

The use of viewing posture to control visual processing by lateralised mechanisms

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Summary

Chicks were trained and tested to run to a dish and feed from it under one of four conditions. In three of these, the dish was covered by a light lid that the chicks readily learned to remove. The square lid (SL) had slightly protruding corners, so that it could be removed by a blow of the bill at a range of positions. A round lid (UL), which fitted snugly, could best be removed by inserting the bill into a medial U-shaped indentation. A round lid (STR), which fitted all the way round to the edge of the dish, could be removed by grasping and tugging a centrally placed piece of string. The final dish had no lid (NOL). The dish and the layout of the arena were otherwise identical under all conditions. Chicks trained and tested with lids predominantly fixated the dish during approach with the right eye and showed leftward deviation from the direct line of approach (which facilitated right eye use). NOL chicks fixated with the left eye and deviated rightwards. The right eye is thus used when a motor plan has to be set up and sustained. The use of the left eye is expected when topographical information has to be used. Here, the approach was so simple and practised that the assumption of left eye viewing is likely to be a default condition. It would facilitate detection of any change in layout.

A standard set of head positions were used, particularly

by SL and NOL chicks, showing that the head was aligned with some reference point, perhaps the centre of the dish. These fell into two series (used by both eyes), and in both the peaks of frequent use were 10° apart. One (20°, 10°) was probably generated by head saccades ending with the bill pointing directly at the dish (0°). The other (35°, 25°, 15°) is best explained by slight divergence of the optic axes. The 25° right eye position was consistently used by STR chicks at the beginning of approach. The STR condition requires the most difficult manipulation, and the manipulandum is most obvious from a distance. This is consistent with right eye use during establishment of a motor plan. Head postures consistent with divergence were also used when close to the dish under conditions where choice between targets was necessary. This was clear in the NOL condition, where the chick could see the food grains as it approached. Here, it is likely that both eyes are used in independent search. If so, it may be that divergence is used as a strategy during establishment of a motor plan (as in STR chicks) to increase the independence of the right eye system.

Key words: eye use, visuomotor control, lateralisation, chick, *Gallus gallus*.

Introduction

The use of either the left or right eye (LE, RE), according to the nature of the task in hand, is well established for birds and fish. The left lateral visual field is used in wide-field search by domestic poultry *Gallus gallus domesticus* when searching the sky after alarm (Evans et al., 1993), and by kookaburra *Dacelo novaeguineae* when perched and searching the ground for food (Rogers, 2002). Chicks use the left lateral field when viewing a strange and potentially disturbing stimulus (a live rat) and the right when viewing an object (a live hen) that is likely to evoke approach (Dharmaretnam and Andrew, 1994). In general, chicks use the RE (or ear) when a decision has to be made, such as whether to approach. They use the LE (or ear), when it is necessary to establish whether a complex stimulus is identical with one that has been previously

encountered (Miklósi et al., 1996; McKenzie et al., 1998; Vallortigara et al., 2001). A very similar dichotomy is present in zebrafish *Brachydanio rerio*: the right frontal field is used when viewing a novel object or scene, and the left, when the same object or scene is seen for a second time (Miklósi et al., 1998). Since the RE is also used when fixating a target that will be bitten (Miklósi and Andrew, 1999), it is likely that its use in viewing a completely novel stimulus is associated with decision making. The shift to LE use occurs when the task is to establish identity with a past experience.

We recently (Andrew et al., 2000) showed that chicks use the RE in an approach to a visible target that they intend to manipulate with the bill, but the LE in very similar approaches, when they cannot see the target that has to be manipulated.

Here, it seems that the processes of decision include the establishment and maintenance of a motor plan. We argued (see also Andrew, 2002) that such lateralised visual control of motor response is likely to be the most ancient form of motor lateralisation.

We present here new experiments, and also further data and analysis from an experiment that was briefly and partially reported in Andrew et al. (2000). We show that different viewing postures (within the overall use of either the LE or RE) are used when establishing the motor plan, and when maintaining it. Further, head postures during viewing allow us to distinguish periods when a motor plan is set up from ones in which a decision is being carried out or a specific target for response is sought.

Materials and methods

Male chicks *Gallus gallus domesticus* (ISA Brown) from a commercial supplier (ISA, Peterborough, UK) were housed on arrival (day 2 of life) in groups of three, in grey-painted aluminium cages (23 cm×23 cm×30 cm). Cages were lit from above by 25 W light bulbs that also provided additional heat. Food (chick starter) and water were available *ad libitum*.

