

THE IMMINENCE OF BEHAVIOURAL CHANGE AND STARTLE RESPONSES OF CHICKS

by

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(With 9 Figures)
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I. INTRODUCTION

The motivational state of an individual is likely to change during a bout of activity, the degree of change varying according to the activity. If that activity serves a function such as maintenance of nutrient level there is a maximum likely duration of its continued occurrence before repletion is reached. As repletion approaches, some of the causal factors necessary for the occurrence of eating must be declining and the probability that an eating bout will end will be increasing. This would not be the reason for the termination of an activity which is subordinate to others, that is to say one whose occurrence is determined entirely by the appearance of gaps between dominant activities. Eating, however, is dominant to at least some other activities, for example in doves (McFARLAND, 1974). Even in the case of a subordinate activity, or an activity dependent upon causal factors which do not change during the course of a bout, motivational state is still changing during a bout because other causal factors will be changing. Hence, if a bout of behaviour is interrupted, the probability that any particular behaviour will replace the ongoing behaviour may change as the bout progresses.

The previous paper (FORRESTER & BROOM, 1980) describes the startle responses of 6-day-old chicks when their surroundings are changed by the illumination of a torch-bulb on the wall of the home pen. The responses differ according to which activity is occurring, or has been occurring, during the 5 seconds prior to that change. The chicks compared in the experiments reported here were all engaged in one of two activities

but, at the time of testing, different amounts of time had elapsed since the beginning of the bout. The responsiveness of 6-day-old chicks which had just started feeding was compared with that of chicks for which the termination of the feeding bout was imminent. Similar experiments were carried out on chicks which were preening at 2, 4, and 6 days of age.

When describing a collection of samples of behaviour it is most useful to express the durations of the behaviours, or of the intervals between them, logarithmically (NELSON, 1964, SCHLEIDT, 1965). This has been done in this study in the determination of the minimum inter-bout interval by means of a log survivor curve (NELSON, 1964; WIEPKEMA, 1968; DELIUS, 1969; van RHIJN, 1977). The method is described in detail by SLATER (1974, 1975). This is not the only way to assess bout-length (MACHLIS, 1977) but was used as it provides a convenient means of classifying points in bouts into those where the bout is likely to continue, *e.g.*, 2-3 seconds after the start, and those where there is a high probability of imminent transition to another activity.

II. METHODS

The methods were similar to those described in the previous paper (FORRESTER & BROOM, *l.c.*) with the following exceptions. The eggs were incubated throughout development in our laboratory. The chicks were observed for 5 minutes, before startling by torch-bulb illumination and for a further 10 minutes whilst the torch-bulb remained illuminated. The 3W torch-bulb was fixed to the rear wall of the pen when startling chicks which were feeding. This position of the bulb was then similar, in relation to the chick, to that at the front of the pen when the chicks were preening. Other experiments indicated, however, that the position of bulb had no effect on responsiveness (CULSHAW, 1977). The statistical tests are 2-tailed Mann-Whitney U tests.

Experiment 1. In order to determine bout-length, 15 undisturbed chicks were watched for several hours on days 2, 4 and 6 and their behaviour recorded.

Experiment 2. Chicks aged 6 days were watched by a silent observer through a one-way screen and their behaviour was recorded until feeding occurred. The observer continued to record behaviour in detail but moved a switch after feeding had continued for 2 seconds. For 15 chicks this resulted in immediate illumination of the bulb but for 15 others the bulb was illuminated after a delay, determined from the bout-length measurements, so as to coincide with the predicted end of the bout. For these latter chicks, recording was terminated if feeding stopped before bulb illumination. The decision as to whether to illuminate the bulb at the beginning or the end of a bout was always taken prior to any recording. Each chick was tested once only, either at the beginning or at the end of a bout. None of the chicks had seen any illumination change since being placed in the pen from the darkened incubator.

Experiment 3. The methods were the same as in Experiment 2 except that the chicks were preening the wing. 15 chicks were startled at the beginning of the bout and 15 at the predicted end of the bout on day 2, day 4 or day 6. The lengths of preening bouts were calculated separately for the three ages.

