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S21-5 Use of head position by birds to determine mode of analysis of what is seen

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Abstract Task properties determine which eye birds use in viewing. Thus the right eye system (RES) is used during visual control of manipulation and response, and the left eye system (LES) for wide search and other tasks requiring diffuse attention. As well, biases are imposed at different ages that are probably not generated by the current task. These biases determine what kinds of stimuli are found interesting. The changes in behavior that result are appropriate to the stage of development reached. Thus, in domestic chickens, shifts in bias are associated with such phases as close following of the mother, exploration of the environment, and learning about strange conspecifics. In addition, the assumption of specific head postures, coupled with standard eye positions, allow the bird to control the extent to which the RES and LES are responsible for visual analysis. This can be simple: for example, viewing by the right eye alone when planning a manipulation, or by the left eye alone when approaching a site at which the target of response cannot yet be seen. Or it can be complex, and involve both systems though with one still leading. The implications of these varying strategies of eye use, so different from our own experience, are discussed.

Key words Visual analysis, Right eye system, Left eye system, Head positioning

1 Introduction

Birds, and probably most vertebrates other than higher mammals, must see the world in a way quite different from ourselves. For most of the time their eyes are diverged in the "primary position of gaze" (Wallman and Pettigrew, 1985). The two eyes then see different areas of the world, right and left. The main lateral fixation points, which involve specialized foveae in some but not all birds (Walls, 1942), lie at around 60° to the longitudinal axis. In the domestic chicken, on which much of the work considered here has been carried out, the fixation point is about 63° (Dharmaretnam and Andrew, 1994), and it is not specialized beyond a slightly enhanced density (Ehrlich, 1981) and regularity of placement of receptors (Morris, 1982). This arrangement is important because there is evidence in the chicken (below) that the use of the main lateral fixation point has more to do with positioning the object of interest in a standard way on the retina than with making use of higher acuity of resolution.

One consequence of the far lateral placement of the lateral fixation points is that the two eyes can never be brought into register, as our foveae always are, so that both see the same object. While the eyes are in the primary position of gaze, the frontal fixation areas are also diverged, so that binocular vision does not occur. The independent functioning of the two eyes is enhanced by the fact that accommodation is entirely independent (Schaeffel and Howland, 1987), and eye movements, although often synchronized, move in different and independent directions (Wallman and Letelier, 1993). Not only do the visual systems fed by right and left eyes (RES and LES) process different information, since they see different things, but they do so in different ways. As a result, RES and LES can elaborate different records of the same visual experience.

When both eye systems are attending to the same stimulus, two different strategies can be used. In one, the head may turn so that the two lateral fixation points are used alternately. Although this strategy has not been studied experimentally, it would allow the specialized abilities of the two sides of the brain to be brought to bear in turn on the single target of current interest. In the second strategy, the eyes may converge so that the frontal fields become binocular. Binocular fixation then allows both eye systems to see the stimulus simultaneously. Again there is clearly a single object of interest. However, it will be argued below that during such fixation it is more likely that a single visual strategy is applied, such as how to respond under visual guidance.

2 The role of head position

Head position is used by birds to ensure that the eye system, RES or LES with abilities appropriate to the task in hand, will analyze the object of interest. Two different strategies are available. As already noted, the head may be turned so that only one eye can see the object. Alternatively, the head may point more nearly at the object but turned so that it is clearly averted to the right or the left visual hemifield. In the second case, part of the retina of the other eye may or may not see the stimulus. The key point is that it lies in one hemifield. Mechanisms of this sort have been described for vertebrates as widely separated as zebrafish (Miklósi et al., 1998) and rhesus monkeys (Hauser et al., 1998). In humans there is direct evidence that perceived position of a stimulus determines which side of the brain undertakes its analysis (Pierson et al., 1983).

A by-product of this ability is that the side on which a bird unexpectedly detects a stimulus will affect the kind of response that may be evoked. No doubt there are costs as a result, but these are evidently outweighed by the ability to choose and sustain processing by the appropriate eye system, using head posture.

