



Review article

The active construction of the visual world

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ABSTRACT

What we see is fundamentally dependent on where we look. Despite this seemingly obvious statement, many accounts of the neurobiology underpinning visual perception fail to consider the active nature of how we sample our sensory world. This review offers an overview of the neurobiology of visual perception, which begins with the control of saccadic eye movements. Starting from here, we can follow the anatomy backwards, to try to understand the functional architecture of neuronal networks that support the interrogation of a visual scene. Many of the principles encountered in this exercise are equally applicable to other perceptual modalities. For example, the somatosensory system, like the visual system, requires the sampling of data through mobile receptive epithelia. Analysis of a somatosensory scene depends on what is palpated, in much the same way that visual analysis relies on what is foveated. The discussion here is structured around the anatomical systems involved in active vision and visual scene construction, but will use these systems to introduce some general theoretical considerations. We will additionally highlight points of contact between the biology and the pathophysiology that has been proposed to cause a clinical disorder of scene construction – spatial hemineglect.

1. Introduction

Although our experience of the visual world seems temporally and spatially continuous, the sensations we derive it from are not. Saccadic eye movements constitute a series of discrete fixations, interspersed by rapid movements. Little meaningful visual information is obtained as the eyes sweep from one fixation to the next (Bridgeman et al., 1975) and, at any moment, the proportion of the visual field from which any high resolution information is sampled is tiny. These observations, seemingly so contrary to perceptual experience, can be reconciled under the metaphor of perception as hypothesis testing (Gregory, 1980; Friston et al., 2012a, b). By forming hypotheses about a continuous world, saccades can be deployed as experiments to adjudicate among alternatives. Note, however, that such experiments are necessarily designed in a biased, unscientific, manner (Bruineberg et al., 2016).

This view implies the perception of space is fundamentally tied to motor representations, as visual input at a point in space is the consequence of an experiment (saccade to that location) (Zimmermann and Lappe, 2016). This enactivist take on perceptual synthesis means that objects in the visual field become hypotheses or explanations for ‘what would I see if I looked there?’. In this review, we will describe the neuronal apparatus used to perform these experiments – and thereby implement active vision (Wurtz et al., 2011; Andreopoulos and Tsotsos, 2013; Ognibene and Baldassarre, 2014; Mirza et al., 2016). This functional anatomy consists of the brainstem network which gives rise to

the nerves to the extraocular muscles. The superior colliculus is an important structure in this network, receiving input from both sub-cortical and cortical regions. Particular focus will be afforded structures that determine the choice of saccade target, and the mechanisms by which the data from previous saccades are combined, accumulated or assimilated to construct a seamless temporal experience (Marchetti, 2014). These mechanisms can fail in the damaged brain, and a common syndrome resulting from this failure is spatial hemineglect. Patients suffering from this fail to attend to one side (typically the left) of visual space (Halligan and Marshall, 1998). One manifestation of this attentional deficit is a decreased frequency of saccadic sampling in the neglected half of space relative to the other (Karnath and Rorden, 2012). This is despite intact early visual processing of stimuli on the neglected side, as evidenced by electrophysiology (Di Russo et al., 2007) and neuroimaging (Rees et al., 2000). We will try to address some of the links between the neurobiology of visual scene construction, and the consequences of its disruption. A number of theoretical concepts recur throughout this review. These include consideration of the mnemonic processes required for scene construction, the relationship between eye movements and attention, and the inferential (Bayesian) nature of these processes.

2. Brainstem oculomotor control

All forms of eye movement rely on the connections from the cranial

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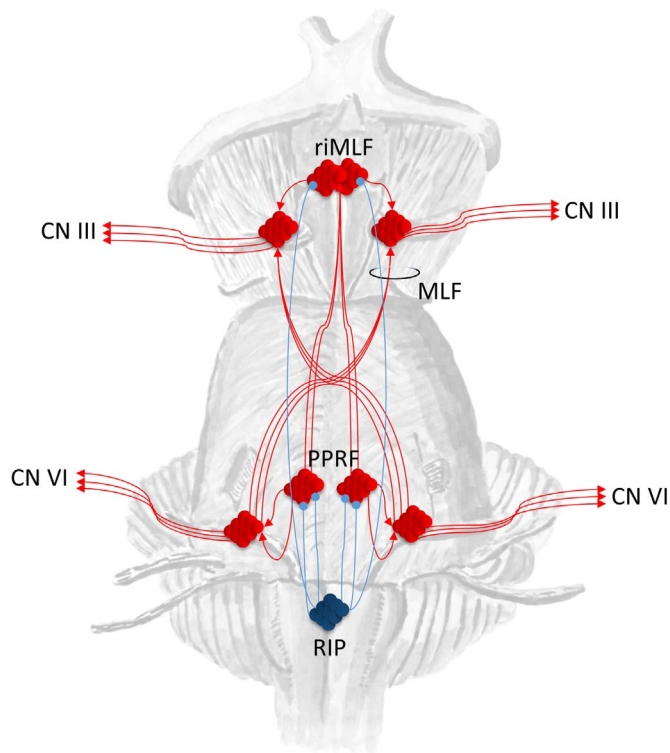


