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HOW DO HENS VIEW OTHER HENS? THE USE OF LATERAL AND BINOCULAR VISUAL FIELDS IN SOCIAL RECOGNITION

by

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(With 2 Figures) (Acc. 24-IV-1995)

Summary

When shown familiar and unfamiliar birds at different distances, hens viewed birds 0.7 m or 1.4 m away with modal head angles between 54° and 72° from the midline, using the lateral visual field but viewed birds closer (less than 20 cm) binocularly, with the head within 18° either side of the midline (Expt. 1). When faced with a choice between a familiar and an unfamiliar bird at different distances, hens chose the familiar bird if the choice could be made 8 cm away but their choices were random if they had to chose 66 or 124 cm away (Expt. 2). This suggests that hens may be unable to discriminate familiar from unfamiliar birds except when they are very close to them. Observations of freely moving birds suddenly confronted with another hen (Expt. 3) showed that even when the object bird was familiar, it was in all cases initially scrutinized from a close distance (26 cm or less), which is consistent with the hypothesis that hens are unable to recognize other birds except when close enough to view them with the myopic lower frontal field. Reasons for this constraint on social recognition are discussed.

Introduction

The eyes of many birds have different retinal areas specialised for viewing different aspects of the environment. For example, chickens, pigeons and other ground-feeding birds have a gradient of myopia in the lower frontal field that enables them to obtain a sharp image of close objects on the ground as they walk along at the same time as being able to use the lateral field of the two eyes to give them a near-panoramic but still focussed view of more distant objects (FITZKE *et al.*, 1985; HAYES *et al.*, 1987; HODOS & ERICHSEN, 1990). Measurements of the distance from which such birds scrutinize food objects (GOODALE, 1983; MACKO & HODOS, 1985) show

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that they pause at that distance which gives a sharply focussed image in the myopic lower frontal field which projects onto the upper temporal quadrant – 'red field' – of the retina (ERICHSEN *et al.*, 1989). Such findings have led to the widespread assumption that the main if not the only function of the lower frontal binocular field is to enable a bird to peck at food objects. All other visual functions, including the initial detection of food, detection of enemies and discrimination of conspecifics are assumed to be carried out using the lateral visual field (BISCHOF, 1988; GÜNTÜRKÜN *et al.*, 1993) or by the emmetropic upper binocular field used when the bird is looking at distant objects straight ahead and above the eye-beak axis (ERICHSEN *et al.*, 1989; ANDREW & DHARMARETNAM, 1993).

In the course of a study on how hens recognize familiar flock mates, however, it became apparent that these birds also used their lower frontal binocular field in social interactions, many of which involve either pecking or close scrutiny of other birds from distances and angles comparable to those used in pecking food. I now describe three experiments that suggest that not only do hens use the front binocular field for the recognition of familiar conspecifics but that, furthermore, they may be unable to discriminate birds from their own and other flocks unless they are close enough to bring the head of the other bird within the focussing distance of the myopic lower frontal field.

The starting point for the study was the well-established phenomenon that chickens in small groups form stable dominance hierarchies or 'peck orders' (Schelderup-Ebbe, 1922; Wood-Gush, 1971; Rushen, 1982). Although it is unclear whether whether hens recognize each other as individuals (ZAYAN, 1989; BRADSHAW, 1991), there is clear evidence that they respond differently to other hens depending on whether they are familiar with them. For example, chickens and red junglefowl (from which modern breeds derive) associate preferentially with familiar individuals (DAWKINS, 1982; KEELING & DUNCAN, 1991; SULLIVAN, 1991; BRADSHAW, 1992) and show much more aggression towards unfamiliar than familiar birds (HUGHES, 1977; ZAYAN, 1987), a fact that is of considerable importance for hen welfare and the design of husbandry systems. Discrimination between familiar and unfamiliar individuals appears to be visual (GUHL & ORTMAN, 1953) but little is known of how hens make the discrimination between familiar and unfamiliar birds. A number of studies have used photographic images to study how hens discriminate

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between individuals (e.g. CANDLAND, 1969; RYAN, 1982) but are subject to the objection that the hens may not perceive these as representing real birds (BRADSHAW & DAWKINS, 1993). Consequently, studies of hens interacting with live birds are essential.