III. RESULTS

1. Determination of bout-lengths.

Since the aim of these experiments was to compare the effects of interrupting chick behaviour at an early or a late stage in a bout of feeding, or of preening, it was necessary to determine the mean bout-length for these activities. The sequences of pecks during feeding are separated by brief gaps. In order to measure bout-length we wished to distinguish such gaps from the intervals between bouts of feeding. There are sometimes short intervals between bouts which are indistinguishable from long gaps within bouts. When analysing undisturbed behaviour it was necessary to establish some criterion to be used in order to decide that a bout had ended. This was done by plotting log survivor functions, of gap or interval length for feeding and for preening. In these log survivor functions, the log of the frequency of gaps of a particular length is plotted in a negatively cumulative fashion against the gap-length. If the lengths of gaps were distributed randomly then the function would have constant slope, for the slope is proportional to the probability of occurrence of any particular gap-length. If the distribution of events is clustered, the log survivor curve will show a steep initial drop. If the probability of a further event, after a cluster of events, is low and does not change with time then the function will have a shallow unchanging slope after the initial steep drop. The discontinuity point between the steep drop and the shallow, unchanging slope gives a useful indication of the length of the shortest interval between bouts.

Since it was not possible to obtain enough data from each chick, during one day of age, to determine its feeding and preening bout-length, data were collected for 15 undisturbed chicks and used in Experiments 2 and 3. All gaps between continuous feeding movements were measured for each of the chicks at 6 days of age. In total, 377 gaps were measured and the log survivor function is plotted in Fig. 1. The first and sharpest discontinuity is at 10 seconds, after which there is a constant, lower probability over at least four points. A sequence of feeding not followed within 10 seconds by further feeding was called a bout and the lengths of all bouts on the same records of behaviour were measured. For 49 bouts of feeding the mean bout-length was 83.8 seconds. Our criterion for a point at which the ending of the bout, and change to another activity, was imminent was therefore established as 84 seconds. Bout termination is much more likely at this stage in the bout than after 2 seconds.

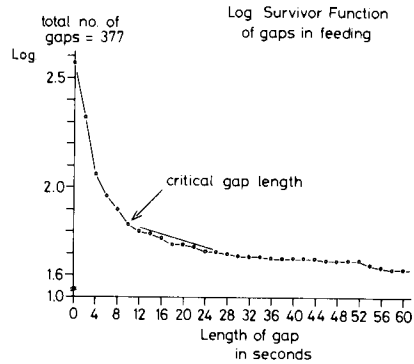


Fig. 1. For feeding, the logarithm of the total number of gaps remaining after successive subtraction, is plotted against the length of gap in seconds. The line is drawn to emphasise the position of the shallow unchanging slope after the initial steep drop. The discontinuity point at the beginning of this slope is used as the critical gap-length in determining when a bout has ended. (see text for further explanation.)

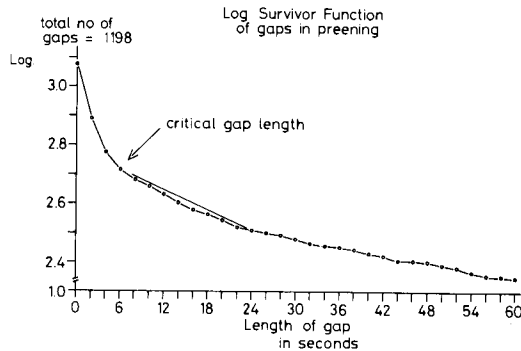


Fig. 2. Legend as Fig. 1. but for preening.

Similar data on gaps between preening movements were collected for 15 chicks on days 2, 3, 4, 5, and 6. The distribution and mean length of gaps did not vary with age (CULSHAW & BROOM, in prep; CULSHAW, 1977) so all 1198 gaps were used when compiling Fig. 2. The steep initial slope in the log survivor function persists until 6 seconds, after which there is a constant slope until another, much smaller, discontinuity at 22 seconds. Using a critical gap-length of 6 seconds, the mean lengths of bouts were 11.9 seconds at 6 days ($n = 125$), 10.2 sec at 4 days ($n = 89$) and 8.4 seconds at 2 days ($n = 108$).

