	×	30	30
3			×	×	×	×	×	×	×	75	30
4			×	×	×	×	×	×	×	30	35
5			×	×	×	×	×	×	×	30	70
6			×	×	×	×	×	×	×	25	35
7			●0.5							35	25
8			○2.5						●3.5	40	95[2]
9									●1.5	35	35
10			○1						●4	35	80
11			○1.5						●●6.5	25	30
12			○2						●●7.5	30+20	20
13			●2.5							30+10	30
14			○3						●5	30	40
15			×	×	×	×	×	×	×	40	60
16			●1.5							35	25
17			○2						●3.5	30	30
18			○1						●4	35	45
19			×	×	×	×	×	×	×	25+20	35
20			○1.5						●●●13	30	30
21			●1							30+30	25
22			○2						●1	35	30
23			○2.5						●●10	25	25
24									●●6	40+35	35
25			○1						●●7.5	30	30
26			○3						●●●12	30	30
27			○2						●●●13	45+35	—
28			○1						●3.5	50	—
29			○2						●5	30+20	30
30			○0.5						●●9	30+25	30
31			○1						●●7	30	40
32			○1						●1	40	30
33			○2						●●6	20+15	35
34			○1						●●5.5	35+20	45
35			○2.5						●●9.5	20+20	30
36			○4.5						●4.5	45+15	25
37			○3.5						●2.5	30+20	30
38			○1.5						●3	35+15	30
39			○2.5						●●8	25+20	30
40			×	×	×	×	×	×	×	35+25	65
41									●●●10.5	25	35
42			○1.5						●3.5	25+20	25
43			○1.5						●●9.5	30+20	40
44			○2						●3.5	25+15	20
45			○1						●●8	30	25
46			○2						●2.5	35	35
47			○3						●●●12	50	35
48			○2						●5.5	55	40
49			○2						●●●●16.5	40	45
50			○4.5						●●7.5	25+10	40
51									●●6	30	40
52			○3						●2.5	30	85
53			○2.5						●3.5	30	—
54			○1						●●6.5	25	55
55			No observation for troublesome of Timechecker							30	30
56			×	×	×	×	×	×	×	—	40
57			○1						●4	30	30
58			○1						●1	35	45
59			○2						●●6.5	30	45
60			×	×	×	×	×	×	×	30	80
61			○1.5						●1	30	25
62			×	×	×	×	×	×	×	20	35
63			×	×	×	×	×	×	×	30	45
64			×	×	×	×	×	×	×	20+10	—
65			×	×	×	×	×	×	×	25	105
66[3]			×	×	×	×	×	×	×	—	40

[1] The trip of W151 was begun at 10:35:40 on Nov. 09, and W301 was caged all day long.

[2] A Japanese honeybee invaded the observation hive just before W151 returned.

[3] The last trip finished at 16:02:15.

genes shared between insects and mammals (Carroll, 2005, p.9).

In the central nervous system, 2 *hox* (=homeobox) gene-sets, the *nk* and *pax* gene-sets, were discovered to be common to insects, annelids and vertebrates (Denes *et al*., 2007). One area of neocortex which orders the human language is called the Broca's area, whose tool-kit gene is identified as *FOXP2* (Lai *et al*., 2001). This gene group has been discovered not only in humans but also in many mammals and birds (Enard *et al*., 2002). It is unknown whether there is an an area in the insect microbrain analogous to Broca' s area in the human megalobrain. Broca's area may have evolved after diverging from the protostomia.

On the other hand, there is a similarity on the structure of the first olfactory nerve center between insects and mammals (Hildebrand & Shepherd, 1997). Recently, the common *Mahya* genes were discovered in honeybees, zebra fishes and mice (Tsuchimoto *et al*., 2005). *Mahya* genes encode novel secretory proteins, and are expressed in the brain area related to the odor. Tsuchimoto *et al*. (2005) suggest that *Mahya* genes may be involved in learning and memory and in processing of sensory information in Hymenoptera and vertebrates.

2. The time lag of recruitment to the waggle dance by W151

Within the above genetic background, a worker honeybee, W151, performed her waggle dance a total of 188.5 times on Nov. 2 (cf. Table 7). If the information contained in her waggle dance was read among her nestmates, we would expect many foragers to be immediately recruited to the feeding station where W151 had been. However, it was not until the next day that 4 recruited foragers appeared at the 180-m-feeder. What, then, is the explanation for this time lag of recruitment? The assumption of a time lag is not contained in the dance language hypothesis. W151 also performed her waggle dance vigorously (272.5 times) on Nov. 9 without the disturbance of recruited foragers, but recruited foragers never appeared at the feeder within the next day (cf. Table 14). This observed time lag of recruitment evidence against the dance language hypothesis.