Chicks were trained singly on days 3, 4 and 5 of life. Food was removed 2 h before training, which occurred in a rectangular arena (32 cm×90 cm) in a quiet experimental room. The arena (Fig. 1) was lit from above by fluorescent ceiling lights, and indirectly by incandescent bulbs on two sides of the room, arranged so that the arena was lit uniformly. A black cylindrical pot (height 2.5 cm, diameter 3 cm) containing a shallow layer of food was placed in the middle of one of the shorter walls. The chick was placed at the opposite end of the arena from the dish, at the mid point of the wall, and facing the dish, which was approximately 30 cm away along the major axis of the arena.

On day 3, a row of food crumbs led the chick directly to the food dish. In those conditions in which the dish was covered by a light paper lid, there were also crumbs on the lid. When the chick pecked these, the lid usually fell off, revealing the food inside the dish, from which the chick then fed readily. The amount of food present on the floor and lid was progressively reduced in later trials, until the chick ran directly to the dish, removed the lid (if one was present), and fed from the dish. There were three training sessions per day, each involving at least six runs to the dish. The chick was allowed to feed for several seconds, and then was held away from the dish with one hand whilst any crumbs that had been thrown to the floor were removed. The final session on day 5 (test session) was recorded by a video camera placed directly above the arena. This session was made up of 4–7 trials, according to the readiness of the chick to continue running to the dish.

Four conditions were used (Fig. 1). Each

chick was trained and tested under only one condition. In the no lid (NOL: 16 chicks) condition the dish was uncovered. In the square lid (SL: 19 chicks) condition, the dish was covered with a square lid (3 cm×3 cm), placed symmetrically so that one corner faced the chick, and two others were at the sides of the dish. The lid projected enough for it to be removed by a peck or sideways blow at a variety of points around its perimeter. In the U-shaped lid (UL: 23 chicks) condition, the lid was circular (4 cm diameter) with a rounded indentation that was positioned directly facing the chick. The lid could most easily be removed by pushing the bill into the space provided by the indentation. In the string lid (STR: 8 chicks) condition, the dish was covered with a circular lid (3 cm diameter) that did not protrude over the edge of the dish. It could be removed most easily by grasping a piece of white string (3 cm long, 3 mm diameter) that was attached to the centre of the lid. Its tip was marked with a black dot that evoked pecking and so facilitated learning. The tip turned over and was directed towards the chick as it approached.

NOL were divided into two batches. In the first, eight NOL were compared with seven SL, and in the second, eight NOL were compared with eight STR. Data from two other batches of UL and from one batch of SL were combined with that from the first two to produce bodies of data for within-condition analyses.

The video recordings were analysed, taking measurements as the chick crossed each of three reference lines running perpendicular to the direct line from the start point to the dish centre. These were 10 cm (DIST), 20 cm (MID) and 27 cm (CLOSE) from the start point (Distant: DIST; Mid: MID; Close: CLOSE). The CLOSE point was just before the dish was reached. The measurements taken were the displacement of the centre point of the head from the direct line of approach, and the angle between the longitudinal axis of the head (bill tip to head centre) and a line from the head centre to the centre of the dish. Head angles were measured to the nearest degree and then assigned to a series of 5° bins, starting with 'binocular' (3° left to 3° right), and then in successive blocks

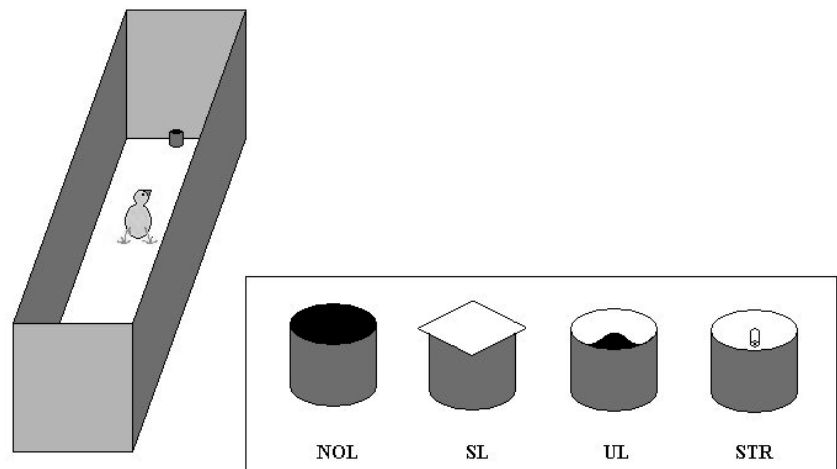


Fig. 1. Layout of the experimental arena and the dish conditions: no lid (NOL), square lid (SL), lid with U-shaped indentation (UL) and lid with protruding string (STR).

(3–7°, 8–12°, 13–17° and so on). These are termed 5°, 10° and 15° (and so on) from their central angle.