2. Interruption at beginning or end feeding bouts (6-days-old).

Feeding is an activity which is inhibited when a chick is startled (BROOM, 1969). As expected, therefore, it occurred rarely during the first two minutes after the illumination of the torch-bulb in the chick's home pen. The frequency of feeding pecks at this time was less than 5% of that which undisturbed chicks would have shown during a comparable period after starting a feeding bout (CULSHAW & BROOM, in prep). Chicks startled at the end of a feeding bout (84 seconds after the start) did not resume feeding during the 10 minutes that the bulb was illuminated. Those startled at the beginning of a bout (2 seconds after the start), however, were more likely to feed at a low level during minutes 3-10 after bulb illumination (Fig. 3).

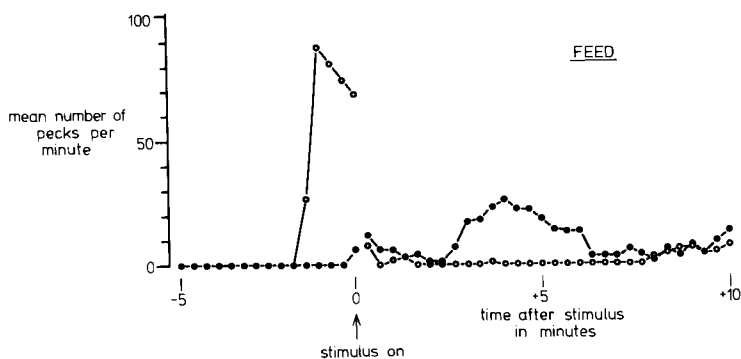


Fig. 3. The mean number of pecks at food per min. by 15 6-day-old chicks, is plotted for successive 20 sec. periods during 5 min. whilst undisturbed and during the 10 min. after the illumination of the bulb on the wall of the pen. Key: ● stimulus on (bulb illumination) at the beginning of bout of feeding, ○ stimulus on at end of bout of feeding.

The most obvious aspects of the startle response of young chicks after bulb illumination are a period of reduced activity, associated with fixating the bulb, followed by a period of increased activity which may be associated with loud peep calls and jumping as well as fixating (BROOM, 1966, 1969; FORRESTER & BROOM, *l.c.*). In this experiment the first type of response was shown by all birds but few showed much increase in locomotor activity or loud calling. As shown in Figs 4 and 5, the proportion of time fixating the bulb or immobile during the first 5 minutes after bulb illumination was clearly greater amongst chicks startled at the end of the bout of feeding than amongst those startled at the beginning. Undisturbed chicks which have started to feed are rarely recorded fixating the bulb or immobile but occasionally crouch and often walk or peck at non-food objects during the next 5 minutes. (FORRESTER & BROOM, *l.c.*;

CULSHAW & BROOM, in prep). In Experiment 2, chicks started at the beginning of a feeding bout sometimes crouched and closed their eyes during minutes 5-10 after bulb illumination. They were slightly more likely to peep and less likely to walk or peck than chicks startled at the end of a bout. None of these differences was large. The area within 5 cm. of the bulb was avoided by those startled at the end of the bout (0-60 seconds after illumination $p < 0.01$, 0-5 minutes and 5-10 minutes $p < 0.05$). Hence these chicks also avoided the adjacent food container.

3. Interruption at the beginning or end of preening bouts (2, 4, or 6-days-old).

Preening the wing, like feeding, is an activity which is inhibited when a chick is startled (BROOM, 1969). Undisturbed chicks are likely to preen again within 5 minutes (FORRESTER & BROOM, *l.c.*; CULSHAW & BROOM, in

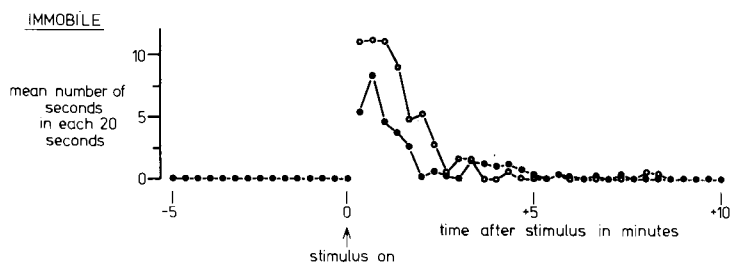


Fig. 4. The mean number of seconds that the 15 6-day-old chicks fixated the bulb during each successive 20 second period is plotted for 5 min. whilst undisturbed and for 10 min. after the illumination of the bulb. Key (as Fig. 3): ●-beginning, ○-end. First 5 min. after bulb illumination beginning v. end $p < 0.05$.

