Visual cortex: **Looking into a Klein bottle**
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Arguments based on mathematical topology may help in understanding the organization of topographic maps in the cerebral cortex.

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The English neurologist Hughlings Jackson inferred the presence of a topographic map of the body musculature in the cerebral cortex more than a century ago, from his observations of the orderly progressions of seizure activity across the body during epilepsy. Topographic maps of one kind or another are now known to be a ubiquitous feature of cortical organization, at least in the primary sensory and motor areas. Every medical student learns that there is a distorted map of the body surface in somatosensory cortex, known as the 'homunculus', and that in the visual cortex there is an orderly map of visual space.

Continuous mappings such as these, from one two-dimensional surface onto another, are easy to visualize. However the cortex seems to be capable of much more complex mappings. In a previous dispatch [1], I discussed theoretical work which suggested that many properties of visual cortex organization might be a consequence of mapping a five-dimensional stimulus space onto a two-dimensional surface as continuously as possible. Recent experimental results, which I shall discuss here, add to this complexity because they show that a stimulus attribute not considered in the theoretical studies — direction of motion — is also systematically mapped on the surface of the cortex. This adds to the evidence that continuity is an important, though not overriding, organizational principle in the cortex. I shall also discuss a demonstration that certain receptive-field properties, which may be indirectly related to direction selectivity, can be represented as positions in a non-Euclidian space with a topology known to mathematicians as a Klein bottle. First, however, it is appropriate to consider the experimental data.

It has long been known that neurons in the visual cortex are selectively responsive to the orientation of an edge or line stimulus. Many studies have examined how preference for stimulus orientation varies with position in the cortex, and have shown a common pattern of organization in a variety of species, including cats, ferrets, tree shrews and monkeys (Fig. 1). Nearby regions in the cortex typically have similar preferred orientations, and preferences generally change smoothly with position [2]. In all species so far examined, 'iso-orientation domains' — neighbourhoods of cells with similar orientation preferences — tend to be short narrow strips with pointed ends, with a periodic spacing of about 1 mm. Different domains often meet at points known as singularities. These points are easily identified in Figure 1, in which the colour cycle red–orange–yellow–green–blue–violet represents the 180° cycle of possible orientation preferences.

There are only two ways in which a single set of orientations (or colours) can be smoothly arranged around a singularity: one in which the orientations rotate clockwise as one moves in a clockwise loop around the singularity (Fig. 2a), and the other in which the orientations rotate anti-clockwise (Fig. 2b). Mathematicians classify these arrangements as half-rotation singularities of sign +½ and –½, respectively, because a full cycle of orientations covers a range of 180°, which is only half of the possible 360° range of angles in a rotation. To my eye, at least, positive singularities resemble a horseshoe crab, whereas negative singularities resemble a scalloped triangle. There are approximately equal numbers of the two types of singularity in the visual cortex, with a density of between three and eight per square millimetre, depending somewhat on location and species [2,3].

Figure 1
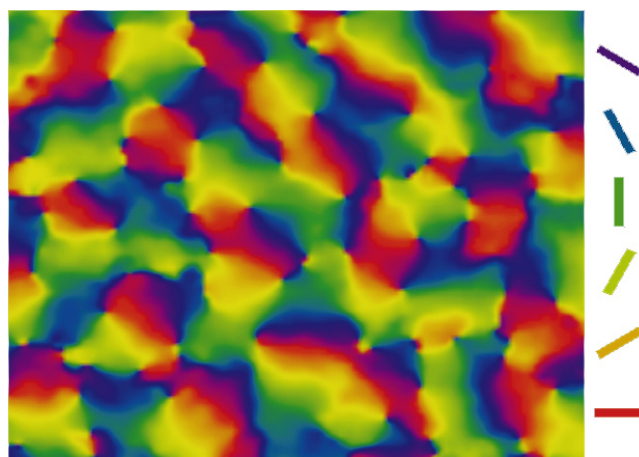
How stimulus orientation is mapped onto the surface of the visual cortex. Colours show the stimulus orientation which best activates each region of the cortex. Note that the preferred orientation changes smoothly with position everywhere, except at singularities, where a single complete set of colours meets. The data were obtained by optical recording from the visual cortex of a macaque monkey [2]. (Reproduced with permission from [2].)