3. What is the starting and ending difficulty?

In all of our experiments using the feeder, the activity of *dancing* (***DA***=***Da***^{r}+***Da***^{t}+***Da***^{w}) was low during the starting period, much like a human who has gotten up on the wrong side of the bed. *Shaking* (***Sh***) and *trembling dancing* (***TD***) were often observed during the starting period. Low activity of *round dancing* (***Da***^{r}), *transition dancing* (***Da***^{t}) and *waggle dancing* (***Da***^{w}) were observed during the ending period, much like a human who becomes very tired at evening time. Only ***Sh*** was frequently observed during the ending period. For the time being, we refer to these situations as "the starting difficulty" and "the ending difficulty". Both difficulties seem to have physiological causes, which were recognized also in Ohtani (2000) and Ohtani (2002). In other words, waggle dances seem to appear only in the best physiological conditions, rather than being controlled by foragers themselves.

4. The influence of recruited foragers hardly danced

Ohtani *et al*. (2005) discussed the dance appearance rate (dAr= the number of dance performances / the number of flights) in many visitors. From the data of Ohtani (2000), Ohtani (2002) and Ohtani *et al*. (2005), it is shown that many visitors to a feeder become poor dancers after visiting a crowded feeder.

In this trial, *dancing* (***DA***) of W151 was clearly influenced by the 4 recruited foragers. The activity of 4 recruits reduced the dAr of W151 (cf. Tables 8-11), and in reverse, the presence of W151 stifled the ***DA*** of the 4 recruits.

From the experiments with the caged and released recruits, it is clear that the influence of the recruits remained for a long time after the recruits were caged, but emerged immediately after a recruit was released (cf. Tables 12 & 13). It is conjectured that the cause of this influence is the scent of the recruits.

5. The physiological aspect of dance performances

We have observed many dance performances in recent years (Ohtani, 2000; Ohtani, 2002; Ohtani *et al*., 2005). Honeybees perform different dances at different times. No dance, *shaking* or *tremble dancing* are often observed at the start of a day. *Round dancing* and *transition dancing* are often observed on successive trips, sometimes with interspersed trips featuring no dance. *Transition dancing* is divided into five sub-forms with gradually increasing waggle number. *Waggle dancing* is observed at certain feeder distances (over 100 m), under favorable weather conditions, and in strong sunlight. These restrictions seem to disqualify the dancing as a language, which should be unaffected by surroundings. If dance performances are to be regarded as a sort

of physiological response, their properties should be constant like a sneeze in a set of physiological conditions. Wenner (2002) proposed that the waggle dance is not a signal but a symptom according to the forager's experience.

A honeybee forager is forced many times to go to and from the feeder. Repeated flights may lead to a sort of labor saving. The excessive excitement in flying may accumulate in the nervous system of the forager. It may cause the thoracic muscles of the forager to work. That is, the forager might be "pseudo-flying" on the comb surface. The same muscles and nervous system used for waggle dances are also used usually in flying and walking. If the dance performance of honeybees is caused by the leaking-out of accumulated excitement from flying, it would be not eliminated by natural selection because it is neutral in evolution. Other expressions of the above conjecture are as "a ritualized reenactment" by Wilson (1980, p.203) and "a miniaturized reenactment" by Seeley (1985, p.83; 1995, p.36).

Acknowledgements

I thank 5 people for their help in collecting data: Ms. Hiroko Kajiwara, Mr. Yutaka Arakawa, Ms. Yumiko Kikuchi, Hisayo Suzuki and my sons (Ichigo and Masaki Ohtani).

References

Brückner, D. (1976) Vergleichende Untersuchungen zur Temperatur- praeferenz von ingezüchteten und nicht-ingezüchteten Arbeit- erinnen der Honigbiene (*Apis mellifica*). *Apidologie*, **7**, 139-149.

Carde, R. T. (1984) Chemo-orientation in flying insects. In W. J. Bell and R. T. Carde, *Chemical Ecology of Insects*, pp.111-124. NewYork: Chapman and Hall.

Carroll, S. B. (2005) *Endless Forms most Beautiful: The New Science of Evo Devo and the Making of the Animal Kingdom* (a Norton paperbook 2006). 350pp. W. W. Norton & Company, London.

Denes, A. S., Jékely, G., Steinmeltz, P. R. H., Raible, F., Snyman, H., Prud'homme, B., Ferrier, D. E. K., Balavoine, G. and Arendt, D. (2007) Molecular architecture of annelid nerve cord supports common origin of nervous system centralization in Bilateria. *Cell*, **129**, 277-288.

Enard, W., Przeworski, M., Fisher, S. E., Lai, C. S. L., Wiebe, V., Kitano, T., Monaco, A. P., and Pääbo, S. (2002) Molecular evolution of *FOXP2*, a gene involved in speech and language. *Nature*, **418**, 869-872.

Free, J. B. (1960) The distribution of bees in a honey-bee (*Apis mellifera* L.) colony. *Proc. R. ent. Soc. Lond. (A)*, **35**, 141-144.

Frisch, K. von (1967) *The dance language and orientation of bees*. (paperback edition, 1993) 566p., Harvard Univ. Press, Cambridge.

