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# Learning Experiments on Individual Recognition in Budgerigars (*Me lopsittacusundulatus*)

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*With 9 figures*

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## Abstract

By means of learning experiments individual recognition in budgerigars was demonstrated. In a 2-choice situation 2 ♂♂ and 3 ♀♀ discriminated clearly between 2 object birds. Characteristics used for identification were predominantly of the head. Budgerigars can recognize conspecifics by means of optical characteristics alone. Training also enabled 2 ♂♂ to discriminate between colour slides of 2 object birds. In training, budgerigars discriminated only between greatly differing calls. When presented with slides and distance calls of 2 object birds, 2 ♂♂ chose mainly according to optical stimuli.

Budgerigars are able to recognize each other, as was inferred from observations of mate-specific behaviour (Trillmich 1976 a). The present paper confirms this conclusion by an independent method and attempts a first step in analysing the underlying performance. Learning experiments were deemed especially suitable for this purpose, as the kind of stimuli responsible for individual recognition can thus be analysed under well controlled conditions.

Few authors have so far tried to demonstrate that birds can recognize each other exclusively by visual characteristics (Bennett 1939, Guhl and Ortman 1953, Noble, Wurm and Schmidt 1938, Tschanz 1959 [on egg recognition in Common Murres]). On the other hand there is much definite evidence that audition alone suffices for individual recognition in birds (e. g. Cowan 1974, Emlen 1971, Falls and Brooks 1966, Ingold 1973, Mundinger 1970, Tschanz 1968, White 1971; review in Beer 1970).

Birds are, however, generally associated with keenness of sight. Most species hunt visually (searching image: Tinbergen 1960, Croze 1970, Müller 1974), and the selectivity of their visual hunting is impressively demonstrated by the many insect mimicry systems presumably evolved under the selective pressure of visually hunting bird predators (Wickler 1968). Birds also identify predators by optical cues (Curio 1975, Hinde 1954, Schleidt 1961). The brilliantly coloured and adorned plumage of ♂♂ of sexually dimorphic bird groups (e. g. Phasianidae, Paradisaeidae) offers morphological evidence that optical releasers play an essential part in the social behaviour of most species (e. g. Howell and Bartholomew 1952, Immelmann 1959, Lorenz 1941, Marler 1961, Nicolai 1964, 1968 a and b, Stout and Brass 1969, Tinbergen 1959).

Accordingly, the visual acuity of most bird species cannot be doubted (for physiological evidence see Sillman 1973). But, presumably because of methodological difficulties, much less is known about the importance of optical characteristics for individual recognition in birds. The learning experiments, therefore, centred upon the analysis of visual recognition.

## 1. Experiments on discrimination between live birds

### Methods

*Housing of test birds:* 2 ♂♂ and 3 ♀♀, which will be referred to as the 'subjects', were trained to discriminate between other budgerigars — the 'objects'. Subjects and objects were housed together in a room, caged singly or in twos. They were maintained on L : D 12 : 12.

*Discrimination training:* In the course of the first training sessions the weight of the subjects was reduced to approx. 80 % of their former free-feeding weight. The subject bird was placed in the start arm of a Y-maze (Fig. 1) in a neighbouring sound-proofed room; this arm could be shut off by a raisable PVC screen. At the end of each side arm a cage was placed containing an object bird. When the screen was raised the subject could see into both cages; if he then ran to the bird designated in the experiment as 'positive' he was allowed to feed for 10—15 s. If he chose the 'negative' bird he was at once driven back from the empty feeding tray to the start arm, and the screen was lowered. If the subject did not choose within 5 s of the lifting of the screen he was encouraged to leave the start arm by an air current from a ventilator. Screen and ventilator could be operated from a darkened anteroom into which the birds could not see.

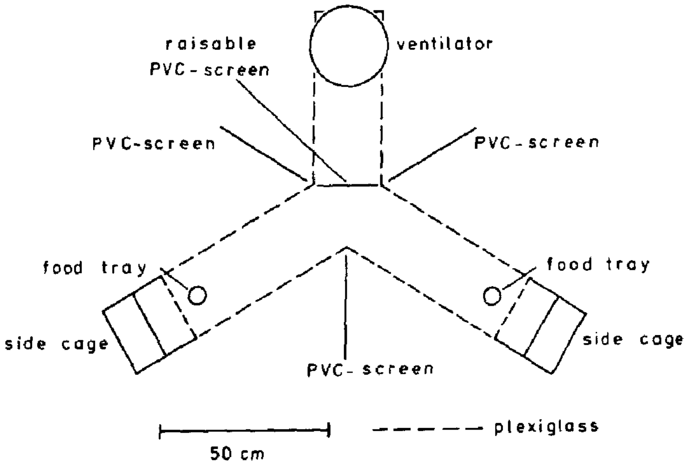


*Fig. 1:* Y-maze. The birds in the side cage sit on perches 10 cm high. Side cages are removable and can be exchanged between trials

The side cages were removed after each trial while the screen was closed, even when they were then replaced as before. Thus the subject could hear but not see the movement. Feeding trays were also removed after each trial and freshly filled. Manipulations were always undertaken in the same order, so that no particular sound sequence could cue the subjects regarding the future positions of the object birds.

Side cages were exchanged according to a quasi-random series of numbers, restricted only in that the same object bird was not presented more than 3 times running on the same side, to prevent the development of position habits (Southerland 1961). This quasi-random series consisted of 160 numbers, of which 20—50 (depending on the subject's responsiveness) were used at each session, starting at a different number every day. The subjects had to choose 20 to 50 times each morning and afternoon, 5 days a week. If approx. 70 % of their choices were correct, food was given on a variable interval schedule of reinforcement every 2nd or 3rd trial on average, to counteract the extinction of the choice reaction in later tests without reward.

In all choice situations labelled 'Test', in which the subjects were tested for learning success or generalization, choices were either reinforced at both the positive and the negative bird or at neither.

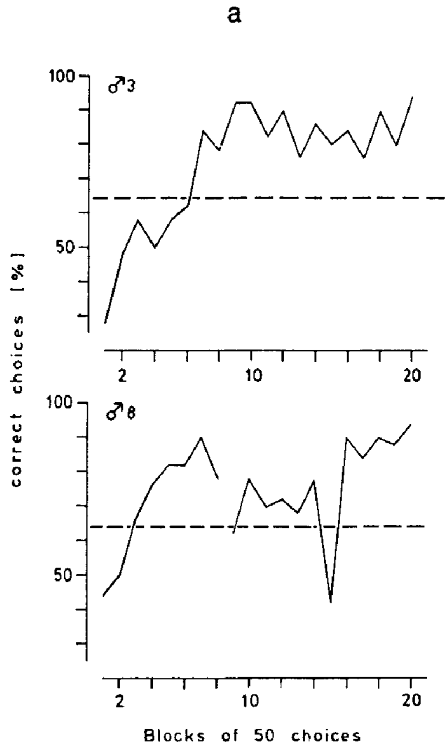
*Position habits:* In the first training sessions, confronted with new problems or alterations in the experimental set up, all birds tended to develop a position habit. This habit was broken by offering the positive bird continuously on the side avoided until the subject bird finally chose it there. The training then proceeded normally.

*Statistical test:* If the subject birds choose at random or according to a position habit, then positive and negative birds should be chosen with equal frequency. The $\chi^2$-test was applied to determine whether the choices were significantly different from this expected value.

## Results

### a) Discrimination between 2 individuals

Usually after 3 or 4 days the subject birds were accustomed to the Y-maze, and chose on their own initiative directly after the screen rose. ♂♂ showed a significant learning success after 200—400 choices, ♀♀ after 300 to



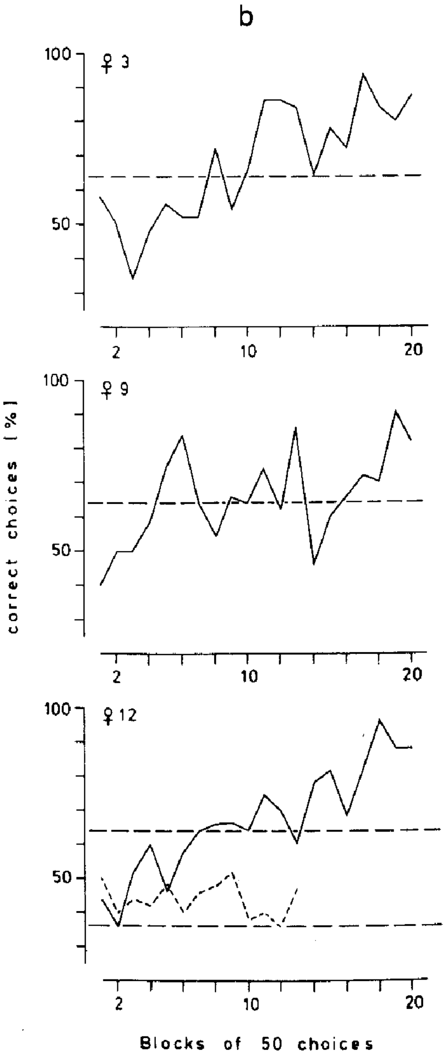


*Fig. 2:* a) Learning curves of ♂♂. Percentage of correct choices per block of 50 trials. Values above the dashed lines are significant ($p < 0.05$). Above: ♂3 chose between ♀3 (mate, positive bird) and ♀2. Below: ♂8 chose between ♂12 (positive bird) and ♂13. Training was interrupted after 8 blocks and continued 20 days later. b) Learning curves of ♀♀. Above: ♀3 chose between ♂3 (mate, positive bird) and ♂11. Middle: ♀9 chose between ♂8 (mate, positive bird) and ♂12. Below: The lower dashed line gives the significance limit for wrong choices ($p < 0.05$) (see text). ♀12 first chose between ♀13 (positive bird) and ♀14 (dotted curve). ♀12 later chose between ♀13 (positive bird) and ♀15 (continuous line)

600 (Figs. 2a, b). ♂♂ were more active in training and seemed less nervous, sitting in a normal posture between trials and sometimes singing; unlike the ♀♀, they hardly ever showed escape reactions. Their quicker learning was probably due to this, and they reached a more or less even niveau of about 85 % correct choices sooner than the ♀♀.

