

## ONGOING BEHAVIOUR AND STARTLE RESPONSES OF CHICKS

by

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(With 11 Figures)

(Acc. 5-VIII-1979)

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### 1. INTRODUCTION

A description of the behaviour of an animal provides information about the motivational state of the animal at that moment, although some limitations of such inference have been pointed out by McFARLAND & SIBLY (1972) and SIBLY & McFARLAND (1974). Additional information is provided by describing the sequence of behavioural events before or after that time, whether or not experimental constraints have been imposed on the animal. The techniques used in many studies of motivation neglect to take into account short-term variations in motivational state and assess responses, and hence state, by measurement of a very narrow range of behaviours. Motivational state is often manipulated by restricting the possible activities of the animal, *e.g.* by deprivation. When the restriction is lifted, the state is usually assessed by measuring the frequency, duration or intensity of occurrence of one or two behaviours.

In our experiments there is no deprivation or other restriction, except for confinement singly in a cage. The technique which we have used has been to interrupt behaviour sequences by a change, in its surroundings, which the animal can readily detect. The ensuing modification of the animal's behaviour is of the kind which is often referred to as a startle response. This response involves an initial scanning and orientation followed by an increase in the frequency of some activities, such as those associated with escape or immobility, and a decrease in the frequency of other activities, such as those concerned with maintenance. In order to assess the effects of interrupting the behaviour sequence, it is necessary to record many measures of behaviour. We compare in detail the behaviour

after the change with that of similar animals whose surroundings are not changed. This provides a useful estimate of the response.

The startle response must depend on the motivational state at the time that behaviour is interrupted. It may also be delayed or affected by the extent of the physical difference between the ongoing and succeeding activities (FORRESTER, 1979) or by the relative difficulty of changing away from the existing attention channel (ANDREW, 1976). If behaviour does partially reflect motivational state then responsiveness will often differ according to the ongoing behaviour. FENTRESS (1968a & b) demonstrated that voles, *Clethrionomys britannicus* and *Microtus agrestis*, respond in a different way, to an object passed overhead, according to whether they were walking or grooming at that time. Our experiments extend those of FENTRESS but with a different animal, the domestic chick, and with studies of animals disturbed when carrying out one of ten different activities. The experimental procedure and the responses reported are similar to those described by BROOM (1966, 1968, 1969a, b).

## 2. METHODS

The subjects in these experiments were White Leghorn/Light Sussex hybrid chicks (*Gallus gallus domesticus*), which were 6 days old when observed. On the 17th day of incubation they were transferred from a commercial hatchery, Thornbers of Twyford or Ross of Andover, to a darkened incubator in the laboratory, where they hatched 4 days later. The chicks were removed to their individual home cages (Fig. 1) 4 to 12 hours after hatching.

The under-floor heating of the cages, which were arranged side-by-side, provided an internal temperature gradient from the front to the rear of 30°C to 26°C. An air-

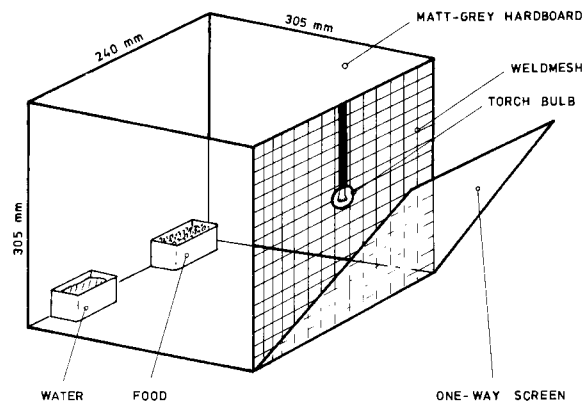


Fig. 1. An individual chick's cage. Such cages were arranged in a row of twelve and were heated by a hot water pipe situated under the floor at the front of the cages. Food and water were replenished automatically from behind the rear wall.

conditioned, sound-proofed room housed only these cages, which were shrouded by dense black cloth. Lighting was continuous from an overhead fluorescent tube. The experimenter, always unobservable to the chicks, viewed them through a one-way screen. The food and water were ad-lib, being automatically replenished from reservoirs behind the rear wall.

