Integration of visual and auditory space in the mammalian superior colliculus

Laurence R. Harris*, Colin Blakemore† & Michael Donaghy‡

The Physiological and Psychological Laboratories, University of Cambridge, Cambridge CB2 3EG, UK

Recordings of eye movements and single-neurone microelectrode recordings of the superior colliculus in cats show that, for each saccadic movement, their eyes start near to the centre of the orbit so that the coordinates of visual and auditory space are aligned, and complex neural compensation of auditory or visual inputs to the superior colliculus is unnecessary.

EYES and ears are specialized for detecting events at a distance. Both vision and hearing can be used to localize objects in external space—a function of utmost importance to any animal anxious to avoid its predators or discover its prey. One part of the brain, the midbrain tectum (which in mammals consists of the superior and inferior colliculi), seems especially concerned with the analysis of spatial information derived from both the eyes and the ears. In animals of diverse phylogeny[1-6] there are neurones in the midbrain that have spatially restricted receptive fields in auditory or visual space and which respond when a sound or light stimulus appears (or preferably moves) within the appropriate, limited region of space. These systems of sensory neurones are topographically organized to form neural 'maps' of auditory and visual space across the midbrain tectum.

The idea that the roof of the midbrain is devoted to the analysis of positional information in external space is supported by the existence there in some species of other mechanisms for localization. The superior colliculus (SC) of cats[7], mice[4] and hamsters[8], as well as having both visual and auditory input, has a topographical representation of the body surface including the whiskers; neurones in the inferior colliculus of the bat[9] may play a part in echo location; and in the SC of the viper there is even a spatial representation of signals from the IR pit organs in the snake's face[10].

Damage to the tectum interferes with an animal's ability to 'orient' towards stimuli: indeed, lesions of the hamster's SC produce a visual defect that renders the animal seemingly blind to novel events in its visual field[11]. In the cat, removal of one SC (which represents primarily the opposite half of space) produces neglect of the contralateral hemifields[12]. Also, lesions of the colliculus in monkeys cause deficits in the timing of eye movements[13].

Further evidence for the importance of the SC in initiating orienting movements towards sounds or sights comes from the fact that electrical stimulation of this structure in unanaesthetized animals elicits movements of the eyes, head, ears and body towards the opposite side of space[14,15].

Correspondence of visual and auditory representations in the superior colliculus

The integrity of the perceptual world clearly demands correlation of positional signals from all sensory systems and especially of messages from the eyes and ears. An animal must know that an object that it both sees and hears is a single thing at one place in space; responses initiated by either auditory or visual cues must be harmonized and coordinated.

The deep layers of the mammalian SC seem ideally equipped for the correlation of spatial cues from the eyes and ears,

for here there are superimposed auditory and visual representations[7,8,16-18]. Neurones in the rostral part of the SC respond to sounds or sights directly in front of the animal, whereas for those further back, visual and auditory receptive fields are shifted into the contralateral hemifield of space. Indeed in cats, many individual cells receive both auditory and visual input[16]: the activity of such neurones could be thought of as providing pure, positional information regardless of the sensory channel mediating it.

In support of this concept, Wickelgren[16], working on the deep layers of the SC in paralysed cats, found such bimodal cells to have their visual and auditory receptive fields (though large) well matched in their horizontal eccentricity in space. Each neurone responded to either a spot of light or a small sound source presented in one particular region of the field. Could such cells in the cat's SC be responsible for the functional integration of visual and auditory space, triggering orienting movements towards peripheral objects whether identified by their visual appearance or by the noise they make?

The effect of eye movements: Pöppel's paradox

This hypothesis, though attractive in its simplicity, is paradoxical. Cells are able to respond selectively to sounds at a particular position by using the relative timing or intensity of sound at the two ears as the cue to direction: the coordinates of auditory space are defined with respect to the ears and hence the head. The positions of visual receptive fields are, however, defined with respect to the retina. As the eyes can move in their orbits, the coordinates of visual and auditory space used by bimodal neurones should, as Pöppel[19] has pointed out, be torn apart every time an eye movement occurs. Unless some compensatory process occurs, bimodal neurones in the SC should provide ambiguous directional information whenever the eyes are deviated from the straight-ahead position.