Mean displacement and mean angle were calculated for each chick for each of the three reference lines in the approach, using data from all the test trials. Measures of right or left bias were based on the number of trials in which each was shown, converted to a ratio as (right/right+left). Overall heterogeneity between lid conditions was examined with general linear model analysis (SPSS for Windows, Release 10). In the case of preferred angular positions of the head, the measure used for overall analysis was the number of occurrences n of each head position (10°, 15°, 20°, 25°) in the formula $(n_{15}+n_{25})-(n_{10}+n_{20})$ for each individual, combining data for the RE and LE. If the most probable distribution of head positions was followed, i.e. the nearer the positions were to pointing directly at the target (0°) the more commonly they were used, then this measure would tend to be negative. When examining the significance of bias within a condition, Wilcoxon signed-ranks tests (T^+) were used (Siegel and Castellan, 1988). All probabilities are two-tailed, with the exception of pairwise tests comparing frequency of head angles in two adjacent bins. Here the only direction of difference of interest was that the bin further from the binocular position should be the larger.

Results

Tracks

In lid conditions, the tracks deviated from a direct line of approach towards the chicks' left side, tending to bring the RE to bear on the dish (see below). In the no lid (NOL) condition, deviation was to the right side, tending to bring the LE to bear on the dish (Fig. 2). In each statistical test a single measure (mean amplitude of displacement to left or right) was used for each individual (see Materials and methods). Behaviour was strikingly consistent between individuals for each condition (Fig. 2). The differences between lid conditions were significant [repeated-measures analysis of variance (ANOVA), $F_{3,62}=13.118$, $P=0.001$]. Multiple comparisons (Tukey HSD) showed that all lid conditions differed significantly from the NOL condition (at the preset level $P<0.05$), but that none of the lid conditions differed in pairwise comparisons.

Comparisons of a lid condition with NOL were possible within a single batch for SL and NOL, and for STR and NOL. In both cases, the lid condition differed significantly from NOL ($F_{1,13}=44.382$, $P<0.001$; $F_{1,14}=13.892$, $P=0.002$).

The most obvious reason for the right and left deviations from the direct line of approach is that they are a consequence of bringing the LE or RE to bear on the dish. However, this needs confirmation. It would be possible for a chick to run indirectly to the dish (for some unknown reason) and to hold its head in positions that would allow either RE or LE use.

A single mean measure of bias in eye use (R/R+L) was calculated for each point of approach for each chick, based on which eye was directed towards the dish in each of the test trials.

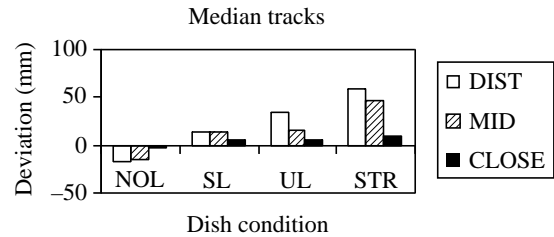


Fig. 2. Median values for the mean displacement of the track from the direct line of approach for individual chicks. Values are shown for three reference points in the chick's journey to the dish: distant (DIST), mid (MID) and close (CLOSE) (see Materials and methods). Displacements to the chick's left (which would bring the right eye to bear on the dish) are shown as positive. Displacements to the right (which would bring the left eye to bear) are shown as negative. These are largely confined to NOL chicks. Almost all conditions departed significantly at all three points from an even distribution of right and left displacement: P values for DIST, MID and CLOSE, respectively, are: NOL, $P=0.004$, $P=0.013$, $P=0.024$; SL, $P=0.018$, $P=0.044$, $P=0.0001$; UL, $P=0.001$, $P=0.002$, $P=0.040$; STR, $P=0.016$, $P=0.016$, $P=0.066$. See Fig. 1 legend for description of dish conditions and Materials and methods for details of chick numbers and trials.

There was overall significant variation between conditions (repeated-measures ANOVA: $F_{3,62}=12.176$, $P<0.001$), which was due to RE use in the lid conditions and LE use in the NOL condition. All pairwise comparisons between NOL and each of the lid conditions, based on measures at all three points, were significant at $P<0.05$.

At the DIST point there was significant bias to RE use in all lid conditions (STR, $N=7$, $T^+=27$, $P=0.031$; UL, $z=2.903$, $P=0.0038$; SL, $z=2.495$, $P=0.0126$). In the NOL condition there was significant bias to LE use ($N=15$, $T^+=116.5$, $P=0.0004$). The corresponding values for MID were: STR, $N=8$, $T^+=33$, $P=0.039$, UL, $z=3.081$, $P=0.002$; SL, $z=1.825$, $P=0.068$; NOL, $N=12$, $T^+=76$, $P=0.0014$; and for CLOSE: STR, $N=7$, $T^+=17$, NS; UL, $z=2.086$, $P=0.037$; SL, $z=1.916$, $P=0.056$; NOL, $N=14$, $T^+=74$, NS.

