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Bi-sensory, striped representations: comparative insights from owl and platypus

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Abstract

Bi-sensory striped arrays are described in owl and platypus that share some similarities with the other variant of bi-sensory striped array found in primate and carnivore striate cortex: ocular dominance columns. Like ocular dominance columns, the owl and platypus striped systems each involve two different topographic arrays that are cut into parallel stripes, and interdigitated, so that higher-order neurons can integrate across both arrays. Unlike ocular dominance stripes, which have a separate array for each eye, the striped array in the middle third of the owl tectum has a separate array for each cerebral hemisphere. Binocular neurons send outputs from both hemispheres to the striped array where they are segregated into parallel stripes according to hemisphere of origin. In platypus primary somatosensory cortex (S1), the two arrays of interdigitated stripes are derived from separate sensory systems in the bill, 40,000 electroreceptors and 60,000 mechanoreceptors. The stripes in platypus S1 cortex produce bimodal electrosensory–mechanosensory neurons with specificity for the time-of-arrival difference between the two systems. This ''thunder-and-lightning'' system would allow the platypus to estimate the distance of the prey using time disparities generated at the bill between the earlier electrical wave and the later mechanical wave caused by the motion of benthic prey. The functional significance of parallel, striped arrays is not clear, even for the highly-studied ocular dominance system, but a general strategy is proposed here that is based on the detection of temporal disparities between the two arrays that can be used to estimate distance.

1. Introduction

Owl vs platypus: Natural selection has been running so many different experiments on brains, for such a long time, that we can often learn much from a judicious comparative approach to questions of sensory processing. For example, as suggested by Lorenz [1] one can ''get behind the mirror of Kantian uncertainty about the world'' by looking for common features of sensory design that have evolved independently to solve the same sensory problem. Common features of this kind have been incorporated into the different solutions adopted by various organisms as they coped with different phylogenetic constraints to solve similar kinds of sensory problems. One such problem, central to this meeting, is the calculation of the distance of objects in the environment, a measure of crucial importance to predators who must tune their motor apparatus to catch mobile prey. Because distance cannot usually be derived directly from the sensory epithelium, it is particularly illuminating to compare the solutions adopted in evolution to the problem of object distance. The solution may be particularly direct in the case of the platypus, *Ornithorhyncus anatinus*, which catches mobile prey in total darkness using a combination of electroreception and mechanoreception [2], as it is in the computation described by Gerhard von de Emde for distance determination by ''his'' electric fish, *Gnathonemus petersii*, in this volume.

In this paper I deal with two unusual evolutionary solutions of this kind, drawn from studies of the owl and the platypus, both of which perform extraordinary feats of prey capture. In both examples, there is a striped array that carries out a comparison between two separate representations that are oriented in parallel stripes that interdigitate, like the ocular dominance columns so well characterised in primate and carnivore visual cortex. In the case of ocular dominance columns, each eye is represented separately in alternate columns and the overall function is thought to be connected with stereoscopic vision and the detection of binocular disparity. In the case of the owl and platypus, the role of the

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stripes is even more obscure, since they involve two non-topographic visual inputs and mechanoreceptive and electroreceptive inputs, respectively. I will outline a general strategy for detecting disparities between two different sensory systems that is applicable to all three of these systems.

Owl corticotectal system: In the case of the owl, stereopsis is achieved despite the absence of the visual pathway features that bring this about in mammals. Since owls have a total crossing in the optic chiasm, with literally only one ganglion cell in ten thousand erring to make an ipsilateral connection [3], it was often inferred that human-like binocular vision was impossible in the owl. I first noticed that Walls [4] had drawn this inference when I was a student in the 1960s and had determined at that time to try test its validity by recording directly from the owl. Harvey Karten noticed my ambition to work on owls in one of my biographical notes [5] and drew my attention to two facts that proved pivotal for my career, viz: (1) owls have a second optic decussation that might provide a substrate for binocular interaction, even though physiological evidence was lacking at that time [6]; (2) Mark Konishi had a colony of owls and might be interested in looking for physiological evidence of binocular interaction.

Subsequently, Konishi and I showed astonishing functional similarities to cat and monkey visual cortex in the properties of "cortical" neurons in the owl's visual Wulst, a huge structure that occupies almost the complete dorsal surface of the brain in strigid owls (only slightly smaller in tytonid owls like the barn owl). The large size and accessibility, as well as the beautiful topography and lamination, make the visual Wulst of the owl a neurophysiologist's dream. Preparation is also simplified by the almost complete absence of eye movements [7,8]. The functional similarities between carnivore and primate mammalian striate cortex and owl visual Wulst included hemifield representations of each eye that are precisely in register (see Fig. 2), as well as orientation- and disparity-tuning, not to mention some cells that were so exquisitely tuned that we could activate them only by binocular stimulation with a target at a particular depth. This binocular depth system has been studied subsequently by Nieder and Wagner [9] in elegant studies where single units are telemetrically recorded from the Wulst of behaving owls who are discriminating depth in Julesz' random dot stereograms. Julesz' random dot stereograms are the "gold standard" for the demonstration of stereopsis since the other cues to depth can virtually be eliminated (but see Cowey and Porter [10] for an account of the difficulties of demonstrating stereopsis in highly intelligent animals). By combining single unit recording with free movement guided by a stereogram, these studies clearly established a link between the binocular depth cells of Wulst and depth-selective behaviour [11].

In this paper I will deal with a puzzling feature of the major output of these binocular depth cells to the optic tectum, viz: information is integrated from either side of the midline in an interdigitated stripe-like array within the tectum. This array represents and integrates input from binocular neurons in different hemispheres rather than from different eyes, as in the more familiar ocular dominance stripes. I speculate that this odd arrangement may be the first step in the process of encoding distance in a process of wide-field integration that would enable the tectal release of successive motor programs related to distance, while at the same time providing guidance in azimuth and elevation. Despite their impressive disparity selectivity, corticotectal output neurons have relatively narrow receptive fields confined to one hemifield that might prove unsuitable for such combined guidance and sequenced triggering at successively closer "shells" of distance from the prey. A wide-field, cross hemisphere kind of integration might be more appropriate for this process, as envisioned by McIlwain [12] for cat tectum, despite the disturbingly unfamiliar lack of apparent topographic order that is involved in integrating opposite hemifields.