There are at least three possible ways in which each bimodal collicular cell might take account of changes in eye position: (1) The cell's visual receptive field might move with respect to retinal coordinates by an angular distance equal and opposite to each eye movement, thus maintaining spatial correspondence with the auditory receptive field. (2) The cell's auditory receptive field might move in space by an amount equal to each eye movement and in the same direction, to preserve the correspondence. (3) The auditory or visual input to the cell might simply be switched off whenever the eyes are significantly deviated from the central position, at which the auditory and visual receptive fields are aligned.

The first two possibilities seem implausible because they demand rapid and gross reorganization of the connections between the eyes or the ears and the SC each time the eyes move. The third hypothesis, which was not considered by Pöppel, is perhaps somewhat more likely. We have now

Present addresses: *Department of Psychology, University of Durham, Durham DH1 3LE, UK; †University Laboratory of Physiology, Parks Road, Oxford OX1 3PT, UK; ‡The National Hospital for Nervous Diseases, Queen Square, London W C 1 N 3 B G, U K
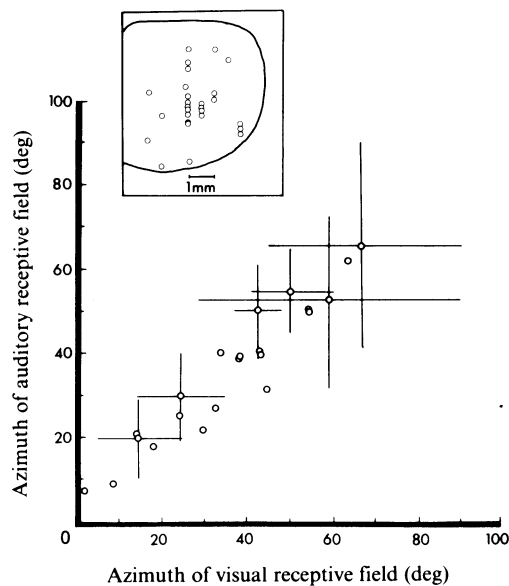
Azimuth of visual receptive field (deg)

Fig. 1 The auditory and visual receptive fields of bimodal cells in the deep layers of the SC are roughly superimposed in space. The inset shows the recording sites (O) of 27 bimodal cells reconstructed with respect to electrolytic lesions and projected on to the horizontal stereotaxic plane within the outline of the right SC. The graph shows the azimuth angle of the centre of the auditory receptive field plotted against that of the visual receptive field for all 22 of the neurones that responded well to the stationary tone used to plot the auditory field. The cat's eyes were centred in the orbits and the head was fixed in the straight-ahead position. For six cells the horizontal extents of the visual and auditory receptive fields are indicated by horizontal (visual) and vertical (auditory) lines.

Testing the three hypotheses

For three adult female cats we used the techniques of Evarts[20] and Schiller and his collaborators[21] to implant silver–silver chloride electrodes[22] around the eyes (for recording horizontal and vertical eye movements electro-oculographically) and a chamber above the SC (for the introduction of glass-coated tungsten microelectrodes to record from single neurones).

We trained each animal to accept being wrapped in a cloth bag and to lie inside a padded box. Its head protruded through a large aperture and was attached to a superstructure that could be used either to measure horizontal and vertical head movements[23] or to fix the head in one position. With training the cats soon accepted these procedures.

To stimulate cells visually, a spot of light was back-projected on to a translucent hemisphere (radius 57 cm) placed directly in front of the cat. Auditory receptive fields were plotted quantitatively by measuring the responses of cells to quiet tone bursts (duration 225 ms, frequency 1.2 kHz) emitted from a small radio earphone suspended from a crane whose centre of rotation was co-axial with the cat's head and whose angular position was varied in 10° steps over 180° in front of the cat and monitored by a potentiometer. The electro-oculogram (EOG) was calibrated[15,24] and the position of the eyes was monitored as a two-dimensional display on a storage oscilloscope. For subsequent computer analysis, horizontal and vertical EOG signals were recorded on tape, together with the neurone's action potentials, the voltage corresponding to the position of the auditory stimulus and pulses to indicate each onset of the sound.