The aim of the first experiment reported here was two-fold. The first aim was to provide quantitative information on how hens view each other when they are suddenly confronted with a live bird that might or might not be a member of their own group -i.e. before and during the process of deciding whether it was a familiar or an unfamiliar individual. The second, complementary, aim was to document what views of the other bird hens have when they make such a decision. For example, if hens always view each other' with the lateral visual field, then they would see only the sides of each others heads and, as a result, might rely particularly on cues visible from the side, such as the shape of the comb. If they show evidence of behaving differently towards members of their own group and unfamiliar birds with some views and not others, this would in itself suggest hypotheses as to what cues they might be using. In this first experiment, the head and body angle between two hens were monitored with overhead video cameras when a visual barrier between them was suddenly removed to reveal either a familiar or an unfamiliar hen at one of three distances.

Experiment 1

Methods.

Animals.

Twelve ISO Brown hens were used for this experiment. Six were designated as test hens and six as object hens. They were housed together with others in two pens (each 3.5×1 m) with an opaque plastic screen separating the two pens so that the two groups were in visual but not auditory isolation. There were 8 birds in each pen, all marked with coloured leg bands. The hens had been living in these groups for approximately 10 weeks. 'Familiar' birds were those from the same pen; 'unfamiliar' were those from different pens. The pens were in a room heated to a constant temparature of 19-20° C on a light-dark cycle of 14 hours light and 10 hours darkness. The floor was covered in wood shavings and the birds were fed on a commercial mixture of grain and mash on an *ad libitum* basis. Each pen contained a wooden nest box and two perches.

Apparatus.

Two circular cages (42 cm diameter and 54 cm high) were used to constrain the distance between two hens. One hen was put in each cage. The lids of the cages were made of clear perspex so that the hens were clearly visible to overhead cameras. The sides of the cages were made of 1 cm vertical dowelling set 6 cm apart and the hens could put their heads out through the gaps. The hens could turn round in the cages but, by moving the two cages, their position relative to one another could be controlled to within the distance they could move within the cages. The cages were placed at one of three distances from one another: 1.4, 0.7 or 0 m (touching). Two video cameras were placed over each cage separately, 1 m directly above it. The signals from both cameras were fed into a Digital WJ-MX production mixer which put both pictures onto a single tape using a Sony BNR Betamax videorecorder.

Procedure.

The two cages were set up according to a pre-arranged plan of distance and whether the hens were familiar to one another. Each of the 6 test hens was tested a total of 6 times, at each of the three distances and with either a familiar or an unfamiliar object hen in the other cage. Different hens received their 6 tests in different orders. Before a test, a piece of wood was placed between the cages so that the hens could hear but not see each other. The two hens (the test bird and the object bird) were put in the cages and allowed 2 minutes to settle down. After this period, videotape records were made for 10 minutes. For the first five minutes, the barrier remained in place. It was then removed for the second period of five minutes.

The videotapes were subsequently analysed by measuring the head angle of the test bird relative to the object bird to the nearest 18° every second. Other behaviour patterns that were described from the videotapes were preening, pecking at the floor, raising neck feathers and escape attempts (repeatedly putting head through the bars on the side of the cage away from the other hen).

Results.

The head angles of the test birds relative to the object birds are shown in Fig. 1, which shows the frequency distributions of angles for all 6 birds, during the first 20 seconds after the barrier was removed. At the longest (1.4 m) distance and the middle distance (0.7 m), there is a bimodal distribution with peaks at 54-72° either side of the midline but for the closest distance, when the cages were touching, the most frequent angles lie within 18° either side of the mid-line. For statistical analysis, the number of seconds (out of a possible 20) where the head angle was within 18° of straight towards the other bird was used as the dependent variable and the data subjected to a 3-way 'hens' (blocks) \times distance \times familiarity ANOVA (SOKAL & ROHLF, 1969, p. 348) with repeated measures. There was a highly significant effect of the distance between test bird and object bird on the head angle (F = 16.28; df = 2,10; p < 0.001) but no effect of whether the object bird was familiar or unfamiliar (F = 0; df = 1,10; p > (0.75) and no interaction between familiarity and distance (F = 0.55; df = 2,10; p > 0.75). There was no significant difference in the use of the left or right eye (p > 0.1). The numbers of other behaviours (preening, escape attempts, hackles raised) recorded were too small for statistical compari-