♀12 had first to discriminate between 2 sisters (♀13 positive and ♀14 negative) looking very similar to the human observer. In the course of 650 presentations there was not the slightest indication of any learning progress (Fig. 2b, below). In most sessions she chose the positive bird in less than 50 % of the trials, the reason being that as she often showed a position habit, the positive bird had repeatedly to be kept on the other side for a number of trials.

♀12 was next presented with ♀13 (positive) and ♀15. Here she learned to discriminate roughly as quickly as the other 2 subject ♀♀ learned to discriminate their mates from other ♂♂ (Fig. 2b).

All 2 ♂♂ and 3 ♀♀ trained learned to discriminate between 2 budgerigars of the same or opposite sex. Discrimination in both cases was learnt equally fast. Whether or not the positive bird was the mate had no evident influence, in this situation, on the speed of learning.

### b) Control experiments

Control experiments were arranged to establish whether the subjects might be able to pick up cues about the next position of the positive bird, instead of having to differentiate between object birds at each presentation.

As soon as the 5 subject birds had learnt to choose the positive bird reliably, food was provided on both sides or neither side in the subsequent 20—50 trials. Under these conditions they continued to choose the positive bird significantly more often ($p < 0.01$). This confirmed that they could not see the food, nor were they cued to it by any reaction of the positive bird.

Alterations in the manipulation sequence in exchanging the side cages also caused no measurable changes in the choices of the 5 subjects.

If after 20 choices the positive bird was placed in the cage of the negative bird, and vice versa, then the 3 so tested subject birds still chose the positive bird significantly more often during the next 20 trials. The cage therefore was not used as a means of identification.

The behaviour of ♀12, who did not learn to differentiate between ♀13, and ♀14 in 650 trials, also shows that manipulations gave no cues which side to chose. This is also apparent from some of the further experiments, described below, in which the birds failed to discriminate between positive and negative object birds.

### c) Tests introducing one new object bird

The control tests had shown that the subject birds chose between the 2 object birds, and used no other cues. If, then, they had learnt to recognize the object birds individually, they should be able to distinguish them from new object birds, not yet presented in the experiments.

*A new bird instead of the negative bird:* When the subjects had learnt to choose the positive bird significantly more often, discrimination against a new bird as yet unused in the experiments was tested. All birds except ♀9 (who did not discriminate ♂8 from ♂1) could distinguish the new birds from the familiar positive birds (Table 1). ♀9 rated a new bird (♂17) as positive over against the familiar positive bird. ♀12 had to be trained instead of tested in 3 out of 4 sessions, as she quickly developed a position habit. But in these sessions of 20 trials each she can hardly have learnt the discrimination.

In the 2-choice tests the subjects could discriminate the positive birds from 4—6 others, therefore they recognized them individually.

*Table 1:* Tests with new birds substituted for the negative bird

| Subject birds | Object birds | Choices | p ($\chi^2$-test) |
|---|---|---|---|
| ♂ 3 | ♀ 3 : ♀ 5 | 45 : 5 | < 0.001 |
| | ♀ 3 : ♀ 6 | 48 : 2 | < 0.001 |
| | ♀ 3 : ♀ 8 | 16 : 4 | < 0.01 |
| | ♀ 3 : ♀ 11 | 51 : 19 | < 0.001 |
| ♂ 8 | ♂ 12 : ♂ 1 | 46 : 4 | < 0.001 |
| | ♂ 12 : ♂ 3 | 29 : 1 | < 0.001 |
| | ♂ 12 : ♂ 5 | 6 : 0 | - |
| | ♂ 12 : ♂ 14 | 18 : 2 | < 0.001 |
| | ♂ 12 : ♂ 15 | 17 : 3 | < 0.01 |
| | ♂ 12 : ♂ 16 | 18 : 2 | < 0.001 |
| ♀ 3 | ♂ 3 : ♂ 5 | 39 : 20 | < 0.02 |
| | ♂ 3 : ♂ 6 | 17 : 3 | < 0.01 |
| | ♂ 3 : ♂ 9 | 36 : 14 | < 0.01 |
| ♀ 9 | ♂ 8 : ♂ 1 | 11 : 9 | < 0.7 |
| | ♂ 8 : ♂ 13 | 50 : 20 | < 0.001 |
| | ♂ 8 : ♂ 14 | 19 : 1 | < 0.001 |
| | ♂ 8 : ♂ 15 | 16 : 4 | < 0.01 |
| | ♂ 8 : ♂ 16 | 16 : 4 | < 0.01 |
| | ♂ 8 : ♂ 17 | 11 : 29 | < 0.01 |
| ♀ 12 | ♀ 13 : ♀ 2 | 17 : 3 | < 0.01 |
| | ♀ 13 : ♀ 5⁺ | 18 : 2 | < 0.001 |
| | ♀ 13 : ♀ 16⁺ | 17 : 3 | < 0.01 |
| | ♀ 13 : ♀ 17⁺ | 16 : 4 | < 0.01 |

⁺ Training, not test.

*A new bird instead of the positive bird:* The subjects had also to choose between the familiar negative bird and a new bird instead of the positive bird (Table 2). All chose the new bird significantly more often. This bird had been presented to 3 of these subject birds in immediately prior tests as new (negative) bird, and had been so regarded (compare Tables 1 and 2). Apparently the subjects had not learnt the new bird as 'negative' during the prior test. ♀12 was again trained instead of tested for discrimination of the new bird. As she had initially taken much longer to learn, she cannot have learned the new bird as positive in 30 trials, in which she chose incorrectly only 6 times.

Thus, all subjects preferred the new (positive) bird to the familiar negative bird.

*Table 2:* Tests with new birds substituted for the positive bird

| Subject birds | Object birds | Choices | p ($\chi^2$-test) |
|---|---|---|---|
| ♂ 3 | ♀ 9 : ♀ 2 | 45 : 24 | < 0.02 |
| | ♀ 11 : ♀ 2 | 40 : 9 | < 0.001 |
| ♂ 8 | ♂ 17 : ♂ 13 | 46 : 24 | < 0.01 |
| ♀ 3 | ♂ 6 : ♂ 11 | 22 : 8 | < 0.02 |
| ♀ 9 | ♂ 13 : ♂ 12 | 37 : 15 | < 0.01 |
| ♀ 12 | ♀ 18 : ♀ 15⁺ | 24 : 6 | < 0.01 |

⁺ Training, not test.

All subjects recognized both birds presented in the 2-choice situation individually. They estimated them, in accordance with their training, as stimuli either promoting or inhibiting approach, as has often been shown for simpler stimuli (TERRACE 1966). As normally the object birds were silent during the trials, the subject birds must have discriminated visually.

### d) Position of optical cues enabling individual recognition

Characteristics of the head seem particularly important for individual recognition in many bird species (GUHL and ORTMAN 1953, MARLER 1961, NICE 1943, NOBLE, WURM and SCHMIDT 1938). To find the position of the optical characteristics making individual recognition possible, upper or lower parts of the positive and negative object birds were increasingly concealed by opaque glass, and the point at which the subject could no longer discriminate was determined. During these experiments training to the positive bird was continued.

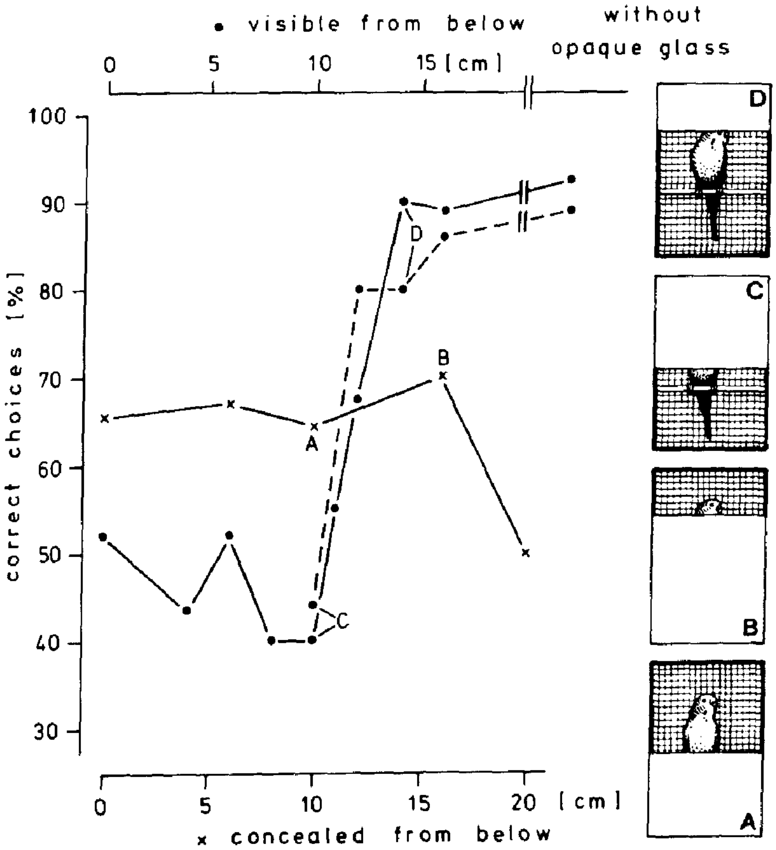


*Fig. 3:* Determination of the degree of concealment beyond which individual recognition is no longer possible. Lower abscissa: Object birds concealed from below. The grade of concealment for points A and B of the curve of ♂3 (marked with crosses) is shown in pictures (right, below). Upper abscissa: Object birds concealed from above. Continuous line: ♀9. Dashed line: ♂8. The grade of concealment of the object birds at points C and D is shown in the pictures (right, top)

For ♂3, each point in Fig. 3 represents 30—58 choices, for ♂8 40—60 choices and for ♀9 15—165 (on average 70) choices. Object birds presented to ♂3 were concealed from below. Tail, legs (with colour-bands) and underparts could be concealed (A in Fig. 3) without affecting ♂3's ability to discriminate. If an opaque glass pane 16 cm high was placed in front of the positive and negative birds (B in Fig. 3), they streched up on their perches so that just their heads were visible. Even in this situation ♂3 was able to discriminate the positive from the negative bird significantly. But behind 20 cm high opaque glass the birds were quite invisible and ♂3 failed to discriminate.