Chicks were watched and their activities recorded using a keyboard and a remotely-located Edgcumbe-Peebles event recorder. In the initial series of studies (controls), the undisturbed behaviour of a chick was recorded in detail, for at least 60 seconds following the occurrence of one of ten activities. For the subsequent series (experimentals), a 60 second illumination of the bulb on the front wall of the home cage was initiated, by the experimenter, during one of the same activities. The illumination of the 3 Watt bulb raised the luminance at the centre of the cage, reflected from the front, from 45 to 75 lux. The ten ongoing activities were: immobility — no movements other than breathing; crouching — abdomen in contact with the floor; preening — moving bill in contact with body surface; pecking the floor or walls; walking — one or more steps in any direction; drinking — bill in contact with the water and subsequent swallowing; feeding — pecking at the food; monocular fixation — directing one eye towards the bulb whilst the head is held still; loitering — standing, not engaged in any of the above activities; pausing — loitering which had persisted for less than 5 seconds. Some behaviours which were recorded occurred rarely in undisturbed chicks and were not used as categories of the ongoing activities. These were: jumping — both feet off the floor; peeping — a loud call, characteristic of 'distress' (COLLIAS & JOOS, 1953; ANDREW, 1964); binocular fixation — directing both eyes towards the bulb whilst the head is held still.

During analysis of the behaviour records, chicks were classified as, for example, preening if they had been preening during the 5 seconds prior to an experimental or control period. The behaviour of a total of 192 chicks was recorded. The numbers in any ongoing behaviour category are quoted in the results Figures. These numbers vary slightly because of occasional event-recorder malfunction and because of the limitations described in the results for the latency of response measure. Statistical tests used were the Fisher-exact test (Figs 3 to 9) and the Mann-Whitney test (Figs 2, 10 and 11). All probability figures quoted are two-tailed.

### 3. RESULTS

The typical response of a 6 day old chick to the illumination of a bulb was as previously described by BROOM (1966, 1969a). In the current experiments most, but not all, responses began with a brief spasm of muscular contraction and orientation toward the bulb. Periods of immobility and crouching and subsequent periods of jumping and peeping followed and were partially overlapped by bouts of fixation of the bulb. The probability of particular behaviours occurring during the illumination period varied in a regular way according to the ongoing activities. As a consequence of the results described below, these have been arranged as the series of increasing responsiveness used in the figures.

A practicable definition of the start of the response was the first occurrence of whichever of jumping, peeping, immobility, crouching or fixation of the bulb had not also occurred during the pre-illumination 5 seconds. As a further check that a resumption of undisturbed behaviour

was not scored as a response, the first occurrence of immobility was not included as a response if the bird had been crouching previously. The latency of response differed according to the ongoing behaviour (Fig. 2). There were many reliable differences in response latencies, *e.g.* between birds which had been crouching or feeding and even between those which had been preening or pecking.

The probability of jumping, peeping and fixating the bulb, monocularly or binocularly, was increased by the illumination of the bulb (Figs 3, 4, 5 & 6). The ongoing activities may be grouped to represent the phase of

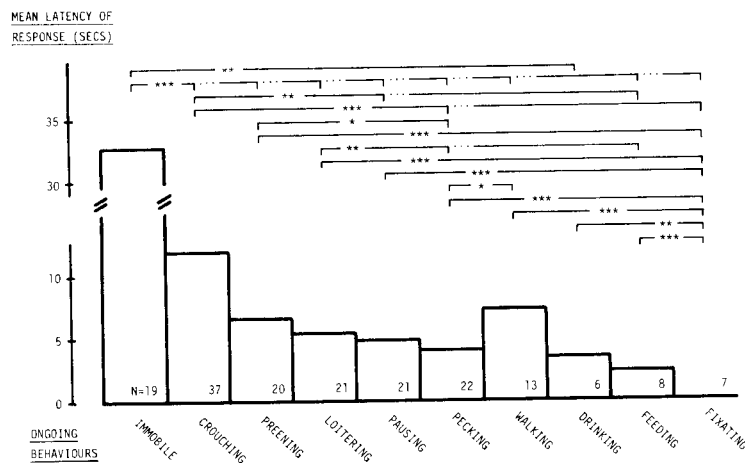


Fig. 2. The mean latency of response (see text) after bulb illumination for each of ten ongoing activities. For comparisons between chicks showing the different ongoing behaviours: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

