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Does an increase in reward affect the precision of the encoding of directional information in the honeybee waggle dance?

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Abstract *Apis mellifera* foragers perform waggle dances to communicate the presence of highly desirable nectar sources to their forager-mates. Each waggle dance consists of several waggle-runs (straight movements of the dancer closely aligned on the comb surface) that carry spatial information that the dance followers can use to locate the food source being advertised. To address how this complex motor display responds to unpredictable fluctuations in its main triggering stimulus, i.e., sucrose stimulation, we analyzed the effects of an increase in reward on the direction of consecutive waggle-runs as well as other components of the waggle dance. Results show that a sudden increase in reward may increase the directional scatter among consecutive waggle-runs, especially those performed at the beginning of the dance. However, a simultaneous and rapid increase in the duration of the signal—together with a more regular alignment of the later waggle-runs within the signal—seems to compensatethe initial increase in directional scatter so that the transfer of directional information remains effective. These results point out that the regulation of dance maneuvers depends on the dancer's motivation to forage.

Keywords *Apis mellifera* · Waggle dance · Directional information · Communication

Introduction

Forager honeybees (*Apis mellifera*) perform waggle dances to communicate the presence of highly desirable food sources to their forager-mates (von Frisch 1965). When the nectar source is fairly far from the nest, dancing foragers perform fast and short forward movements straight ahead on the comb surface, return in a semicircle in the opposite direction and start the cycle again in regular alternation. Each waggle dance consists of several of these cycles, which are rather similar motion patterns. The straight portion of this course, called a waggle-run, consists of a single stride performed in a strange gait in which all six legs hold onto the comb most of the time (Tautz et al. 1996) and is emphasized by lateral waggling motions of the abdomen (von Frisch 1965). The length of each waggle-run increases with the distance that the forager had flown to reach the food source being advertized (von Frisch and Jander 1957). It has also been shown that the length of a single waggle-run is affected by the optic flow experienced during the flight and that the retinal image flow that bees experience while flying provides them with some means of monitoring the distance traveled (Srinivasan et al. 2000; Esch et al. 2001; Tautz et al. 2004). In addition, the angle of each waggle-run relative to the upward direction of the comb correlates with the direction of the flight relative to the sun's azimuth in the field and sun-linked patterns of polarized skylight (von Frisch 1965).

Throughout a single waggle dance, the dancer's movements are closely followed by a variable number of nest-mates (von Frisch 1965). Although the mechanisms underlying the acquisition of information by these followers remain unknown (Michelsen 2003), previous evidence indicates that the dance followers perceive both the direction and the duration of the single waggle-runs (von Frisch 1965; Michelsen et al. 1992; Seeley 1995; Michelsen 2003). In the case of nectar sources, the key stimulus that triggers the waggle dance is the presence of sugar solution (as a reward) at a given feeding place. Thus, the amount and sugar concentration of the discovered nectar must exceed a threshold that was previously defined by the forager's central nervous system according to several properties of the feeding place, the

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dancer's past foraging experience and, in addition, several stimuli available inside the nest (Núñez 1970; Seeley 1995). Besides direction and distance, dances also encode the profitability of the nectar source, i.e., a high profitability both enhances the number of waggle-runs and the intensity of the dance maneuvers and decreases the time interval between consecutive waggle-runs (von Frisch 1965; Waddington and Kirchner 1992; Seeley and Towne 1992; Seeley et al. 2000; De Marco and Farina 2001).

Interestingly, a feature of the waggle dance is that consecutive waggle-runs are performed with some directional scatter. This means that the directions of single waggle-runs usually diverge from each other, erring alternately to the right and left of the main nector. Early works have demonstrated that the distance to be flown to reach the nectar source that is being advertised is an important factor affecting these divergences (von Frisch 1948; Gould 1976; Towne and Gould 1988). Changes in the insects' general motivation, however, usually promote variations in their spontaneous responsiveness to different external stimuli (Mc Farland 1971). This type of variations might also influence the control of a complex motor display such as the waggle dance. In honeybees, several works have shown that changes in different types of motion patterns can be explained by considering simultaneous variations in the insect's general motivation. Karl von Frisch and Martin Lindauer (1955), for instance, showed that flight speed depends on the sugar concentration offered at an artificial feeder. They have then proposed that the power-output of a forager bee depends on its motivation to forage. In addition, it was suggested that several aspects depend on the insects' foraging motivation: the bees' metabolism and their movements while foraging on a flower patch (Balderrama et al. 1992; Moffat 2000), as well as the short flights (Wei et al. 2002) that foragers perform after collecting nectar at an artificial feeder (through which they learn specific visual cues related to the food source location).