Head positions

Chicks are known to use precise and standard head positions when viewing objects at a distance with one or other lateral visual field. Under these circumstances there is a narrow peak in frequency of head positions that is centred on 62–63° from the direct line of sight to the object (Dharmaretnam and Andrew, 1994). This degree of consistency suggests that a standard eye position is usually assumed when viewing from a distance. It is likely that the 62–63° peak involves the avian 'primary position of gaze' (Wallman and Pettigrew, 1985), in which the eyes are held diverged to a standard degree. A second standard relative position of the optical axes in birds is binocular convergence just before pecking, including a further series of small vergences (approximately 3° in pigeon *Columba livia*) as the head descends towards the target (McFadden, 1994).

A final point to note is that the present data often show well-

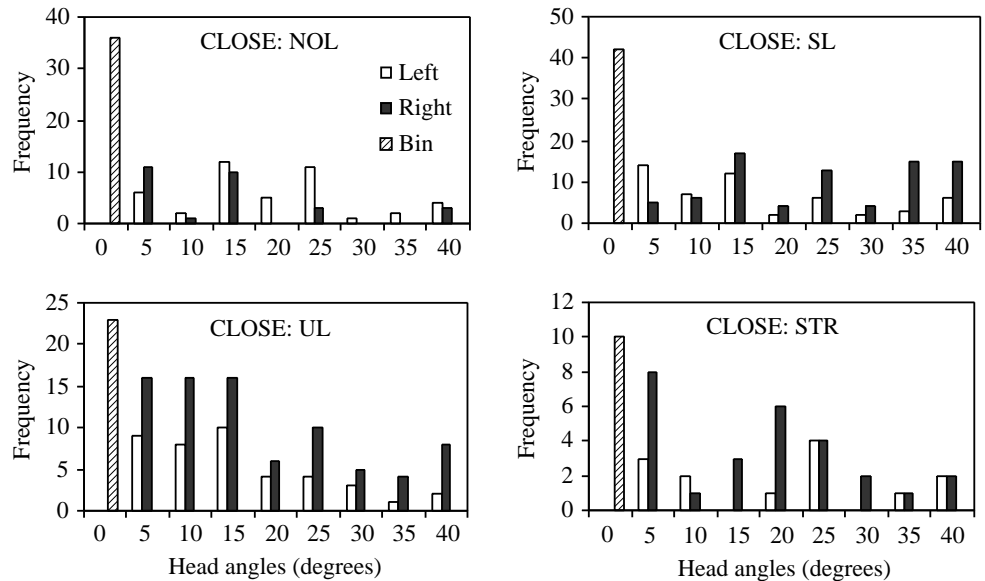


Fig. 3. Frequencies of occurrence of particular head positions for the four dish conditions NOL, SL, UL and STR for the CLOSE reference point (measurement position nearest to the dish), combined for all individuals. The data are blocked into 5° bins (head angles) (see text for details). Analyses based on single scores for each individual are given in the text. See Fig. 1 legend for description of dish conditions. Bin, bincular (0°).

defined standard head positions relative to the centre of the dish, even when quite close to it (a few centimetres at most, at the CLOSE point). This suggests that the retinal area important for viewing is aligned in some standard way with the object of interest (the dish), perhaps with its centre. A similar alignment is probably needed to explain the standard head positions described by Dharmaretnam and Andrew (1994) for chicks that were viewing objects such as a live hen or rat. Although the distance between chick and stimulus object in that study was approximately 55 cm, the objects could be 15 cm or more in length, when turned broad-side on. This could introduce variation of as much as 15° if the head were turned to examine different features, which would certainly have obscured the sharply defined and standard peaks in frequency of use. It follows that the head and retina are aligned with some characteristic feature of large objects of interest. This suggests either that analysis of different local features can be carried out over a relatively wide area of the retina, or that once the alignment is taken up small eye movements allow scanning.

Fig. 3 shows the frequency of occurrence of particular head positions for chicks at the CLOSE point near to the dish. From these data the number of occurrences of each head position for both eyes at 10°, 15°, 20° and 25° was entered in the formula $x = (n_{15} + n_{25}) - (n_{10} + n_{20})$ for each individual. If the most probable distribution of head positions occurred, i.e. the nearer the positions were to pointing directly at the target (0°) the more commonly they were used, then this measure would tend to be negative. The calculated values showed a clear preference for 15° and 25° in NOL (median $x=2$) and SL (median $x=1$) chicks. There was significant heterogeneity between lid conditions (univariate ANOVA, $F_{3,62}=3.256$, $P=0.027$), because this preference occurred only in SL and NOL animals (median $x=0$ for UL; median $x=-1$ for STR). In both, the measure was positive and significantly different from random (Wilcoxon signed-ranks test; for SL, $N=15$, $T^+=106$, $P=0.0034$; for NOL,