behaviour in which they occur, viz. 'inactive'; immobile, crouching, preening, loitering; and 'active'; pausing, pecking, walking, drinking, feeding, fixating. For example, inactive undisturbed birds are more likely to be crouched during the subsequent minute than are active birds (Fig. 7, control data,  $p < 0.001$ ). Those which were preening are more likely to crouch than those which were feeding ( $p < 0.01$ ). On the other hand, inactive undisturbed birds are less likely to peck or feed during the subsequent minute (Fig. 9, control data,  $p < 0.001$ , feeding: 4% of birds after inactive, 30% of birds after active,  $p < 0.001$ ). In the experimental periods, the previously active birds had a higher probability than those which had been inactive of jumping, peeping and fixating, but a lower probability of crouching. The active birds, however, did show a signifi-

cant increase from the control level in the probability of crouching (Fig. 7). Less than 10% of the birds showed immobility during the control periods, except for those which had been crouched or immobile. More than 75% of the birds, however, in all ongoing behaviour categories other than fixating, were recorded as showing some immobility during the experimental period. Preening was slightly more likely in inactive birds, particularly for those which had been preening (Fig. 8). Preening after illumination of the bulb was an overshoot of the previous activities, since only one bird stopped preening and then resumed. Feeding was absent from the illumination period, except for a few birds which had been feeding previously, but pecking at other than food did occur and was more likely in active birds (Fig. 9). This pecking was not directed at the illuminated bulb.

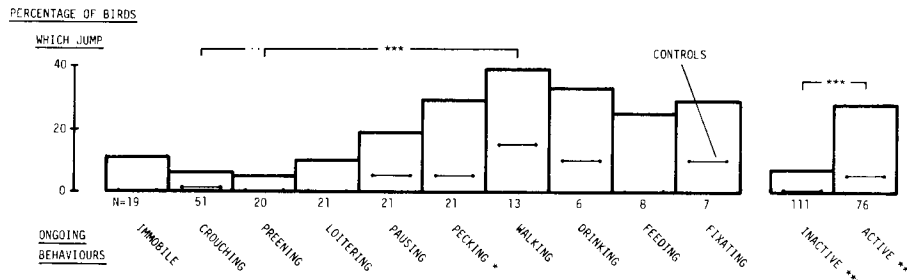


Fig. 3. The percentage of birds which jumped during the 1 min. bulb illumination period is shown for each of ten ongoing behaviours. Four behaviours, immobile to loitering, are summarised as "inactive" and the remaining six, are summarised as "active". In addition to the comparisons between chicks showing the different ongoing behaviours (as in Fig. 2), comparisons between control and experimental chicks were made (probability values indicated after the name of the ongoing behaviour).

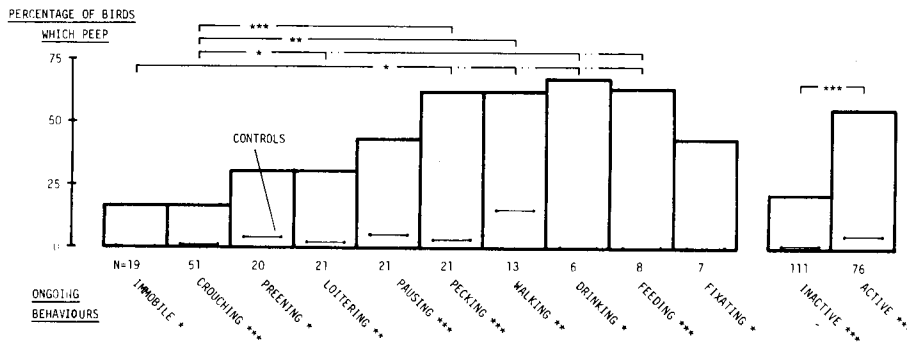


Fig. 4. Legend as for Fig. 3, but for peeping.