Hence, one might view a complex set of repetitive motion patterns that are finely controlled, such as the waggle dance (which does not occur randomly but in response to a well-defined set of stimuli), as a self-regulated motion system that exhibits its own dynamic for processing internal information and which operates under intrinsic feedback mechanisms (Wiener 1948; von Holst and Mittelstaedt 1950; von Holst and von St Paul 1960). According to this point of view, the output of such a system will definitely oscillate whenever the system as a whole faces unpredictable variations in its main triggering stimulus (Küpfmüller and Poklekowski 1956). This would happen, for instance, when a single bee that regularly forages on a given feeding site experiences an unexpected increase in reward. Under these circumstances, the sudden increase in sucrose stimulation (which enhances the insect's motivation to forage) would trigger short-lived oscillations in the values of those internal parameters that regulate the motion patterns of the waggle dance. This might negatively affect the control of the dance maneuvers, increasing, for instance, the directional scatter of consecutive waggle-runs, which may in turn diminish the precision of the encoding of directional information. Yet, as a behavioral output evolved to encode information (von Frisch 1965; Seeley 1995), the properties of the waggle dance (conceived as an autonomous system, Wiener 1948) should allow the entire signal to face unpredictable reward variations in such a way that, in spite of possible changes in the regulation of the dance maneuvers, the information being transferred remains useful. This becomes especially relevant if we consider that honeybees face an ever-changing nectar offer (Visscher and Seeley 1982). In the present study, we attempted to address how a complex communicating motor display such as the honeybee waggle dance responds to unpredictable variations of its main triggering stimulus. To this end, we analyzed the effects of a sudden increase in sucrose stimulation on the direction of consecutive waggle-runs as well as other components of the waggle dance.

Methods

A colony of nearly 4,000 *Apis mellifera ligustica* bees (with queen and workers) was placed in a two-frame observation hive (von Frisch 1965) located inside the laboratory. These bees had not been used for research before the experiments. In addition, they were not naive with respect to the study area since the colony was taken directly from the apiary located near the laboratory. Labeled bees were trained to forage individually on a feeder located 160 m away from the hive. There they were presented with a single artificial flower connected to a set of rate-feeders (see Núñez 1966, 1970), each delivering scented sugar solution (80 μl mint essence per liter of solution) at a constant flow rate of 5 μl per minute. The rate-feeders offered different sucrose concentrations (0.6, 1.2, 1.8 and 2.4 M). In this way, we were able to rapidly change the sucrose concentration delivered by the flower when the trained bee (whose behavior was being recorded) stayed inside the hive in between its consecutive foraging bouts. Since the flower delivered sugar solution only when the trained bee was present at the feeder, the offered solution did not accumulate during the corresponding foraging pauses. Experiments were conducted between March and May in the Experimental Field of the Faculty of Exact and Natural Sciences of the University of Buenos Aires (34°33′S, 5°26′W).

Experimental series

Each experiment started when a single trained bee was allowed to collect sucrose solution individually at the feeder. To diminish possible oscillations in the insects' foraging motivation at the beginning of each trial during the experiment, trained foragers collected the initial concentration of the corresponding experimental series for approximately 1 h before the recordings were begun. In each series, a bee made five successive visits to the feeder. We performed six different experimental series, which differed either in the sucrose concentration offered or in the reward stability. The first three series offered steady-state reward conditions for all five successive visits by the trained forager; the bees were given a constant sucrose concentration of 1.2 M ($n=4$), 1.8 M ($n=7$) or 2.4 M ($n=4$). The three remaining series offered transient reward conditions, in that they presented the bees with a sucrose concentration of 0.6 M throughout the initial four visits, and then with an increased sucrose concentration of 1.2 M ($n=3$), 1.8 M ($n=6$) or 2.4 M ($n=9$) in the last visit. Thus we evaluated independently the effects of the sucrose concentration offered and a sudden increase in reward on the foragers' dance behavior. Comparisons were made among data collected in the last visit of each of the experimental series.