Figure 2
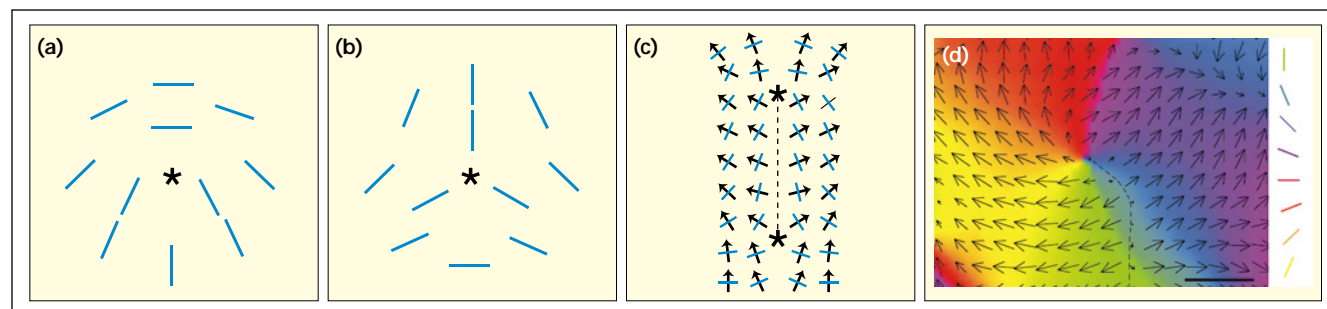
(a,b) Arrangement of orientations giving rise to half-rotation singularities: (a) of sign + ½, and (b) of sign – ½. (c) An attempt to map direction preferences continuously onto two nearby orientation singularities, showing the necessity of connecting them by a line singularity in direction preference. (d) A detail from a combined orientation and direction preference map obtained by Weliky *et al.* [9]. Colours code for orientation preference and arrows show direction preference. An orientation singularity is present in the centre of the figure, and a line singularity in direction preference originates in it. The scale bar = 0.2 mm. (Reproduced with permission from [9].)

The functional significance of the singularities, if there is one, has yet to be identified. It is possible that they are an accidental outcome of a developmental process which does not specify in advance the orientation specificity of each region of cortex. Initial preferences might either be random, or pre-specified in a small number of different locations; in either case, if one tries to generate a continuously varying pattern of orientations, singularities are almost certain to result. Try drawing several randomly oriented lines on a piece of paper and interpolating smoothly varying orientations between them, and you will often find that the smooth pattern is unavoidably interrupted by singularities.

Many cells in the visual cortex respond selectively not only to the orientation of an edge, but also to the direction in which it is moved. For example, some cells respond to a vertical edge only when it moves to the left, others will respond when the edge moves to the right. There are also non-selective cells which respond well to either direction of motion, while nevertheless being highly selective for orientation. Direction selectivity is a common property of neurons in the primary visual cortices (areas 17 and 18) of mammals such as cats and ferrets, although in primates this property is most fully developed in the visual area known as medio-temporal (MT) cortex (or V5).

The preferred direction for moving long bars and edges will, almost by definition, be orthogonal to the preferred orientation, in one of two possible ways. For shorter bars, it is possible for direction and orientation preference to be unrelated, although it seems that preferences are usually close to orthogonal [4]. (This may be explained by reference to the so-called 'aperture problem', which asserts the impossibility of determining the velocity of a moving edge when only a small portion of it is visible; the brain may solve the problem by first coding the velocity of the edge in a direction perpendicular to its orientation, and then extracting the actual velocity by combining velocity information from differently oriented edges of the same object.) Given this, and evidence that the direction preferences of nearby neurons tend to be similar [3–6], it is of interest to consider how an orientation map, containing numerous singularities of sign ±½, might constrain the organization of a direction preference map.