The durations of particular response behaviours also varied according to the preceding activities. The percentage of the 60 second illumination period spent crouching was higher for the previously inactive birds (Fig. 10), as to a lesser extent was the percentage spent immobile (Fig. 11). Chicks which had been engaged in any previous activity except immobility spent a mean of 33 to 42 seconds fixating the bulb during the minute of its illumination. The greater latency of response amongst previously immobile chicks accounted for the reduced duration of their fixation.

Chicks which had been immobile showed a high likelihood of crouching and further immobility in the control period, but little

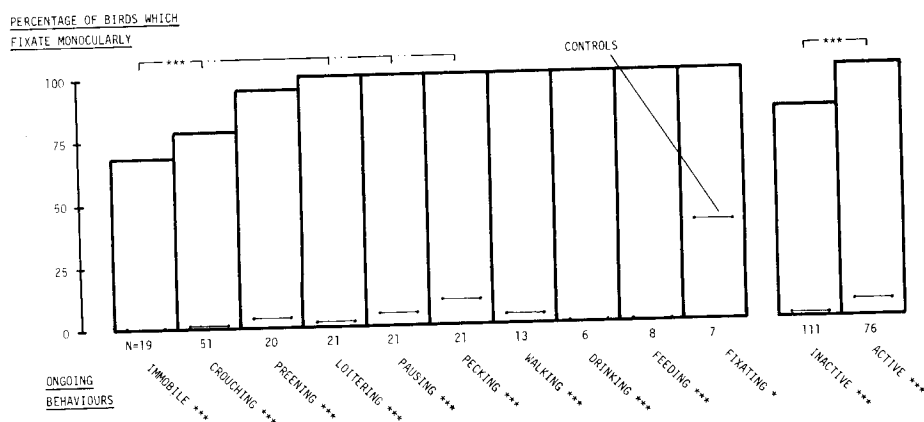


Fig. 5. Legend as for Fig. 3, but for monocular fixation.

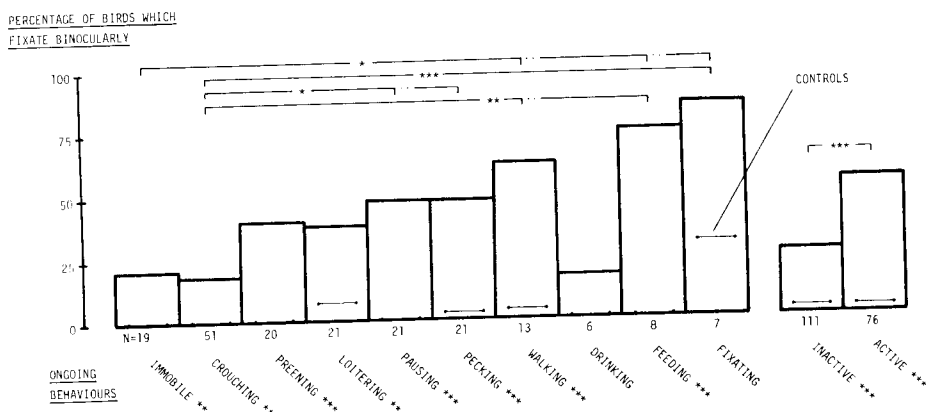


Fig. 6. Legend as for Fig. 3, but for binocular fixation.

likelihood of other behaviour. In the experimental period, these birds were a little more likely to fixate, jump and peep. Such differences between the experimental and control periods can be regarded as overt responses. Responses of previously crouched birds were essentially similar to those of birds which had been immobile, except that the time taken to respond was less and fixation was more likely. If preening when disturbed, the response was a reduction in preening and pecking, compared with control birds, and an increase in immobility, fixating and peeping. If loitering or pausing, the birds' responses resembled those of birds which had been preening but there were indications of an increase