Measurements

At the observation hive, we video-recorded the dance behavior of the trained foragers. The hive was illuminated by a fluorescent lamp (i.e., diffuse light) placed directly above the hive, in order not to disturb the direction of the dances. Data were obtained from videotapes. For the dances that insects displayed after returning from their fifth foraging bout, we measured the angle (in degrees) of single waggle-runs relative to vertical and the total number of waggle-runs. Two different approaches can be used to estimate the precision of the directional information encoded in the dances. On the one hand, a simple measure of the directional scatter of the waggle-runs (which assumes accurate corrections for changes in the sun's azimuth whenever dances occurring all day are compared) probably leads to the most sensitive estimation of the precision of the directional information. On the other hand, it is also possible to measure the divergences between the angles of consecutive waggle-runs. This may somewhat exaggerate the directional scatter. However, it simplifies comparing the precision of the directional information being transferred through different dances (as revealed by the degree of similarity among their consecutive motion patterns). Since we examined only those dances displayed in the last visit of the experimental series and, in addition, we excluded the behavior of the dance followers from the analysis (i.e., a quantitative evaluation of the effectiveness of the directional message was not made), the divergences between the angles of consecutive waggle-runs were used to compare dances under both steady-state and transient reward conditions. We then calculated the ''divergence angle'', as the differences between the angles recorded from consecutive waggle-runs. Each value was calculated as the direction of a single waggle-run minus the direction of the previous one (minimum 0° to maximum 180°). Thus, the first divergence angle in a given dance is associated with the second waggle-run displayed by the dancer. Data from different dancers were then averaged for each of the waggle-runs (considered sequentially) performed throughout the entire motor display. In addition, we calculated the ''mean divergence angle'' associated with each of the six different reward programs. In doing this, we first averaged the divergence angles obtained from the dances of individual bees (one divergence angle per bee per reward program), and then the divergence angles from different insects were averaged for statistical comparisons. Together with the directions of the waggle-runs, the directions of the consecutive turns within each dance (either to the left or to the right) were recorded. We also compared the average number of waggle-runs displayed by individual bees. Finally, for each of the different reward programs, we also calculated the ''dance precision'', as the median value of divergence angle in the frequency distribution of all the divergence angles recorded per program. The lower the median, the higher the dance precision.

Statistical analysis

Data were analyzed by means of two-way ANOVA and planned comparisons (Zar 1984).

Results

Figure 1 shows the divergences between the angles of consecutive waggle-runs as well as the relative frequency distribution of these divergences for each of the different reward programs (see the histograms). Results are presented according to the sucrose concentration (a: 1.2 M, b: 1.8 M and c: 2.4 M) and the reward stability offered by the different series (steady-state reward programs: black circles and bars, transient reward programs: white circles and bars, see Methods).

Under both steady-state and transient reward conditions, the foragers that collected 1.2 M sucrose solution showed divergence angles that ranged from 0° up to 130° approximately (Fig. 1a, black and white circles). Maximal values were 123 and 143 for the steady state and the transient reward programs, respectively (Fig. 1a, see the black and the white bars in the histogram). We found no difference in the mean divergence angle between both types of programs (Table 1, $P=0.07$, planned comparisons). The mean number of waggle-runs was also similar in both programs (Table 1, $P=0.7$, planned comparisons). Dance precision seemed to be lower in the steady-state reward program (Fig. 1a, see the histogram), although no statistical comparison was possible.

Divergence angles were smaller and more regular throughout the entire dance when the trained bees collected 1.8 M sucrose solution under steady-state reward conditions (Fig. 1b, black circles). Values ranged from 0° up to 85° (see the black bars in the corresponding histogram). In the transient reward program; however, the divergence angle was variable and higher, especially at the beginning of the dance (Fig. 1b, white circles). It ranged from 0° up to 163° (Fig. 1b, see the white bars in the histogram). As a result, the mean divergence angle was higher in the transient reward program (Table 1, $P = 0.003$, planned comparisons). In addition, dance precision was higher in the steady-state reward program. As shown previously, the mean number of waggle-runs did not differ statistically when the results from both types of programs were compared (Table 1, $P = 0.85$, planned comparisons).

The divergence angles were also low and regular throughout the entire dance when the insects collected 2.4 M sucrose solution under steady-state reward conditions (Fig. 1c, black circles). They ranged from 0° up to 85° (with the exception of one 143° difference, Fig. 1c, see the black bars in the corresponding histogram). In the transient reward program, the divergence angles were clearly higher at the beginning of the dance (Fig. 1c, white circles), ranging from 0° up to 175° (see the white bars in the histogram). In this case, however, the insects showed lower and less variable divergence angles shortly after their initial waggle-runs (Fig. 1c, white circles). In addition, they performed a higher number of waggle-runs in the transient reward program (Table 1, $P = 0.001$, planned comparisons). As a consequence, the mean divergence angle did not differ statistically when the results from both types of programs were compared (Table 1, $P = 0.69$, planned comparisons). Dance precision also seemed to be higher in the transient reward program (Fig. 1c, white vs black bars).

