Hemispheric collaboration in food search in the domestic chick

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ABSTRACT In the domestic chick there is evidence of early development of age-dependent biases of control by the right or the left forebrain hemisphere and this was used to examine the differing roles of the two hemispheres in food search. In normal search for food grains hidden under the sawdust in the test arena, with both eyes in use, the left hemisphere appears to initiate approach and to attempt to identify potential food on entirely local cues. The right hemisphere uses topographical cues to guide locomotion to the location where food has been found in the past.

ABSTRAK Di dalam perkembangan awal anak ayam terbukti adanya penglibatan umur kecenderungan kawalan hemisfera kanan atau kiri pada otak hadapan dan ini dipergunakan untuk mengkaji pelbagai tugas kedua-dua hemisfera itu dalam pencarian makanan. Dalam ujian normal, mencari butiran makanan yang terkambus di bawah debu kayu di dalam arena dengan menggunakan kedua belah mata, hemisfera kiri mengawal gerakan menghampiri dan pengecaman potensi makanan hanya berdasarkan tandaan lokal. Hemisfera kanan menggunakan tanda topografi untuk mengarah geraklaih ke lokasi di mana kedapatan makanan sebelumnya.

(hemispheric collaboration, food search, domestic chick)

INTRODUCTION

Hemispheric specialisation has been well established in the domestic chick by using procedures which restrict direct sensory input to one or other hemisphere. Chicks using the left eye are able to choose between objects to which they are socially attached on the basis of small changes in the visual appearance of the objects, which are ignored by right-eyed chicks [1]. Chicks using the right nostril (and thus the right hemisphere) have a similar advantage in choice on olfactory cues [2]. Left-eyed chicks have substantial advantage in orientation by visual cues, both distant and close, in order to find a search area [3]. These findings suggest a special competence of the right hemisphere in analysing spatial patterns and in the recognition of small or subtle changes in visual stimuli. (The term 'hemisphere' is used, following convention, to refer to the structures contralateral to the seeing eye, which in birds receives the dominant visual input, and whose specialisation, it is assumed, is responsible for the differences between right- and left-eyed chicks).

Right-eyed chicks (using the right eye and have the left eye occluded) come to select food grains in preference to distracting inedible pebbles faster than do left-eyed chicks [4]. We argue here that the left hemisphere may be particularly important in determining whether responses, such as feeding pecks or approach to food, shall be emitted or not.

Lesions and other insults to one hemisphere have been used to establish hemispheric specialisations in other birds [5] and in non-human mammals [6]. However, there is very little evidence bearing on the way in which animals may make use of hemispheric specialisation under normal conditions. One strategy which appears to be used by chicks is to use either right or left hemisphere in analysis according to stimulus properties: thus the right eye is used to look at a hen and the left to look at a small novel object [7]. Here, it is likely that the type of the analysis of stimulus properties determines which hemisphere is engaged.

One particularly interesting behaviour for the study of hemispheric interaction in the control of response is food search. When birds search for food which is patchily distributed, they have available to them local cues which could potentially identify classes of patch (e.g. amongst lichen, under flakes of bark) and more distant cues which might allow return to particularly profitable patches. At the same time, they have to be able to identify particular food items. Rogers and Andrew [8] studied domestic chicks searching for food grains in an environment where potential 'food patches' were identified by the presence of black squares on the floor of the experimental arena. Birds proved to be responsive both to position of the patches and the presence or absence within a patch of a single camouflaged grain. Both patches and grain could be shown (by measurement of targetting head movements) to be detected at similar substantial distances, so that

chicks had open to them at least two different strategies of choice at any particular point in search. One possible way of simultaneously conducting two strategies of selection would be to associate each strategy with one hemisphere (and so with one eye).

In an earlier study [3] in which search guided by local visual cues (objects within the arena) could be distinguished from that guided by more distant cues, (topographical features of the environment), we showed that left-eyed male domestic chicks (LE) were in general much better than right-eyed (RE) male chicks in the use of both types of cue. Although RE searched intensely for food across the whole arena with sawdust covered floor, they showed little concentration of search in the areas defined by cues previously associated with food. Even under special conditions (day 8: unique bias for RE), when some guided search occurred, only local cues were used. Chicks using both eyes resembled LE in their effective use of distant cues, so that it seemed likely that the right hemisphere (receiving the direct input from the left eye) was predominantly responsible for the use of such cues during food search.