If however the subject birds were shown only tail, legs (with colour-bands) and underparts, by concealing all but the lowest 10 cm of the object birds with opaque glass (C in Fig. 3), then neither ♂8 nor ♀9 was able to discriminate between them. If the opaque pane was raised to a height of 14 cm (D in Fig. 3), then both these birds could choose accurately between the object birds.

Sharp inflections occur in the curves (Fig. 3) at different points depending on whether the object birds were concealed from above or from below. In the former case the birds in their side cages bent down from the perch to look under the pane, in the latter case they stretched up to see over the pane. In both situations reliable discrimination ceased when the subject birds could no longer see the heads of the object birds.

It is the head, therefore, that carries sufficient identification characteristics for individual recognition. As the view of the whole body minus the head was insufficient to allow discrimination, it must be assumed that the body alone carries either no individual characteristics, or at the most markings which do not by themselves allow identification by other budgerigars. The subject birds did not treat artificial characteristics, such as colour-bands, as an aid to identification. This experiment again demonstrates that the subject birds discriminated visually.

### e) The function of head patterning in (individual) recognition

There is striking variation in budgerigar head patterning. Number and size of the black throat spots, the size of the blue cheek stripes and the area of the yellow forehead vary from bird to bird. This applies to both domesticated budgerigars and to those in the wild, as an examination of specimens (collected and kindly made available by Dr. de S. DISNEY in Australia) in the Australian Museum of Natural History in Sydney showed. Moulting quickly effects strong pattern change, particularly of throat spots and cheek stripes.

In the first discrimination training, ♀12 could not distinguish between the 2 very similar sisters ♀13 and ♀14 (Fig. 2b, below). Even after successful training to choose between ♀13 and ♀15, she still failed to discriminate between ♀13 and ♀14.

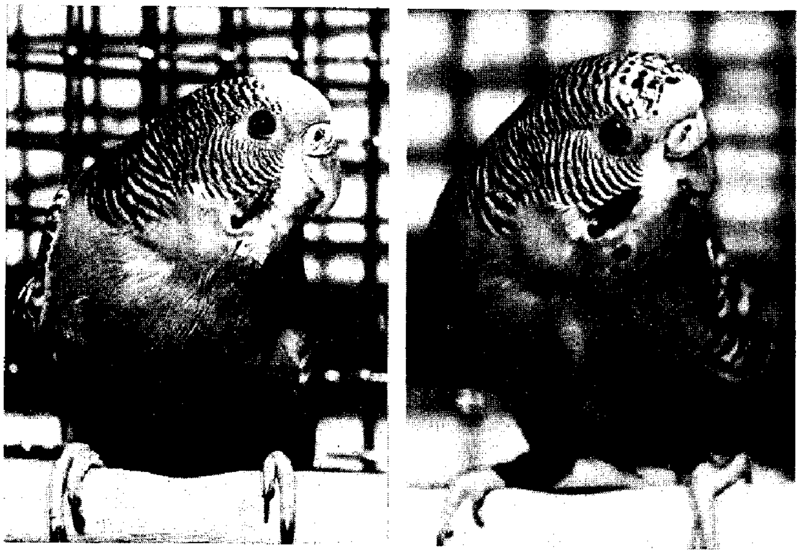


*Fig. 4:* Alterations of head patterning.
Left: ♀14 with throat spots concealed. Right: ♀14 with painted forehead

This was an opportunity to find out which artificial alterations of head patterning would enable ♀12 to discriminate between the 2 ♀♀. To see whether ♀12 reacted to changes of the head, the most striking sexual characteristic of the budgerigar was first altered — the cere colour. The cere is blue in male budgerigars, brown in ♀♀. The cere of ♀14 was painted blue, and ♀12 discriminated significantly between the sisters (♀13 : ♀14; 17 : 3).

The blue colour was then washed off the cere, and ♀14's black throat spots were covered with pieces of yellow adhesive tape, giving her a completely yellow throat (Fig. 4). ♀12 was again trained to discriminate between ♀13 and ♀14. Out of 80 trials she chose according to position habit 20 times, in the 60 remaining choices she ran 26 times to ♀13, 34 times to ♀14 ($p < 0.3$). She could not therefore use the difference in throat patterns of the 2 ♀♀ as identification clues, or learn to do so within 80 trials.

The pieces of adhesive tape were removed from ♀14's throat spots, and approximately the back half of the yellow forehead was painted with wavy black lines (Fig. 4). ♀13 and the painted ♀14 were again presented to ♀12, who chose ♀13 significantly more often (29 : 11; $p < 0.01$), after having initially chosen 30 times according to position habit. It proved impossible to remove the painted head-patterning from ♀14 completely, a suggestion of grey remained. When ♀12 was presented with ♀13 and ♀14 again, she chose ♀13 (17 : 3). She could therefore discriminate between the 2 ♀♀ by means of forehead patterning. Immature budgerigars are patterned with wavy lines over the whole forehead, down to the base of the beak. It is thus not established that this experiment tested an individual characteristic, rather than an age criterion.

Another experiment confirmed that budgerigar throat spots and cheek stripes are not necessary for individual recognition. Would the mates of 6 pairs reunite after being separated for 20 days, if throat spots and cheek stripes had been removed in the meantime?

For 3 weeks, 6 pairs remained together in an aviary; at this time all the birds were firmly mated, i. e., the mates allopreened, beak touched and the ♂♂ fed their partners (Trillmich 1976a). All 6 ♀♀ were then removed to an aviary unknown to any of the birds, while the ♂♂ stayed in the initial aviary. 19 days later the black throat spots and blue cheek stripes were completely cut off, so that all the birds had uniformly yellow faces. The ♂♂ were released to the ♀♀ in their aviary on the morning of the 20th day, and the pairs were at once observed for 90 min. That evening the birds were observed for an h; similarly on mornings and evenings of the following 2 days.

Mates of 3 pairs found each other immediately and showed partner-specific behaviour. 2 more pairs reassociated during the observation time. Partners of the 6th pair ignored each other and all other birds. The probability that 5 of 6 pairs came together as before separation at random is $p = 0.0013$ (see Trillmich 1976b for the calculation of this probability).

As it can therefore be excluded that the pairs formed at random, the birds must have recognized each other without the head patterning. They may have used other optical, or else acoustical characteristics (see description of the individuality of distance calls, below). But throat and cheek stripes are not necessary for individual recognition in budgerigars; which does not preclude their possible use for recognition, in combination with other characteristics.

## 2. Discrimination training to slides

It has been shown in the experiments described above that optical stimuli are of great importance for the recognition of individual budgerigars. Statements on the relative importance of optical and acoustical stimuli for individual recognition can be made only if it is possible to manipulate the two separately.

This and the following 2 sections describe experiments to determine whether the birds react to either a purely optical or a purely acoustical display, in a way that could be described as individual recognition. A purely optical display was attempted with colour slides, a purely acoustical display was achieved by playing distance calls from a tape recorder.

### Methods

The 2 trained ♂♂ chose more reliably, and gave the impression of being altogether more composed in the training situation than the ♀♀. The ♂♂ were therefore chosen for training to the colour slides of object birds. Fig. 5 shows the experimental set-up for this

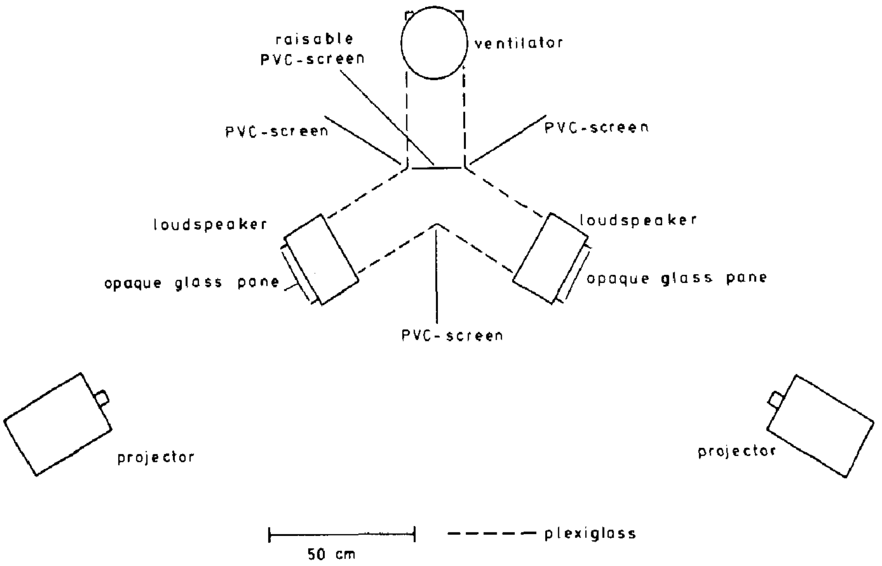


*Fig. 5:* Modified Y-maze for training to slides and/or distance calls. Coloured slides of the object birds were projected simultaneously in life size onto 2 opaque glass panes. Distance calls of each bird could be played back from either side by loudspeaker. Further explanations in text

training (and for training to discriminate between distance calls, see below). In place of the side cages with the live birds were opaque glass panes onto which slides could be projected, showing the object birds sitting in various postures at various points on the side cage perches. The slides were so shown that the birds appeared life-sized and the right way round as viewed by the subject bird. Slides were projected with a 110 V 50 W bulb (projector: Revue A 240, with Isco-Göttingen 1 : 2,8/85), the distance from the opaque pane being 80 cm. The background illumination on the pane was greater than in the presentation of live birds. The subjects were trained to discriminate between 10 or 16 different slides of each of the 2 object birds. Variations were achieved in that any of the 10 or 16 slides of the positive bird could be shown over against any of the 10 or 16 slides of the negative bird, according to a random series. Otherwise the experiments were conducted as described for those with live birds.