Because of the way we measured the directional differences between consecutive waggle-runs, there would be two ways that the bees may change their dances so that they show different divergence angles when they experience either a steady-state or a transient reward program. On the one hand, bees might alternate regularly between left and right turns when dancing and show divergence angles that do not depend on the directions of the turns (either left or right). On the other hand, bees might alternate less regularly between left and right turns when dancing. Because waggle-runs made after one type of turn (either to the left or to the right) tend to have a different direction than waggle-runs made after the other one, the angles between consecutive waggle-runs might be smaller if a bee does not alternate between left and right turns when dancing than if it does alternate between left and right turns. Throughout the present experiments, however, the probability of recording two consecutive turns in the same direction (either left or right) within a dance ranged between 0.017 and 0.019. Hence, the differences in the divergence angles we observed throughout the different reward programs can be explained only by considering directional differences that did not depend on the directions of the turns within the dance.

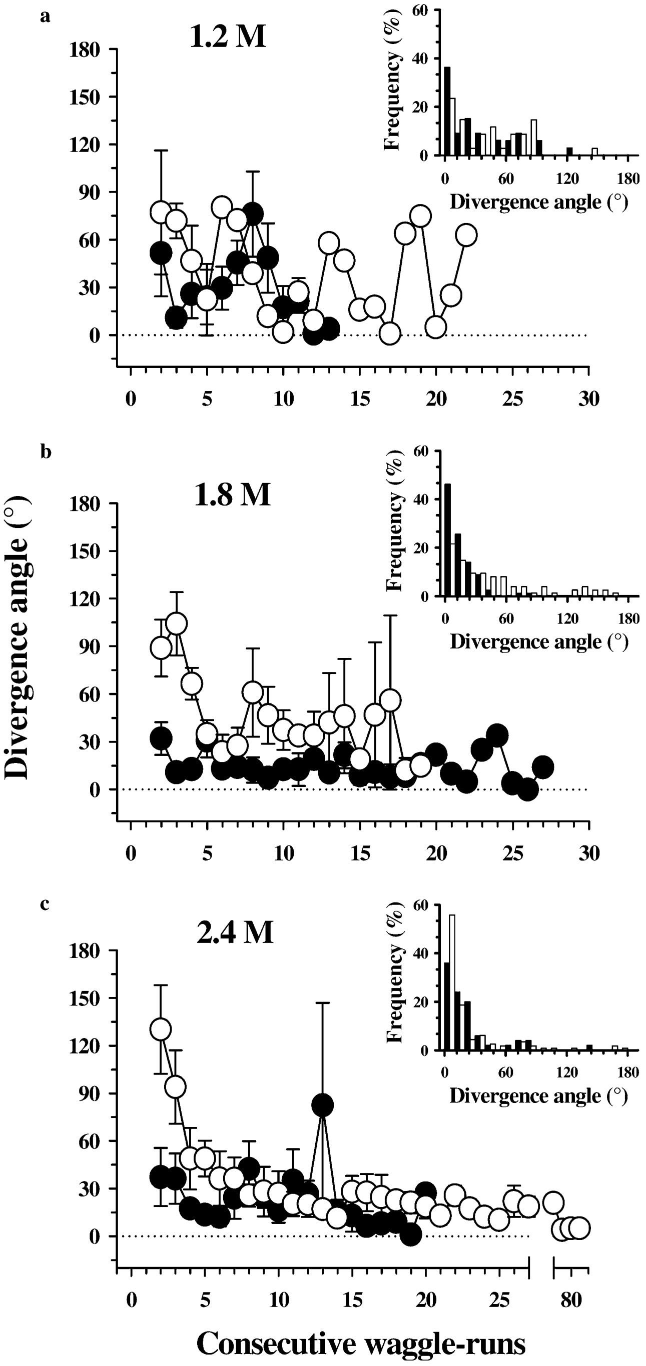

Fig. 1 For each reward program, the figure shows the divergence angles (mean ± SE, in degrees), defined as the differences between the angles recorded from consecutive waggle-runs. Each value was calculated as the direction of a single waggle-run minus the direction of the previous one (minimum 0° to maximum 180°). Data from different dancers were then averaged for each of the waggle-runs (considered sequentially) performed throughout the entire dance. The *absence of error bars* indicates data from only one dancer. *Black circles* indicate steady-state reward conditions. *White circles* indicate transient reward conditions (see Methods). Results are presented according to the sucrose concentrations offered: **a** 1.2 M; **b** 1.8 M and **c** 2.4 M. For each of the different reward programs, the histograms show the frequency distribution of all the divergence angles recorded per program (steady-state *black bars*; transient *white bars*)