Platypus primary somatosensory cortex (S1) stripes: The example from the platypus sensory system also involves a stripe-like array that integrates inputs from two different systems, like the ocular dominance stripes of striate cortex and the tectal stripes representing dual hemispheric corticotectal inputs in the owl tectum. As with the owl corticotectal system, the puzzle of the stripes in platypus S1 is incomplete because of the problems of working on such unusual and nationally-admired animals as platypus. Nevertheless, one can piece together a coherent story that involves the platypus making a comparison of mechanical signals and electrical signals coming from the same moving prey in the water. The S1 stripes allow the integration of the mechanoreceptive and electroreceptive systems, with individual bimodal neurons responding to both mechanical and electrical signals at a particular time delay. The arrangement may act as a "thunder and lightning" device that gives prey distance as a function of the delay between the instantaneous electromyogenic signal and the later-arriving mechanical signal.

2. Methods

2.1. Owl corticotectal system

Four barn owls (*Tyto alba delicatula*) and 2 grass owls (*Tyto capensis*) were used. As we could see no difference between the data from the visual systems of these two species, we have combined them.

Corticotectal neurones in Wulst: The owl was anaesthetised with ketamine (10–15 mg IMI) and attached to

a stereotaxic frame using a bolt glued to the exposed dorsal surface of the skull using cyanoacrylate glue and dental acrylic. A life-sized model of the owl brain and an owl skull were used to orient the bolt on its universal joint so that direct line-of-sight access behind the orbit could be obtained to the optic tectum, through a groove revealed on the anterolateral surface of the forebrain, once cancellous bone had been removed. The anterior pole of each optic tectum was exposed by dissection of the overlying bone and the use of an operating microscope with axial illumination as previously described [3,6] and a small hole made in the dura using 23 g needles bent into hooks. Multiple injections of 0.1–0.3 μl retrograde tracer were made 100–200 μm below the surface using a glass micropipette glued with dental acrylic over the barrel of the microsyringe and a custom microinjection apparatus that advanced the plunger under stepping motor control. Rhodamine isothiocyanate was injected on one side and fluorescein isothiocyanate on the other. The bone defect was covered with tissue soaked in Sofradex® (dexamethasone (as sodium metasulphobenzoate) 0.05%, framycetin sulphate 0.5%, gramicidin 0.005%). Survival time was 20–40 h. After euthanasia with separate injections of overdoses of ketamine and pentobarbital sodium, the owl was perfused with heparinized saline followed by 2% paraformaldehyde in phosphate buffer. The total perfusion time of fixative was limited to 20 min. This figure was chosen after some trial and error to achieve the appropriate balance between the need for a firm brain to slice in the vibratome and the problem of leaky somata on injection that seemed to follow too prolonged a fixation time. Sections were cut roughly normal to the surface of the Wulst at 300 μm on a vibratome, mounted in glycerol and examined on a Zeiss Axioscop using two separate, standard rhodamine and fluorescein filters, as well as a cube that enabled the simultaneous visualisation of rhodamine and fluorescein.

Retino-tectal ganglion cells: The eyes were removed, a cut made at the corneo-scleral junction and placed in lysine-periodate paraformaldeyde solution [13]. The retinas were dissected free of the pigment epithelium and mounted ganglion cell layer up, on glass slides freshly coated with 2 layers of Gatenby's chrome alum/gelatine solution. They were mounted in glycerol and examined in the same fluorescence microscope system as for the corticotectal neurons.

Orthograde projections to the tectum from Wulst: In a separate experiment, a large craniotomy exposed the whole dorsal surface of the Wulst. Multiple injections were made using the same microinjection apparatus as used in the tectum, except that the tracer was HRP. The brownish staining of the Wulst after injection was used to gauge the spacing of the injections so that complete coverage of the Wulst was achieved. This required about 20 separate injections. Survival was 40 h. A whole mount of optic tectum was made by unrolling it and placing it under a glass slide and brass weights as previously described for mammalian cerebral cortex [14]. HRP projections were revealed by the TMB method of Mesulam [15].

3. Optical recording

The tectal surface was exposed as described for the labelling experiments and protected from drying with high-viscosity silicone. The camera (Optical Imager 2000) was focussed 300 micra below the surface of the tectum and images acquired every second as described previously [16]. Visual stimulation was carried out in 30 s blocks under light ketamine anaesthesia (~10 mg/kg). During each block, visual stimulation was confined to a single hemifield by means of a black velvet drape that was taped to the owl's vertical meridian as projected onto a spherical translucent dome, 57 cm radius, that was centred on the owl's eyes. The tape reduced visual stimulation at the vertical meridian along a 1° wide strip. The hemifield being stimulated was switched by flipping over the velvet drape at the beginning of each block until 20 blocks had been collected. Visual stimuli projected onto the dome were moving, high contrast dark bars of different orientations and size that had been shown previously to be effective in driving superficial Wulst neurons. As many as 10 bars could be visible in one hemifield at one time.

3.1. Platypus mechanoreception and electroreception

The physiology and neuroanatomy underlying the combined, ocular-dominance-column-like cortical representation of bill mechanoreception and electroreception has already been described [17]. In these earlier experiments, the hypothesis that bill mechanoreception might involve water-borne vibrations was not entertained, so there was no systematic investigation of the effect of varying the precise temporal relations between time of arrival of water-borne electrical and mechanical stimuli. Platypus became unavailable for these kinds of experiments in 1997, so retrospective analysis was the only possible way to test the hypothesis. It could be seen that all bimodal units showed a form of temporal facilitation where the peak activation for combined electrical and mechanical stimulation shifted to an earlier time compared with unimodal stimuli. The magnitude of this shift varied from 5 to 15 ms in the small number of neurons that could be studied. In the absence of more specific data, which are unlikely to be collected in the present climate of opposition to this kind of work on the platypus, it seems reasonable to conclude that these bimodal cortical neurons are particularly interested in the relative timing of the electrical and

mechanical events and the times of special interest would be in this same range where temporal facilitation has been known to occur.