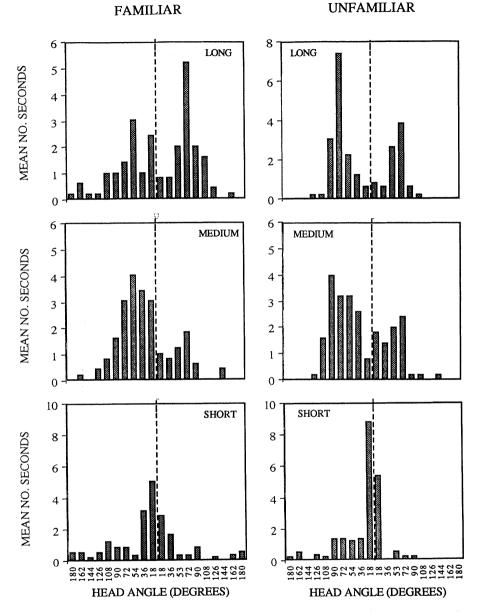


Fig. 1. Head angles shown by 6 hens in the first 20 seconds after removal of a barrier to reveal either a familiar or an unfamiliar hen at three different distances between cages (Long = 140 cm; Medium = 70 cm; Short = 0 cm). Each bar shows the mean number of seconds spent by the 6 birds with the head at that angle, with the standard deviations represented as vertical lines. The major dotted vertical line shows where the beak points directly towards the other bird; bars to the right or left of this line indicate viewing with the right or left eye respectively.

son but it was notable that the only occurrences of hackle raising (4 hens) and escape attempts (2 hens) were in the close unfamiliar tests.

Discussion.

When a hen was suddenly shown another hen 0.7 or 1.4 m away, it viewed the other bird by turning its head sideways to an angle that was variable but tended to lie between 54° and 72°, which is consistent with the fact that they were using the lateral visual field to view it. This is comparable to ANDREW & DHARMARETNAM'S (1993) finding that domestic chicks have two peaks of head fixation, one at 30-39° and another at 60-69°, which they argue indicates monocular fixation using the lateral field on the basis of their calculated limits of binocular fixation in the chick as about 27°. BISCHOF (1988) also found that zebra finches commonly fixate food grains with the head at about 60°. However, when the other bird was very close (10-20 cm), it was viewed frontally, within 18° either side of a line pointing directly at the other bird. This suggests that the other bird was being viewed binocularly since 18° is within the known limits of the binocular field of both the chick (ANDREW & DHARMARETNAM, 1993) and the pigeon (NALBACH *et al.*, 1990).

The lack of difference in head angles between familiar and unfamiliar bird tests suggests that this binocular scrutiny was part of the recognition process rather than or at least as well as part of an aggressive response to a strange bird. Furthermore, it was only in the close unfamiliar tests that any consistent differences in behaviour (hackle raising, aggressive pecking or escape attempts) were apparent at all and these occurred only after the binocular looking. If binocular scrutiny is indeed part of the process by which hens discriminate familiar from unfamiliar hens then this suggests that they may be unable to make this discrimination unless they are very close to one another, possibly not unless they are close enough to be able to focus the other hen in their myopic lower frontal field. To test this idea, the next experiment was designed to see whether hens ability to discriminate familiar from unfamiliar hens was related to their distance from the other bird.

Experiment 2

The sight of a feeding bird is an attractive stimulus to other hens and hens prefer to feed near familiar birds (BRADSHAW, 1992). In this experiment,

hens were given a choice between feeding near a familiar hen and near an unfamiliar one but forced to make the choice at different distances from them. The hens were forced to make their choices at different distances by placing a barrier between the two target hens and varying the length of the barrier.