Table 1 For each reward program, the mean number of waggle-runs (± SE) is presented together with the mean divergence angle (± SE) and the dance precision (median)

	Reward program					
	Steady-state			Transient		
	1.2 M	1.8 M	2.4 M	1.2 M	1.8 M	2.4 M
Waggle-runs[†]	8 ± 1.9^{a}	11 ± 3.0^{a}	12.5 ± 2.8^{a}	11 ± 5.2^{a}	12 ± 2.4^{a}	37 ± 6.1^{b}
Mean divergence angle (°)[‡]	$31 \pm 6.3^{a,b}$	19 ± 4.6^{a}	25.5 ± 3.6^{a}	54 ± 13.2^{b}	49 ± 8.5^{b}	29 ± 6.3^{a}
Dance precision (°)	27	12	18	39	34	9

[†] Two-ways ANOVA: interaction factor $F(2,27) = 3.4$, $P = 0.049$; Single effects: steady-state $F(2,27) = 0.14$, $P = 0.86$; Transient $F(2,27) = 10.4$, $P = 0.0004$; 1.2 M $F(1,27) = 0.12$, $P = 0.7$; 1.8 M $F(1,27) = 0.03$, $P = 0.85$; 2.4 M $F(1,27) = 12.3$, $P = 0.001$. Different letters indicate differences between the different experimental series (planned comparison, $P < 0.01$).

[‡] Two-ways ANOVA: interaction factor $F(2,27) = 1.87$, $P = 0.17$; Reward program effect: $F(2,27) = 9.43$, $P = 0.005$; Concentration effect $F(2,27) = 1.75$, $P = 0.19$. Different letters indicate differences between the different experimental series (planned comparison, $P < 0.05$)

We next addressed the effects of the offered reward by comparing results from the three different steady-state reward programs (Fig. 1, black circles). Results gave no difference in the mean divergence angle recorded for the different concentrations (Table 1; 2 M vs 1.8 M, $P = 0.27$; 1.2 M vs 2.4 M, $P = 0.65$; 1.8 M vs 2.4 M, $P = 0.54$; planned comparisons). We also found no difference in the mean number of waggle-runs, although a tendency was recorded which indicated a positive correlation between the number of waggle-runs and the offered sucrose concentration (Table 1; 2 M vs 1.8 M, $P = 0.69$; 1.2 M vs 2.4 M, $P = 0.6$; 1.8 M vs 2.4 M, $P = 0.85$; planned comparisons). On the contrary, when the data from the transient reward programs were compared (Fig. 1, white circles), results showed that variations in both the mean divergence angle and the mean number of waggle-runs may appear, depending on the magnitude of the offered increase in reward, i.e., the mean divergence angle decreased and the mean number of waggle-runs increased when the insects experienced a fourfold increase in reward (i.e., from 0.6 M to 2.4 M) (Table 1, mean divergence angle: 1.2 M vs 1.8 M, $P = 0.64$; 1.2 M vs 2.4 M, $P = 0.03$; 1.8 M vs 2.4 M, $P = 0.03$; waggle-runs: 1.2 M vs 1.8 M, $P = 0.9$; 1.2 M vs 2.4 M, $P = 0.002$; 1.8 M vs 2.4 M, $P = 0.0004$; planned comparisons).

Discussion

Forager honeybees cope with fluctuations in nectar resources by exchanging information about resource opportunities (von Frisch 1965; Seeley 1995). In doing this, they usually take advantage of the waggle dance, a well-known behavior that has been studied extensively (von Frisch 1965; Seeley 1995). In the waggle dance, the direction of the waggle-runs carries information that the dance followers can use to locate the food source being advertised (von Frisch 1965). Although the mechanisms through which the followers acquire the spatial information encoded in the waggle-runs remain unknown (Michelsen 2003), previous results indicate that those insects that keep close contact with the dancer are stimulated to visit the prospective food source (von Frisch 1965; Seeley 1995) after following a relatively low number of waggle-runs (von Frisch and Jander 1957; Gil and Farina 2002). Additionally, once in the field and close to the target, recruited foragers also use olfactory and visual cues to identify the food source previously signaled by the waggle dance (von Frisch 1965, Tautz and Sandeman 2002).