Precision of correspondence of visual and auditory receptive fields

We studied 27 bimodal cells (giving responses of roughly similar strength to optimal visual and auditory stimulation) in the deep layers of the SC. 50% of the cells recorded in the colliculus

below 1.2 mm from the surface were bimodal. The inset in Fig. 1 shows the position of each recording site at which a bimodal cell was found. With the cat's head held in the straight-ahead position, her attention was constantly attracted to the centre of the hemisphere, and fixation at the centre was constantly checked from the two-dimensional display of eye-position. The position of the visual receptive field of the neurone was plotted by monitoring the responses elicited by a small moving spot (~2° in diameter) back-projected on to the hemisphere. Then the hemisphere was removed, all the room lights extinguished and the horizontal extent of the auditory receptive field plotted out by setting the height of the small loudspeaker on the same level as the middle of the visual receptive field, swinging the crane to various positions in front of the cat's head and recording the responses to tone bursts. Only five of the 27 bimodal cells could not be studied in this way because they failed to respond to the pure tone and were excitable only by more complex sounds such as key-jingling or finger-snapping.

Eye position was constantly monitored throughout this procedure. Rapid recalibration of the EOG, by the simple procedure[15] of examining the range of signals produced as the cat made eye movements over the whole oculomotor range, showed little change in the d.c. level or gain of the EOG within the period of darkness in these experiments.

All bimodal cells were spatially selective in their responses to sound and visual stimuli, although in some cases, especially for cells in the more caudal part of the colliculus, representing the more peripheral field, visual and auditory receptive fields were rather large and their borders not sharply defined. However, we were satisfied that our data confirmed Wickelgren's[16] observation that, with the eyes in a straight-ahead position, visual and auditory receptive fields are quite well aligned and usually of about the same horizontal extent. The graph in Fig. 1 plots the horizontal position of the centre of the auditory receptive field against that of the centre of the visual receptive field: total horizontal extents are also indicated for six typical cells.

Is there compensation of the visual receptive field during eye movement?

We did not attempt to measure possible minor variations in the dimensions, sensitivity or retinal positions of the visual receptive fields of bimodal cells during deviation of the eyes. However, for a number of bimodal cells we did informally replot the visual receptive field while attracting the animal's attention to various points on the hemisphere and hence producing deviation of the
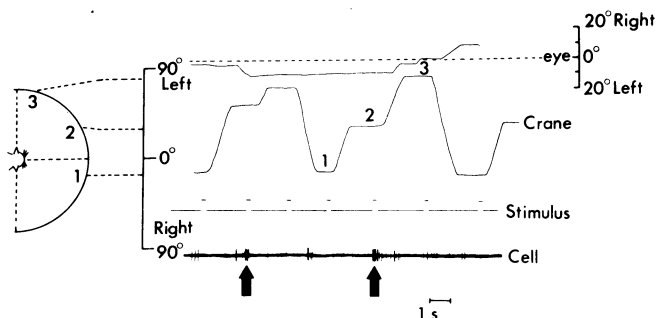