$N=16$, $T^+=105$, $P=0.0001$). Thus there are peaks in frequency of use at 15° and 25° in SL and NOL that are absent (or less well developed) in STR and UL. Comparison of each peak with the sector adjacent to it that was nearer to 0°, showed significant differences for both the 15° and 25° peaks (for SL, 15°, $N=13$, $T^+=80$, $P=0.007$; and 25°, $N=15$, $T^+=95$, $P=0.024$; for NOL, 15°, $N=8$, $T^+=36$, $P=0.004$; and 25°, $N=13$, $T^+=86.5$, $P=0.001$). Further, for SL the frequency at 35° was significantly greater than that at 30° ($N=12$, $T^+=66$, $P=0.034$), suggesting periodicity of repetition, with peaks 10° apart.

The patterns of head position frequency for NOL and SL also resembled each other at the MID and DIST points (Figs 4, 5). At both points, the use of the dominant eye (left for NOL, right for SL condition) was so predominant that analysis was confined to these data. At the MID point 20° was used more often than 15° ($N=18$, $T^+=138.5$, $P=0.017$), and at the DIST point 10° was used more than 5° ($N=23$, $T^+=205.5$, $P=0.04$).

In general, STR chicks show no clear peaks in the frequency of use of head positions. However, at the DIST point (Fig. 5), there was a significant difference between 25° and 20° for the RE ($N=6$, $T^+=21$, $P=0.016$).

At the CLOSE point further resemblances in the pattern of frequency of head positions can be seen between NOL and SL. Subordinate and dominant eyes both show a peak at 15°, but the 25° peak is largely confined to the dominant eye. In addition, in both conditions, 0° is by far the most commonly used position, whereas in UL and STR chicks the frequency of use of 0° is more similar to that of 5° (Fig. 3), even though in these latter two conditions there was a single central target at which the bill could be directed. The frequency value for the 0° bin thus was compared with the mean of the right and left 5° bins: 0° was used more frequently than the 5° bins for NOL ($z=2.90$, $P=0.004$) and SL ($z=3.007$, $P=0.002$).

At the DIST point, the pattern for UL is similar to that of SL, with suggestion of a peak in RE use at 10°. However, at

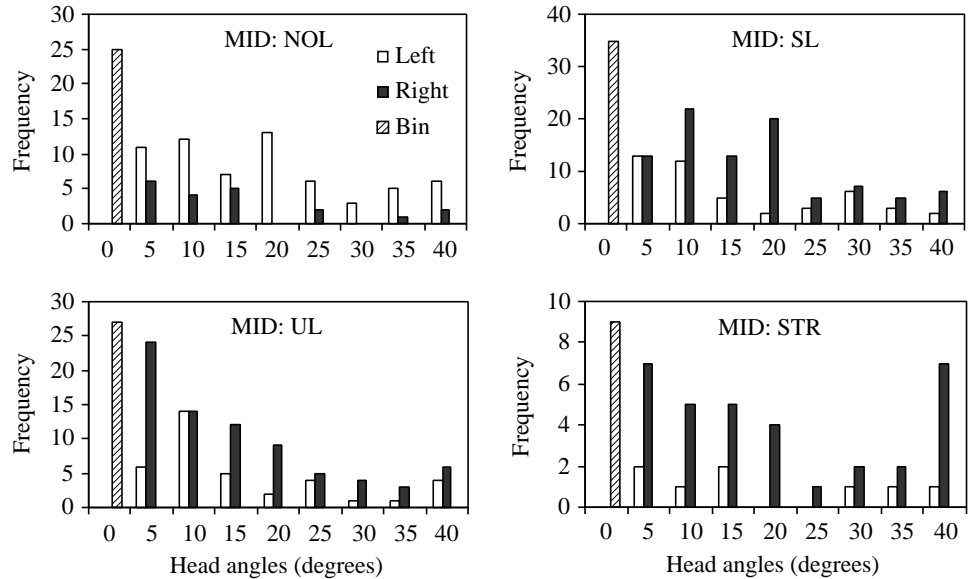


Fig. 4. Frequencies of occurrence of particular head positions for the four dish conditions NOL, SL, UL and STR for the MID reference point (middle measurement point). All other conventions as in Fig. 3. Bin, binocular (0°).

MID and CLOSE, there are no clear peaks in RE use in UL chicks, in contrast to the SL condition. At the CLOSE point UL chicks made similar use of all RE bins from 0° to 15° . There is a significant difference between UL and SL chicks in the relative use of 0° and 5° for the RE (Mann–Whitney test, $U=132.5$, $P=0.029$).