3.1.1. Relative timing of mechanical and electrical stimuli

In contrast to the propagation of waves at the water surface, where the velocity is well described [18], there is little information about the velocity of particle motion underwater, particularly under the natural conditions that would prevail when platypus catch benthic prey. So a device was constructed to measure this directly under water in semi-natural conditions where a known prey item produced a tail-flick. A wooden "paddle" (swizzle stick 2 mm diameter × 5 cm long) was attached to a piezo-electric device to record particle motion. The increase in mechanical leverage enabled us to record mechanical disturbances in the water up to 50 cm away from the tail flick of the red claw yabbie (*Cheronax* Sp). This crustacean was the platypus' major dietary item at the time and that we knew that it could be detected at that distance. A bipolar electrode was connected to a pre-amplifier circuit to record the electromyographic signal associated with the tail flick. The probes were placed in the same water used in the platypus aquarium in a plastic tank approximately 1 m × 1 m × 0.4 m deep. Tailflicks were provoked from the yabbie by gently tapping with a stick and the resulting electromyographic potentials, along with the mechanical disturbance recorded at different distances from the two probes. The effect of changing water depth on the latency of the mechanical wave was studied as well as the distance between probe and yabbie.

4. Results

4.1. Owl

4.1.1. Ipsilateral and contralateral corticotectal neurons originate from the same topographic location in Wulst

Ipsilaterally- and contralaterally-projecting corticotectal neurons were found intermixed at the same location in the Wulst, even when injections had been placed in small sites that represented topographically incongruent locations when the tectal and Wulst retinotopic maps were considered together. For example, contralaterally-projecting corticotectal neurons could be labelled on the vallecular margin of the Wulst, representing the vertical meridian, from a tectal injection at the anterior pole of the contralateral tectum, which represents locations 20° into the ipsilateral hemifield. Despite the intermingling of neurons with crossed and uncrossed destinations of their axon terminations in the tectum, we rarely encountered an individual neuron with evidence of label from both tecta. Such bilaterally-projecting neurons were seen in less than 1% of cases (9 double-labelled neurons compared with 1010 single-labelled neurons). This is shown in Fig. 1 and the geniculo-striate visual pathways of the owl are outlined in Fig. 2. The integration of corticotectal pathways with the retinotopic organisation of the geniculo-striate pathway is shown in Fig. 3.

4.1.2. Morphology of injected corticotectal neurons

Corticotectal neuron morphology varied widely, with different size and complexity of dendritic tree and marked variation in spine density. We saw no obvious difference between the morphology of the ipsilaterally and contralaterally-projecting neurons. The overall dendritic morphology of corticotectal neurons shared some similarities to that of mammalian corticotectal neurons with the exception that they lacked the apical dendrites that are characteristic of mammalian pyramidal neurons.

4.1.3. Ipsilateral and contralateral corticotectal projections interdigitate in tectum

The separation of crossed and uncrossed corticotectal neuronal populations observed with retrograde label was reinforced by examination of the anterograde label, which was distributed to the tectum in a stripe-like

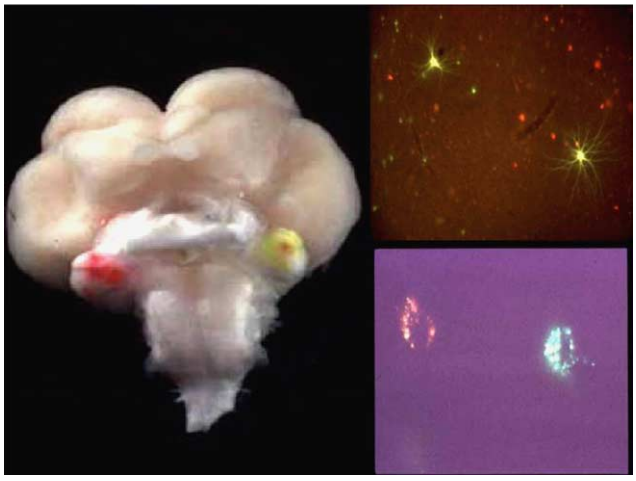

Fig. 1. Ipsi-, contra- and bilateral corticotectal neurons. Left: Ventral view of *Tyto* sp. brain shows reddish rhodamine dump in right anterior tectum and greenish fluorescein dump in left anterior tectum, both having been placed by direct visualisation of the midbrain following a dissection that obviates the need for a needle track and the risk of placing dye along the injection path. Upper right: After separate fluorescein and rhodamine injections in each tectum, corticotectal neurons were labelled in the Wulst, side by side at the same topographic location. Note nearby red and green neurons. Despite this intermingling of ipsi- and contra-laterally projecting corticotectal neurons, it was rare to find a corticotectal neuron with label from both tecta. Bottom right: The absence of double labelling implies that there must be separate sites within the tectum that receive ipsilateral and contralateral projections at the appropriate topographic location. This implication was verified by orthograde projection studies (Fig. 4), and optical recording (Fig. 5).

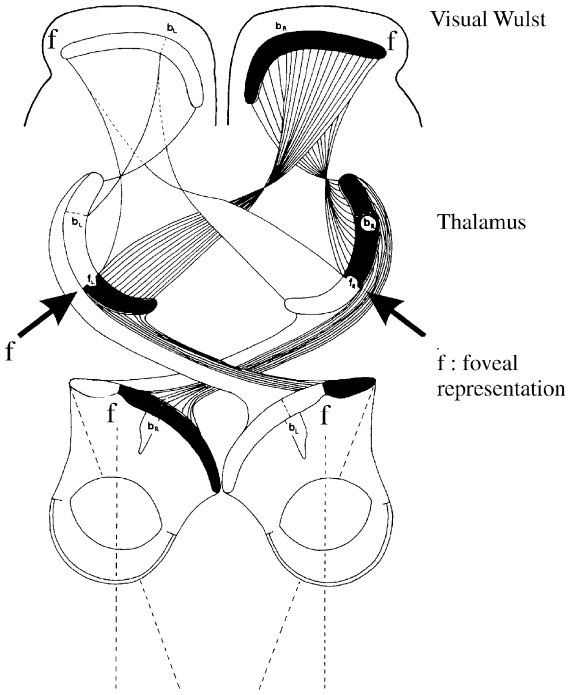

Fig. 2. Geniculostriate visual pathways of Owl. A second decussation enables integration of information from the same hemifield of each eye despite the complete decussation in the optic chiasm. Contrast this integration of both eyes into a single hemifield map in each hemisphere with Fig. 3, which shows the complex arrangement in the midbrain, where an input from the whole contralateral retina interacts with non-topographic inputs from the each Wulst representing both hemifields of space. f-Fovea, or foveal representation (marked by arrow in thalamus, showing that the complete contralateral retina is represented in this relay nucleus, in contrast to the partial representation in the visual Wulst).