We present here new evidence for the nature of the collaboration of right and left hemispheres in food search, and show that each hemisphere appears to play a part consistent with the specialisations reviewed above. In order to do this we take advantage of the fact that there are age-dependent shifts in hemispheric dominance during development in the chick [9]. Recent evidence has confirmed this and shown that bias reaches maximum values on two days: to the left hemisphere on day 8 and to the right on day 11. This means that binocular birds can be compared under conditions of strong bias to either hemisphere or with little or no bias. We use new measures taken from already published experiments, as well as data from unpublished experiments.

MATERIALS AND METHOD

Male chicks were housed singly, in cages (23.0 x 25.5 x 35.5 cm), through the transparent fronts of which could be seen the room in which training and testing were carried out. Training began on day 3 of life (where the day of travel from the hatchery was treated as day 1). Food was removed from the home cage about 3 hours before training. Each chick was placed in a square tray (57 x 57 x 10 cm), the walls of which were marked with a variety of coloured patterns (paper strips to form horizontal and vertical bars or crosses), so that position in the tray could be determined by reference to wall features. For analysis the tray was treated as divided into nine equal squares (i.e. four corners, four mid-way and one central square). Food was always presented in the same corner square, which was further identified by two small bottles (height 8.5 cm), in which the area between the bottles was where the food was placed. On the first day of training, food (BOCM Starter crumbs) was visible in a patch of floor cleared of the sawdust, with which the floor was otherwise covered to a depth of 1-2 cm, and the chick was placed in the food area and encouraged to eat by tapping on the floor there. On the next day there were three, and thereafter two training trials a day, starting with the chick being placed in the centre of the tray; it was placed on alternate trials with right or left eye turned towards the food area. On the second trial of the third day the food was covered with sawdust. From this time on the chick had to use cues internal to the tray or the more distant features of the room (or both) to locate the food.

On test days (the start of testing was days 7 and 8 for experiments 1 and 2 respectively), a first trial was given under training conditions, with food present; at a second trial in the afternoon the tray was rotated through 180°, and there was no food present. In these 'rotated tray' tests there were two areas of search (corners) prescribed, one by cues internal, and one by cues external to the tray. We distinguish these as 'local' and 'distant' respectively. Chicks were assigned throughout to one of three conditions: right-eyed (RE), left-eyed (LE) or binocular (BIN). In monocular groups the eye not in use was covered for 30 minutes before the trial with a paper patch (25 x 25 mm; sticky sided 'masking tape'), which was stuck to the down around the eye; the patch was removed immediately after the trial, and had no obvious effect on behaviour in the tray (apart from changes in the use of orienting cues). Patches were not worn for days of training, so the task was initially learned in all cases with both eyes in normal use. Tracks followed by the chick were recorded by an observer on a standard plan of the tray. Two measures were considered here: length of track in particular squares, which gives an indication of persistence of search in a particular locality (since chicks moved forwards continuously whilst searching), and heading of departure

from the central start point. The second measure was taken from the point of first crossing of an imaginary circle, centred on the midpoint of the tray (from which the chick started) and with a radius of 15 cm. Data for track measures which compare track lengths in the two corner squares, which were specified respectively by local and distant cues, have already been presented for the main experiment (Expt 1) which is discussed here [3]. We consider here for the first time the relative use by the three groups of the neutral corners, not specified by orienting cues, and the departure headings. In a second (previously unpublished) experiment the effect of moving only the bottles is examined. Here the bottles were moved to the middle of one wall, so that for the first time they were not associated with a corner.

The data were analysed using mostly analysis of variance (ANOVA) from the Genstat package. Non-parametric tests included Mann-Whitney and Fisher Exact tests. Statistical tests for the incorrect headings were applied to the actual angular deviation from the nearer of the two correct bearings (135° local cues, 315° distant cues). Changes in the chosen heading was used for each individual, with improvement (close to correct bearings) scored positive and worsening choice, a negative. Two-tailed probabilities were quoted and results were considered to be significantly different when the values (p) were less than 0.05.

RESULTS

Experiment 1. Initial headings

Changes between days were significant or suggestive for LE (day 8 vs. day 9, p = 0.052; day 8 vs. day 11, p = 0.024). The patterns of change between day 8 (left hemisphere bias) and day 11 (right hemisphere bias) differed for LE vs. RE (p = 0.032) and suggestively for LE vs. BIN (p = 0.052). BIN and RE showed parallel changes with poor initial orientation on days 9 and 11 and good initial orientation on day 8, whilst LE showed the opposite pattern. Both RE and LE thus showed poor performance on the days when there was bias to control by the hemisphere which did not receive direct visual input (day 8 for LE, day 11 for RE). When there was orientation to cues, both RE and LE tended in their initial headings to orient to local cues (almost certainly the conspicuous bottles), whereas on day 8 (when BIN oriented well), BIN were almost equally likely to head

towards distant or local cues (Table 1). This difference between BIN and the monocular groups was significant for those birds which showed orientation to cues (p = 0.034, Fisher's Exact test).