## Results

Having learnt to discriminate between living birds, ♂3 and ♂8 were tested to see whether they reacted similarly to slides of these birds. 3 slides each of ♀3 and ♀2 were shown to ♂3, 16 slides each of ♂12 and ♂13 were shown to ♂8. Neither subject bird chose at first, but both grew accustomed to the new conditions after 5—10 presentations. Their choices gave no indication that they associated the slides in any way with the live birds to which they had been trained (Table 3,1.).

♂3 was then trained to choose between 10 slides of each of his object birds, ♂8 was trained to choose between 16 slides of each of his. Table 3, 2. shows that the subjects learned to discriminate reliably between positive and negative slides.

In a test ♂3 was shown 'head' slides of ♀3 and ♀2, with whose slides he had just been trained. The slides were of the ♀♀ sitting on the floors of their cages, so that only their heads could be seen when projected. ♂3 was apparently unable to discriminate between these 'head' slides of the 2 ♀♀ in accordance with the foregoing training to normal slides (Table 3,3.).

Control tests were run with new slides of the same object birds, to determine whether the subjects had merely learnt a colour pattern by heart, or had

*Table 3:* Discrimination training to colour slides

| | Subject birds | Object birds | Choices | no. of slides | p ($\chi^2$-test) |
|---|---|---|---|---|---|
| 1. Test: Generalization from live birds to slides | ♂ 3 | ♀ 3 : ♀ 2 | 35 : 39 | 3 : 3 | < 0.7 |
| | ♂ 8 | ♂ 12 : ♂ 13 | 15 : 13 | 16 : 16 | < 0.8 |
| 2. Training to slides: total choices | ♂ 3 | ♀ 3 : ♀ 2 | 108 : 62 | 10 : 10 | < 0.001 |
| | ♂ 3 | ♀ 19 : ♀ 12 | 253 : 165 | 10 : 10 | < 0.001 |
| | ♂ 8 | ♂ 12 : ♂ 13 | 88 : 36 | 16 : 16 | < 0.001 |
| 3. Test: 'head' slides of 2 ♀♀ | ♂ 3 | ♀ 3 : ♀ 2 | 43 : 55 | 5 : 5 | < 0.3 |
| 4. Test: new slides | ♂ 3 | ♀ 19 : ♀ 12 | 54 : 27 | 3 : 4 | < 0.01 |
| | ♂ 8 | ♂ 12 : ♂ 13 | 27 : 7 | 6 : 6 | < 0.001 |
| 5. Test: Generalization from slides to live birds | ♂ 3 | ♀ 19 : ♀ 12 | 64 : 31 | - | < 0.001 |

actually classified positive and negative slides into categories corresponding to positive and negative birds. The birds' choice of the new slides corresponded to their choice of the familiar ones (Table 3,4.).

In a further control, ♂3 was trained from the outset to distinguish between slides of ♀♀19 and 12 (10 each) (Table 3.2.). These object birds were known to the subject, but he had not been trained to choose between them. ♂3 learned to discriminate between the slides within 160 trials (97 : 63; $p < 0.01$). He was then tested with the live birds pictured in the slides. As shown in Table 3,5., he significantly discriminated between the live birds in the same way as he had learnt to discriminate between their slides (Table 3,2.).

According to these results, the subject birds had not only learnt and responded to a number of independent colour patterns, but they extracted features from the slides enabling them to classify a number of new slides of positive and negative birds. Slides of ♀19 and ♀12 supplied ♂3 with sufficient information to enable him to discriminate correspondingly between the live birds.

## 3. Training to distance calls

### Description of the individuality of distance calls

Can budgerigar calls serve to identify an individual? This question was investigated before birds were trained to discriminate acoustically between individuals. Distance calls of 10 ♂♂ and 11 ♀♀ were therefore recorded and the intra- and interindividual variability of the calls compared.

The distance calls were recorded in an anechoic room and in a soundproofed room with echo suppression, and evaluated with a Sonagraph 6061B of Kay Electrics.

Calls of different individuals can easily be distinguished from the sonagrams, whereas all calls of one individual resemble each other closely (Fig. 6). Most distance calls fall into 3 rough categories, easily distinguishable to the human ear.

*Type 1:* The frequency of the call rises and falls repeatedly, e. g. the calls of ♂♂ and those of ♀9 (Fig. 6). *Type 2:* Other calls begin with a relatively high frequency (4.0—4.5 kHz), falling more or less evenly to a much lower frequency, as e. g. the calls of ♀11 (Fig. 6). *Type 3:* The calls have a somewhat

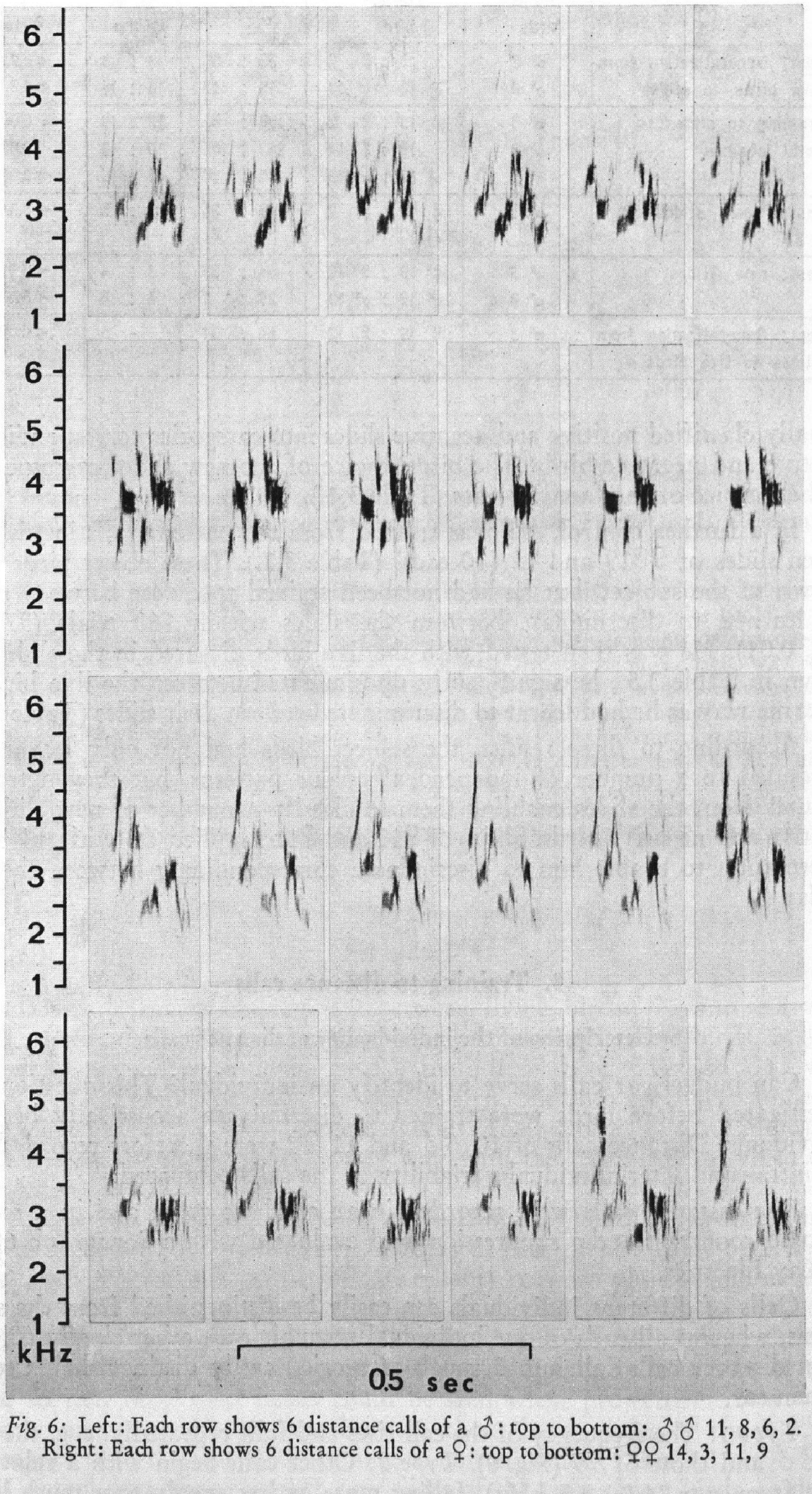
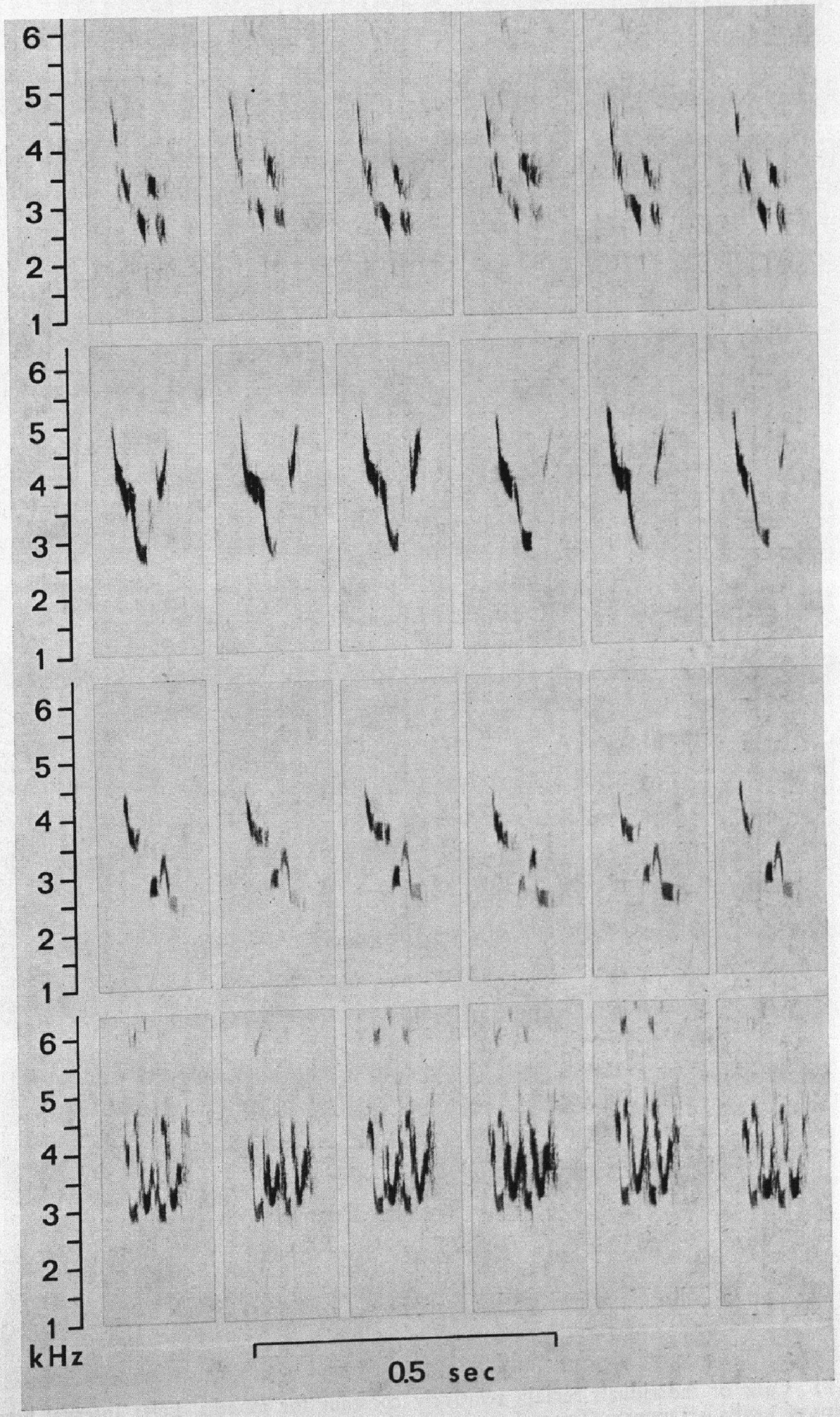