Fig. 2 A sample record from the experiment in which tone-burst stimuli were presented in the dark while the head was held. The position of the tone was randomized and the animal was encouraged to move her eyes. The top trace represents the horizontal eye position (approximate amplitude calibration on the right; interrupted line indicates the centre of the oculomotor range). The second trace shows the position of the crane that carried the loudspeaker (amplitude calibration on the left, with a sketch of the arrangement showing three positions labelled 1, 2 and 3, corresponding to the parts of the trace labelled). The third trace shows the duration of each 1.2 kHz tone burst (duration 225 ms). The bottom trace is an oscillograph recording of action potentials from a bimodal cell. Movements of the crane and noises produced by the experimenter elicited some activity between test stimuli. Clear responses to the tone are indicated by arrows.
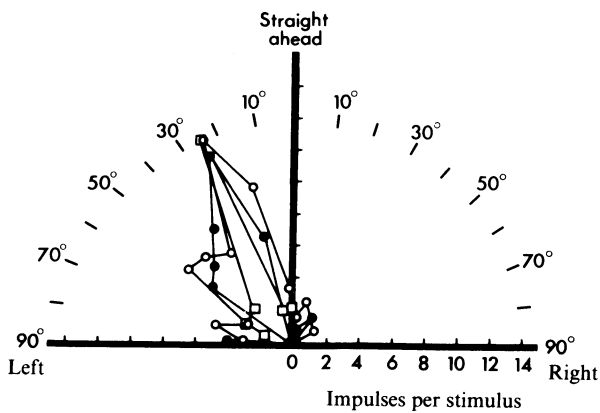
Straight
ahead

90°
Left

0 2 4 6 8 10 12 14

90°
Right

Impulses per stimulus

Fig. 3 Quantitative determinations of the spatial location and extent of the auditory receptive field of a bimodal cell. The visual receptive field for this unit was centred ~25° to the left of the vertical meridian of the visual field. Tone stimuli were presented randomly at different positions in front of the cat with the head held in darkness. The animal was encouraged to deviate her eyes. The response (mean number of impulses in the 500-ms period following the onset of the tone averaged over at least five stimulus presentations) is plotted along the radial axis of the polar graph. The average standard deviation is 2.7 impulses per point. The angle of this polar plot represents the angular horizontal position of the loudspeaker. Data are plotted for three conditions of eye fixation: eyes centred (within 7° of straight ahead; O), eyes deviated more than 7° right (□) or left (●). The auditory receptive field seems to be unchanged in spatial position and in sensitivity during deviation of the eyes.

eyes away from the central position. In no case was there any evidence of an obvious change in the retinal position of the receptive field: it always moved with the eyes and, except for possible brief changes in sensitivity associated with saccadic movements themselves[15,25], no bimodal cells seemed to suffer dramatic reduction in visual sensitivity during deviated gaze. We therefore reject the first hypothesis described above, as well as the possibility of strong attenuation of the visual input during deviated gaze (hypothesis (3)).

Is there compensation of the auditory receptive field during eye movement?

To test the second hypothesis we performed a detailed quantitative experiment on three bimodal cells (though the result was confirmed informally on many more). For each cell a series of ~500 auditory stimuli was delivered in total darkness with the cat's head held straight ahead and with the position of the crane randomly varied from tone to tone. We took care to deliver tones only when the crane was stationary and the room silent. In addition, between tone stimuli, the cat's attention was frequently attracted by tapping or speaking to persuade her to deviate her gaze away from the straight-ahead position. A commentary on the progress of the experiment was made on the voice channel of the tape recorder. Thus we randomized the position of controlled auditory stimuli while the eyes were sometimes straight ahead, sometimes deviated right, sometimes left.

Figure 2 is a typical example of the records obtained, showing eye position, crane position, sound stimuli and the activity of the cell. Note that although the cell was frequently active between the tone stimuli, in response to the relatively loud attention-attracting noises, only two of the tone bursts (marked with arrows) elicited clear responses.

In an off-line computer analysis, the responses of the neurone to tones at each position in auditory space were averaged for three ranges of gaze position: eyes straight ahead (within 7° of the resting position); eyes deviated >7° right of centre; eyes deviated >7° left. The data available allowed at least five responses to be averaged for every stimulus condition.

Figure 3 shows the results for one bimodal cell that had its visual receptive field centred about 25° left of the midline. Each point represents the average number of impulses in a 500-ms interval following the onset of the tone. Points are plotted on polar coordinates, the radial axis indicating the magnitude of the response. The data collected within each of the three ranges of gaze position are plotted with different symbols and clearly the maximum response was always of about the same magnitude and always occurred with the loudspeaker placed ~25° to the left of the midline, whatever the position of the eyes. The auditory receptive field did not move with the eyes, neither was the auditory input switched off when gaze was deviated. This result, which was reproduced in two other cells whose receptive fields were centred about 45° and 70° from the midline, seems to eliminate the remaining hypothetical forms of compensation described above.