It is not difficult to see that, if direction preferences are arranged as continuously as possible around a half-rotation orientation singularity, only half of the complete range of direction preferences can be present (Fig. 2c). If a loop is drawn around a singularity, orientations will change continuously along its circumference, but direction preferences must necessarily flip once, or an odd number of times. This argument holds for any size or shape of loop, provided only one half-rotation singularity is present inside. As a result, at least one (or an odd number) of line singularities, across which direction preferences flip by 180°, must extend from each orientation singularity. These lines can begin and end only in singularities, although closed loops are possible, as are line crossings. It is easy to verify these points diagrammatically, by constructing smoothly changing patterns of lines and orthogonal arrows.

Arguments that cortical maps of direction preference might have these properties were first put forward almost 10 years ago [3]. At that time, the evidence [3–6] suggested some degree of local continuity, while surface maps obtained from closely spaced microelectrode recordings allowed tentative reconstructions of line and point singularities in area 18 of the cat [3]. This evidence was not completely convincing, however — it was possible that interruptions and reversals in direction preference might be more numerous than the mapping studies suggested,

Figure 3
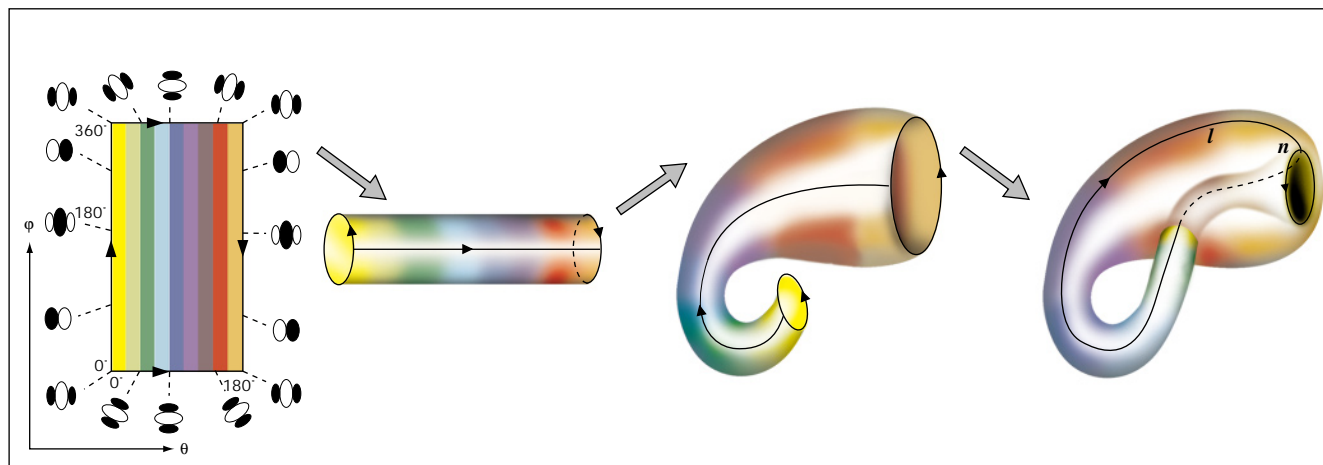
Demonstration of how a Klein bottle may be constructed from the symmetry properties of simple cell receptive fields. On the far left, receptive-field orientation is plotted on the horizontal axis, and receptive-field phase, which corresponds to the layout of excitatory (white) and inhibitory (black) subregions within the receptive field, is plotted on the vertical axis. Any combination of orientation and phase can be represented as a position within the rectangle. A continuous surface across which these parameters vary smoothly can (only) be constructed by joining together opposite edges of the rectangle to form a Klein bottle, as shown on the far right. (Modified from [10].)

and it was not clear what might happen to direction preferences close to a line singularity. If direction preferences deviated from being orthogonal to the preferred orientation, the topological arguments would be weakened or invalidated; if the direction preferences disappeared, the singularity would effectively vanish.

