How development of the visual system leads to visual perception

The formation of a retinotopic map allows transmission of visual stimuli from the photoreceptor cells to the Lateral Geniculate Nuclei (LGN) in the Thalamus. The primary visual cortex receives information from the LGN and integrates it, allowing processing in multiple cortical areas. The developmental processes which lead to this ordered relaying of information are highly regulated and result from a combination of embryonic development and interaction with the environment. The study of healthy or diseased visual systems has greatly increased our knowledge of visual perception, and may lead to an increased understanding of what consciousness is.

The visual percept can be defined as the internal image produced in the cortex in response to external stimuli received through the retinas. This requires integration of vision with other processes in the brain to produce a coherent and contextual interpretation of our surroundings.

Historically, the study of visual perception utilised head injury patients who had lesions in particular areas of the brain. Using such patients, Gordon Holmes proposed the idea of a retinotopic map in 1918 when he observed that specific lesions caused individual and accountable defects in 'sight' (Holmes, 1918). More recently, induced lesion studies in higher primates have enabled greater understanding of each specific region. The lateral geniculate nucleus (LGN), part of the thalamus, relays information to the primary visual cortex (V1 cortex) in the occipital lobe (Dacey, 2004). Other basal areas also receive visual information needed for movement, balance and fear responses. The integration of each branch of the visual brain is essential for producing an internal percept; however it is the visual cortex where higher processing of information occurs (Dobkins, 2009).

The connection between the eyes and the higher processing centres is tightly regulated. During development a morphogen gradient guides migrating axons from the retina to the brain (Erskine and Herrera, 2007). Study in this area has used lower vertebrate models such as zebrafish, where the tectum has similar connections to the LGN and Superior Colliculus of humans (Meyer et al., 2003).

Ephrin is a short range secreted repulsive signal which is highly expressed in the posterior tectum. Posterior retinal cells have a high concentration of the Ephrin receptor, Eph, which prevents them migrating towards the posterior tectum. Anterior retinal cells, with no Eph-receptor, make connections with the posterior tectum (Scicolone et al., 2009, Erskine and Herrera, 2007). Together this will produce a crude map which links the retina and the tectum. Refinement of neural connections during development adds detail to the retinotectal map, allowing a high degree of specificity. The refinement is brought about by the initiation of electrical signalling in the developing neurons. This process is extremely plastic; in a zebrafish model using a GFP tagged synaptophysin in combination with a Red fluorescent tagged axon, it can be seen that only 20% of axon branches and 30% of synapses survive to maturity, and the average lifespan of axons during development is 20 minutes (Meyer et al., 2003).

In higher vertebrates the basic connectivity is complicated by the crossing over of optic nerves in the optic chiasm. The left hemisphere receives stimuli from the right visual field, and vice versa. Nerves from the nasal half of the receptive field are termed contralateral and undergo crossing over whilst the temporal half, the ipsilateral, remains in the same hemisphere. At the level of the LGN, a six layered stratified structure can be observed. The contralateral axons project to layers 1, 4 and 6, and the Ipsilateral axons to layers 2, 3 and 5 of the LGN. At this point information remains segregated in terms of quality (for example colour or contrast) and also origin. The LGN projects to the V1 cortex; over 80% of the cells here receive input from both eyes (Lachica et al., 1992).

Bishop can be credited with the idea of parallel visual processing; different visual qualities are transferred from the retina to the brain via unique and individual pathways (Bishop, 1933). Current estimates state there are 80 functionally and anatomically distinct neuron types within the retina and these transmit information to at least 12 separate ganglionic pathways (Dacey, 2004). This condensation is required due to the anatomical bottleneck of the optic nerve; each ganglia type tiles the retinal field with minimal overlap, thus reducing the number of neurons needed to cover the

visual field. The three most prevalent ganglia types are Midget, Parasol and Bistratified (Nassi and Callaway, 2009). Midget ganglia are the major component of the parvocellular pathway; that is the reception of image detail such as shape and colour. Their small dendritic field means each ganglion corresponds to a small area of the retina allowing detailed information such as red-green colour and shape to be transmitted (Dacey et al., 2005). Parasol ganglia transmit a broad monochromatic signal which forms the magnocellular pathway; fast axonal conductance and a large dendritic field size allows them distinguish broad temporal changes, but less spatial acuity (Nassi and Callaway, 2009). Bistratified ganglia contribute a blue-yellow colour opponent to the koniocellular pathway, which carries a broad range of information to the LGN. Its exact function in the V1 cortex has yet to be determined (Chatterjee and Callaway, 2003, Hendry and Reid, 2000). Both the magnocellular and Parvocellular pathways project to layer 4 of the V1 cortex (Lachica et al., 1992).