*Fig. 6:* Left: Each row shows 6 distance calls of a ♂: top to bottom: ♂♂ 11, 8, 6, 2. Right: Each row shows 6 distance calls of a ♀: top to bottom: ♀♀ 14, 3, 11, 9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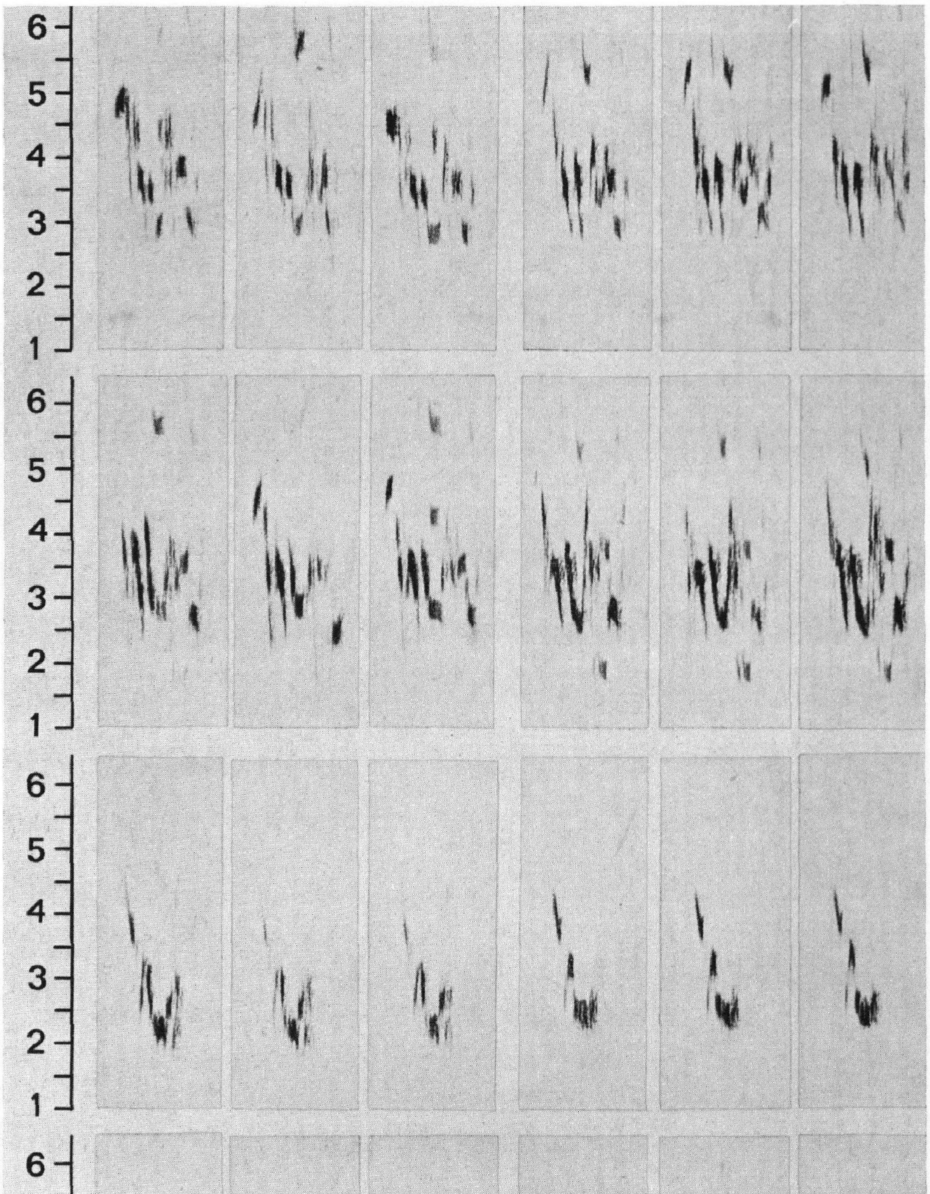
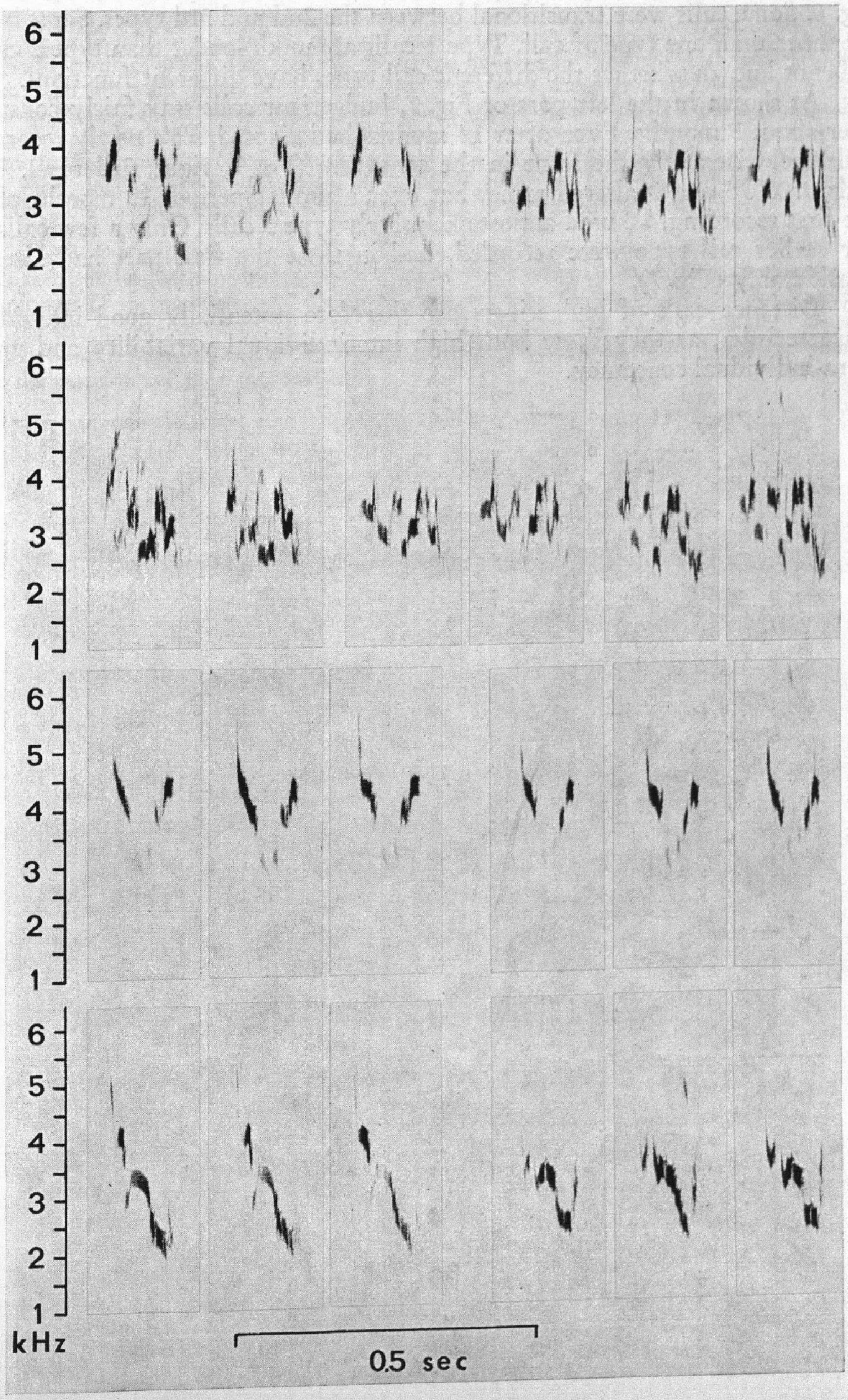


*Fig. 7:* Calls of individuals remain relatively constant for months. Left: Interval between groups of 3 calls is 3 months. Top to bottom: ♂♂ 13, 12, 8, ♀12. Right: Top row ♂5, interval between groups of calls approx. 16 months. 2nd row ♂3; 3 groups of 2 calls, recorded Nov. 1973, Feb. 1975 and July 1975. 3rd row ♀5, interval between the 2 call groups approx. 14 months. Bottom row ♀2, interval between call groups approx. 15 months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kHz
0.5 sec

U-shaped sonagram frequency pattern, and occurred only in ♀♀, e. g. ♀3 in Fig. 6. Some calls were transitional between the 2nd and 3rd types. Some birds use more than one type of call. Type 1 calls are much louder than type 2 calls. It is not known whether the different call types have different functions.