It now appears that the arrangement suggested by the topological arguments may in fact be correct. A study of area MT of the owl monkey [7], in which neuronal responses to stimuli moving in different directions were measured using the optical recording technique [2], has shown that direction preference varies continuously across the surface of the cortex, except in elongated regions which extend from, and connect together, half-rotation orientation singularities. A preliminary report from the same laboratory [8] suggested there is a similar map in area 18 of the cat. Recently, Weliky *et al.* [9] have demonstrated the presence of an ordered map of direction preference in the visual cortex of the ferret: here, narrow strips of poor direction selectivity divide regions with similar preferred orientations but opposite direction preferences (Fig. 2d). As in the owl monkey, the linear strips intersect with the orientation singularities.

Tanaka [10] has also applied topological arguments to the organization of the visual cortex. The starting point is the two-dimensional Gabor function commonly used to model the receptive-field profiles of simple cells [11], which make up a substantial percentage of visual cortical neurons. This function has associated with it an orientation and a phase angle, which, like direction preference, is cyclic over a 360° range. Any combination of orientation and phase angles can be plotted as a position in a rectangle on a two-dimensional plane; if the edges of the rectangle are joined up, then a surface across which these parameters vary continuously is formed. The only way to do this, however, is to construct the curious object known as a Klein bottle, which has a single closed surface and no interior (Fig. 3).

This result allows Tanaka to investigate the likely properties of a cortical map in which receptive-field orientation and spatial phase vary smoothly. The technique used to do this comes from a branch of mathematics known as homotopy theory, and considers the behaviour of a loop drawn on the surface of the Klein bottle. For most biologically plausible mappings, in which points on the surface of the bottle are mapped continuously onto small regions of cortex, it will generally be the case that any loop on the surface of the bottle will map to a loop on the cortex. If the loop on the bottle can be shrunk to a point, the cortical region inside it does not contain a singularity. This will be true of many loops, but not all — for example, the two drawn on the Klein bottle in Figure 3 cannot be shrunk to a point, no matter how they are deformed or moved across the surface of the bottle. The corresponding line on the cortex will therefore encircle a singularity, which would be either an orientation or a phase singularity, depending whether the loop is of the type labelled *l* or of the type labelled *n* in Figure 3.

This is an elegant demonstration, although unfortunately there is little compelling experimental evidence that spatial

phase varies systematically with position in the cortex. Given the cortex's liking for continuity, however, this may yet turn out to be the case. Even if phase is not systematically mapped, Tanaka's arguments will apply equally well to other properties that can be shown to be topologically equivalent to orientation and phase. Although, at first sight, direction selectivity might seem to be such a property, there are some important differences. Firstly, receptive field phase and direction preference have been found experimentally to be unrelated, although other kinds of phase relationship are important in many models of direction preference. Secondly, in Tanaka's formulation, smooth reversals in direction preference are allowed, because of the existence of intermediate values of phase corresponding to a lack of direction selectivity — these are the symmetric fields with phase values of 0° or 180°. This is probably the reason why line singularities are not predicted by this analysis.

The new experimental data suggest the existence of common organizing principles in the cortex, inasmuch as the maps of orientation and direction preference found in ferret area 17, cat area 18 and owl monkey area MT are similar. Continuity seems to be important, as observed for many other variables, although it now seems that the cortex is not averse to a clean cut when continuity cannot be achieved. It is nevertheless a bit of a puzzle why the direction map is as discontinuous as it is. It would not be difficult, in principle, to replace the half rotation orientation singularities with point direction singularities, around which a full 360° cycle of direction preferences could be arranged, together with two complete sets of orientation domains: this would render the line singularities unnecessary. That this does not occur suggests, perhaps, that the orientation map develops first, and that the direction map is forced to conform to it at a later stage. Alternatively, there may be a functional advantage in having neurons with similar orientation preferences, but opposing direction preferences, brought close together in some regions of the cortex. Whatever the answer, reasoning based on topological arguments may be increasingly helpful in attempting to understand how the world, Klein bottles and all, is unfolded onto the surface of the cortex.

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