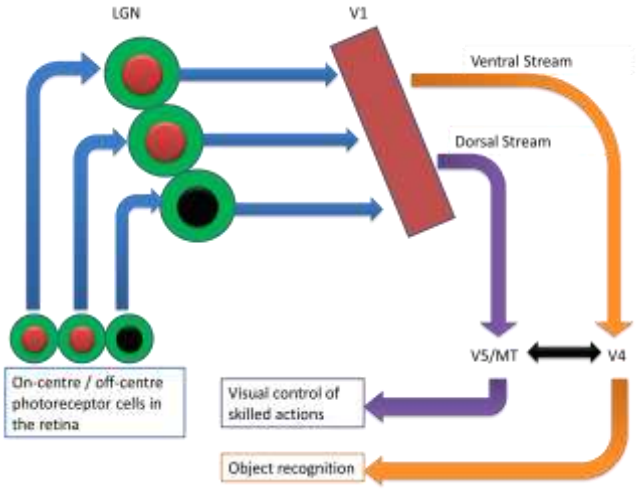

Figure 1. **The primary visual cortex (V1) is responsible for integration of visual information.** The retinal photoreceptor cells are arranged in a centre-surround format, which is either activated (on-centre) or repressed (off-centre) in response to light selectively hitting the centre area. This information is transmitted through distinct ganglia types to the LGN and other basal areas. The LGN relays information to layer 4 of V1, where stellar cells integrate information to produce distinct streams. Pyramidal neurons transmit this information to other visual cortex areas. The Dorsal stream travels to the medial temporal (MT) area, where visual control of skilled actions is mediated. The ventral stream travels to the 4th visual cortex where object recognition is produced. Both information streams use the same retinal information for different purposes. Crosstalk exists between each pathway.

It is at the cortical level where information is integrated to form a percept. The currently favoured hypothesis is that information from the LGN is integrated in the V1 to form new streams of information (Figure 1). The cortex develops from neuroblasts at the ventricular zone; a transient increase in β1 laminin causes detachment of stem cells from the basal lamina, allowing them to migrate along glial processes to form the cortical plate. Successive generations of axons migrate through this layer to form a striated structure(Loulier et al., 2009). In humans, the layering is initiated during foetal growth but is refined throughout childhood until the age of 8-10 (Slack, 2006),

by which point each layer will have morphological and functionally distinct neuron types. This raises interesting questions as to whether the function is specified in the developing ventricular zone, or by specific electrical activity during growth (Loulier et al., 2009).

The method of connectivity between the LGN and the V1 cortex was investigated by Hubel and Livingstone using Kittens. The right eye lids of new born kittens were sewn shut for varying periods of time, and once opened functional testing on the visual pathways was carried out. Closing an eye for the first six weeks after birth resulted in functional blindness; cortical space normally covered by connections from the right eye had been taken by those from the left eye. This suggested that activity dependant competition occurs at the cortical level for neuronal connections (Livingstone and Hubel, 1984). Closing both eyes for the first six weeks of development led to both eyes being functional once re-opened, as neither eye was able to out-compete the other. Cortical development occurs in a Hebbian manner; those neurons with simultaneous activity during development will innervate similar areas of the V1 cortex, and this will lead to formation of distinct information streams leaving the V1 cortex (Nassi and Callaway, 2009). Studies in mature monkeys where either eye had been closed for varying periods of time showed that radioactive glucose traces would form a columnar pattern in relation to which eye had been closed (Livingstone and Hubel, 1988). This columnar organisation has been explored further using electrode readings from individual neurons. Ocular dominance columns will be activated in response to activity from one eye only, and within this column light orientation specific columns exist (Dacey, 2004). Whilst in the retina and LGN the antagonist centre surround system is used, here each individual area will respond to bars of light of a particular orientation (Figure 1). It is thought the transformation from a circular representation of the visual field to the columnar organisation causes a reorganisation of visual information allowing it to be processed in different cortical areas. The best characterised of these pathways are the dorsal stream and the ventral stream (Yabuta et al., 2001). The dorsal stream passes from the V1 cortex to medial temporal (MT) area. Lesions to the MT can cause Akinetopsia; this condition leads to loss of movement perception, and motion is transferred as a series of still images. Lesions in the V4 cortex

disrupt the ventral stream and lead to Achromatopsia where colour vision is entirely lost, and light is perceived in a monochromatic array. These conditions show that the ventral pathway is involved in object recognition whilst the dorsal stream is involved in the visual control of skilled actions (Milner and Goodale, 2008). These two areas utilise the same information received by the retinas and integrate it with other external information and previous experience to produce a response. It is interesting to note that these two pathways have significant cross talk, particularly in the area of binocular disparity (Janssen et al., 1999, Uka et al., 2000). Each eye produces a slightly different image, and this is essential for nearly all components of perception. The dorsal stream uses gross disparity to orient and guide actions in a three dimensional manner, whilst the ventral stream uses the finer detail of disparity to integrate texture and three dimensional shape which are important for object recognition (Janssen et al., 2003, Umeda et al., 2007).

This essay has briefly covered the anatomic pathways laid down during development, and how this transmits the required information for visual perception. However, the dorsal and ventral streams are not end points in the visual pathway – transmission of information into the frontal cortical area provide the critical link to learning, memory and language (Schendan and Stern, 2008). This integration of processes is responsible for our seamless interaction with our environment. Future work in the area will focus on the complex interactions between these processes, with the aim of understanding how the brain fully integrates itself with the outside world.

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