At the MID point for UL there is no elevation of the frequency of use of 0° relative to 5° that is present in SL chicks (Mann–Whitney test, $U=146$, $P<0.001$). These patterns suggest that UL chicks fail to maintain a standard fixation point relative to the dish as they approach. One explanation for this would be a shift in attention to the large notch, into which the bill will be inserted, at some point during the approach that varies between trials and individuals.

It is worth emphasising that the test arena and position and dimensions of the target dish was the same for all conditions. The observed differences in head position were due to decisions by the chick that in turn derived from the nature of the tasks.

Discussion

We identified peaks in frequency of head positions with a periodicity of 10° , i.e. at 10° and 20° , or 15° , 25° and 35° . One possible reason for having head saccades of a standard size is suggested by the way in which chicks scan when in a strange place (Andrew and Dharmaretnam, 1993): they use regular head saccades, that are perhaps 30° in amplitude. Such regularity is likely to facilitate the rapid identification of previously seen features following a head turn, since it means that features transfer predictably between a series of retinal loci (i.e. whatever falls on A will transfer to B and then C). In the strange environment, no particular feature is the centre of attention. Instead, the whole environment is scanned by a series of head saccades, accompanied by body turns when necessary.

The regularity of the peaks in the present data suggest that similar predictable transfer of features is important here too, but based on much smaller amplitude (10°) head saccades, made whilst attention is directed to a particular area or target.

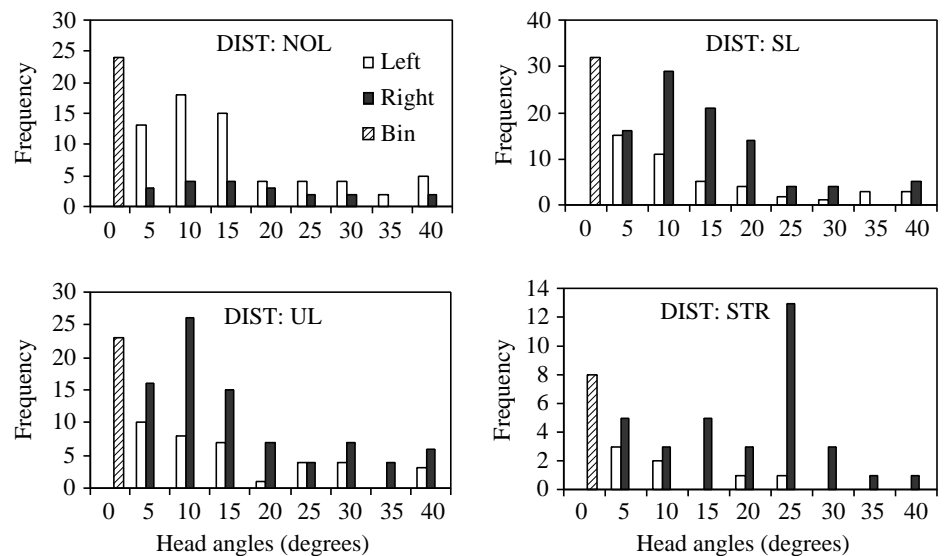


Fig. 5. Frequencies of occurrence of particular head positions for the four dish conditions NOL, SL, UL and STR for the DISTANT point (measurement point further from the dish). All other conventions as in Fig. 3. Bin, binocular (0°).

The existence of two series of peaks, displaced relative to each other by 5°, is best explained by supposing that the 10° and 20° peaks occur when the eyes are converged to the position used during binocular fixation. Note that 0° is then a part of the 10° and 20° series, with head turns towards 0° ending in binocular fixation. The series 15°, 25°, 35° is hypothesised to occur when the eye in use is diverged by 5°. It can be seen most clearly in SL and NOL at the CLOSE point (Fig. 3), suggesting that such divergence occurs, in SL and NOL chicks, at or near to the CLOSE point. In both SL and NOL animals, it is likely that selection of specific targets occurs as the chick approaches this point. This must be true for NOL, since the food grains could not be seen until the chick was close to the dish. In the case of SL, there was no single obvious best place to apply the bill. The lid could be removed by a blow at a variety of places around the rim. Selection of a particular target for the bill thus could well have occurred only when close to the dish. The other feature of interest of the CLOSE point data from NOL and SL is that (at least for the 15° peak) they involve the subordinate eye almost as much as the dominant. This is consistent with the use of both eyes in search, so that the head turns to best use whichever eye has detected a possible target. Both eyes are used independently when chicks search for food grains scattered over the floor (Rogers and Andrew, 1989). Divergence during such searching may make it easier for each eye system to work independently, by bringing the eyes out of binocular register.

The UL condition differs from SL and NOL in that attention is likely to shift during approach from the dish as a whole to the notch. The hint of a peak in the frequency of head positions at 10° for the DIST point suggests that at least some chicks began the approach with the alignment to the dish that was observed in SL and NOL chicks to occur up to the CLOSE point. A shift in alignment during the approach in UL birds would obscure any detailed pattern of preferred head position.