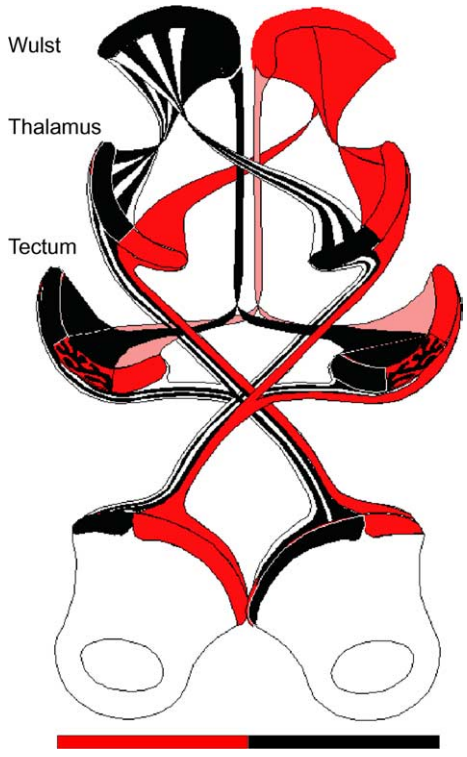

Fig. 3. Bilateral, non-topographic corticotectal projection from Wulst back to midbrain tectum of Owl. Pathways devoted to the right hemifield are depicted BLACK, while pathway devoted to the left visual hemifield are depicted RED. Note that each Wulst (top structure) is devoted exclusively to a single hemifield, but that both subcortical stations, the thalamus (second from top) and midbrain tectum (immediately above eyes) have inputs from both hemifields. The feature of interest in the present paper is the middle third of the mediolateral extent of each tectum, where there are inputs from both Wulsts to the same region (indicated by stippling). These corticotectal inputs to the same tectal zone must perforce be non-topographic, since they represent opposite hemifields 20° on either side of the vertical meridian. These disparate corticotectal inputs do not mix, but instead occupy separate interdigitating stripe-like arrays. The function of such intermingled, non-topographic, inputs from the telencephalon is an intriguing puzzle whose solution could illuminate the general question of the role played by disparate inputs that are mixed in the same array.

fashion, with the stripes roughly parallel to the horizontal meridian. This is shown in Fig. 4. The stripe-like corticotectal projection was confined to the middle third of the tectum, corresponding to the retinotopic input from the vertical meridian to around 20° contralateral in the visual field of the tectum. We did not succeed in achieving complete, separate labelling of the anterograde corticotectal system from both Wulsts, but we infer that the pattern of stripes observed on each side are interdigitated, this being a more likely and logical alternative than an arrangement where the orthograde stripes from both Wulsts are superimposed and the intervening regions receive no corticotectal input at all.

Optical recording: We were able to verify this unexpected arrangement using optical recording while alternately stimulating each hemifield. The images were normalised by division of one hemifield's image by the opposite hemifield's image. This division procedure should only result in patterned activity if inputs converge onto the same tectal locations from opposite hemifields. Optical recording (Fig. 5) revealed a zone of absent activity at the antero-medial edge of the tectum, in the topographic region know to get input from the ipsilateral hemifield. Adjacent and more lateral to this region there was a vertical strip with intense activation in stripe-like zones whose boundaries ran roughly parallel to the horizontal meridian. This zone corresponds to the region where ipsilateral and contralateral corticotectal inputs converge, and where the overlying retinal projection corresponds to a vertical strip between the zero vertical meridian and a vertical meridian at azimuth +20° contralateral (see Fig. 5).

The optical recording result confirms the inferences about the projections made from the retrograde and anterograde projection studies. In particular, it shows that both hemifields make a contribution to the activation of the same site in tectum, an outcome that could only come about if there was a strong (non-topographic) input to the region from the contralateral Wulst. The

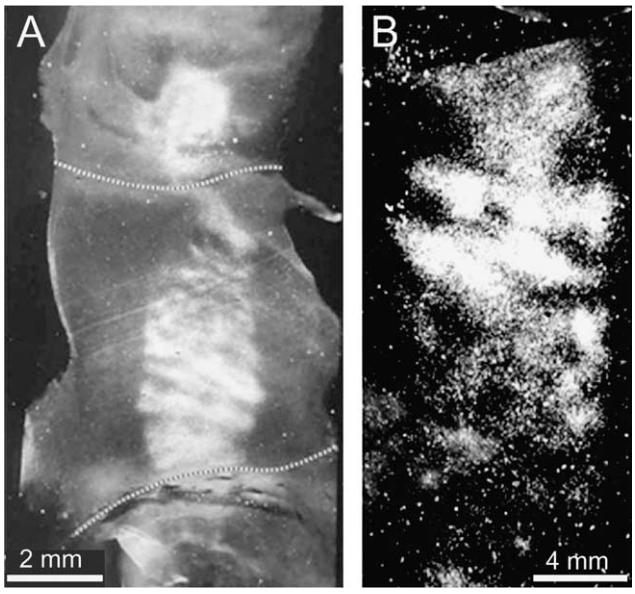

Fig. 4. Orthograde transport from total extent of contralateral Wulst to whole-mounted optic tectum of Owl. Horseradish peroxidase, reacted with TMB, is shown after anterograde transport from the contralateral Wulst. Magnification in the right panel is twice the magnification in the left panel. Anterior pole of the tectum is to the left in each panel; Dorsal and medial is towards the top in each panel. Note the absence of input to the anterior pole of the tectum where it would be expected on the basis of retinal topography, since the tectum has retinal input here from −20° to 0°, just like the contralateral Wulst. Note also that the sharply-defined vertical strip of corticotectal input is broken into roughly horizontal bands.

interdigitation of two arrays, one from each Wulst, certainly confirms the principle put forward here that this involves the encoding of differences between the arrays, particularly when one realises that in this case the arrays represent opposite hemifields (Fig. 6)!

4.1.4. Ipsilateral and contralateral corticotectal projections integrate mirror-symmetric regions of visual space

It was not possible to verify electrophysiologically the topographic relations between the corticotectal system and the retinotectal system. While the direct retinal topography could be demonstrated, it was not possible to define the corticotectal input clearly in terms of the expected binocular depth-selective responses from a wide field, including the ipsilateral 20°. Elucidating this system physiologically may require more work on state of anaesthesia or on examining the possibility of binocular depth inhibition against a background of retinally-induced excitation.