Methods.

Animals.

Ten hens, drawn from the same groups that had been used in the previous experiment, were used. Housing conditions were similar to those used previously and this experiment was done approximately two weeks after the first.

Apparatus.

Two target hens, one familiar (from the same group as the test hen) and one unfamiliar (from the other group) were placed in circular cages (42 cm diameter and 54 cm high) with walls made of 1cm dowelling placed 6cm apart so that they could be clearly seen by the test hen. In front of each cage was placed a small (8 cm) dish containing chicken mash. The cages of the two target birds were visually separated from one another by a hardboard barrier which was one of three lengths: 'short' = 56 cm, which was enough to prevent the target birds seeing each other and projected 8 cm in front of the target bird cages; 'medium' = 114 cm and which projected 66 cm and 'long' = 172 cm and which projected 124 cm. A start box ($430 \times 400 \times 480$ cm high) for the release of the test hen was placed 1800 cm away from the target hens. The start box had both a perspex and a wooden door. The floor between the start box and the target hens was marked into 600 cm sections with adhesive tape so that the position of the test bird could be easily recorded.

Procedure.

Each of the 10 test hens received 4 choice tests at each of the three distances. To control for possible effects of position, the familiar bird appeared on the right in two of the tests and on the left in the other two. To control for the possibility that one of a pair of hens fed more vigorously or was more attractive for reasons other than its familiarity, each test bird was tested with two separate pairs of target birds, the target hens were changed frequently and a given target bird appeared as both the 'unfamiliar and the 'familiar' to different test hens. In two of the four choice tests given to one test hen, the same two target birds were presented, once with the familiar bird on the left and then immediately afterwards with the familiar bird on the right. In the other two tests, carried out on another day, another pair of target birds was used, again with a change in the position of the two birds. To control for the effects of the order in which birds received their short, medium and long barrier tests, different individuals received these in different orders according to a pre-arranged schedule.

For each test, the test bird was placed in the start box with both doors down. After 1 minute, the wooden door was raised, leaving only the clear perspex door in place. After 30 seconds, this was raised and the test bird was free to leave. The times when it moved into each section of the apparatus were recorded with a stopwatch as was the time taken to feed at one of the dishes in front of the target hens. A choice was considered to have been made when the hen started to feed and tests were stopped if no choice had been made for 5 minutes.

Results.

The choices made by the hens are shown in Fig. 2. For each hen, the 4 choices it made in each of its three types of test (short, medium or long barrier) were expressed as a single percentage for familiar hens for that test type. Statistical analysis was done on angular transforms of the original data. There was a highly significant effect of barrier length on the choices for feeding with a familiar hen (2-way ANOVA F = 10.95; 2,18; p < 0.001) as well as a significant difference between hens (F = 2.85; 9,18; p < 0.05). With the medium and long barriers, the hens' choices were no different from chance (p > 0.1; Binomial test) and only with the short barrier was a preference for familiar hens apparent (all 9 hens that made a choice showed a preference for familiar target birds; 1 hen failed to choose; p = 0.02, Binomial test).

In the short barrier tests, the hens were able to make and remake choices at any point between the start box and the final choice to feed and so the paths taken by the hens in these tests were further analysed to see if they gave additional evidence of where hens had made their choices. If hens had made their choices from the start box, they could be expected to have taken a direct path to the familiar hen. If, on the other hand, they made their choices only much closer, their paths could be expected to be longer than the direct path as they would have to correct themselves as they moved. Since the position on the grid and time of crossing each line had been recorded, the paths could be reconstructed. For all 9 birds for which familiar hens were chosen (one bird chose one unfamiliar and three 'no choices' and was discounted from this analysis), hens took longer paths (mean = 2201 cm) than expected (= 1800 cm; $\chi^2 = 23.14$; p < 0.01).

Discussion.