As shown in the left part of Fig. 7, budgerigar calls stay fairly constant over about 3 months. Even after 14 months had elapsed, ♀5's newly recorded calls looked exactly the same in the sonagram (Fig. 7, right, 3rd row). The calls of ♂♂5 and 3 altered somewhat over a similar period. 15 months after the first recording, ♀2 used almost exclusively type 3 calls. Only a few calls of her earlier call type were recorded, and in these the first part had altered considerably (Fig. 7).

Distance calls of budgerigars are therefore potentially good individual characteristics, as they show both high interindividual variability and great intra-individual constancy.

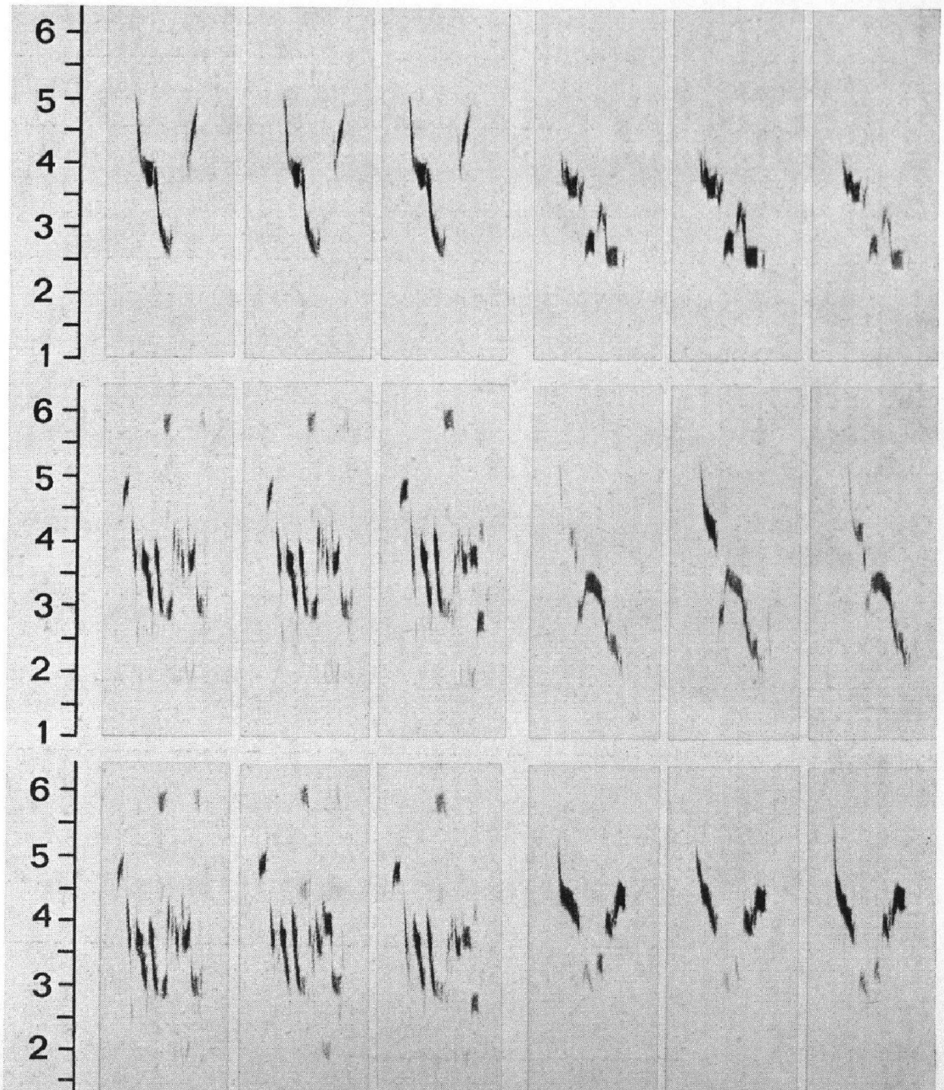
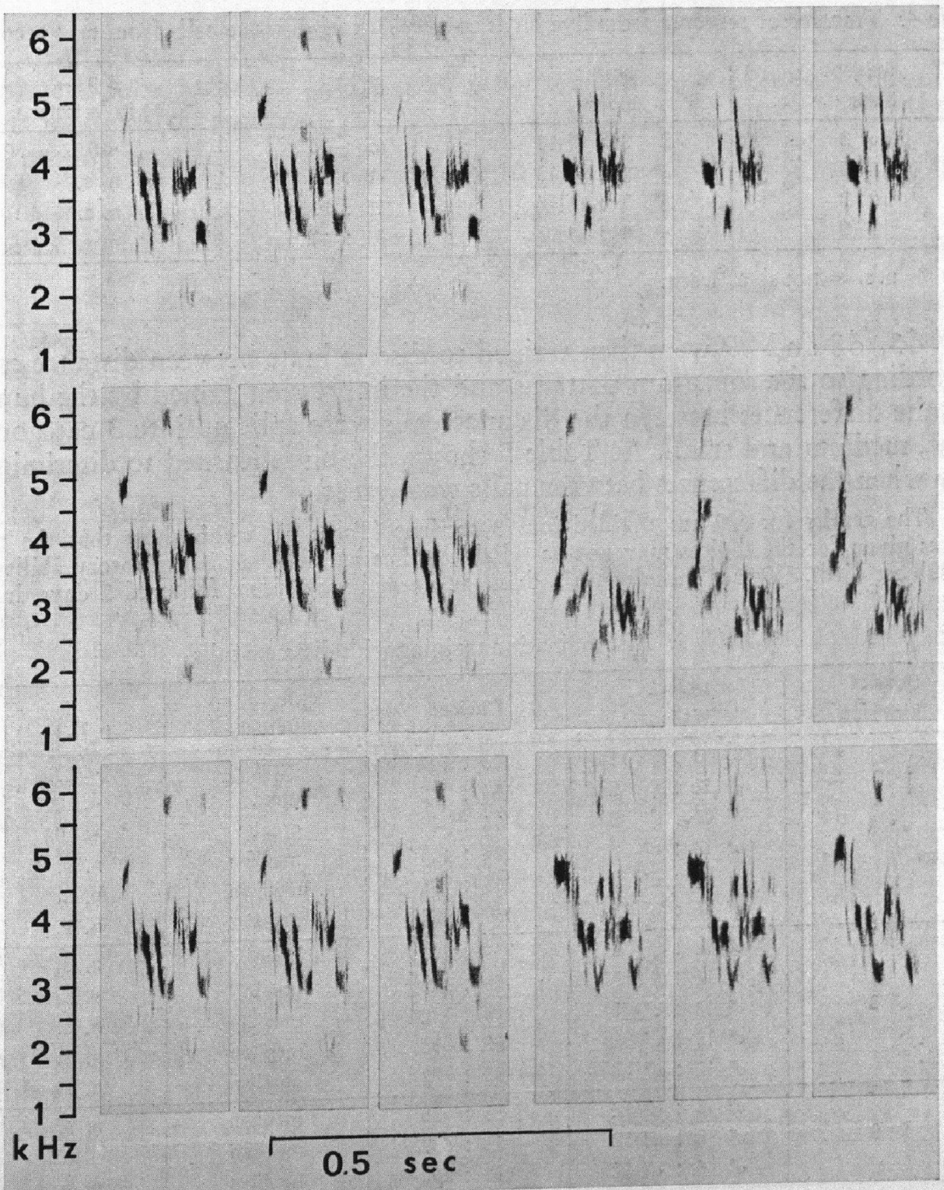


*Fig. 8:* Calls to which birds were trained. Each row shows 3 positive and 3 negative calls. Top to bottom: Left: ♀3 versus ♀11, ♂12 v. ♀2, ♂12 v. ♀5. Right: ♂12 versus ♂8, ♂12 v. ♂2, ♂12 v. ♂13

## Method

Recordings lasting about 6.5 min and containing 45 calls/min were built up from the original recordings of the distance calls of various budgerigars. The calls followed each other at irregular intervals. The calls of the 2 object birds were transferred to 2 tracks of a stereo recorder (Uher Report Stereo IC). These could be played back together from 2 loudspeakers (Isophon, 150—11000 Hz) mounted on the roof of the apparatus (Fig. 5). By means of a switch, track 1 could be played from the right and track 2 from the left loudspeaker, and vice versa. In this way the distance calls could be presented from right or left in a quasi-random sequence corresponding with the presentation of live birds and slides.