Nevertheless, it was possible to show from two different approaches that the arrangement of the corticotectal projection was non-topographic. First, corticotectal neurons could be labelled at the same location in the Wulst from two sites in the opposite tecta that represented mirror locations between 10° and 20° on either side of the midline. This was puzzling to us from the very first experiment when we thought that there

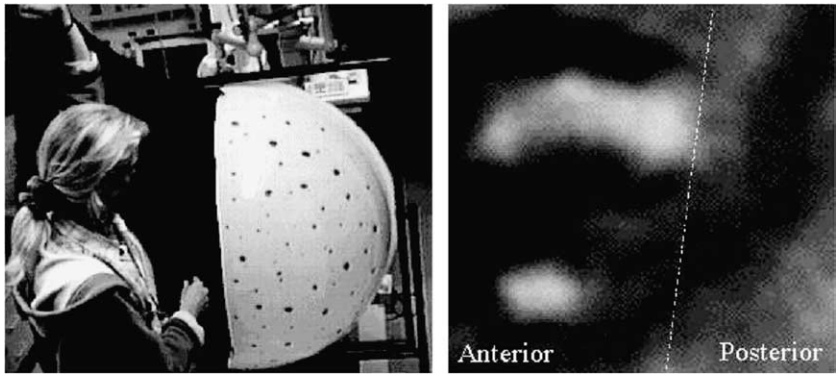

Fig. 5. Optical recording experiment showing corticotectal input from both hemispheres. A translucent dome was used to provide visual stimulation out to 80° azimuth in both hemifields. Black velvet, taped along the zero meridian, was flipped every stimulus cycle of 5 s in order to alternate visual stimulation of each hemifield (left hand side). Right hand panel (representing 1 mm square): dotted line indicates the +20° azimuth region, anterior to which there is bilateral input from both Wulsts into the stripe-like corticotectal region identified with anterograde label. The intrinsic signal was recorded and averaged in each hemifield condition and then the images from each hemifield condition were divided to give a reflection of the relative activity produced by stimulation in the two conditions. There is a zone of absence activity in the posterior part of the image corresponding to azimuths greater than 20°. This control result is to be expected, despite the fact that there was retinal input to this region, if there is no complementarity between the two stimulus conditions. In contrast, anterior to the zero activity zone there is a heterogeneous region, with adjacent high contrast zones, some with horizontal orientations, corresponding to retinotopic regions 0–20° contralateral; this high contrast differential activity implies a high degree of complementarity in the pattern of activity in each stimulus condition and therefore requires that both hemifields (both Wulsts) are converging onto the same tectal location. In other words, this experiment verifies the unexpected anatomical findings of Figs. 2 and 3 that there is a non-topographic overlap of inputs from both Wulsts. Ipsilateral Wulst provides inputs covering azimuths from 0° to +20° visual field contralateral to the tectum, in congruence with the retinal input to the same piece of tectum. In striking contrast, contralateral Wulst provides inputs covering azimuths from −20° to 0° azimuth in the mirror symmetrical part of space. This mirror visual field input from ipsilateral Wulst is arranged in stripes and is connected to the same tectal zone receiving retinal and ipsilateral Wulst input from 0° to +20° azimuth.

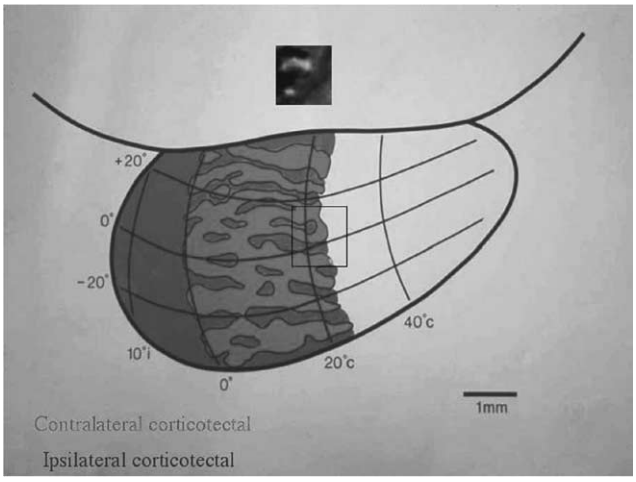

Fig. 6. Surface of the left tectum, anterior pole to the left of figure, showing the three zones of retinotectal vs corticotectal projections. Note the topographic mismatch in the retinorecipient zone from 0° to +20° azimuth, with mirror symmetrical retinotopic positions being represented via the Wulst. Inset shows the 1 mm square window used in the optical recording experiment of Fig. 5 for comparison. The roughly-horizontal zones of activation (white) and inhibition (black) produced by alternately stimulating each hemisphere have similar dimensions and shape to the horizontal striations revealed in the projection from the Wulst. In other words, both Wulsts contribute inputs to the same location in the tectum, even though they represent mirror locations in the two visual fields! Optical recording therefore supports the extraordinary mirror topology imposed upon the retinotopicity of tectum by the very different topographic organisation of the corticotectal inputs at the same location.

might be technical explanations, such as undetected spread of label. Technical explanations have been ruled out in many subsequent experiments that have confirmed the bizarre non-topographic arrangement. For example, the second orthograde experiment confirmed the arrangement, because the contralateral corticotectal projection avoided its topographically-congruent region on the anterior pole of the tectum to innervate the region of tectum that received a retinotopic projection from the mirror-symmetrical region (i.e. visual field ipsilateral to the field locations of that crossed corticotectal system).

It was always easy to be confused by these data, and to assume that you had made some error in coding slides or reversing the section. The reluctance to accept such a counterintuitive arrangement also explains the long latency between the original work and this presentation of the data.

4.2. Platypus

4.2.1. Stripe-like interdigitation of electroreceptive and mechanoreceptive representations in primary somatosensory cortex (S1)

There is a good structure–function relationship between the stripe-like array shown in platypus S1

Fig. 7. Electroreceptors (40,000) [red] and mechanoreceptors (60,000) [blue] in the platypus bill. Note the parasagittal arrangement of electroreceptors. This reconstruction is based on a photomicrographic study of both kinds of receptor pore after their contrasting morphologies had been revealed in the bill using ink. Each receptor's distribution was separately plotted, based upon the different morphology of each. The separate distributions have been combined here using pseudocolour. (See [30] for further details.)

with cytochrome oxidase (CO) staining and the physiological properties of neurons recorded in the two kinds of stripes (Figs. 7 and 8). Neurons in cytochrome-dense stripes were activated by mechanosensitive inputs to the bill, in keeping with the high levels of maintained and driven activity of these neurons. In contrast, the cytochrome-light stripes had neurons that were also electrosensitive, in keeping with the low levels of maintained activity of electrosensitive cortical neurons.