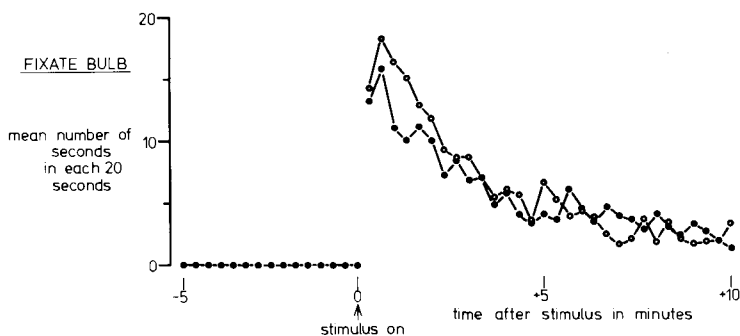


Fig. 5. The mean number of seconds that 15 6-day-old chicks were immobile during each successive 20 sec. period is plotted for 5 min. whilst undisturbed and for 10 min. after the illumination of the bulb. Key (as Fig. 3): ●-beginning, ○-end. First 5 min. after bulb illumination beginning v. end — $p < 0.05$.

prep) but at each of the three ages, little preening occurred amongst chicks startled at the end of a preening bout (Fig. 6). Whereas chicks startled at the end of a bout ceased preening almost immediately, those startled at the beginning of a preening bout often continued to preen for some seconds so that their preening frequency was considerably higher during the first minute after bulb illumination.

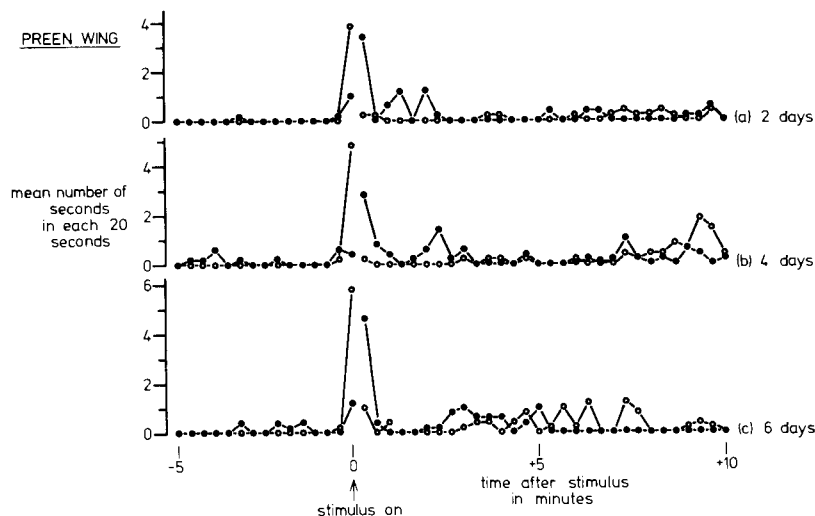


Fig. 6. The mean number of seconds that the 15 2, 4, and 6-day-old chicks preened their wings during each successive 20 sec. period is plotted for 5 min. whilst undisturbed and for 10 min. after the illumination of the bulb on the wall of the pen. Key: ●-stimulus (bulb illumination) at beginning of bout of preening the wing, ○-stimulus on at end of bout of preening. First min. after bulb-illumination, beginning v. end, 2 days $p < 0.01$, 4 days $p < 0.001$, 6 days $p < 0.01$.