The hens had a clear preference for feeding near a familiar rather than an unfamiliar hen but only when the barrier between the target hens was short (8 cm) and they were able to choose which hen to feed with when they were very close to the target hens. When forced to choose at larger distances (66 or 124 cm), their choices were essentially random. This strongly suggests that they could not recognize a familiar hen except when close, but it is still possible that they could in fact discriminate at larger distances but were not sufficiently motivated to do so. The analysis

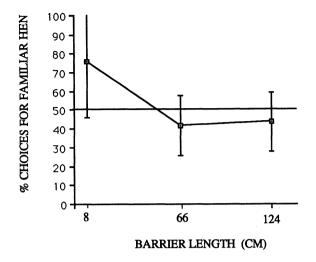


Fig. 2. Choices between familiar and unfamiliar target birds made by hens with barriers of different lengths.

of path lengths in the short barrier tests, however, makes this unlikely. In these tests, where the hens were free to make and then remake their choices at all distances as they approached the target hens, they consistently took longer routes than would be necessary if they had already made their final discrimination when they left the start box. The most likely explanation of this is that they could see hens feeding at the longest distance but could not identify them and then had to correct their routes when they were close enough to recognize familiar from unfamiliar birds.

The results of Experiments 1 and 2 are thus consistent with the hypothesis that hens are unable to tell whether a hen is familiar to them unless they are close (within 30 cm) and unless they view it with the frontal binocular field. How plausible is it that hens use the myopic frontal field for social recognition? HODOS & ERICHSEN (1990) measured the degree of myopia in the frontal fields of birds of different eye heights and found it to be consistent with the values predicted by FITZKE *et al.* (1985) from the following equation:

 $R = \sin A/H = 1/V$

where R is the state of the eye in diopters (D), A is the angle of elevation below the horizon, H is the pupil height (vertical distance from eye to ground) and V is the viewing distance to an object on the ground.

For adult broiler chickens (pupil height = 54.0 cm), HODOS & ERICHSEN give the degree of myopia in the lower field of -1.4D for A= 60°. However, egg-laying hens are considerably smaller than broilers and their eves are consequently nearer the ground. Substituting an eve height of 32 cm (DAWKINS, 1985) in the above equation gives a value of myopia of between -2D and -3D for an elevation of 60°. This means that the hens used in this study would be unable to view the head of another bird in clear focus at distances greater than 1/2-1/3 m. If the front binocular field is indeed used for the discimination of familiar from unfamiliar birds, then we should expect that when hens make such a discrimination, they should position themselves within this distance. While it is impossible to obtain accurate measurements of the distances and angles from which freely moving birds view each other, such observations can be used to see whether the hypothesis that the lower binocular field is used in social recognition is within the bounds of plausibility. For example, if hens never come near enough to each other to be able to use the myopic lower field, then the hypothesis would have to be discarded. If, on the other hand, even hens that are familiar scrutinize each other from a close distance, the hypothesis is at least worth testing further. What is meant by 'close' can also be specified more accurately. The outer predicted limit would be 33-50 cm since beyond this, objects could not be clearly focussed by the myopic lower field. The inner limit would be set by the near point of accommodation which for chickens has been estimated to be about 5 cm (SCHAEFFEL et al., 1986).

Experiment 3

A visual barrier between two familiar hens was suddenly removed and the subsequent behaviour of both birds was recorded on videotape. For ethical reasons (to avoid the fights that were likely occur between birds that were strangers to each other) the two hens were always from the same group but had been separated for a few minutes and then observed in a place that was unfamiliar to both of them. It was reasoned that if two familiar hens that had been together in their home pens within ten minutes previously still investigated each other from a close distance, this would be strong evidence that recognition of familiar group members depended on the frontal visual field.

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Methods.

Eight of the hens that had been used for the previous experiment were used for this series of observations. They were placed one at a time in an arena $(700 \times 2000 \text{ cm})$ at one side of which there was a wooden barrier. A member of the bird's home group (a different one for each bird) was placed behind the barrier so that the two birds could not initially see each other. After two minutes, the barrier was removed and the behaviour of the two birds was observed for a further five minutes. The whole sequence was recorded on videotape using a camera positioned 2 m from the birds, to the side. Estimates of distances between hens were obtained by measuring the size of a real hen's head, measuring this on the videotapes and then applying the appropriate correction for the observed distance on the tapes. Since it was impossible to know which part of another hen's head a bird was looking at, the distance between the eyes of the two birds was measured. Obviously, if the hen was in fact looking at, say the tip of the comb, this would tend to be a over-estimate.