By studying bimodal neurons that receive both electrosensitive and mechanosensitive it was possible to examine their interaction. Unfortunately, these experiments were terminated by lack of unavailability of platypus just as we realised the importance of varying the relative timing of the two inputs. Nevertheless, it was clear that bimodal neurons had different latencies when activated electrically or mechanically. Because there was no opportunity to check on the preferred latency difference for bimodal stimulation before platypus experiments ceased, this preference has been assessed retrospectively in a variety of units from the latency difference in the two sensory modalities. The latency difference varied from 0 to 15 ms from unit to unit, with a mode around 7 ms. For the purposes of this paper, it is assumed that there would be optimal bimodal stimulation when stimuli arrived with latency differences corresponding to these differences.

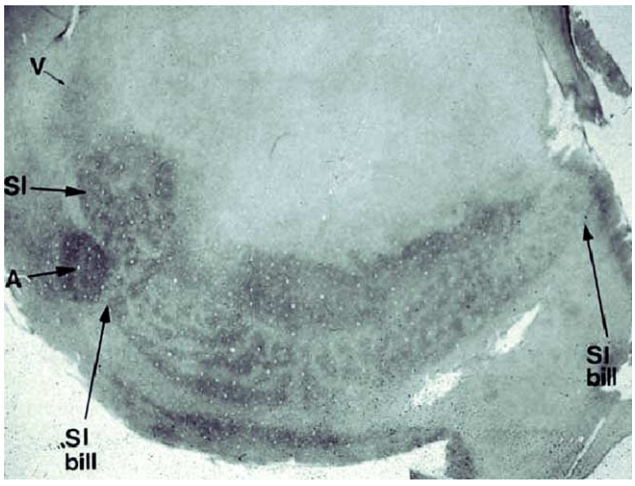

Fig. 8. (A) Cytochrome oxidase preparation of flattened Platypus S1 cortex to show stripe-like arrangement in the bill representation. The two arrows labelled S1 bill show the very large extent of the bill representation within primary somatosensory cortex (S1). The rest of the body's representation (labelled S1) is much smaller. The stripe-like arrangement in "S1 bill" has been shown to correspond to the two different sensory inputs from the bill, electrosensory and mechanosensory, with the cytochrome oxidase-rich stripes corresponding to the mechanosensory division, which has much higher spontaneous activity than the electrosensory division.

5. Discussion

5.1. Functional significance of the dual representation of the ipsilateral hemifield in optic tectum

The present study has established that the ipsilateral hemifield is represented twice in the owl's tectum: first as a result of direct retinal input, since the tectum receives a representation of the complete retinal field of view, as in most vertebrates with the exception of primates and relatives. The second source of input concerning the ipsilateral hemifield derives from corticotectal neurons in the contralateral Wulst, which have a highly-defined projection to the intermediate layers of the tectum. Since the Wulst neurons convey information that cannot be derived directly from the retinal input (such as information about binocular depth), the second innervation pattern from the Wulst is at first sight reasonable. What is much more difficult to understand is that the input to the tectum from the contralateral Wulst is not in topographic register with the local retinal input. To be in register, the contralateral Wulst input to tectum would have to project to the anterior-medial-most zone of the tectum which represents visual space 20° ipsilateral to the vertical meridian. Instead, the contralateral Wulst input to tectum innervates a tectal zone that is separated from the anterior-medial pole and receives both retinal and ipsilateral Wulst input from the 20° of visual field immediately adjacent to the vertical meridian.

In other words, there is a topographic mismatch between the projections from the ipsilateral and contralateral Wulsts to the tectum with mirror-symmetrical positions 20° ipsilateral and contralateral to the vertical meridian being represented in this part of the tectum. This arrangement is illustrated in Fig. 4.

What functional role could such connectivity serve? How does one explain an organisation where each tectum has a region subserving the same part of visual space, 20° on either side of the midline, that receives input from both ipsilateral and contralateral forebrain and that seems deliberately to ignore the precise topography for which the visual system is noted?

Encoding of large disparities: The first possibility is that this would enable the encoding of very large retinal disparities, like those seen in the optic tectum of plethodontid salamanders where there is a mirror arrangement of retinotectal inputs from each eye [19]. The problem with this interpretation is that the cortico-tectal inputs concerned are already binocular and highly-tuned for much smaller retinal disparities. It is hard to see what purpose would be served by such a recombination from binocular neurons on either side of the midline when the Wulst neurons are already so exquisitely tuned for disparity.

Depth and motor control: An alternative explanation is offered by a consideration of the owl's predatory life style. In a stoop, the owl must execute a sequence of motor programs that are each linked precisely to distance from the prey such as extension of wings and alula, extension of talons etc. Since the visual guidance for such programs comes from the centre of the visual field, by necessity, some form of cross-midline integration or right/left balancing would be inevitable to ensure that the precise depth information was also consistent with a precise central heading toward the prey. The non-topographic cortico-tectal inputs described here could play an important role in such a process for a number of reasons.

(a) First they are already highly processed for binocular depth discrimination and would provide the precise information necessary to guide the strike.

(b) Cross-midline integration would be mediated by the unusual corticotectal topography.

(c) Segregation of mirror inputs into separate stripe domains permits independent hemispheric control of the region and a possibly superior neural apparatus for dealing with ambiguity.

Motion shear: A third possible role for this system was suggested by Herman Wagner after I presented the puzzling data at Treilles. Van der Willigen, with Wagner and colleagues [20,21] has shown an unexpected interdependence of motion perception and stereopsis in the owl, which can transfer learned cues from a stereopsis task to a similar motion parallax task, but cannot use motion parallax to solve a similar stereo task. This

asymmetry is consistent with a role for the corticotectal system in transmitting to the tectum information about an object that is visible stereoscopically but not monocularly. If monocular parallax is sufficient for the disambiguation of a motion contour at the tectal level, as suggested by recording experiments in the pigeon's tectofugal pathway [22], the asymmetry could be explained by the presence of a strong input from Wulst to tectum, which could convey the stereo information, but not in the reverse direction. Further support for this idea is provided by the fact that some tectal neurons have extremely complex, wide-field integrative properties for the extraction of contour information about objects moving in a flow field. Some of this complexity could have a corticotectal contribution. If motion and stereo information were segregated in the Wulst, even a strong contribution of motion processing to the corticotectal system would be compatible with an asymmetry, since the Wulst stereo processing could still contribute to tectal motion processing, but not vice versa.

