The vocal expression of feeding motivation and frustration in the domestic laying hen, *Gallus gallus domesticus*

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Abstract

Thwarting of feeding behaviour in the laying hen results in an increase in stereotyped pacing, displacement preening, and the gakel-call. These behaviours therefore reflect the frustration arousal caused by the thwarting of feeding behaviour. This raises the question whether the level of frustration also varies with the intensity of the motivation to perform the thwarted behaviour. This study investigated the relationship between the intensity of the motivation and level of frustration on the one hand and the gakel-call on the other hand. In Experiment 1, the strength of the motivation to feed was varied by thwarting hens in their feeding behaviour in an operant procedure after different durations of food deprivation 0, 8, 23 and 47 h. Trend analysis showed that with increasing hunger state, an increasing number of gakel-calls was given. No effect of treatments on temporal characteristics of the gakel-call was found. In Experiment 2, the level of frustration was varied by reducing or increasing the duration of access to food for food-deprived hens compared to the duration of access during training. It was assumed that a shorter duration of access to food compared to training would elicit frustration, which in turn would affect the performance of behaviours indicative of thwarting. However, we found neither a relation between the number of gakel-calls nor the temporal features of the gakel-call and the duration of access to food. Possibly, the differences between treatments were not large enough to induce differences in frustration level. Also, other factors that might have influenced the motivation are discussed.

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1. Introduction

In laying hens, it has been found that thwarting of feeding behaviour is expressed through a specific vocalisation, the gakel-call (Zimmerman and Koene, 1998). A gakel-call typically consists of a whining, elongated note, followed by a variable number of short notes. Thwarting of feeding behaviour is also known to elicit escape behaviours, an indication of the aversiveness of the situation, and subsequent stereotyped pacing (Duncan and Wood-Gush, 1972a,b). It is, however, not known whether the intensity of thwarting and the strength of the thwarted motivation to feed are reflected in the number of gakel-calls and temporal characteristics of this call.

The first aim of this study is to investigate whether a change in motivation to feed, induced by different durations of food deprivation, affects the gakel-call which is given in response to the thwarting of feeding behaviour.

Besides deprivation, the incentive value of a reward is another determinant of motivation. According to Amsel (1992) frustration is “an aversive state that results from non-reward, reduced reward or delayed reward in the presence of a history of reward”. This aversive state might affect the behaviours reflecting the frustration arousal resulting from the thwarting of feeding behaviour. In this way, the level of frustration might be reflected in the number of gakel-calls and other temporal characteristics of this call. So, a second experiment was done to examine the relation between frustration and the gakel-call.

In conclusion, we investigated the following research questions: is an increasing duration of deprivation as a measure of increasing motivation to feed reflected in an increasing number of gakel-calls during thwarting of feeding behaviour? Does an increased motivation to feed result in a change in mean length and number of elements per gakel-call? Furthermore, is an increasing intensity of frustration expressed in a higher number of gakel-calls and a change in mean length and number of elements per gakel-call?

2. Experiment 1

2.1. Materials and methods

2.1.1. Animals and apparatus

Sixteen non-naive hens, eight Brown Warrens and eight White Leghorns, from a previous experiment (Zimmerman and Koene, 1998) were used. In this earlier experiment, the hens had been conditioned in a classical and operant procedure and after that, had been subjected to both a control and extinction session in a food context. In the present experiment, the hens were housed individually in cages (139 × 50 × 50 cm) containing a nest and a dust box. Food (commercial poultry mash) and water were available ad libitum outside the experimental treatments. The light period fell between 4:00 AM and 8:00 PM.

A Skinnerbox was located in a sound-attenuated room next to the room where the hens were housed. This Skinnerbox was operated through a personal computer standing in the same room.
2.1.2. Experimental procedure

All hens were habituated to the Skinnerbox and the experimental environment during a total of 45 min on 3 consecutive days. Next, the hens were deprived of food for approximately 8 h and subjected to a number of sessions in which the instrumental response of key pecking was shaped. After the shaping sessions, the hens were deprived of food for 23 h and subjected to a series of 15-min conditioning sessions. In such a session, a trial started with an interval of 35 ± 10 s, then a light was lit for 10 s during which a hen could peck a key to make a food magazine come within reach and eat for 5 s. A training session consisted of approximately 20 trials. All hens were subjected to one training session a day. A hen was considered to be trained sufficiently when she pecked the key and fed in all trials during three consecutive sessions.

After training, the 16 hens were subdivided in four groups and all hens in each group were subjected to an extinction session after the following durations of food deprivation: 0 (Dep0), 8 (Dep8), 23 (Dep23) and 47 (Dep47) h. The treatments were assigned to the groups in a balanced way. In an extinction session, the food magazine was presented with a Plexiglas cover. Thus, the hens were thwarted in their feeding behaviour. For every hen, one extinction session was run per day. Between extinction sessions, hens were subjected to a training session in which they received a food reward in each trial to prevent a carry-over effect of one treatment on the subsequent one. The training and extinction sessions were carried out in the afternoon after the hens had laid their egg.