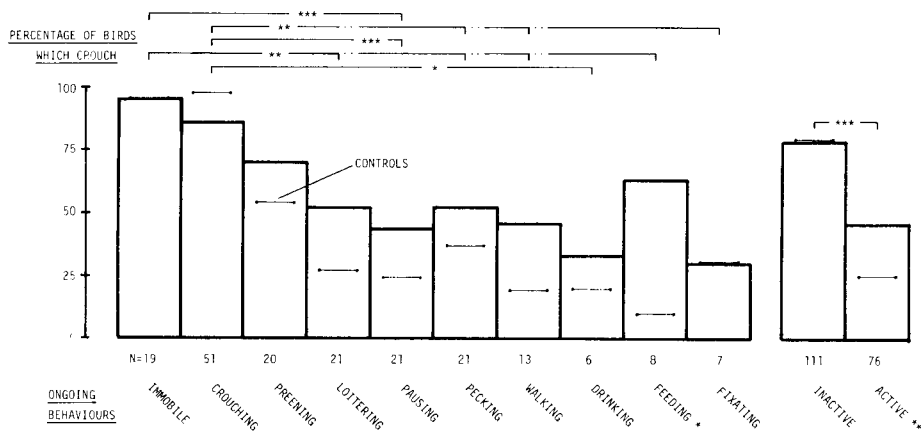


Fig. 7. Legend as for Fig. 3, but for crouching.

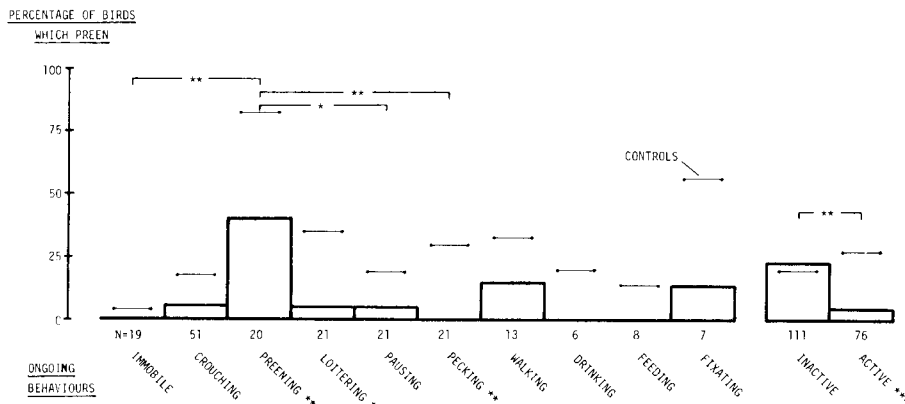


Fig. 8. Legend as for Fig. 3, but for preening.

in escape behaviours. Chicks which had been pecking or walking showed reduced pecking, preening and feeding and enhanced likelihoods of jumping, peeping, fixation and immobility. The form of the response can be seen from the Figures to vary according to ongoing behaviour, the relatively inactive being most likely to show a longer and clearer immobility response and the relatively active showing a more pronounced escape response. The most obvious escape response and the least immobility was shown by birds which had been fixating the bulb just prior to its illumination.