Results.

All observed instances of the subject and target hens being within 40 cm (eye to eye distance) of each other are shown in Table 1. In all tests, one or more of the following 'close-up' behaviours were seen: (i) comb pecking (CP) – one bird gives a sharp downward peck onto the front of the other bird's comb (ii) mutual looking (ML) – both birds face each other from the front with their heads approximately level (iii) one-way looking (OL) – one bird looks down onto the comb of the other one. In each encounter,

TABLE 1. Occurrence (and duration) of mutual looking (ML), one-way looking (OL) and comb pecking (CP) when hens were within 30 cm (eye-

Hen	lst minute	2nd minute	3rd minute	4th minute	5th minute
1	ML (1 s)				
	OL $(2 s)$				
	CP				
2	ML (1 s)				
3	ML(1 s)				
	OL (at) (1				
	s)				
	CP (at)				
4	ML (2 s)				
5	ML (32 s)				
6	ML (7 s)				
7	ML (2 s)	ML (5 s)			
	ML (4 s)				
8	ML (1 s)	OL (4 s)			
		OL(1 s)			

to-eye) of each other in the 5 successive minutes of Experiment 3

The mean distance (eye-to-eye) for ML = 13.4 cm (N = 10; SD = 6.57; min = 4.5 cm; max = 26 cm). The mean distance for OL = 13.7 cm (N = 4; SD = 3.06; min = 10.3; max = 16.3). 'at' means test hen was recipient rather than giver of CP or OL.

therefore, at least one bird viewed the head of the other at distances of less than 30 cm and in most instances much closer than this. At least one incident of this close-up viewing took place within the first minute of every test, and often not thereafter, strongly suggesting it was part of a recognition process that took place even when birds were familiar with each other.

Discussion.

Even when birds were familiar to each other and had been in the same home pen together within the last 10 minutes, each encounter (sudden appearance of a bird in an unfamiliar place) was quickly followed by the two birds coming close (within 30 cm and often much closer) to each other, close enough to be consistent with the hypothesis that the myopic lower frontal field was being used to recognize a familiar group member. In two cases, actual pecking of the comb of the other bird was observed, clearly indicating use of the myopic 'pecking field'. Even where no actual pecking occurred, hens scrutinized each other 'head on' from short distances when they initially met another bird. Even though this scrutiny often lasted for only a few seconds, it seemed to be necessary for the hens to establish the identity of the other bird, which was then largely ignored for the rest of the test.

Much of the behaviour of domestic hens involves very close contact with other birds and in many cases actual pecking. Allopreening, such as gentle pecks to feathers, and beak-pecking are common amongst groups of birds that are familiar with each other (LILL, 1968; WOOD-GUSH & ROWLAND, 1973; VESTERGAARD *et al.*, 1993) and provide opportunities for close and prolonged scrutiny of other birds. Aggressive behaviour also involves pecks to the head of the opponent (RUSHEN, 1982) and it is reasonable to assume that the accurate delivery of aggressive pecks uses the same lower frontal field specialisations as that of food pecking. The fact that the beak is used for so many different functions means that many different kinds of behaviour from fighting to mutual grooming and recognition may make use of the same visual specialisations as have been evolved for efficient food pecking.

General discussion

The evidence from these three experiments lends support to a particular and somewhat surprising hypothesis about the way in which hens discriminate familiar from unfamiliar conspecifics. This is that they are unable to make such a discrimination unless they are within 8-30 cm. which would bring the head of the object bird within the focussing distance of the binocular myopic lower visual field.

This is not because hens lack the visual capability for making complex discriminations at bigger distances, since RYAN (1982), BRADSHAW & DAWKINS (1993) amongst others, have successfully trained hens to discriminate photographic slides of individual hens placed at distances of over 1m. In drawing conclusions about social recognition in hens, a distinction should perhaps be made between what hens can be trained to do in an operant conditioning experiment and what they spontaneously do in more natural situations.