Table 1. Percentage of birds showing 'incorrect headings' (i.e. headings outside 20° sectors on either side of the bearing of the centre of the corners respectively specified by local and by distant cues).

Group	Day		
	8	9	11
BIN	25	58.3	54.5
RE	25	75	63.6
LE	58.3	0	18.2

Experiment 1: Track in search

BIN performed well on all days, largely concentrating on the corner specified by distant cues (Fig. 1; and [3]). They showed little change across days in the use of such cues, unlike LE, which rose to BIN levels only on the day of maximum bias to right hemisphere control (day 11: Fig. 1). Testing [3] continued to day 15, and this marked use of distant cues continued on later days in LE, resulting in sustained and significantly better performance than that shown by RE. The other monocular group, RE, also showed its best performance on the day of bias to the hemisphere receiving input from the seeing eye (left hemisphere, day 8); even so the chicks made little use of distant cues at this time, orienting mainly to local cues (Fig. 1).

We are concerned here chiefly with the pattern of search across the three corners which are not specified by distant cues. Amongst these, LE predominantly visited the corner specified by local cues, whereas BIN distributed visits almost equally between the three (Fig.1). It is not possible to tell whether this represents a complete abandonment of guidance of search by past experience, with the chick passing through or pausing in corners because of the constraining walls of the arena, or whether it represents a relaxation of the criteria for identification of the local area in which food is normally to be found.

RE showed a third pattern, in that on the one day when they showed good orientation (day 8), they visited the corner specified by local cues persistently, but the
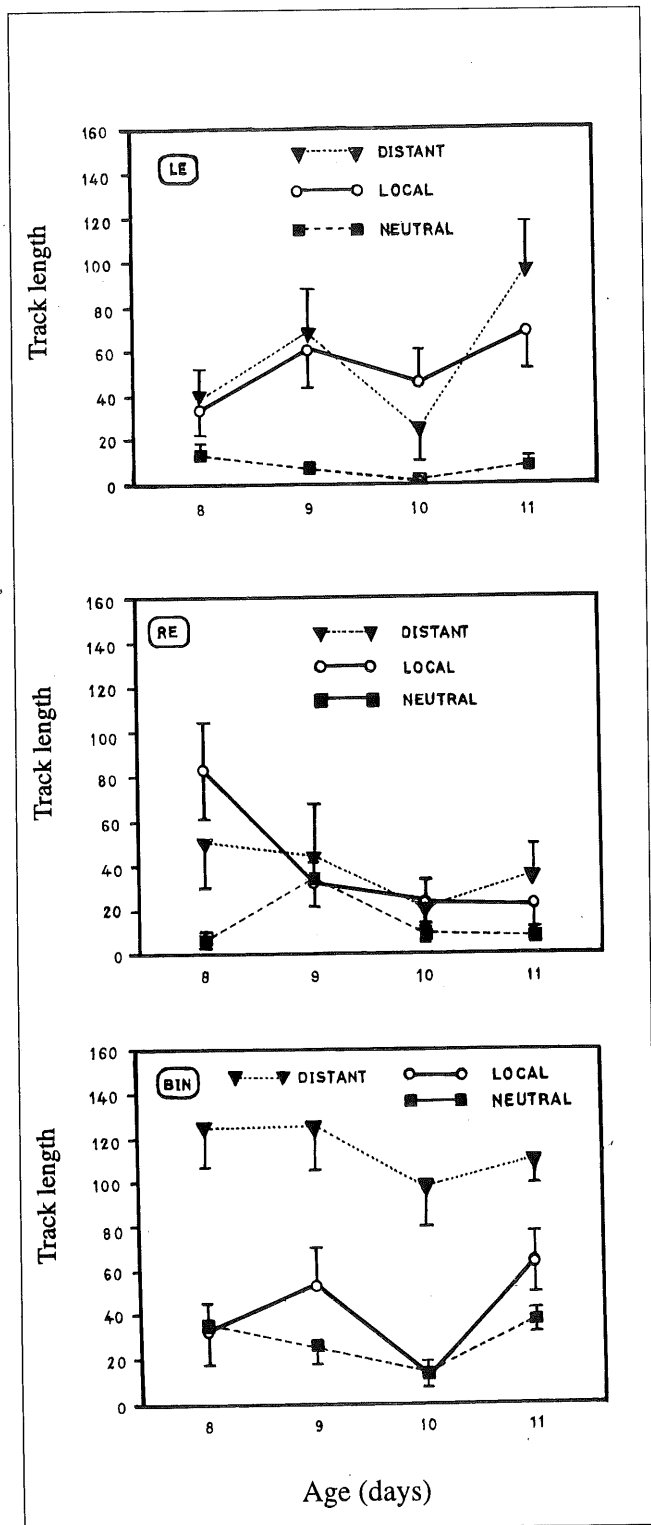
Figure 1. Track length (cm) for search in three groups of chicks: using their left eye (LE), right eye (RE) or both (BIN). Two corners were respectively specified by LOCAL and DISTANT cues, while two other corners were not so specified (NEUTRAL: the values used are for the sum of search in the two corners divided by 2, so as to produce a value comparable to those for the other two corners).