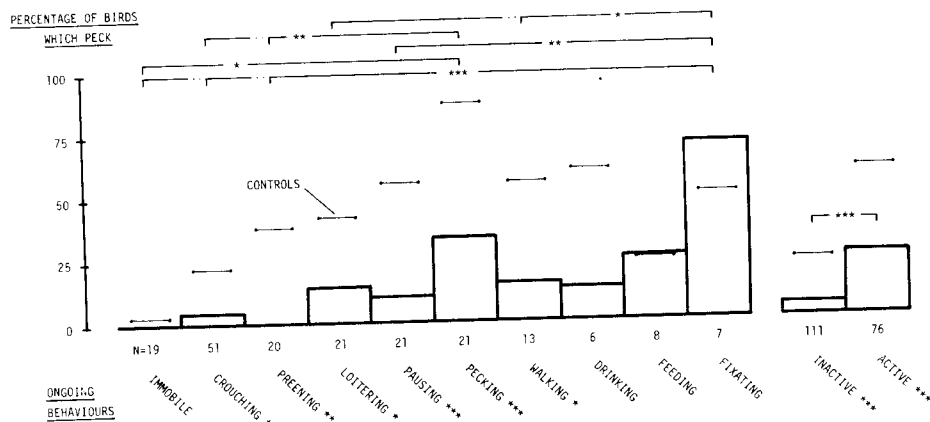


Fig. 9. Legend as for Fig. 3, but for pecking.

#### 4. DISCUSSION

The results clearly demonstrate that the responsiveness of chicks, differing in their ongoing behaviours, varies in both nature and degree. Analysis of the behaviour after interruption by the experimental change confirmed the existence of two response components, immobility and escape (BROOM, 1969). Individual birds showed aspects of each component, but less active birds showed a greater immobility response and more active birds showed a greater escape response. In other studies (FORRESTER, in prep.), the probability of showing the immobility or the escape response was found to be affected by the type of change to which chicks were subjected. Stimulation of the diencephalic region of the chick brain has been shown to elicit behaviour patterns which are apparently the same as these responses (ANDREW & OADES, 1973). An "escape-hide-freeze" system was identified, the responses being alternatives if strongly



stimulated in the periphery of the relevant area of the brain, but mixed if weakly stimulated at its centre. In some circumstances it will be most advantageous for an animal to show an immobility response whereas in others, the escape response will be more appropriate. It appears that there is some overlap in the neural systems controlling which response will be shown. Our observations about the precise context in which the responses are shown help to explain the working of the system for making decisions about which response will predominate.

The change in behaviour, which occurred when the bulb was illuminated, was greater for most measures if the chick had previously

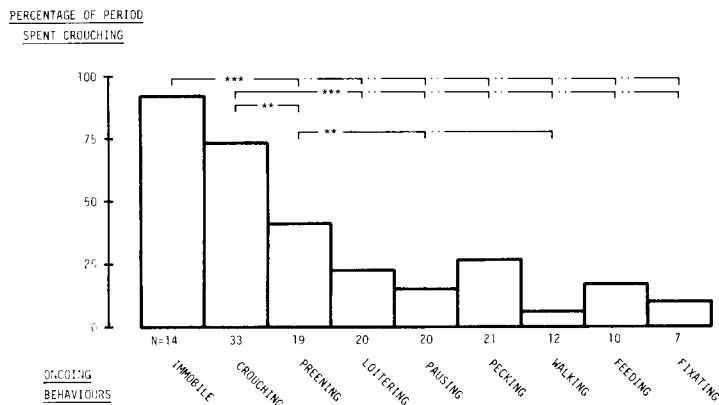


Fig. 10. The mean percentage of the 1 min. bulb illumination period spent crouching is shown for each of ten ongoing behaviours. Results of comparisons as in Fig. 2.

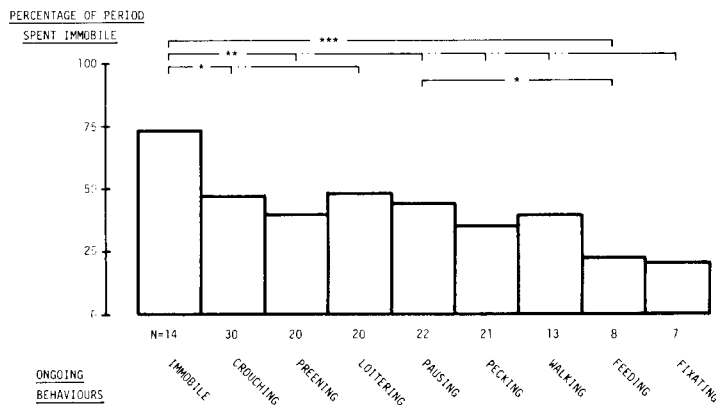


Fig. 11. Legend as for Fig. 10, but for immobile.

been active than if it had been inactive. These differences in the magnitude of the responses are correlated with other aspects of responsiveness in chicks. BROOM (in prep.) illuminated a bulb in the chick's cage for 10 second periods, regularly, once each minute. The responses habituated very rapidly (median = 2 trials) if the chick had been crouched, but awake, at the beginning of the first trial. The responses of the chicks which had been standing and pecking the ground at the beginning of the first trial, however, habituated slowly (median = 16 trials).