Playback of distance calls began 3—5 s before each trial and continued until the subject arrived at the feeding tray in one of the arms of the Y-maze. A false choice resulted in the termination of the playback, and the subject was immediately driven back to the start arm and the screen lowered. A correct choice meant the continuation of the calls until the end of the 10—15 s feeding time. The recorder was then switched off, the bird was driven back into the start arm and the screen lowered.



The sound volume of the calls varied at the centre of the Y-maze, where the subject made its choice, between 75 and 80 dB. The sound volume of calls of live birds sitting in the side cages was 80—87 dB.

## Results

After the subject birds had learnt to discriminate between live birds, they were tested for their acoustical discrimination between the distance calls of these birds, to see whether their reactions were similar in both situations.

Table 4 shows the results of these tests. The distance call sonagrams of the object birds are shown in Fig. 8 and Fig. 6 (♂6).

Of all 4 birds tested, only ♂3 reacted to the distance calls in the same way as to the live birds. The 3 other subject birds showed no preference for the recorded calls of either individual. These tests could not be continued indefinitely as the birds developed position habits. According to the sonagram (Fig. 8) and the impression gained by the human ear, of all the birds tested ♂3 was presented with the most different calls.

*Table 4:* Transfer of response from live birds to playback of distance calls from tape recorder

| Subject birds | Object birds | Choices | p ($\chi^2$ - test) |
|---|---|---|---|
| ♂ 3 | ♀ 3 : ♀ 11 | 45 : 24 | $< 0.02$ |
| ♂ 8 | ♂ 12 : ♂ 13 | 48 : 52 | n. s.$^{+}$ |
| ♀ 3 | ♂ 3 : ♂ 6 | 16 : 23 | n. s. |
| ♀ 9 | ♂ 8 : ♂ 12 | 21 : 18 | n. s. |

$^{+}$ n. s. = not significant.

♂3, ♂8 and ♀9 were then trained to discriminate between distance calls. According to the sonagram patterns and the impression gained by the human ear, the differences between the distance calls were split up into 3 categories: great, medium and small. As Table 5 shows, the birds learned to discriminate only when the differences between calls were great.

The results for ♀9 are divided into 3 sections (Table 5), which show that the total figures given for the choices may not be reliable indications of the discriminatory ability of the subject birds. ♀9 was initially trained in the normal way; there followed 2 days during

*Table 5:* Discrimination training with distance calls

| Subject birds | Object birds | Choices | call differences | p ($\chi^2$ - test) |
|---|---|---|---|---|
| ♂ 3 | ♀ 3 : ♀ 11 | 143 : 107 | great | $< 0.05$ |
| | ♂ 12 : ♀ 2 | 184 : 126 | great | $< 0.001$ |
| | ♂ 12 : ♀ 5 | 74 : 46 | great | $< 0.02$ |
| | ♂ 12 : ♂ 8 | 168 : $163^{+}$ | medium | n. s.$^{++}$ |
| | ♂ 12 : ♂ 2 | 115 : 94 | medium | n. s. |
| | ♂ 12 : ♂ 13 | 147 : 163 | small | n. s. |
| ♂ 8 | ♂ 12 : ♀ 2 | 219 : 201 | great | n. s. |
| | ♂ 12 : ♀ 5 | 168 : 123 | great | $< 0.01$ |
| | ♂ 12 : ♂ 8 | 146 : 152 | medium | n. s. |
| | ♂ 12 : ♂ 2 | 58 : 52 | medium | n. s. |
| | ♂ 12 : ♂ 13 | 63 : 82 | small | n. s. |
| ♀ 9 | ♂ 8 : ♂ 12 | 28 : 36 | medium | n. s. |
| | ♂ 8 : ♂ 12 | 21 : $7^{+++}$ | medium | $< 0.01$ |
| | ♂ 8 : ♂ 12 | 293 : 300 | medium | n. s. |

$^{+}$ First training session: 34 : 16, $p < 0.02$.
$^{++}$ n. s. = not significant.
$^{+++}$ Loudspeakers erroneously exchanged.

which the loudspeakers were erroneously exchanged, and in which she was rewarded for a choice of the negative call (♂12), and driven back without food when she chose the positive call (♂8). During this time she showed a significant preference for the call of ♂8. In one sequence she chose his calls 12 times running, for which the random probability is only $(1/2)^{12}$. When the error was corrected and approach to the call of ♂8 was rewarded again, she failed in the course of about 600 trials to discriminate reliably.

Presented with the distance calls of ♀3 and ♀11, which ♂3 had distinguished spontaneously and estimated in the same way as he had the live birds, he at first learned to choose ♀3's calls. Later on he chose the calls of each bird equally often, and finally developed a position habit. A similar development in the course of training was observed in the reactions of ♂8: presented with a new two-choice series, he frequently began by choosing the new call (♂12 remained the positive object bird during all his training in distance call discrimination), then switched to the familiar positive call, and finally chose both equally often.

## 4. Determination of the relative importance of optical and acoustical characteristics in the training situation

In the training situation it was possible to present optical and acoustical characteristics separately. This was an obvious opportunity to test which of the 2 sets of characteristics was more heavily relied upon by the subject birds in the training situation.

*Table 6:* Relative importance of slides and distance calls

| | Subject birds | Object birds + : - | choices between + : - | no. of slides | $\chi^2$ | p |
|---|---|---|---|---|---|---|
| 1. Training: slide + calls between tests (2) | ♂ 3<br>♂ 8 | ♀ 3 : ♀ 11<br>♂ 12 : ♂ 13 | 185 : 55<br>216 : 128 | 10 : 10<br>16 : 16 | 70.4<br>22.5 | $<0.001$<br>$<0.001$ |
| | | | slides (+) : calls (+) | | | |
| 2. Test: calls exchanged | ♂ 3<br>♂ 8 | ♀ 3 : ♀ 11<br>♂ 12 : ♂ 13 | 70 : 40<br>64 : 36 | 10 : 10<br>16 : 16 | 8.2<br>7.8 | $<0.01$<br>$<0.01$ |

♂3 and ♂8 had first been tested to see whether their live-bird learning would be transferred spontaneously to the presentation of slides and distance calls (Table 3,1. and Table 4). Immediately after these tests — without intermediary training to slides or distance calls — both ♂♂ were trained to discriminate between slides and distance calls of their respective object birds. After some time both birds learned to discriminate (Table 6,1. and Fig. 9).

Tests were then interposed in the normal training: the distance calls of the 2 object birds were exchanged, and each presented together with the slide of the unrelated object bird. In these tests both ♂♂ chose the slides of the positive object birds significantly more often than their calls (Table 6,2).

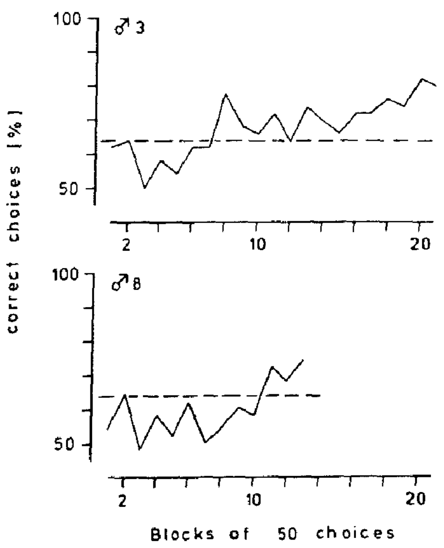


*Fig. 9.* Learning curves in training to slides and distance calls combined. ♂3 chose between ♀3 and ♀11, ♂8 between ♂12 and ♂13. Presentation as in Fig. 2

♂3 chose the slides of the negative bird significantly more often ($p < 0.01$) when they were presented together with the call of the positive bird than in the normal situation. This means that ♂3 used both slide and call for his discrimination, but laid more emphasis on the slides. ♂8 chose the slides of the negative bird with equal probability in both situations.

This result agrees well with the results of training to distance calls, in which it was seen that ♂3 could distinguish reliably between the calls of ♀3 and ♀11, but neither of the 2 ♂♂ could distinguish between the calls of ♂12 and ♂13.

## Discussion

### a) Demonstration of individual recognition

It has been shown to be very probable that both partners of a budgerigar pair recognize each other individually (TRILLMICH 1976a). It may therefore be presumed that in these experiments subjects had to learn the training situation, rather than the discrimination between individuals, especially if one of the 2 object birds was its mate.

Budgerigars of both sexes could differentiate between various ♂♂ and ♀♀ in the experiments. All birds trained learned to master the discrimination task. Both partners of a pair can therefore recognize each other individually.

It was surprising to find that ♀12 could not discriminate between ♀13 and ♀14 in the training situation. To judge from their behaviour, other birds in the aviary could distinguish between the two. But of course they had at their disposal more behaviour characteristics to enable discrimination than had ♀12, who was required to choose between two still and silent ♀♀. In addition, ♀12 panicked several times. A slight tendency to escape, however, can reduce discrimination performance in a choice situation considerably (BERNSTEIN 1957, SOUTHERLAND 1961). The failure of ♀12 is therefore presumably an artifact of the training situation. But as she later succeeded in distinguishing between ♀13 and ♀15, it may be assumed that ♀13 and ♀14 looked very much alike, even for budgerigars. Her case is, however, a reminder that the performance of the other trained birds may reasonably be considered minimal.

### b) Visual discrimination

It was possible to conclude from the experiments with live birds that, as the object birds remained for the most part silent, the subject birds could discriminate between them by means of visual characteristics. Olfactory recognition is extremely unlikely in parrots, as their olfactory brain is one of the smallest known in birds (WENZEL 1973).

*Possible optical identification features:* For the budgerigars in these experiments, features of the head region were most important for discrimination. Features attracting the attention of humans, such as colour-bands or a bent tail feather, were not used by the birds for identification. These results agree with observations and experimental findings of other authors for other bird species (GUHL and ORTMANN 1953, LORENZ 1935, HEINROTH in LORENZ 1935, NICE 1943, NOBLE 1936, NOBLE, WURM and SCHMIDT 1938).