other two (neutral) corners hardly at all; on other days, they showed little or no distinction between corners. As a result of these differences between groups there were significant interactions (EYE.DAY: $F_{6,99} = 3.28$, p = 0.005; EYE.CORNER: $F_{2,132} = 12.26$, p < 0.001; EYE.DAY.CORNER: $F_{6,132} = 3.71$, p = 0.002). Restrictions revealed all three pairwise comparisons between groups showed significant differences: LE vs.RE: EYE.CORNER, $F_{1,88} = 7.70$, p = 0.007; EYE.DAY.CORNER, $F_{3,88} = 4.31$, p = 0.007. LE vs. BIN : EYE.CORNER, $F_{1,88} = 28.37$, p < 0.001. RE vs. BIN: EYE.DAY, $F_{3,66} = 5.66$, p = 0.002; EYE.DAY.CORNER, $F_{3,88} = 6.06$, p < 0.001). This reflected the greater use of LOCAL cues on day 8 by RE and on the other days by LE, together with a similar level of use of both LOCAL and NEUTRAL by BIN, which varied little with age.

Experiment 2
A different batch of chicks was used for this experiment. RE and LE were tested on the standard procedure and in addition were given a test by moving the local cues. In this test the arena remained unrotated, but the main local cues (i.e. the bottles) were moved away from the usual corner. Despite this, LE unambiguously used the bottles to guide search as well as distant cues (Fig. 2). Search was clearly not distributed at random (SQUARES: $F_{4,120} = 18.333$, p < 0.001), and the pattern of search changed between pretest and test (TEST.SQUARES: $F_{4,120} = 4.426$, p = 0.002; EYE.TEST. SQUARES: $F_{4,120} = 7.007$, p < 0.001). This was largely due to LE, where restriction revealed the same interaction to be significant ($F_{4,64} = 13.358$, p < 0.001); the corresponding interaction in RE was not significant. RE were clearly making rather poor use of all orientation cues, and so it is not surprising that they were little affected by the movement of local cues. The important finding is that LE did follow the bottles.