During the extinction sessions, vocalisations were recorded on videotape using an external microphone (Bandridge BMC 660) and a videorecorder (Panasonic AG-6200). From the videotape, the gakel-calls were digitised with the Signal software program (Engineering Design, 1992). From those recorded gakel-calls that contained no background noise the mean duration, the mean number of notes and the mean length of the first four notes were determined with the Signal software program.

2.1.3. Statistical analysis

A repeated measurements analysis was used in the GLM-procedure in the SAS statistical programme (SAS Institute, 1989) with strain, group, and treatment as factors. A square-root transformation on the number of gakel-calls was used to reach normality. A polynomial contrast was made to take into account the quantitative values of the treatments of deprivation. Furthermore, a trend analysis was done to test whether a linear or quadratic relation existed between the duration of deprivation and the number of gakel-calls.

The effect of strain, group, and treatment on mean duration and number of notes per gakel-call were determined in a repeated measures analysis in SAS.

3. Results

No effect of strain or group on the number of gakel-calls was found. There was a significant effect of duration of deprivation ($F_{1,14} = 12.21$, $P < 0.001$) on the number of gakel-calls. In treatment Dep47, the hens gave significantly more gakel-calls than in
treatments Dep8 ($P < 0.05$) and Dep0 ($P < 0.001$) (Fig. 1). Trend analysis revealed a significant positive relationship between the duration of food deprivation and the number of gakel-calls; this concerned both the linear ($F_{1,14} = 26.31, P < 0.001$) and quadratic component ($F_{1,14} = 6.13, P < 0.05$).

A significant effect of treatment ($F_{3,11} = 3.09, P < 0.05$; Fig. 2a) on the mean duration of a gakel-call was found. It was not possible to carry out trend analysis for the mean duration per gakel-call, because of the small number of hens ($N = 11$) that produced gakel-calls of sufficient sound quality. A post-hoc test showed that in treatment Dep0, the mean duration per gakel-call was significantly longer than in treatment Dep47. A significant effect of treatment ($F_{3,11} = 3.34, P < 0.05$; Fig. 2b) was also found on the mean number of notes per gakel-call. A post-hoc test showed that the gakel-calls in treatment Dep23 consisted of more notes than in treatment Dep0.

No significant correlation (Spearman rank correlation) was found between mean length and number of notes per gakel-call.

4. Experiment 2

4.1. Materials and methods

4.1.1. Animals and apparatus

For this experiment, 20 naive ISA Brown hens of 22 weeks of age were used. They were housed individually in the same cages as the hens in Experiment 1. When not stated otherwise, food mash and water were available ad libitum. The light period fell between 4:00 AM and 8:00 PM.
4.1.2. Experimental procedure

All hens were subjected to the same schedule of habituation and training as the hens in Experiment 1 with the following exception that in Experiment 2, the hens were allowed access to a 10-s food reward unlike the 5-s food reward provided in Experiment 1.

After training, the hens were subdivided in four groups. Two hens were left out of the test because they failed to acquire the operant task. All hens of each group were subjected to four conditioning sessions, which differed in the duration of access to food: 0 (Food0), 3 (Food3), 10 (Food10) and 30 s (Food30). The order in which the hens were
subjected to the four sessions differed between groups. In the Food0 treatment, the food magazine came within reach for 10 s but was covered with Plexiglas. The assumption was that treatments Food0 and Food3 would induce frustration, because of the reduction in reward (Amsel, 1992), whereas treatment Food10 would create no frustration compared to the training. Treatment Food30 was assumed to be a bonus.

The hens were subjected to one test session each day. Test sessions were carried out after 2:00 PM after all hens had laid their egg. Between test days, hens were subjected to a training session to prevent an effect of a treatment on the subsequent one.

Vocalisations were recorded on videotape. Gakel-calls were digitised with the Signal® software programme (Engineering Design, 1992). Again, from those recorded gakel-calls of good sound quality, the mean duration and mean number of elements per gakel-call were calculated.

4.1.3. Statistical analysis

For each bird, the mean number of gakel-calls per intertrial interval was calculated in order to correct the mean number of gakel-calls for the different number of trials in the different treatments. Since the test session in all treatments had the same duration and the same intertrial interval and because the duration of the food rewards differed between treatments, this meant that the mean number of trials also differed between treatments.