The STR task was unique in that the manipulandum was conspicuous from the start, and also required careful grasping, rather than the sideways blow of the bill that occurs when a chick cannot reach food because of an obstacle. Both are likely to have required a motor plan to be set up at the beginning of the approach. The greater use of the 25° right head position at the DIST point by STR chicks may be associated with setting up such a motor plan. It has been argued above that the use of this head position in SL and NOL chicks at the CLOSE point was associated with the selection of a specific target for the bill.

The use of extreme head positions such as 25° or 35° for RE viewing may function to prevent the left eye system (LES) from attending to the target, and thus give the right eye system (RES) full control over establishing and sustaining a motor plan.

The key finding of the present study is the importance of the RES in motor control. This may be widespread in birds. Hunt (2000) gives indirect evidence that New Caledonian crows *Corvus moneduloides* use the RE when making a tool from the hooked edge of a pandanus leaf: here a series of skilled movements are carried out under RE control. In the pigeon

(Zeigler et al., 1994) adjustment of gape to the size of the object to be grasped is under visual control. If this is true also of the chick, then the evidence cited here implies that the RES is responsible. Further aspects of RES motor control are likely to be acting to sustain the motor plan against distraction: the use of the 25° RE head position has already been discussed as a strategy contributing to this.

The RES also appears to record cues to which attention is directed during the performance of a response under visual control. When marsh tits *Parus palustris*, with one eye covered, recover food items recently hoarded with both eyes functional, they use local properties of the site itself, when searching with the RE, but spatial position within the general environment when using the LE (Clayton and Krebs, 1994). A comparable condition in chicks is suggested by their tendency to turn towards objects seen in the right hemifield when searching using local cues, but to the left hemifield when using topographical cues (Tommasi et al., 2000). Chicks also use information from the general environment to determine the geometric centre of an arena when using the LE, but use local landmarks when using the RE (Vallortigara, 2000; Tommasi and Vallortigara, 2001).

There is evidence suggesting that the RES records the outcome of the response to a stimulus, in the chick. After feeding on one type of food, the attractiveness of that type of food is reduced. Such 'devaluation' affects choice based on dish characteristics that are predictive of food type, but only during RE, and not LE use (Cozzutti and Vallortigara, 2001). Note that if the RES holds such information, this will further improve the ability to control the motor response correctly with the RE.

The use of the LE in the NOL condition deserves comment. Orientation by topographical features is better with the LE than with the RE (Rashid and Andrew, 1989); however, this can have mattered little in the simple direct approaches to the dish that were made in the tasks used here. Nevertheless, a default strategy of LE use during approach to sites where no manipulandum is visible might be advantageous. Detection of novelty is more likely when use of the LE is forced (Vallortigara and Andrew, 1991). Spontaneous use of the LE as a default strategy may thus make it more likely that unexpected change will be detected (Andrew et al., 2000).

There has been no study of possible improvements in manipulation, when the chick is forced to use the RE. However, chicks with one eye covered show better performance in the pebble floor task when using the RE (Rogers and Anson, 1979). Here, one type of small target (familiar food grains) has to be rapidly selected from amongst a mixture of two types of target. Pecks at the second type, inedible and unfamiliar small pebbles, are scored as errors. There is no special manipulation to be planned. Nevertheless, two features of the task call for effective motor control. Firstly, this is a task in which the speed of pecking is such that the ability to inhibit responses to incorrect targets must be crucial. Secondly, the cues used in selection have to be derived from immediate prior experience of the outcome of response.

We propose that the assumption of specific head angles in viewing is also functional, and that it serves to regulate the degree of control by one or other eye system and of the interaction between them. Such regulation occurs whether the RE or LE is in use. It thus forms a second and relatively independent mechanism.

Current evidence indicates that the specialisations of the RES and LES in birds may be summarised as follows: RES focuses on the target of response, controls the motor response and records both the response and its outcome. The LES uses diffuse attention in the analysis of the layout of the environment, and uses multiple cues to assess identity or novelty. It is likely that this would be largely incompatible with the control of the response. Note that it is not argued that the RES does not use information relating to spatial patterning at all. The local cues that distinguish hoarding sites for marsh tits probably could only be reliably discriminated one from another if the relative positions of features within the pattern were taken into account.

The current findings underline the importance of studies that, like the present one, allow study of lateralisation under normal conditions. They suggest that differential viewing is used to allow the eye system appropriate to the task in hand to dominate, even with both eyes readily able to see the target.

