1 Abstract

All organisms wishing to survive and reproduce must be able to respond adaptively to a complex, changing world. Yet the computational power available is constrained by biology and evolution, favouring mechanisms that are parsimonious yet robust. Here we investigate the information carried in small populations of visually responsive neurons in Drosophila melanogaster. These so-called `ring neurons', projecting to the ellipsoid body of the central complex, are required for complex visual tasks such as pattern recognition. Recently the receptive fields of these neurons have been mapped, allowing us to investigate how well they can support such behaviours. For instance, in a simulation of classic pattern discrimination experiments, we show that the patterns of output from the ring neurons matches observed fly behaviour. However, performance of the neurons (like flies) is not perfect and can be easily improved by addition of extra neurons, suggesting the neuron’s receptive fields are not optimised for recognising abstract shapes. A conclusion which casts doubt on cognitive explanations of fly behaviour in pattern recognition assays Using artificial neural networks, we then assess how easy it is to decode more general information about stimulus shape from the ring neuron population code. We show that these neurons are well-suited for encoding information about size, position and orientation, which are more relevant behavioural parameters for a fly than abstract pattern properties. This leads us to suggest that in order to understand the properties of neural systems, one must consider how perceptual circuits put information at the service of behaviour rather than how they preserve visual information.

Introduction

As with many animals, vision plays a key role in a number of behaviours performed by the fruitfly

Drosophila melanogaster, including mate-recognition [1], place homing [2], visual course control [3], collision-avoidance [4], landing [4] and escaping a looming object (like a rolled newspaper, for example) [5]. The benefit of studying these visually guided behaviours in Drosophila is the range of neurogenetic techniques which give a realistic chance of understanding the neural circuits that underpin them. With that goal in mind, we focus on recent work [6] which mapped the receptive fields of a set of visually responsive neurons, the ring neurons of the ellipsoid body. These neurons are surprisingly small in number given that they are key for certain complex behaviours, such as short term spatial memory, pattern discrimination or place memory [7, 9]. To understand their role in these behaviours, we used modelling to bridge the gap between neurogenetic data and behaviour by evaluating neural responses during simulations of fly experiments. In this way we investigate how small populations of visual neurons in Drosophila provide behaviourally relevant information.

In laboratory assays flies show interesting spontaneous visual behaviours. For instance, flies will orient towards bar stimuli [10, 11] and in a circular arena with two diametrically placed bars will walk between them for long periods. This spontaneous preference for elongated vertical bars is reduced as the bar is shortened until free-flying flies show a spontaneous aversion to small cube stimuli [12]. In addition a number of studies have investigated the process of pattern recognition and its neural underpinnings [7, 13, 14]. The standard paradigm involves putting a fly into a closed-loop system where it is tethered in a drum, on the inside of which are two visual stimuli alternating every 90\_ (Figure 1E). As the fly attempts to rotate in one direction, the drum counter rotates in closed loop, giving the illusion of the fly moving in a stable world. To elicit conditioned behaviour, if the fly faces one of the patterns it is punished by a heat beam. Over time if the fly is able to differentiate the patterns it will preferentially face the unpunished pattern. This procedure has been used to demonstrate that flies can differentiate stimulus pairs such as upright and inverted `T' shapes, a small and a large square, and many others [13]. That is, flies seem to possess a form of pattern recognition and pattern memory analogous to the better studied pattern memory of bees [15-17]. Interestingly, both bees and flies fail systematically to discriminate certain pattern pairs.

The control of these visual behaviours is dependent on the central complex of flies, a brain area thought to be involved primarily in spatial representation and mediation between visual input and motor output [18]. The central complex comprises the ellipsoid body, the fan-shaped body, the paired noduli and the protocerebral bridge [19]. This part of the brain has been characterised as the site of action selection and organisation and is claimed to be homologous to the basal ganglia in vertebrates [20]. A particular class of neurons that project to the Ellipsoid Body of the central complex are `ring neurons', which are known to be involved in visual behaviours (R1: place homing [2, 21, 22]; R2/R4m: pattern recognition [7, 13, 14]; R3/R4: bar fixation memory [8]). Here we examine how the Ring neurons contribute to these behaviours, by simulating the visual input as it would be processed through this small population of visually responsive cells. In particular, we can address why flies might be unable to discriminate certain pattern pairs, whether the neurons are tuned for pattern recognition and if not, what visually-guided behaviours are these cells suited to.

In order to do this, we leverage research which has described the receptive field properties of have two classes of ring neuron in the Drosophila ellipsoid body [6]. The two subtypes of ring neuron investigated were the R2 and R4d ring neurons, of which only 28 and 14, respectively, were responsive to visual stimuli. The cells were found to possess receptive fields (RFs) that were large, centred in the ipsilateral portion of the visual field and with forms similar to those of mammalian simple cells [23] (for details of how the receptive fields were estimated, see Section 5.1). Like simple cells, many of these neurons showed strong orientation tuning and some were sensitive to direction of motion of the stimuli. The ring neuron RFs, however, are much coarser in form than simple cells, are far larger, are less evenly distributed across the visual field and respond mainly to orientations near the vertical. This suggests that ring neurons might have a less general function than simple cells [24]. In mammals, the population of simple cells means that small high contrast boundaries of any orientation are detected at all points in the visual field. Thus the encoding provided by simple cells preserves visual information and acts as a `general-purpose' perceptual network, feeding into a large number of behaviours. In contrast, the coarseness of the receptive fields of ring neurons, allied to the tight relationship between specific behaviours and sub-populations of ring neurons suggests instead that these cells are providing economical visual information that is likely tuned for specific behaviours.

To investigate such issues, we here use a synthetic approach whereby investigations, in simulation, of the information provided by these populations of neurons can be related to behavioural requirements, thus `closing the loop' between brain and behaviour. We show how the population code is well-suited to the spontaneous bar orientation behaviours shown by flies. Similarly, we verify that our population of simulated ring neurons are able to explain the success and failure of the fly to discriminate pairs of pattern. Upon deeper analysis, we demonstrate that certain shape parameters { orientation, size and position { are implicit in the ring neurons' outputs to a high accuracy, thus providing the information required for a suite of basic fly behaviours. This contrasts with the rather limited ability of ring neuron populations (and flies) to discriminate between abstract shapes, casting doubt on cognitive explanations of fly behaviour in pattern discrimination assays.