Chicks which are preening are very seldom recorded during the next 10 minutes fixating the bulb, immobile, or peeping. They do not walk much in that time but they do sometimes feed or crouch (CULSHAW & BROOM, in prep). Chicks startled at the end of a bout of preening fixated the bulb for longer at each age (Fig. 7) and were immobile for longer at 4 and 6 days (Fig. 8). There were no large differences, related to the timing of bout interruption, for other measures of behaviour. Walking and jumping were slightly more frequent, 5-10 minutes after bulb illumination, amongst 2 and 4-day chicks startled at the end of the bout (Fig. 9). Some of these chicks showed stereotyped locomotor movement from side to side at the front of the cage. Activities which were more likely amongst chicks

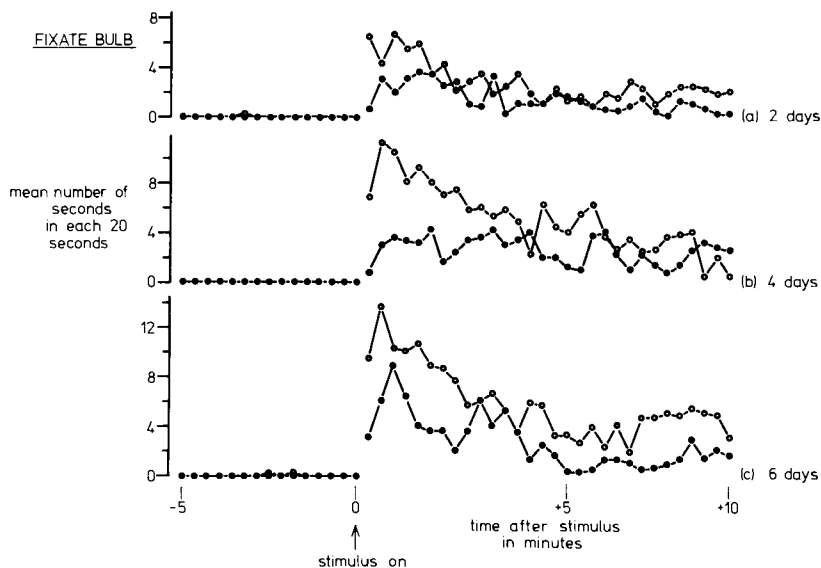


Fig. 7. The mean number of seconds that the 15 2, 4, and 6-day-old chicks fixated the bulb during each successive 20 sec. period is plotted for 5 min. whilst undisturbed and for 10 min. after the illumination of the bulb. Key (as Fig. 6): ●-beginning, ○-end. First min. after bulb illumination, beginning v. end, 2 days $p < 0.01$, 4 days $p < 0.01$, 6 days $p < 0.01$.

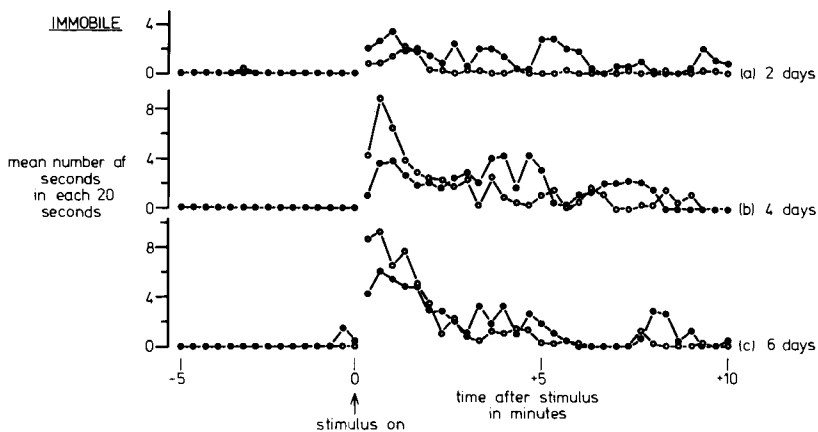


Fig. 8. The mean number of seconds that the 15 2, 4 and 6-day-old chicks were immobile during each successive 20 sec. period is plotted for 5 min. whilst undisturbed and for 10 min. after the illumination of the bulb. Key (as Fig. 6): ●-beginning, ○-end. First min. after bulb illumination, beginning v. end, 4 days $p < 0.01$.