The type of response also differed after different ongoing behaviours. The results of FENTRESS (1968a & b) are a further example of the effects of ongoing behaviour on responsiveness. The response of voles in an alley, to an overhead moving object, was fleeing if the ongoing behaviour was walking or had been walking several seconds before. FENTRESS interpreted this result as indicating an underlying "activity tendency". In our chicks, the higher probabilities of jumping, walking and peeping and the lower probabilities of crouching and immobility after the more active ongoing behaviours, support this concept. In addition, the slight overshoot of preening, pecking and feeding into the experimental period is similar to the temporary continuation of voles' grooming, after a disturbance, reported by FENTRESS. Such persistence of specific activities indicates that, at least at first, the levels of the causal factors which predominated in the previous motivational state are maintained above the threshold necessary for that behaviour to be shown. The functioning of the mechanism which determines which behaviour is shown at a moment, the behavioural final common path (MCFARLAND & SIBLY, 1975), must entail the assessment of the priorities of the different possible activities. Investigations of two ongoing behaviours, feeding and preening, have shown that chicks are less responsive near the beginning of a bout than near the end of a bout (CULSHAW & BROOM, 1980). Less immobility and crouching were shown and there was greater persistence of the ongoing activity, if behaviour was interrupted near the beginning of a bout. A possible explanation for the persistence of behaviour at a time when other causal factors must be increasing is the existence of a mechanism for minimising inefficient vacillation between behaviours. In a situation where causal factors rise and fall at very frequent intervals, for example where those causal factors are the immediate result of sensory changes, equally rapid alternation of behaviours would often be functionally undesirable. A temporary 'locking on' mechanism would have the result that the duration of an activity was seldom less than a minimum and that interruption of the activity would be easier as the effects of the

mechanism declined. Such a mechanism could operate by positive feedback which might depend solely on internal factors or might involve the persistence of attention to relevant cues (ANDREW, 1976).

Three inter-related aspects of the relationship between ongoing behaviour and the type and degree of responsiveness are now considered. Firstly, the physical nature of the behaviour may influence the ease with which responses can be organised (FORRESTER, 1979). The term "physical nature" includes the muscular tonus involved, the posture, the general orientation, the level of activity, and the particular muscles in use. For example, efficient fleeing by chicks is physically more difficult after crouching than after feeding. Secondly, the nature of the chick's attention will also influence the response to a change in the chick's surroundings. Attentional variables include the orientation of the sensory receptors, the relative importance ascribed to different sensory inputs, and the 'set': the data-processing task the chick is engaged in at the time. A decreased responsiveness of chicks to small changes, following testosterone treatment, was shown by ANDREW (1976) to be due to persistence of attention to cues relevant to a particular task. Thirdly, ongoing behaviour is itself an indication of the motivational state and which causal factors are predominating at the time. Our control data demonstrate some of the temporal associations between behaviours, for example crouching is much more likely to occur during the minute following preening than in the minute following feeding. Responsiveness must depend upon motivational state but need not reflect it exactly (McFARLAND & SIBLY, 1972). Certain types and intensities of behaviour might result from different motivational states and also some states are "unobservable", *i.e.* the behavioural repertoire available at the time cannot exactly express that state.