If this schema is correct, cooperation at the tectal level between the motion and stereo systems could help maintain the owl's orientation to a dimly visible prey outline during a strike. In this situation, it would be paramount to integrate across the midline so that the prey was not "lost" as it moved from one part of the visual field to another. The double representation in each tectum would ensure that this did not happen and that there was no resulting disadvantage at the vertical meridian of the very precise binocular decussation in the Wulst.

5.2. Interhemispheric competition

Paradoxically, the need to integrate across the midline seems to be ignored by the corticotectal inputs where they converge from each hemisphere onto one tectum. The stripe-like segregation of inputs from each hemisphere suggest instead a form of competition between the independent sources of information. Given the difficulty of the owl's prey acquisition task in disambiguating a poorly visible prey, perhaps this competition is an apparatus to deal with ambiguity. If there were two "opinions" about the nature of the prey's contours, perhaps this is where the rivalry between them would take place.

In discussions about the owl's superb spatial abilities, the emphasis is usually upon the accuracy of localisation of a sound source or visual target. In the present case, I am proposing that there is large-scale generalisation across azimuthal space for the 40° or so represented by the mirrored ipsilateral hemifields of each hemisphere while maintaining tight specificity for depth by virtue of the disparity sensitivity of the corticotectal neurons. This region could then generate a series of concentric "shells" at different distances from the owl that would provide the depth information needed for each program of the stoop sequence, but would also provide a wide field within which to operate necessary manoeuvres such as course corrections. The convergence of symmetrical inputs from both hemispheres onto the same midbrain location could also serve an important role in centring the owl's course by balancing potential biases for one hemifield.

5.3. Stereovision vs monocular movement parallax

Owls show a paradoxical asymmetry in their ability to take advantage of spatial cues that might be explained by the corticotectal system that I have just described. While an owl trained on a random dot stereogram can transfer the information about the hidden stereo contour to a kinematogram that uses similar contours, it is unable to benefit from a transfer in the reverse direction. Training on the kinematogram does not permit the owl to generalise the hidden contours hidden within the motion parallax cues of the kinematogram to the detection of similar shapes hidden within a stereogram [23]. This surprising asymmetry could be explained if we focus more attention on the role of midbrain tectum in behaviour, as I am attempting to do in this paper. Since the major output of the Wulst is to the optic tectum, a consideration of its corticotectal role, in relation to the function of the tectum, might help explain the paradoxical asymmetry in the following way.

It is known that the tectum can perform sophisticated motion parallax tasks (e.g. [22]). If tectal circuitry is sufficient to generate the disambiguation of a contour in the kinematogram, without any contribution from the Wulst, then it follows that this ability might be enhanced by an augmenting contribution from the corticotectal system about a camouflaged stereo contour, given that stereo is a recognised specialty of visual processing in the Wulst. Since stereo information comes to the tectum only via the binocular pathways of the corticotectal system, and there is no obvious tectum-Wulst reverse projection, one might expect that the specialised tectal system for motion parallax might not be able to pass that expertise readily to the Wulst system, in contrast to the ready transfer in the reverse direction by the elaborate corticotectal system that I have just described. The behavioural asymmetry could thus be explained by this fundamental asymmetry in the connectivity of the corticotectal system, coupled with a primary role for the tectum in object detection by motion parallax.

Such an account places great weight on the role of the tectal system in motion processing by the owl. This emphasis is not in line with current evidence from the primate visual system, where motion and stereo paths seem to travel side by side through V1. On the other hand, there is considerable evidence for the view origi-

nally expressed by Karten that the tectofugal pathway is homologous to the primate dorsal stream involving MT, with its unusual, "primary qualities" such as developmentally early and heavy myelination. Elaborations and modifications related to the formalisation and fovealisation of the primate visual system may make it difficult to recognise the possible phylogenetic origins of the dorsal stream from the tectofugal system. Certainly, a primary role of the tectofugal system in object disambiguation by colour and monocular parallax is well-documented in the majority of vertebrates except primates.

5.4. Interhemispheric switching of corticotectal systems

Finally I would like to draw attention to a remarkable feature of the corticotectal system that I have described: the segregation into stripes is based upon the hemisphere of origin of the fibres. How can this fact be encompassed by the schema for bimodal stripe-like arrays that I have put forward, where disparities between the arrays are measured? What kind of disparities could exist between the two hemifields of visual space only 20° from the midline? Any existing disparities might be reduced even further by the fact that there are both crossed and uncrossed corticotectal projections which would tend to equalise visual inputs to the relevant part of each tectum.

This is a further puzzle that would require for its solution some electrophysiological recording data from both stripes during the owl's performance of a task. A promising line of investigation here would be to use ambiguous stimuli, both because there are experimental links between interhemispheric competition and perceptual ambiguity [24] and because it is reasonable to postulate that the disparity between the two arrays might have as much to do with the different cognitive styles of each hemisphere (birds show hemispheric lateralisation too [25]) as with different sensory inputs, given that the latter will be minimised by the pattern of projections.

5.5. Integration of separate systems using interdigitated stripe-like arrays

The diverse observations on the even more diverse species that I have described can be linked by a common underlying pattern of organisation, where different representations are integrated via a bimodal sensory array with a pattern of stripe-like interdigitations. The platypus S1 array brings together two independent samples of the world, from electroreceptors and from mechanoreceptors. The striped array represents separate sensory streams emanating from the bill organ, each receiving information about prey in the same aquatic environment. The owl's corticotectal system also has two interdigitated, stripe-like representations, but in this case they emanate from separate hemispheres and have the puzzling feature that they would appear to bring together visual information from non-topographic regions about 20° on either side of the midline.

Since I do not have all the pieces of the puzzle that might help explain the significance of these patterns of organisation, it may be helpful to start with a general discussion on the theme of stripe-like arrays, which have been described in a number of systems, such as the ocular dominance column system of carnivore and primate V1, (where the representations of each eye interdigitate), the striosomes of the basal ganglia, (where different cortical input systems interdigitate in a similar way [26]), and the prefrontal cortex (where callosal and parietal inputs are segregated into stripe-like arrays Goldman-Rakic). In all of these cases, the key questions are:

1. Why not fuse the two input systems? If the information from one system is ultimately to be integrated with the other, why go through an intermediate stage with this particular stripe-like architecture, where the representations are split along one dimension?