Fig. 1. Brainstem control of saccadic movements This schematic shows some of the brainstem nuclei involved in the generation and control of saccadic eye movements. The paramedian pontine reticular formation (PPRF) is responsible for the generation of horizontal saccades, through its influence on the ipsilateral abducens nucleus, which gives rise to cranial nerve (CN) VI. A subset of neurons in the abducens nucleus projects to the contralateral oculomotor (CN III) nucleus in the midbrain, via the medial longitudinal fasciculus (MLF), ensuring conjugate eye movements occur. The PPRF additionally projects to the rostral interstitial nucleus of the MLF (riMLF), which generates vertical saccades. ‘Omnipause’ neurons in the nucleus raphe interpositus (RIP) synchronise the onset of vertical and horizontal components of saccades. The superior colliculus (not shown) influences both the PPRF and RIP. Excitatory connections are shown in red, while inhibitory connections are shown in blue. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

nerve nuclei in the midbrain (CN III), the pons (CN IV), and the medulla (CN VI) to the extraocular muscles. Saccadic eye movements depend specifically upon the connections to these nuclei from the paramedian pontine reticular formation (PPRF) and the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF). The former generates horizontal saccades (Cohen et al., 1968; Henn, 1992), and the latter vertical (Büttner-Ennever and Büttner, 1978). Other important influences come from the vestibular system (Baker and Highstein, 1978), and the cerebellum (Berretta et al., 1993), but these will not be covered here. A subset of neurons within the PPRF monosynaptically target the ipsilateral abducens (CN VI) nucleus (Strassman et al., 1986). From the abducens nucleus, some neurons have axons which first decussate, then ascend as part of the MLF, to the oculomotor (CN III) nucleus in the midbrain (Sparks, 2002). The PPRF can use this pathway to initiate conjugate eye movements in the ipsilateral direction. An additional anatomical pathway allows the PPRF to influence the riMLF (Büttner-Ennever and Büttner, 1978), ensuring it can generate saccades with a vertical directional component (see Fig. 1 for a summary of this anatomy).

Saccadic movements are rapid movements that occur between short periods of fixation. In order to maintain fixation between saccades, PPRF ‘burst’ neurons are tonically inhibited by ‘omnipause’ neurons, located in the nucleus raphe interpositus (RIP) (Büttner-Ennever et al., 1988). These cells cease firing immediately before a burst of firing in the PPRF cells, but resume before the saccade is complete. ‘Omnipause’

neurons may have a role in synchronising different directional components of saccade generation, as the RIP also projects to the riMLF (Büttner-Ennever and Büttner, 1978). The electrophysiological correlates of the fixation and saccadic phases suggest the brain treats saccadic eye movements as a series of discrete events, consistent with the view that attentional processes are both serial and discrete (Buschman and Miller, 2010).

2.1. The superior colliculus

An important input to the PPRF, and the RIP, is the superior colliculus (Raybourn and Keller, 1977). This is a midbrain structure, found at the same level as the oculomotor (CN III) nucleus. The superior colliculus represents visual space according to several integrated topographic maps. Superficially, it contains a retinotopic map, making use of the input it receives directly from the optic nerve (Schiller and Stryker, 1972). Intermediate layers are thought to house a motor map, with each location corresponding to a potential saccadic target (Sparks, 1986). Deeper layers have maps that exhibit multisensory features, including somatosensation (Stein et al., 1989; Peck et al., 1993). Some accounts of collicular function propose that it contains a saliency map (Zelinsky and Bisley, 2015; Veale et al., 2017), and mediates attention to salient locations. Attention here refers to planned or performed eye movements leading to foveation of the ‘attended’ location. This is a distinct process to attention as ‘gain control’ (Hillyard et al., 1998; Feldman and Friston, 2010) of sensory streams (that does not necessarily depend upon oculomotor contingencies). The colliculus receives an input from cortical layer V (Fries, 1984). This layer specific input is shared with other structures with a role in salience computations, including the basal ganglia (Shipp, 2007) and the pulvinar nucleus of the thalamus (Shipp, 2003). It is encouraging that many of the areas implicated in attentional selection and salience conform to this laminar input pattern.

Neurons in the superior colliculus can be classified according to distinct electrophysiological profiles. Three broad categories of neurons are identifiable in this way. These are the collicular ‘burst’ neurons, the ‘fixation’ neurons, and the ‘build-up’ neurons (Ma et al., 1991; Munoz and Wurtz, 1995a). The first of the three are found more dorsally, while the latter two are more ventral within the colliculus. ‘Fixation’ neurons are active during fixation, and are found at the rostral pole of the colliculus. These synapse on the ‘omnipause’ neurons of the nucleus raphe interpositus (Gandhi and Keller, 1997), so that decreases in ‘fixation’ neuron activity causes a disinhibition of the PPRF ‘burst’ neurons, resulting in a saccade. The ‘burst’ neurons discharge immediately before a saccade, and the target location of the saccade corresponds to the location of these neurons in the colliculus. ‘Build-up’ neurons have a slowly increasing activity that terminates when a saccade occurs, although this activity is not always followed by a saccade. This observation is important in the context of the premotor theory of attention (Rizzolatti et al., 1987), as this theory suggests that covert attention may correspond to a planned saccade which does not take place. ‘Build-up’ neurons, as a population, have the interesting property that the activity across the population appears to travel as a ‘hill’ across the colliculus towards the rostral pole, which represents the foveal location (Munoz and Wurtz, 1995b).

The notion of a travelling ‘hill’ of excitation corresponds well to a set of theoretical constructs known as attractor networks. Representations of states which evolve in metric space have been extensively modelled using continuous attractor networks (Zhang et al., 2008). These rely on the assumption that a population code is used (Pouget et al., 2000), and there is good evidence to suggest that this is the case in the superior colliculus (Lee et al., 1988). One reason for emphasising this point is that, due to the serial nature of saccadic sampling, the apparent temporal continuity of visual experience requires explanation. The constraints placed upon a ‘hill’ of activity in a continuous attractor network mean that changing representation of one

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