3 Specializations of RES

RES is concerned with the visual control of response. In vertebrates that do not, like ourselves, manipulate the world with paired forelimbs, a crucial property is visual control of the mouth. In birds, this not only includes accurate guidance of the bill to its target, but also the matching of gape size to target size (Zeigler et al., 1993). It is remarkable here that visual control of a medial effector is lateralized in a way reminiscent of human handedness. The most sophisticated example of such control so far described is the use by *Corvus moneduloides* (New Caledonian crow) of the right eye when positioning the series of bites that detach a hooked strip of pandanus leaf to serve as a tool (Hunt, 2000). Eye use in nest construction would clearly repay study in the avian world.

In the chicken, it has been shown that the head is positioned during approach to bring the right eye to bear only when the object to be grasped or manipulated can be seen (Andrew et al., 2000; Tommasi and Andrew, 2002). In such circumstances, the head is turned 25° to the left to bring the right eye to bear. This position is assumed at a considerable distance, and is presumably associated with the establishment and maintenance of the requisite motor plan. When nothing to be pecked or grasped is seen during approach, the head is then turned to bring the left eye to bear. This is best understood functionally as a default condition. Use of the LES improves detection of novelty and analysis of the topographical layout of the environment. Direct approach to visible food hardly requires advanced topographical skills; yet change is always possible in the most familiar of environments, and is predictive of danger. Left eye use may help detection of such unexpected change.

4 Head saccades

When domestic chickens fix on an interesting object at a distance of about 55 cm they use two standard head positions. These center on 35–36° and 62–63°. The latter coincides with the angle of the pupiliary axis of the eye, measured in a relaxed chicken (Wallman and Velez, 1985). It is thus associated with viewing at the main lateral fixation point, with eyes in the primary position of gaze. The other head position (35°) appears to be the first of a series of head positions used during approach to a target. These run from 25° through 15° to 5° (Tommasi and Andrew, 2002). The distribution of preferred head positions suggests that 10° head saccades are usual under such circumstances.

Such peaks of preferred head position when fixating a large object reveal that a standard alignment with the object must be assumed. That the center of the object is aligned initially with the main lateral fixation point is the most likely possibility, but there is no direct evidence for this yet. Were there no such alignment, any peaks of usage would be smeared out by varying choices of points on the object.

The full sequence is likely to follow initial establishment of alignment using the lateral fixation point, succeeded by transfer of this point first to 35°, and then by a series of standard 10° saccades to a point close to but not yet identical with frontal fixation. The most probable function of standardized saccades is to ensure that features of the object transfer in a coherent way across the retina. If a feature picked out by region A transfers predictably first to B and then to C, this will facilitate rapid identification of the feature after each shift, allowing simultaneous analysis of information relating to the object of interest over a wide area of the retina. The breadth of high acuity along the streak connecting central and temporal retinas (Martin, 1993) allows this.

That a further mechanism is involved is suggested by two actual series of head positions, separated by 10°. The second series is 20°, 10° and 0°. When this series comes into use, the point of alignment is on the way to being transferred to the frontal fixation position at 0°, which presumably involves binocular convergence. The data are thus consistent with the use of a slight divergence of the optical axes in the 25°, 15° and 5° series to prevent binocular supply to visual units that would receive such input after full convergence. The head positions that would be associated with such slight divergences are used in search. This is clear for the food dish without a lid experiment, where the saccades are initiated at the point at which food becomes visible and a particular grain must be selected. The same is true for lids where a decision has to be taken exactly where to place the bill around the edge.

In free search over a floor on which food grains are scattered, it is clearly advantageous to involve both eyes. This requires some degree of independence of eye control, in that each eye should be able to move independently to fix on a target. In the next step, the eye system, left or right, that has the more promising target takes control of head position as well (Rogers and Andrew, 1989). The target is captured by the lateral point of fixation, and then the head is turned for frontal fixation during approach and peck. What is here suggested is that independence of analysis continues until binocularity is assumed, and that the critical change probably comes with the establishment of binocular inputs to appropriate visual units. This marks the transition to the kind of single vision that we use.

5 Specializations of LES

In the domestic chicken, the forced use of one or other eye shows that the use of more distant topographical features to locate a site at which food is known to be hidden is enhanced when the left eye is employed (Rashid and Andrew, 1989). When the right eye is used, chickens tended instead to rely on landmarks close to the site. Use of the left eye also increases responsiveness to small changes in the properties of a model social partner (Vallortigara and Andrew, 1991).