But which head characteristics are involved in individual recognition? Neither in the experiment with ♀12, nor in the separation experiment with 6 budgerigar pairs was there any evidence that throat spots played a role in individual recognition. CINAT-THOMSON (1926) concluded from experiments on mate selection that ♂♂ were the more attractive the greater their throat spot size; she conceded, however, that male 'temperament' might be of equal importance. Reservations against assuming that mate selection is based largely on throat spot size were strengthened in my own preliminary experiments. The functional significance of the conspicuous throat spots in budgerigars thus remains obscure.

The features which enabled ♀12 to discriminate between ♀♀13 and 14 are categoric rather than individual. The blue cere 'changed' ♀14's sex, while the forehead painting simulated a young bird moulting into adult plumage. In some adult budgerigars, however, the area of the yellow forehead is small; so these experiments merely indicate that features of forehead patterning may be important for individual recognition.

In some bird species head measurements vary more than those of other parts of the body (DAVIS 1951, MILLER 1941, PITELKA 1951, SCHERNER 1974). MARLER (1961) remarked in this context: '. . . some of the variability may be a positive adaptation to aid individual recognition.' This hypothesis is extremely attractive, as head proportions would change less in the moult than feather patterning, and could also serve monochromatic species in discriminating between individuals.

*Recognition of slides:* Training with slides meant that all acoustical and olfactory individual traits were eliminated, and the optical ones could be tested independently, even if only two-dimensionally. In these experiments, each of 10 or 16 different slides of one object bird could be shown together with any of 10 or 16 slides of the other object bird. The 2 ♂♂ did not merely memorize the slides as positive and negative spot patterns, but allocated them to 2 categories corresponding to the 2 live birds. This is the only possible explanation for the consistent choice of slides of the positive bird by the subject, when shown new slides of both birds. The characteristics learnt from the slides by ♂3 to form this kind of concept even enabled him to identify the live birds.

The construction of very complex concepts has also been demonstrated in pigeons (HERRNSTEIN and LOVELAND 1964, MALOTT and SIDALL 1972). The pigeons learnt to distinguish slides with people from those without, they developed a 'people concept'. The authors did not test whether the 'concept' obtained from the slides could be transferred to live persons, but suspected that it existed prior to training. HUMPHREY (1974) succeeded in showing that rhesus monkeys are not only able to differentiate between slides of conspecifics, but that experience with slides even allowed them to discriminate between slides of individuals of other animal species.

The budgerigars generalized from slides to live birds, but not from live birds to slides. This is probably because in the tests for transfer from birds to slides, the ♂♂ were subjected to a new, unfamiliar lighting, which may have activated an escape tendency, and so reduced their performance. The transfer from slides to live birds, on the other hand, brought ♂3 into another familiar situation. An alternative explanation, not excluding the first, is that transfer from the complete presentation (3-dimensional, moving bird) to the incomplete presentation (2-dimensional, motionless bird) may be more difficult to master than the reverse.

These results allow the conclusion that in the budgerigar, individual recognition is possible by optical means alone.

### c) Acoustical recognition

The budgerigars could distinguish between distance calls only if they differed considerably. If the learning experiments are any indication, a budgerigar in a flock cannot recognize all other individuals by their calls.

Even in the budgerigars' most sensitive frequency range between 1 and 4 kHz their differential frequency sensitivity is slightly less than in man (DOOLING and SAUNDERS 1975). If time resolution in the budgerigar is not much better than in man, then the birds may really be unable to discriminate between very similar calls. Negative results, however, always allow various interpretations; also, some observations during training with distance calls suggest a better discriminatory ability.

Several not mutually exclusive explanations are possible for the birds' failure to differentiate between similar calls.

1. Reflections from the walls of the Y-maze may have obscured differences between calls.
2. The position of the loudspeakers on the roof of the cage-arms could have made the stimulus-reward connection less effective than e. g. in slide training. This would mean that, due to decreased contiguity of stimulus and reward, the birds learned to discriminate only between greatly differing distance calls.
3. COWEY (1968) reported on the difficulties of training an animal to discriminate between 2 parallel acoustical stimuli. Even monkeys learn such a discrimination only with great difficulty in a procedure with reinforcement, but far more quickly in an avoidance procedure. According to COWEY (1968) the difficulty could be partly due to the fact that diurnal animals seek for optical cues, and so come to learn irrelevant characteristics of the situation.
4. The weakness of the reaction to the acoustical stimuli may be partly due to habituation; the birds answered the recorded calls with their own distance calls only during the first 5—10 trials. Similar habituation to acoustical models is known in the wild for other bird species (SCHUBERT 1971, HELB 1973). But as the choice of the positive call was continually rewarded in the experiments, it is hard to understand why the birds should have become habituated to it.
5. When a budgerigar becomes separated from the flock it starts calling loudly, which regularly leads to an answer by birds in the flock. The separated bird then approaches the flock, thus coming again into visual contact with its flockmates. If a bird approaching the source of a distance call expects to come into visual contact with another bird, then the subject birds may have been frustrated during training, as they always approached a calling 'bird' but never made contact with it. This may have eventually induced them to disregard the calls and to choose according to other cues, e. g. position.

### d) Possible interaction of optical and acoustical stimuli

During training, both ♂♂ depended more on optical than on acoustical stimuli. This was not because the presentation of the distance calls sounded too unnatural, for ♂ 3 successfully transferred his choice reaction from live birds to their recorded distance calls.

When slide and call were offered him simultaneously, a significant influence of the distance calls upon his choice behaviour was still apparent after ca. 1000 trials (see p. 390). In a further 250 choices between distance calls without optical stimuli, he soon began to choose each call equally often, and finally developed a position habit. This means that after a while, the acoustical stimuli stopped controlling the choice reaction; but combined with optical stimuli, acoustical stimuli had been shown to retain an influence upon the choice reaction even after 1000 choices. The optical stimulus seems, therefore, to contribute to the persistence of the reaction to the acoustical stimulus.

It may be that acoustical stimuli acquire their full significance for the budgerigar only when combined with optical stimuli. Ducklings of open-nesting species cannot be imprinted on acoustical stimuli without simultaneously being offered optical stimuli (KLOPFER 1959, KLOPFER and GOTTLIEB 1962, FISCHER 1966, COWAN 1974, EISERER and HOFFMANN 1974, summary in HESS 1972). If ducklings are offered an optical imprinting model combined with acoustical stimuli (usually over a loudspeaker in the model) they learn to distinguish these from other acoustical stimuli. In imprinting, the acoustical stimulus boosts the attraction of the imprinting object, which for its part stimulates the young bird to learn fine details of the acoustical stimulus. Such an interaction between optical and acoustical stimuli may also occur in the budgerigar.

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## Summary

The characteristics used by budgerigars for individual recognition were investigated by means of learning experiments.

2 ♂♂ and 3 ♀♀ learned to discriminate between various conspecifics of either sex in a 2-choice situation. Characteristics used for identification were mainly of the head. Experimental alterations of head patterning gave no clear indications of the characteristics involved in individual recognition.

Training enabled 2 ♂♂ to distinguish between colour slides of 2 object birds, and to react accordingly to further, as yet unseen slides of these. 1 ♂ trained with the slides of 2 ♀♀ chose accordingly between the 2 live birds when these were later presented.

Distance calls of budgerigars have characteristics peculiar to individuals. In training, budgerigars discriminated only between greatly differing calls.

2 ♂♂ learned to discriminate between the slides plus attributive distance calls of 2 object birds. When the calls were exchanged and presented with the unrelated slides, the birds chose mainly according to optical stimuli.

The results show that individual recognition is possible from optical stimuli alone; acoustical stimuli were less effective under the experimental conditions.

Possible reasons for the failure of the budgerigars to discriminate between similar acoustical stimuli are discussed, including the hypothesis that the latter attain greater significance in combination with optical stimuli.

## Zusammenfassung

Es wurde versucht individuelles Erkennen beim Wellensittich mit Lernversuchen nachzuweisen und zu analysieren, welche Merkmale daran beteiligt sind.

2 ♂♂ und 3 ♀♀ wurden in einem Y-Labyrinth mit Futterbelohnung darauf dressiert, verschiedene ♂♂ bzw. ♀♀ voneinander zu unterscheiden. Die

Vögel bewerteten den Vogel, bei dem sie belohnt wurden, als zur Wahl stimulierenden Reiz, den anderen als Wahl-hemmenden Reiz. Die verwendeten Unterscheidungsmerkmale lagen vorwiegend in der Kopfregion. Veränderungen der Kopfzeichnung gaben keine eindeutigen Hinweise, welche Merkmale für das individuelle Erkennen verwendet wurden.

2 ♂♂ konnten nach der Dressur verschiedene Farbdias zweier Wellensittiche unterscheiden. Sie reagierten auf weitere, noch nie zuvor gesehene Dias dieser Vögel im Sinne der Dressur. Ein ♂ wählte zwischen 2 ♀♀, auf deren Dias er dressiert worden war, wie zwischen den Dias.

Die Distanzrufe von Wellensittichen besitzen individuenspezifische Merkmale. In der Dressur unterschieden die Wellensittiche nur zwischen sehr verschiedenen Rufen eindeutig.

2 ♂♂ konnten erfolgreich auf die Unterscheidung der Kombination von Dias und entsprechenden Distanzrufen zweier Wahlvögel dressiert werden. Wurden ihnen die Rufe und die Dias anschließend über Kreuz geboten, richteten sie ihre Wahl bevorzugt nach den optischen Reizen.

Die Ergebnisse zeigen, daß individuelles Erkennen durch optische Reize ermöglicht wird, akustische Reize dagegen unter den Versuchsbedingungen weniger geeignet sind. Mögliche Gründe für das Versagen der Wellensittiche in der Dressur auf akustische Reize werden diskutiert, so unter anderem, daß akustische Reize in Verbindung mit optischen von den Wellensittichen stärker beachtet werden.

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