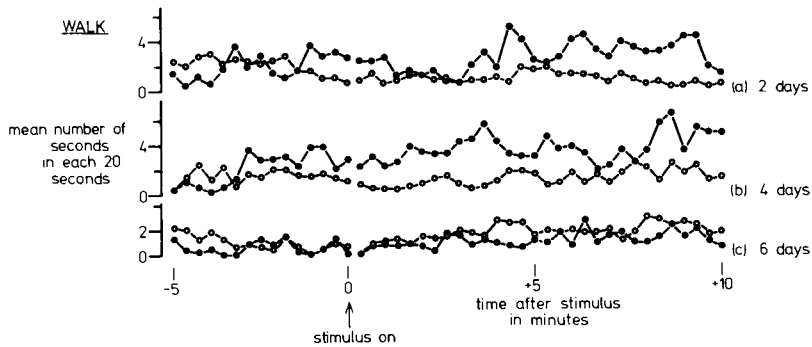


Fig. 9. The mean number of seconds that the 15 2, 4 and 6-day-old chicks walked during each successive 20 sec. period is plotted for 5 min. whilst undisturbed and for 10 min. after the illumination of the bulb. Key (as Fig. 6): ●-beginning, ○-end.

started at the beginning of the bout included crouching (day 2, first 60 seconds $p < 0.05$), preening and eyes shut.

IV. DISCUSSION

The general result of these experiments is that chicks startled at the end of a bout of feeding or preening the wing show a greater startle response and are less likely to continue with undisturbed behaviour than are chicks startled at the beginning of a bout of feeding or preening. Two activities which are characteristic of the response and rare in disturbed chicks, fixating the bulb and immobile with the eyes open, are clearly more frequent amongst chicks startled at the end of a bout. The other component of the chick's startle response involves increased activity and sometimes peeping. It is less frequent in these experimental conditions and shows no clear difference according to the point of behaviour interruption. This fact is further evidence for the idea that there are two components of the response, immobility and escape (BROOM, 1969).

The differences between the startle responses shown by chicks which are feeding, preening *etc.*, are described by FORRESTER & BROOM (*loc. cit.*). In our experiments feeding and preening were suppressed during the 10 minutes after bulb illumination but feeding did occur if chicks were startled at the beginning of a feeding bout and preening did continue briefly if chicks were startled at the beginning of a preening bout. Chicks startled at the end of a bout were immobile and fixated the bulb at first, then started walking and pecking at non-food objects if they had been pecking previously at food. If they had previously been preening they did

not peck but walked and showed stereotyped movements similar to the pacing movements of adult fowl which have been "thwarted" (DUNCAN & WOOD-GUSH, 1972). These are qualitative differences in response which vary according to ongoing behaviour and the timing of the interruption during the bout. The differences in fixating the bulb and immobility are principally quantitative but there are some differences in time-course. Chicks startled at the end of a bout of preening are immobile for much of the first minute after bulb illumination, but for little time after that. This pattern was not shown by 2-day-old chicks. All chicks startled at the beginning, rather than at the end, of a bout of preening showed less immobility but often became immobile some time after the bulb illumination.

In these experiments, as in those of FORRESTER & BROOM (*l.c.*), the behaviour sequence of the chicks is interrupted by a change in the chick's surroundings which evokes a clear but not an extreme response. A drastic environmental change would be likely to initiate extreme changes in motivational state so that the response would depend little upon the previous state. These results do provide, however, clear evidence that the motivational state changes during the course of an activity.

The comparisons between interruption at beginning and end of a bout were similar for chicks of each age. The younger chicks showed less marked responses, as has been reported previously (BROOM, 1969), and there were some differences in the pattern of their response but the chicks startled at the end of the bout showed a greater as well as a different response at 2, 4 and 6 days. In addition to the difference in immobility mentioned above, a difference in the time-course of the response was the more prolonged suppression of walking after bulb illumination in 6-day-old chicks than in those aged 2 or 4 days.

Variations in responsiveness are commonly explained in terms of activation, motivation and attention. Our results demonstrate that attempts to explain all changes in behaviour on the basis of an activation model such as that of DUFFY (1962) are simplistic. Feeding is usually placed high in any activation continuum (MORUZZI, 1969) so it is likely that the activation level would fall during a feeding bout if it changes at all. Preening is often followed by crouching and sleeping (CULSHAW & BROOM, in prep.) and these are generally considered to be low activation behaviours, so activation should often decline during a preening bout. Responses should be greatest when activation is high so simple activation models would predict lower responsiveness at the end of a bout of feeding or preening than at the beginning. The reverse was found in these ex-

periments. Hence, within the time scale and activity range of this study, there is little support for an activation model.