For some cells the auditory receptive field was replotted with the head fixed not straight ahead but at a 45° angle to the right or left with respect to the body axis. In all cases the auditory receptive field shifted by precisely the same angle as the head. The auditory receptive field seems locked to head-centred coordinates, as one would expect if it depends on timing or intensity differences at the ears for its spatial selectivity. The auditory receptive field is not fixed with respect to the eyes nor with respect to the body axis as it does not move with the eyes when the head is stationary and it does move with the head when the head moves.

Recentering of the eyes during gaze shifts

Our results so far indicate that there is no simple mechanism in the cat's SC for compensating for deviations of the eyes. Indeed, we predict that cats might suffer perceptual misalignment of visual and auditory space when the eyes are fixating peripherally. However, further experiments have revealed that a simple motor strategy ensures that this situation very rarely occurs in normal, freely moving cats.
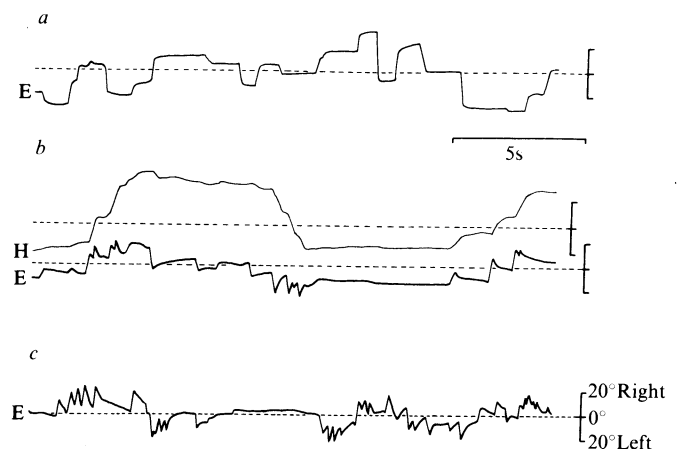

Fig. 4 Records of natural horizontal eye-in-orbit movements (E) and head movements (H) as a cat looks around a well lit stationary scene, in three conditions. The vertical calibration for each trace shows ±20° deviation from the straight-ahead position, which is indicated by an interrupted line. *a*, Head held stationary. The eyes make a series of characteristic saccades with intervening fixations, lasting up to ~2 s, with the eyes deviated up to ~30° from the centre of the orbit. *b*, Head free to move in the head-holder, which transduces head movements but impedes and slows them a little. Now each large eye saccade is accompanied by a head movement in the same direction. The vestibulo-ocular reflex evoked by each head movement results in a compensatory counter-rotation of the eyes, tending to bring them back towards the centre of the orbit. *c*, Head completely unrestrained (hence no trace for head position). Recentering of the eyes after each saccade is now even more efficient, indicating that the head usually executes a movement almost equal in amplitude to that of the eyes. Hence each new change in gaze starts with the eyes near the centre of the orbit.

In these three animals, and in three other cats implanted for EOG recording and head fixation, we used the methods of Blakemore and Donaghy[23,24] to study coordinated movements of the head and eyes during changes of gaze. The superstructure to which the animal's head was fixed could be released to allow relatively free head movement, the horizontal and vertical rotations of which were monitored through potentiometers attached to the axes of rotation. We measured eye movements as the cat simply looked around the room in three conditions: head held still, head free to move in the headholder, and head completely unrestrained (Fig. 4).
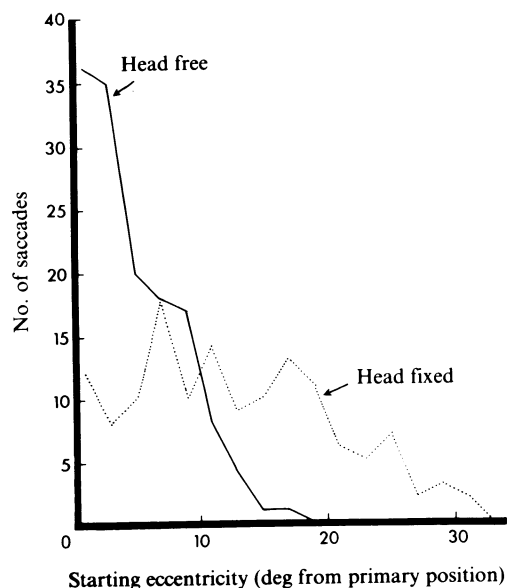