2. Why stripe-like rather than patchy? What is the significance, if any, of the integration from a point in one system, to a line that generalises across the stimulus dimension in the other system?

I am going to try to answer these questions with reference to a set of stripes that I know most about, the ocular dominance "columns" so familiar in V1 of cats and most anthropoid primates. My schema to explain the functional significance of this arrangement can be seen in Fig. 9, a cartoon where I have simplified the complexities of the real system to help draw attention to the features that I consider crucial. I have separated the two sets of stripes in a view that allows one to see how each eye's neural image on its set of stripes might look if a 3D truncated pyramid was presented to both eyes. I have exaggerated the approximate trend for ocular dominance stripes to be oriented parallel to the horizontal meridian (this takes some liberties, especially in the foveal region where the stripes are randomly oriented and therefore have no such bias). The cartoon makes it obvious that such a system will result in binocular neurons of layer 3 having a greater horizontal dispersion of receptive fields on each retina. In other words, the stripes create an anatomical predisposition toward the generation of horizontal disparities, which are one of the crucial elements of stereopsis. In the foveal region where there is no such horizontal bias in the direction of stripes, the system would nevertheless generate a mixture of horizontal and vertical disparities, in keeping with the observation that foveal disparities tend to be isotropic horizontally and vertically and also with the observation that vertical disparities also play an important role in stereopsis.

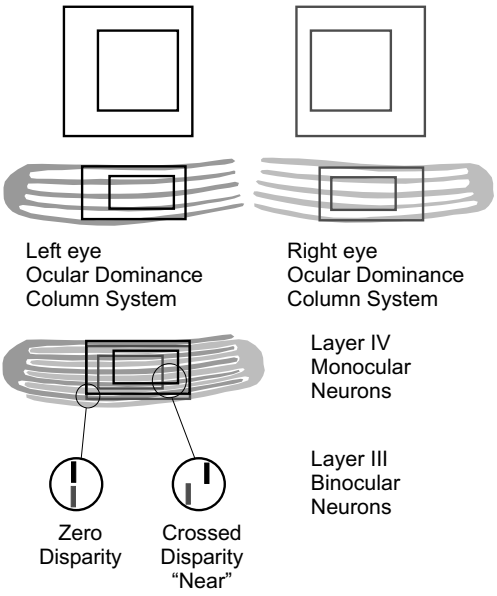

Fig. 9. Disparity-detection in ocular dominance stripes. Two sensory arrays, each dealing with the same sensory world from different viewpoints, are interdigitated by a series of splits that are roughly parallel to the horizontal meridian. Neurons above the stripe-like array integrate both sensory inputs, and so will be specific for bimodal stimulation at different disparities between the two arrays. The choice of horizontal for the split will ensure that the range of variation is mostly horizontal, in keeping with the importance of horizontal disparities in binocular vision. (Note that this over-simplification has been adopted to help make the point and that actual ocular dominance column arrays are more irregular, especially in the foveal representation where both horizontal and vertical disparities would be encoded in this way.) The principle illustrated might be relevant to the bimodal, stripe-like sensory arrays in platypus S1 cortex and owl tectum described here.

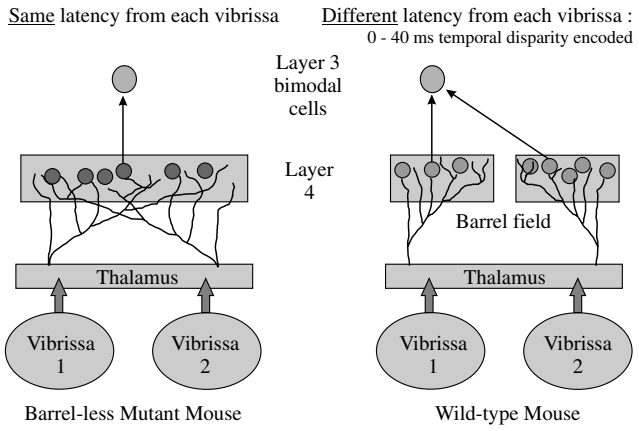

Fig. 10. Generation of specificity for temporal disparity in bimodal neurons of barrel field cortex. In the barrel-less mutant, both inputs connect in layer 3 with no disparity between the time of arrival of inputs from different whiskers. In the presence of barrels, intracortical connections to bimodal neurons in layer 3 from different barrels in layer 4 can generate temporal disparities.

If we accept for the sake of discussion my suggestion for the role of ocular dominance stripes in the generation of binocular neurons that encode retinal disparities, how does this help to answer the general questions I have raised? The question, "Why not fuse?" can be answered readily by reference to both phylogenetic and ontogenetic variation in this system, which shows that this is a question of neural timing and visual resolution. Frank segregation into stripes occurs only in those taxa with high resolution that would be capable of discriminating as asynchronous the slightly different patterns drifting over each eye. If the asynchrony is increased, by introducing a strabismus during development, species that normally show no segregation in this system can be induced to do so (e.g. sheep [27] and owls [3]). There is not space here to go into a detailed comparison of V1 in different taxa, but the principle of delaying fusion in segregated cortical arrays can be well illustrated from a different system which shows beautiful anatomical segregation in Layer IV, but which does not have the distraction of the point-to-line, stripe-like transformation: the barrel field system seen in S1 of many whiskered mammals. Using barrel-field mutants that lack barrels, Welker and colleagues [28,29] have shown that segregation of thalamic inputs into separate barrels in layer 4 plays an important role in the wiring of layer 3 neurons that respond to stimulation of adjacent whiskers at a variety of different asynchronies. In mutants lacking barrel field segregation, inputs from adjacent barrels are "fused" in layer 4 where all neurons respond at similar latency to stimulation of different whiskers. In contrast, wild-type S1 cortex has intracortical connections from layer 4 that represent only a single whisker, and which contact layer 3 neurons that respond to adjacent whiskers with different latencies because of intracortical conduction time. This effect of segregation in generating a range of different specificities for temporal asynchrony can be seen in Fig. 10. The functional significance of this kind of circuitry is immediately obvious for a mouse "whisking" a 3D object, where adjacent whiskers would be stimulated at different degrees of asynchrony as a function of the spatial properties of the object.

Interdigitated stripe-like arrays may therefore perform a general role in detecting small disparities between two different inputs concerned with the same sensory event. By delaying the "fusion" of the two inputs and by splitting the array along an appropriate spatial dimension, the stripes may allow the fine-grained, higher order representation of the disparities in an array of tuned bimodal neurons.

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