References

- Andrew, R. J.** (2002). The earliest origins and subsequent evolution of lateralisation. In *Comparative Vertebrate Lateralisation* (ed. L. J. Rogers and R. J. Andrew), pp. 70–93. Cambridge: Cambridge University Press.
- Andrew, R. J. and Dharmaretnam, M.** (1993). Lateralisation and strategies of viewing in the domestic chick. In *Vision, Brain and Behavior in Birds* (ed. H. P. Zeigler and H.-J. Bischof), pp. 319–332. Cambridge, Mass.: MIT Press.
- Andrew, R. J., Tommasi, L. and Ford, N.** (2000). Motor control in vision and the evolution of cerebral lateralisation. *Brain Lang.* **73**, 220–235.
- Clayton, N. S. and Krebs, J. R.** (1994). Memory for spatial and object-specific cues in food storing and non-storing birds. *J. Comp. Physiol. A* **172**, 371–379.
- Cozzutti, C. and Vallortigara, G.** (2001). Hemispheric memories for the content and position of food caches in the domestic chick. *Behav. Neurosci.* **115**, 305–313.
- Dharmaretnam, M. and Andrew, R. J.** (1994). Age- and stimulus-specific use of right and left eye by the domestic chick. *Anim. Behav.* **48**, 1395–1406.
- Evans, C. S., Evans, L. and Marler, P.** (1993). On the meaning of alarm calls: functional reference in an avian vocal system. *Anim. Behav.* **46**, 23–28.
- Hunt, G. R.** (2000). Human-like, population-level specialisation in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. *Proc. R. Soc. Lond. B* **267**, 403–413.
- McFadden, S. A.** (1994). Binocular depth perception. In *Perception and Motor Control in Birds* (ed. M. N. O. Davies and P. R. Green), pp. 54–73. Berlin: Springer-Verlag.
- McKenzie, R., Andrew, R. J. and Jones, R. B.** (1998). Lateralisation in chicks and hens: new evidence for the control of response by the right eye system. *Neuropsychologia* **36**, 5–58.
- Miklósi, A. and Andrew, R. J.** (1999). Right eye use associated with decision to bite in zebrafish. *Behav. Brain Res.* **105**, 199–205.
- Miklósi, A., Andrew, R. J. and Dharmaretnam, M.** (1996). Auditory lateralisation: shifts in ear use during attachment in the domestic chick. *Laterality* **1**, 215–224.
- Miklósi, A., Andrew, R. J. and Savage, H.** (1998). Behavioural lateralisation of the tetrapod type in the zebrafish (*Brachydanio rerio*), as revealed by viewing patterns. *Physiol. Behav.* **63**, 127–135.
- Rashid, N. and Andrew, R. J.** (1989). Right hemisphere advantage for topographical orientation in domestic chick. *Neuropsychologia* **27**, 937–948.
- Rogers, L. J.** (2002). Advantages and disadvantages of lateralisation. In *Comparative Vertebrate Lateralisation* (ed. L. J. Rogers and R. J. Andrew), pp. 126–154. Cambridge: Cambridge University Press.
- Rogers, L. J. and Andrew, R. J.** (1989). Frontal and lateral visual field use by chicks after treatment with testosterone. *Anim. Behav.* **38**, 394–405.
- Rogers, L. J. and Anson, J. M.** (1979). Lateralisation of function in the chicken forebrain. *Pharmacol. Biochem. Behav.* **9**, 735–740.
- Siegel, S. and Castellan, N. J.** (1988). *Nonparametric Statistics*. New York: McGraw-Hill.
- Tommasi, L., Andrew R. J. and Vallortigara, G.** (2000). Eye use is determined by nature of task in the domestic chick (*Gallus gallus*). *Behav. Brain. Res.* **112**, 119–126.
- Tommasi, L. and Vallortigara, G.** (2001). Encoding of geometric and landmark information in the left and right hemispheres of the avian brain. *Behav. Neurosci.* **115**, 602–613.
- Vallortigara, G. and Andrew, R. J.** (1991). Lateralisation of response to change in social partner in chick. *Anim. Behav.* **41**, 187–194.
- Vallortigara, G.** (2000). Comparative neuropsychology of the dual brain: a stroll through left and right animals' perceptual worlds. *Brain Lang.* **73**, 189–219.
- Vallortigara, G., Cozzutti, C., Tommasi, L. and Rogers, L. J.** (2001). How birds use their eyes: Opposite left-right specialization for the lateral and frontal visual hemifield in the domestic chick. *Curr. Biol.* **11**, 29–33.
- Wallman, J. and Pettigrew, J. D.** (1985). Conjugate and disjunctive saccades in two avian species with contrasting oculomotor strategies. *J. Neurosci.* **5**, 1418–1428.
- Zeigler, H. P., Bermejo, R. and Bout, R.** (1994). Ingestive behaviour and the sensorimotor control of the jaw. In *Perception and Motor Control in Birds* (ed. M. N. O. Davies and P. R. Green), pp. 54–73. Berlin: Springer-Verlag.