BRADSHAW (1991) trained hens to discriminate between two real hens for a food reward in a Y-maze when the birds had to make their choice approximately 0.75m away from the target birds. He was only able to do so, however, after 150-200 trials, which suggested that the task was not a particularly easy one for them. A direct prediction of the hypothesis suggested here is that if hens are conditioned to discriminate between two hens, the task should be relatively easy if they are close to each other but difficult or impossible with distances as great or greater those used by BRADSHAW.

What could possibly be the functional significance of a recognition system that only allows recognition when the hen is so close as to be within striking distance of the beak of another bird and indeed where the posture adopted for recognition (close-up head to head scrutiny) is similar to that of overt aggressive behaviour? In other words, why can't hens recognize each other at safer distances? Potential cues, such as comb shape and size (which differ markedly between individuals) are present and can be used by hens when they are trained in operant conditioning tasks (CANDLAND, 1969). The risk of delaying recognition until very close to a potential adversary are considerable. To see why it may occur, we have to consider how hens form and maintain their social relations.

Hens establish their position in a group largely by fighting, which involves aggressive pecking at the head of another bird (RUSHEN, 1982). Their information about each other thus comes from standing close up together, front to front, and either pecking the other bird or being pecked or both. At this stage, their view of each other is a close-up frontal view. In order to be able to recognize each other at a distance, they would somehow have to link this close-up frontal view to a distant front or side view. The problem would be as to how or even whether they could make this link.

There are three possible hypotheses as to why they apparently fail to do so:

1. The cues used by the hens in the recognition of individuals might be such that they are simply not detectable from further away. Visual cues that are undetectable except when the birds are within a few cm. of each other might be such things as the pattern of pits on the comb or the shape of the nares. It is also possible that other cues such as sounds inaudible to the experimenter or smell could be important. These possibilities could be tested by establishing exactly what cues the hens do use for recognition.

2. The hens might be unable to make the connection between the closeup frontal view that they have seen in a fight and a quite different view of the same individual seen from the side that they might see from a distance. As hens view each other laterally at a distance (Expt. 1), they would often not see the familiar frontal view when first encountering another bird. This hypothesis – that they cannot make the connection between the front and side view of the same bird – could be tested by seeing whether hens can recognize each other from long distances when they see the same view (directly from the front) that they have seen close up.

3. It may be difficult for hens to transfer information originally obtained in the frontal field to the lateral field used for more distant viewing. REMY & EMMERTON (1991) reported that in pigeons a discrimination originally learned in the frontal field did not transfer to the lateral visual field but that the same task learned in the lateral field did transfer to the frontal field. REMY & WATANABE (1993) interpret this asymmetry in transfer as reflecting the natural organisation of feeding behaviour. Ground-feeding birds such as pigeons and chickens originally fixate food objects with the lateral visual field and then fixate food again with the frontal field before pecking. If this interpretation is correct, it would imply that hens might find intraocular transfer of information about social companions from frontal to lateral field difficult or impossible.

These three hypotheses thus make different and testable predictions as to why hens seem unable to recognize familiar individuals except when they are close enough to view them with the myopic frontal field. All three suggest that there is no particular evolutionary advantage in such a 'closeup' recognition system. Rather, the nature of the stimuli they use or the structure of the bird's visual system may impose an inevitable constraint on their ability to recognize other birds from long distances. Although this may seem to us to be a severe disadvantage, it may not be so in the natural environment of the junglefowl where small groups of birds stay together most of the time and only occasionally come across other groups (COLLIAS & COLLIAS, 1967). Other birds do not therefore need to be constantly 'checked out' as they are likely to be familiar. Only if something unusual happens (a new bird appears, a flockmate starts behaving

oddly) would the need for positive recognition occur. In the very unnatural environments of commercial farming, however, where birds are kept in 'flocks' of 2000 or more birds a 'close-up' recognition system may impose more of a penalty and may have important implications for hen welfare that have so far not been considered.

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