The procedure used in the Food0 treatment unintentionally introduced an inequality with the other frustration treatment Food3. The mean length of intertrial intervals in both Food0 and Food3 treatment was the same. However, by presenting a covered feeder during 10 s in treatment Food0 the intertrial period, in which the food magazine was inaccessible, was actually extended for 10 s compared to treatment Food3. It was

![Fig. 3. Mean number of intertrial gakel-calls (mean ± SEM) in the treatments Food0, Food3, Food10 and Food30. Different letters indicate significant differences between treatments below the 0.05 level.](image)
Table 1
Mean duration and mean number of notes per gakel-call (mean ± SEM) in the treatments Food0, Food3, Food10 and Food30

<table>
<thead>
<tr>
<th></th>
<th>Food0</th>
<th>Food3</th>
<th>Food10</th>
<th>Food30</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean duration (ms)</td>
<td>849 ± 71</td>
<td>939 ± 64</td>
<td>1020 ± 96</td>
<td>848 ± 45</td>
</tr>
<tr>
<td>Mean number of notes</td>
<td>1.3 ± 0.1</td>
<td>1.4 ± 0.1</td>
<td>1.4 ± 0.1</td>
<td>1.4 ± 0.1</td>
</tr>
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</table>

decided then to compare treatment Food0 with Food10 and, concerning the varying motivation to feed, make the comparison between treatments Food3, Food10, and Food30.

A repeated measurements analysis was used in the GLM-procedure in the SAS® (SAS Institute, 1989) statistical programme with group and treatments Food0, Food3, Food10 and Food30 as factors. Polynomial contrasts were made to take into account the quantitative values of the food rewards. Trend analysis was carried out to investigate the nature of the relation between intensity of frustration and number of gakel-calls.

5. Results

No significant differences between groups concerning the number of gakel-calls were found ($F_{1,14} = 1.37$, $P = 0.29$). When testing the number of gakel-calls in the treatments with the similar procedures (Food0 and Food10) a significant difference was found ($F_{1,14} = 8.40$, $P < 0.05$). On average, more gakel-calls were given between trials in treatment Food0 (mean ± SEM:1.02 ± 0.1) than in treatment Food10 (0.73 ± 0.1). Repeated measurements analysis revealed no statistically significant differences in the mean number of intertrial gakel-calls between treatments Food3 (0.78 ± 0.1), Food10 (0.73 ± 0.1), and Food30 (0.89 ± 0.2). A trend analysis revealed no significant relation between these treatments and number of gakel-calls (Fig. 3).

No statistically significant effects of group or treatment were found on either mean duration or number of elements per gakel-call (Table 1). No statistically significant correlation (Spearman) existed between the mean length and number of notes per gakel-call.

6. General discussion

The results from Experiment 1 indicate that a higher motivation to feed, induced by a longer time of deprivation, is expressed in a higher number of gakel-calls. However, unintentionally, an inequality between treatments might have been introduced which could have affected the number of gakel-calls. The hens were trained on a 23-h deprivation schedule. In treatment Dep47, the hens were put in a Skinnerbox 24 h later than during training. The resulting frustration, caused by the delayed reward (Amsel, 1992), might have influenced the number of gakel-calls given in response to the
 thwarting of feeding behaviour. So, in treatment Dep47, the motivation to feed might have been affected not only by deprivation, but also by frustration induced by delayed reward.

The relation between the intensity of frustration and the number of gakel-calls was examined in Experiment 2. Intensity of frustration was varied by reducing or increasing the duration of access to the food reward compared to training. A higher number of gakel-calls was recorded when the hens had no access to food compared to 10-s access to food. So, non-reward in a situation that previously had been rewarded resulted in a higher number of gakel-calls, as has been found before (Schenk et al., 1983; Zimmerman and Koene, 1998).

We assumed that the intensity of frustration decreased from treatment Food0, Food3, Food10 to Food30 and that intensity of frustration was related to the expression of the thwarting response. So, we expected the hens to give the highest number of gakel-calls in treatment Food0 and to show a linear decrease from Food10 to Food30. We expected treatment Food30 to produce the lowest number of gakel-calls. However, such linear relationship between treatment and the number of gakel-calls was not found. A possible explanation might be that the differences in the intensity of frustration in this experiment were too small to influence the number of gakel-calls. An alternative explanation for the lack of a difference in the number of gakel-calls between treatments Food3, Food10, and Food30 is the phenomenon of positive feedback of feeding (Wiepkema, 1971). This positive feedback of feeding, in the initial phase of a feeding bout, on the motivation to feed may have counteracted the effect of frustration; in the longer food-access treatments, this effect might have been stronger. However, we can probably reject this interpretation because positive feedback of feeding has never been found in the domestic hen, at least not in chicks (Clifton, 1979).

7. General conclusion

A higher motivation to feed, induced by a longer duration of deprivation, is expressed in a higher number of gakel-calls in laying hens. A change in the intensity of frustration was not found to be expressed in the number of gakel-calls. Experiments on the vocal expression of feeding motivation in laying hens should take into account the possible frustrative effect of food deprivation. The phenomenon of positive feedback of feeding is also something that should be taken into account when studying the vocal expression of frustration in adult laying hens.

References