In explaining our results we consider that one of the ways in which motivational systems operate is by modifying attentional variables. A useful way of describing motivational state is as a point in causal factor space (SIBLY & McFARLAND, 1974). At the beginning of a bout of activity, the causal factors necessary for the occurrence of that activity are at a relatively high level. They may increase during the initial part of an activity because of a positive feedback mechanism. Adult terns or gulls which have started to preen are more likely to stop preening and change to another activity in the very early part of a preening bout than in a bout which has lasted for a third of the mean bout-length (VAN IERSEL & BOL, 1958; VAN RHIJN, 1977). As the bout progresses, levels of some relevant causal factors are likely to decline, partly as a consequence of the activity. At the same time, causal factors necessary for the occurrence of other activities may be increasing. The bout of activity would normally end, either when causal factors necessary for a second behaviour increased to a level which resulted in that behaviour being shown (competition or inhibition during time sharing) or when the second behaviour was disinhibited (McFARLAND, 1974; McFARLAND & SIBLY, 1975).

We postulate that the change in levels of causal factors during the latter stages of a bout initiates an attentional change. Since the animal is carrying out the same type of activity throughout a feeding or preening bout it is likely that some attentional variables remain the same throughout the bout. For example, the orientation of the sensory receptors and the data-processing procedures relevant to this activity may be similar at different stages of the bout. The changes in attentional variables as the end of a bout approaches may include an increased ability to attend to sensory input which is not directly related to the ongoing activity. It is likely that distractibility falls in the first few seconds of a bout of behaviour as the "lock on" mechanism (FORRESTER & BROOM, *l.c.*) comes into effect. The reverse change occurs towards the end of the bout. Such a change in distractibility could explain our finding that responsiveness is greater nearer to the end of a bout than 2 seconds after the beginning. DELIUS (1970) suggested that the rate and level of information processing increases as a point of transition approaches. Perhaps such a mechanism facilitates the changeover from one activity to another and increases the probability that it will occur at the optimum time. Animals whose behaviour is interrupted near the end of a bout are more prepared for response to any sort of change in input and less constrained, than they

were at the beginning of the bout, by the effect of high levels of the causal factors necessary for the ongoing behaviour. Further experiments using these techniques should provide greater insight into the control of behavioural sequences.

SUMMARY

The responses of chicks startled near the end of a bout of feeding or preening were different from, and measurably greater than, those of chicks startled at the beginning of bouts of these activities. This result provides evidence about changes in motivational state during a bout of activity. It is proposed that causal factors, which are changing during the bout, may initiate an attentional change as the point of transition to another activity approaches. Distractibility and information-processing rate may be increased near the end of an activity because the individual can then attend to a greater variety of inputs than it could earlier in the bout. This would maximise the efficiency of the ensuing behavioural change.

In order to carry out these experiments, bouts of feeding and preening were measured using a criterion based on log survivor curves for inter-event gap-lengths. The effects on the response of the time during a bout at which interruption occurs, were shown by chicks of 2, 4 and 6 days of age. The method used in these experiments, the interruption of activities at previously defined instants whilst observing behaviour in detail, affords opportunities for studying the nature of behavioural sequences and their control.