Fig. 5 Histograms showing the frequency of occurrence of eye-in-orbit position during steady fixation in head-fixed (interrupted line) and head-free (solid line) conditions (compare with Fig. 4a, c). The abscissa shows the horizontal position of the eye in the orbit (rightward and leftward deviations pooled) at the start of each saccade. Efficient recentering of the eyes in the head-free condition results in most new saccades starting with the eyes roughly centred in the orbit.

With the head held still the eyes make typical saccadic movements of up to ~40° amplitude with the eyes being held almost stationary for periods of up to 2 s, at deviations in the orbit of up to ~30° from straight ahead (Fig. 4a).

The situation is different when the head is allowed to move (Fig. 4b, c). Gaze changes of more than a few degrees in amplitude are now accomplished by combined movements of the eyes and head, with the eyes' saccade usually starting 25–50 ms before the start of the head movement[23,24]. Large changes in the direction of gaze involve a staircase of saccadic jerks of the eyes superimposed on a large head movement. Whenever the head is in motion, a counter-rotation of the eyes in the orbit, of opposite direction to the head movement and of virtually identical velocity, is superimposed on whatever other

eye movement is occurring. Blakemore and Donaghy[24] and Donaghy[27] have shown that this counter-rotation of the eyes in cats is due to the accurate operation of the vestibulo-ocular reflex. This has the effect of slowing down the saccade if the head begins to move before the eye has reached its target, and of causing a compensatory eye drift in the direction opposite to the saccade as the head movement continues after the end of the saccade (Fig. 4b). As the head rotation is usually of similar angular displacement to the saccadic eye rotation it accompanies, the net effect is to return the eye close to its starting position shortly after each saccade.

The saccadic mechanism can be viewed as a rapid motor system for the fixation of objects of interest, but the complete gaze change in a cat nearly always involves a similar movement of the head that effectively recentres the eyes. Hence, whenever a cat is steadily fixating an object after a whole gaze change is complete, the eyes are nearly always close to the centre of their orbits. This is very clearly shown in records of horizontal eye position when the head is completely unrestrained (Fig. 4c). Nearly all steady fixations occur with the eye close to the orbital centre, and each new change of gaze starts from roughly the straight-ahead position.

Figure 5 plots as a histogram the horizontal starting positions of the eye in the orbit for 70 successive changes of gaze made by each of two cats as they looked around a stationary scene. With the head fixed, the distribution of starting positions has almost constant probability out to 20° deviation and some saccades started with the eyes deviated horizontally by more than 30°. On the other hand, with the head completely unrestrained more than half of all saccades started with the eyes less than 3° from straight ahead in the orbit and very few started with the eyes more than 10° from the primary position.

Paradox resolved for the cat, but not for primates

Pöppel's paradox[19] turns out not to be a problem for the cat. Complex neural compensation of the auditory or visual inputs to bimodal cells is unnecessary because the motor programme used by the cat to look around ensures that the eyes rapidly return near to the centre of the orbit after each saccade. Every time a new peripheral object attracts the cat's attention its SC can safely assume that the eyes are near the primary position, and hence that the coordinates of visual and auditory space are aligned.

On the other hand, for primates, including humans, the paradox still remains. Quite clearly, monkeys and people do not follow every eye saccade with a head movement of nearly identical amplitude. Occasionally fixation is maintained steadily on a peripheral target with the eyes deviated by 40° or more. We know very little about the neural basis of sensory integration in monkeys (and even less, of course, in man) although bimodal cells have been described in the primate SC[28,29]. The greater independence of the head movements in primates makes Pöppel's paradox a real issue once again.

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