DISCUSSION

The reliance of BIN on distant cues, which appear to be used hardly at all by RE but effectively used by LE, implies that the right hemisphere is responsible for orientation in normal search with both eyes in use [3]. The new evidence presented here suggests that the left hemisphere is also strongly involved. Its participation
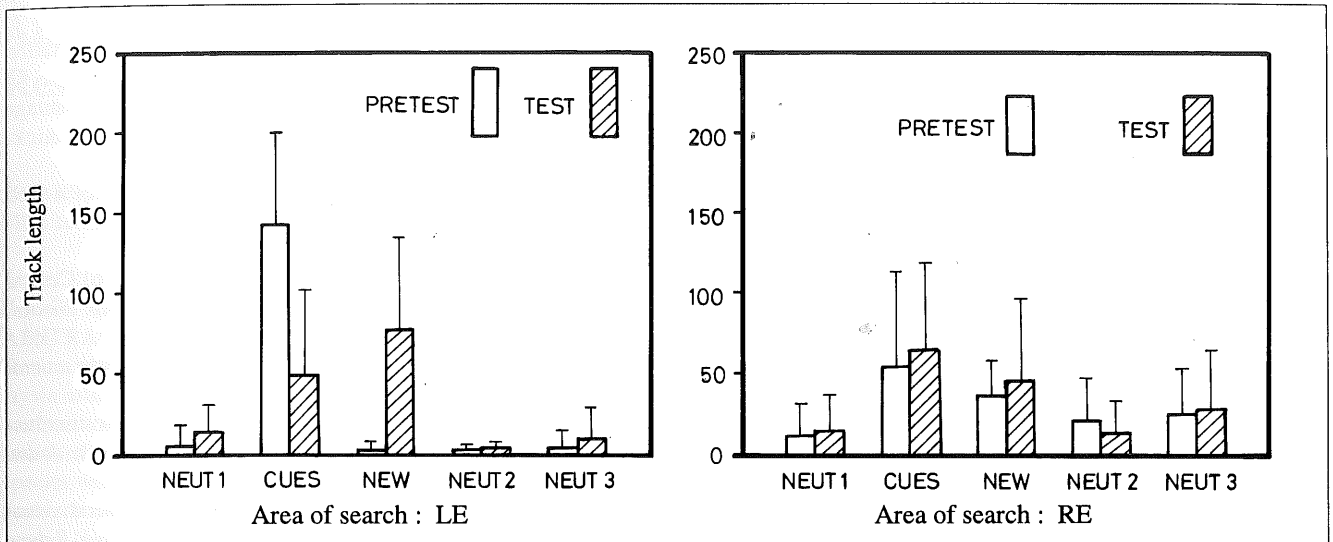
Figure 2. Track length (cm) for search in five of the (imaginary) squares into which the floor was divided. CUES designates the corner square specified by both distant and local cues. At pretest this included the bottles, which at test were moved to the square midway along one wall, which is designated as NEW; well organised search should make no use of this square at pretest but at test, if the bottles were used as important cues, search should increase in NEW. NEUT1 is the corner square opposite to CUES and NEUT2 and NEUT3 are the two other corner squares, neither of which are specified by any orientation cues, and so should have low track scores in well organised search.

appears to be crucial in BIN for the rapid assumption of approach to a target area, since this occurs only on the day of strong bias to left hemisphere control. BIN are then as likely to show an initial heading to distant cues as to local ones; this is consistent with the establishment of collaboration between the two hemispheres rather than with a brief initial period of control by the left hemisphere, which would be expected to orient only to local cues.

The other difference between BIN and LE is also best explained by the participation of the left hemisphere in search in BIN. The near failure of BIN to use local cues, when distant cues are not being used, contrasts with the alternation of search between local and distant cues which is shown persistently by LE. This difference is explained if it is assumed that, in BIN, search for food involving both identification of potential food particles and selection of particular local sites for examination is particularly the concern of the left hemisphere, with guidance to appropriate locations in the arena being provided by the right hemisphere. Under these conditions, it would be possible for search to continue with little or no guidance by locality cues as a result of reduction or change in right hemisphere involvement. It should be noted that, when (on our argument), guidance by orienting cues is the main or only task, which is undertaken by the right hemisphere,

nearly all orientation is by distant cues; only when the right hemisphere has to combine guidance to the correct area with identification of the local zone for search, does orientation by local cues also become important. Indeed, the behaviour of LE suggests that, under these conditions, there is stable specification of local cues, as well as of distant ones. As a result, at least within the period of the test, LE can only alternate between local and distant cues, rather than shifting at times to search which is more widely distributed.

There is independent evidence of special involvement or competence of the left hemisphere in selection of food amongst other targets. When chicks are presented with familiar food grains scattered amongst pebbles of roughly similar size and appearance, RE come to select food alone much quicker than do LE [4, 10].

Experiment 2 showed that LE follow local cues (the bottles) and search near them, when they are moved to different locations within the arena, including a site not at a corner. This is consistent with right hemisphere specification of areas of search by local, as well as by distant cues.

We conclude that in normal binocular search in the chick both hemispheres are involved, with the left hemisphere being responsible for local search and perhaps, in view of the evidence from initial headings,

for ordering approach. The right hemisphere provides guidance in orientation. This collaboration can be sustained with standing bias to either hemisphere. This seems reasonable for a task in which the two hemispheres are engaged in complementary but largely independent aspects of the task. One consequence of the involvement of both hemispheres in different aspects of the task may be a greater flexibility, when a strategy proves to be unsuccessful.

In birds like the domestic fowl, which have independent eye movements [11], it is likely that this hemispheric collaboration is expressed, at least in part, by the left eye being used during search to look at distant orienting cues, whilst the right eye concentrates more fully on identification of food.

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