Preferential LES use of topographical information is also exhibited by marsh tits when hoarding (see below). The greater importance of the right cerebral hemisphere in rats for orientation by topographical features (Adelstein and Crowne, 1991; Cowell et al., 1997) confirms that this condition is general amongst tetrapod vertebrates, and not just confined to humans. Note that the LES links to the right hemisphere in birds.

6 Different memories in RES and LES

It seems certain that the two eye systems must collaborate in many tasks. Direct evidence for this is provided by cases in which each has learned different things about single incidents. Once again, the fact that the two eyes see different aspects provides a simple but powerful control mechanism, according to the hypothesis that each eye system records what it sees and therefore analyses.

The most striking case is provided by hoarding in marsh tits (Clayton and Krebs, 1994), in which both eyes are used differentially. In the experiment, the tit first placed the storage item in a hole surrounded by a specific local specific pattern. There were many such hoarding sites in different areas of the room, each with a different identifying pattern. Immediately after hoarding, the patterns were shifted to different holes. Five minutes later, the bird was reintroduced to recover the item, but now with one eye covered. When the left eye was in use, the bird visited the correct place in the room, but when the right eye was in use it chose the correct pattern in a new position. Given that the original placement was done under visual control by the RES (as expected), then the right eye would see the identifying pattern, whereas the left eye was free to scan the environment.

Cues used to identify the center of an area are another example. Tommasi et al. (1997) trained chickens to find food hidden in the center of an arena. The chickens were then tested in enlarged and distorted versions of the arena. When the left eye was in use, search was concentrated in the geometric center, cued by the point furthest from all walls and averaging estimates in all directions. When the right eye was in use, the chickens searched on a different pattern. They now moved around the full perimeter, always keeping to distances from the nearest wall that had separated the center from the closest point to a wall during control feeding. Exactly such a pattern would be generated if the RES recorded what it saw during feeding, including the lateral view of a wall. The LES, in contrast, would have had to record and integrate a series of views all around the general site of feeding, whether from search during a single or series of sessions.

The visual control of response, once initiated, goes beyond control of a motor plan. It is also necessary to choose an appropriate target, on the basis of past experience of response outcomes. It is likely that the RES is the more important here. In a standard test of acquisition of feeding discriminations, chickens perform better when using the right eye. Familiar food grains are scattered amongst small pebbles of roughly the same size but the grains are stuck down so that they cannot be taken up in the bill. Inhibition of pecks at pebbles develops faster with right eye use (Rogers and Anson, 1979; Deng and Rogers, 1997). The specific involvement of the RES in recording the consequences of response is suggested by the finding (Cozzutti and Vallortigara, 2001) that “devaluation” of a food affects choice of food site only when the right eye is in use. Devaluation is the temporary reduction in preference for an acceptable type of food after a hearty meal of such food.

The hypothesis can thus be extended. The RES may be supposed to use records of past response that include the appearance of the target that was chosen, the nature of the response itself and its outcome. As more and more comparable experiences occur, the cues defining the target will inevitably vary between successive targets, so that the RES is likely to be faced with the need to select key cue dimensions and to establish criteria of match. This would explain its superiority in acquiring discrimination between pebbles and food grains, for example.

Feeding is not the only type of response that is preferentially controlled by the RES. Male zebra finches approach females in a copulatory display in which the right side is directed towards her (Workman and Andrew, 1986). The same is true when testosterone-treated chickens approach a model to copulate (Workman and Andrew, 1986). When a conspecific is perceived on the left, in contrast, chickens are more likely to exhibit aggressive and sexual behavior than when it is seen on the right (Rogers et al., 1985). The same is true of a range of other vertebrates (Andrew and Rogers, 2002). Here motivational changes that result from seeing conspecifics are resisted when the RES is controlling. Such resistance may be part of a necessary ability of the RES to inhibit other responses during ongoing behavior (Andrew, 2002). It will be interesting to see whether this left/right difference is also used to control behavior by choice of eye. Evocation of behavior that is unwise in a particular social situation might be avoided by right eye use.

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