Harrison, J. M. (1987) Role of individual honeybee workers and drones in colonial thermogenesis. *J. Exper. Biol.*, **129**, 53-61.

Hildebrand, J. G. and Shepherd, G. M. (1997) Mechanisms of olfactory discrimination: converging evidence for common principles across phyla. *Annu Rev Neurosci*, **20**, 595-631

Lai, C. S. L., Fisher, S. F., Hurst, J. A., Vargha-Khadem, F. and Monaco, A. P. (2001) A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature*, **413**, 519-523.

Michelsen, A., Andersen, B. B., Storm, J., Kirchner, W. H. and Lindauer, M. (1992) How honeybees perceive communication dances, studied by means of a mechanical model. *Behav. Ecol. Sociobiol.*, 30, 143-150.

Milum, V. G. (1955) Honey bee communication. *Amer. Bee J.* **95**, 127-134

Ohtani, T. (1974) Behavior repertoire of adult drone honeybee within observation hives. *J. Fac. Sci. Hokkaido Univ. VI, Zool.*, **19**, 709-721.

Ohtani, T. (1992) Spatial distribution and age-specific thermal reaction of worker honeybees. *Humans and Nature*, **No.1**, 11-25.

Ohtani, T. (1994) Behaviors in adult queen honeybees within observation hives. I. Behavior patterns. *Humans and Nature*, **No.3**, 37-77.

Ohtani, T. (2000) A preliminary report on the dance performance of honeybees at very near distance from the hive. *Nature and Human Activities*, **No.5**, 27-39.

Ohtani, T. (2002) A report on four dance performances of two worker honeybees visiting the feeding station regularly within 105 m from the hive. *Nature and Human Activities*, **No.7**, 35-52.

Ohtani, T. and Kamada, T. (1980) 'Worker pipping': the piping sounds produced by laying and guarding worker honeybees. *J. Apic. Res.*, **19**,154-163.

Ohtani, T., Ikeno, H. and Wakazono, M. (2005) A report involving no dance and rare dance performances of worker honeybees after visiting the feeding station. *Nature and Human Activities*, **No.9**, 57-75.

Riley, J. R., Greggers, U., Smith, A. D., Reynolds and Menzel, R. (2005) The flight paths of honeybees recruited by the waggle dance. *Nature*, **435**, 205-207.

Seeley, T. D. (1985) *Honeybee Ecology: A Study of Adaptation*

in Social Life. 201 p., Princeton Univ. Press, Princeton.

Seeley, T. D. (1995) *The Wisdom of the Hive*. 302 p., Harvard Univ. Press, Cambridge.

Tautz, J. (1996) Honeybee waggle dance: recruitment success depends on the dance floor. *J. Exp. Biol.*, **199**, 1375-1381.

Tsuchimoto, M., Yasuo, S., Funada, M., Aoki, M., Sasagawa, H., Yoshimura, T., Tadauchi, O., Cameron, S. A., Kitagawa, Y. and Kadowaki, T. (2005) Conservation of novel *Mahya* genes shows existence of neural functions common between Hymenoptera and Deuterostome. *Dev. Genes Evol*. **215**, 564-574.

Yushima, T. (1977) Mating behavior of lepidopterous insects in relation to sex pheromone. *Kontyû, Tokyo*, **45**, 459-470. (In Japanese)

Wenner, A. M. (2002) The elusive honey bee dance "language" hypothesis. *J. Insect Behav.*, **15**, 859-878.

Wenner, A. M. and Wells, P. H. (1990) *Anatomy of a controversy – the question of a* "*language*" *among bees*. xiv+399p., Columbia Univ. Press, New York.

Wilson, E. O. (1980) *Sociobiology: The New Synthesis* (The abridged edition). xi+366p., The Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts and London.

大谷　剛：招集バチによる影響を受けたミツバチ働きバチの尻振りダンス招集効率

180 ｍまで引き伸ばされた餌場に通っている W151 の背番号をつけたミツバチの働きバチは，2007 年の 11 月 2 日に観察巣箱で 188.5 回の尻振りダンスをした．しかし，この日にはこの尻振りダンスの情報で餌場に招集された個体は観察されず，次の日に 4 匹現われ，尻振りダンスはしなかった．この 4 匹の招集バチが現われた影響は，W151 の尻振りダンスの回数の減少となった．W151 は尻振りダンスのほか，シェイキング，身震いダンス，円ダンス，移行型ダンスをした．そのほか，招集バチを実験的に捕らえたり放したりして，尻振りダンス数の減少を確かめた．論議では，ミツバチの脳の研究史を記述したあと，招集の遅れ，立ち上がりと終了間際の無ダンス，そして招集バチの影響について取り上げた．これらの結果は，収穫ダンスが「ダンス言語」説にそぐわない生理的側面をもっていることの証である．

Received: July 30, 2008
Accepted: September 1, 2008