Intriguingly, one feature of the waggle dance is that the consecutive waggle-runs are usually performed with some directional scatter that depends mainly on the distance to be flown to reach the target (von Frisch 1965). Towne and Gould (1988) proposed that this kind of directional scatter might favor a well-suited distribution of recruited forager-mates across natural food sources. In addition, other factors also seem to affect the precision in the direction and indications of the waggle dance. For instance, it has been shown that the nature of the target being advertised, i.e., a nest site or a food source, also affects the alignment of the waggle-runs (Weidenmüller and Seeley 1999). Indeed, the effects of either the distance or the nature of the prospective target on the angular divergences of the waggle-runs rely not only on the properties of the brain circuitry underlying the honeybee dance behavior, but, mainly, on the mechanisms within the brain of the insects employed for computing environmental cues other than sucrose stimulation. However, whenever the waggle dance is conceived as a self-regulated motion system triggered by sucrose stimulation (Wiener 1948), the rules governing the computation of the neural signals involved in the regulation of the dance maneuvers might be also affected by unexpected reward variations (Küpfmüller and Poklekowski 1956). This may lead, for instance, to short-lived oscillations in the control of the dance maneuvers and a decreased precision in the directional indication of the dances, especially if the waggle dance occurs within a motivational context. We addressed this issue under highly controlled foraging conditions.

According to the present results, a sudden increase in reward may affect the divergence angles between consecutive waggle-runs (Fig. 1, Table 1), especially at the beginning of the dance. Whereas a twofold increase in reward affects neither the mean divergence angle nor the number of waggle-runs (Fig. 1a, white and black circles, Table 1), a threefold increase enhances the mean divergence angle but not the number of waggle-runs (Fig. 1b, white circles vs black circles; Table 1). Initially, the latter decrease in the precision of the directional information encoded in the signal seems not to be adaptive, since an effective and rapid recruitment through the dance may enhance the nectar gathering of the colony by enlarging the number of recruited forager-mates. However, after experiencing a fourfold increase in reward, the insects show higher divergence angles at the beginning of the dance, but also a higher number of waggle-runs that are more regularly aligned on the comb surface (Table 1; Fig. 1c, white circles). Consequently, a big improvement in the offered reward enhances the number of communicating events without affecting the mean divergence angle (Table 1). Thus, at least on the signal production side of the communication process (i.e., by considering only the behavior of the dancer) a property of the waggle dance, i.e., a rapid increase in the number of signals together with a more regular alignment of the latest waggle-runs, seem to compensate the initial oscillations of the divergence angles so that the transfer of precise directional information still occurs. From a technical point of view, one would say that a big improvement in the intensity of the triggering stimulus has a double effect on the motor display: it enhances the system's oscillations during its transient regulatory response and, in addition, it leads to a general increase in the amplification of the signals (according to this point of view, differences among individuals must be expected with respect to both effects). Thus, throughout a single dance, a decreased precision in the message transferred at the beginning of the dance would be compensated by an increased number of waggle-runs that carry more precise signals throughout the last part of the motor display. The speed at which the angular imprecision is compensated shortly after the beginning of the signal suggests that the initial divergences result from changes in some physiological parameters associated with the foraging motivational level of the dancer. Moreover, the speed of this compensation also reveals the well-developed functioning of the intrinsic feedback mechanisms regulating the waggle dance and it might also represent an important feature of a complex evolved behavior for encoding information.

Yet our results indicate that the insects' recent foraging experience affects the waggle dance in such a way that the expected degree of similarity among its repetitive motion patterns may decrease transitorily when the foragers experience an unexpected improvement in reward. Effects of the insects' recent foraging experiences on their dance behavior had been reported with respect to both the number of waggle-runs (De Marco and Farina 2001) and the number of round circuits (Raveret-Richter and Waddington 1993), but not with respect to the angular divergence of consecutive waggle-runs. It might be concluded, therefore, that the motor display occurs within a motivational context and that the assessment of sucrose stimulation depends not only on its current level, but also on what the insect expects to experience next, which relies on the background of its experience under the same circumstances and defines its foraging motivation.

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