REFERENCES

- BROOM, D. M. (1966). Changes with age in the domestic chick's reactions to novelty. — *Anim. Behav.* 14, p. 586-587.
- (1969). Reactions of chicks to visual changes during the first ten days after hatching. — *Anim. Behav.* 17, p. 307-315.
- CULSHAW, A. D. (1977). The development of responsiveness in domestic chicks. — Ph. D. thesis, University of Reading.
- DELIUS, J. D. (1969). A stochastic analysis of the maintenance behaviour of skylarks. — *Behaviour* 33, p. 137-178.
- (1970). Irrelevant behaviour, information processing and arousal homeostasis. — *Psychol. Forsch.* 33, p. 165-188.
- DUFFY, E. (1962). *Activation and behaviour*. — Wiley, New York.
- DUNCAN, I. J. H. & WOOD-GUSH, D. G. M. (1972). Thwarting of feeding behaviour in the domestic fowl. — *Anim. Behav.* 20, p. 444-451.
- FORRESTER, R. C. & BROOM, D. M. (1980). Ongoing behaviour and startle responses of chicks. — *Behaviour* 73, p. 51-63.
- IERSEL, J. J. A. van & BOL, A. C. A. (1958). Preening of two tern species. A study of displacement activities. — *Behaviour* 13, p. 1-88.
- MACHLIS, L. (1977). An analysis of the temporal patterning of pecking in chicks. — *Behaviour* 63, p. 1-70.
- McFARLAND, D. J. (1974). Time sharing as a behavioural phenomenon. — *Adv. Study Behav.* 5, p. 201-225.
- & SIBLY, R. M. (1975). The behavioural final common path. — *Phil. Trans. R. Soc. Ser. B.* 270, p. 265-293.
- MORUZZI, G. (1969). Sleep and instinctive behaviour. — *Archs ital. Biol.* 197, p. 175-216.
- NELSON, K. (1964). The temporal patterning of courtship behaviour in the glandulocaudine fishes (Ostariophysi, Characidae). — *Behaviour* 24, p. 90-145.

- RHIJN, J. G. van (1977). The patterning of preening and other comfort behaviour in a herring gull. — *Behaviour* 63, p. 71-109.
- SCHLEIDT, W. M. (1965). Gaussian interval distributions in spontaneously occurring innate behaviour. — *Nature Lond.* 206, p. 1061-1062.
- SIBLY, R. M. & MCFARLAND, D. J. (1974). A state-space approach to motivation. — In: *Motivational control systems analysis*. ed. MCFARLAND, D. J., Academic Press, London.
- SLATER, P. J. B. (1974). Bouts and gaps in the behaviour of zebra finches, with special reference to preening. — *Rev. Comp. Animal* 8, p. 47-61.
- (1975). Temporal patterning and the causation of bird behaviour. — In: *Neural and Endocrine Aspects of Behaviour in Birds*. (WRIGHT, P., CARYL, P. G. & VOWLES, D. M. eds). Elsevier, Amsterdam, p. 11-33.
- WIEPKEMA, P. R. (1971). Positive feedbacks at work during feeding. — *Behaviour* 39, 266-273.

ZUSAMMENFASSUNG

Die Reaktionen von Küken, die gegen Ende eines Fress- oder Putz-‘bouts’ aufgestört worden waren, waren anders und messbar grösser als diejenigen von Küken, die zu Beginn der Anfälle dieser Aktivitäten gestört worden waren. Dieses Ergebnis gibt einen Hinweis auf Änderungen des motivationellen Stadiums während eines Aktivitäts-‘bout’. Es wird vorgeschlagen, dass kausale Faktoren, die sich während des Ablaufens der Aktivität ändern, einen Umschwung in der Aufmerksamkeit bewirken, wenn sich der Zeitpunkt des Übertritts zu einer anderen Aktivität nähert. Die Ablenkbarkeit und die Geschwindigkeit der Informationsverarbeitung kann am Ende einer Aktivität erhöht sein, da das Individuum dann auf eine grössere Vielfalt von Inputs achtgeben kann als es zu einem früheren Zeitpunkt konnte. Dies würde die Wirksamkeit der darauffolgenden Verhaltensänderung maximieren.

Um diese Experimente durchführen zu können, wurden Fress- und Putz-‘bouts’ jede für sich gemessen, wobei Kriterien für die Längen dieser Aktivitäten verwendet wurden, die sich auf ‘log survivor’-Kurven der Intervalle zwischen dem Auftreten dieser Verhaltensweisen beziehen. Die unterschiedlichen Reaktionen, gemäss des Zeitpunktes der Unterbrechung, wurden von 2, 4 und 6 Tage alten Küken gezeigt. Die Methode, die in diesen Experimenten angewandt wurde, nämlich das Unterbrechen von Aktivitäten zu vorher definierten Zeitpunkten, während das Verhalten im Detail beobachtet wurde, bietet Möglichkeiten an, die Natur von Verhaltenssequenzen und deren Kontrolle zu studieren.