The behaviour which an experimenter calls a response is merely one of several possible behavioural sequences which the subject might show. The transitions in behaviour of a chick not subjected to an experimental change still constitute a behavioural sequence resulting from alterations in the levels of underlying causal factors. The experimental changes merely result in different modifications of these levels. If the motivational state of the animal is regarded as being a point in causal factor space (SIBLY & McFARLAND, 1974), then this point is moved by the experimental change. Different ongoing behaviours reflect different starting points in causal factor space and hence the new position following the experimental change can result in different overt expressions in the behaviour. Although the effects of extreme environmental changes on

behaviour might be very similar whatever the ongoing behaviour, our results can explain some of the variations in the behaviour of animals in experimental studies of responsiveness. The behaviour of animals at the time of testing, and the behaviour sequences which are likely if the test change does not occur, could usefully be taken into account in most attempts to assess responses.

#### SUMMARY

The responsiveness of 6-day-old chicks varied in nature and degree according to their ongoing behaviour. Behaviour sequences were interrupted by a novel change, the illumination of a bulb, in the home pen. The behaviour of chicks following the novel change was compared with that of others whose ongoing behaviour was the same but which were undisturbed. The difference between these experimentals and controls, which we define as the response, involved fixation of the bulb and reduced feeding, general pecking and preening behaviour. Some birds showed much crouching and immobility whereas others showed more escape behaviour, for example jumping and peeping. A greater proportion of escape components and a smaller proportion of immobility components was included in the response if the chicks had been active, when the bulb was illuminated, than if they had been inactive. Specific differences in response according to ongoing behaviour included more crouching and less jumping by chicks which had been preening than by those which had been walking.

These results and the fact that certain activities persisted briefly after bulb illumination are discussed in terms of the physical difficulties of change from one activity to another, attentional mechanisms, causal factors and the behavioural final common path. We propose that there is a 'locking on' mechanism which minimises inefficient vacillation between behaviours.

Responsiveness can be very different according to ongoing behaviour, so this fact should be taken into account in any attempt to assess the responses of animals.

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#### ZUSAMMENFASSUNG

Die Antwortbereitschaft von 6-Tage-alten Küken variierte in ihrer Art und Stärke, je nachdem welche Verhaltensweise gerade ablief.

Bei den Experimenten wurden Verhaltenssequenzen durch eine neuartige Änderung im heimischen Gehege — das Aufleuchten einer Glühbirne — unterbrochen. Das Verhalten der Küken, das auf diese Änderung folgte, wurde verglichen mit dem von anderen, deren Anfangsverhalten gleich war, die jedoch nicht gestört worden waren. Der Unterschied zwischen diesen Experimenten und den Kontrollen, den wir als die Beantwortung definieren, schloss Fixierung der Glühbirne, Reduktion des Futterpickens, allgemeinen Hackens und Putzverhaltens in sich ein. Einige Vögel kauerten viel und waren häufig bewegungslos, andere hingegen zeigten mehr Fluchtverhalten, z.B. Aufspringen und Piepen. Waren die Küken beim Einschalten der Glühbirne aktiv gewesen, so war ein grösserer Anteil an Fluchtcomponenten und ein kleinerer Anteil an Bewegungslosigkeit in der Beantwortungen enthalten, als wenn sie inaktiv gewesen waren. Als Beispiel für eine unterschiedliche Beantwortung gemäss der gerade ablaufenden Verhaltensweise sei gegeben dass Küken, die sich geputzt hatten, mehr kauerten und weniger aufsprangen als Küken, die umhergegangen waren.

Diese Ergebnisse und die Tatsache, dass bestimmte Aktivitäten noch eine kurze Zeit nach der Glühbirnenbeleuchtung andauerten, werden diskutiert in Bezug auf die Schwierigkeiten von einer Aktivität zu einer anderen überzuwechseln, Aufmerksamkeitsmechanismen, Kausalfaktoren und den letztlich gemeinsamen Weg des Verhaltens. Wir nehmen an, dass es einen 'Verkettungs'-Mechanismus gibt, der unwirksame Schwankungen zwischen Verhaltensweisen minimal werden lässt.

Die Antwortbereitschaft kann sehr unterschiedlich sein, je nach dem anfänglichen Verhalten; daher sollte diese Tatsache berücksichtigt werden, wenn immer es gilt, Reaktionen von Tieren zu erfassen.