Behavioural Brain Research 317 (2017) 382–392

Contents lists available at ScienceDirect

Behavioural Brain Research

journal homepage: www.elsevier.com/locate/bbr

Research report

Neural correlates of sample-coding and reward-coding in the delay activity of neurons in the entopallium and nidopallium caudolaterale of pigeons (*Columba livia*)

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HIGHLIGHTS

- Delay activity in entopallium represents a neural correlate for the to-be-remembered visual stimuli.
- Delay activity in NCL represents a neural correlate for the upcoming reward.
- Both of these are regions are modulated by external factors and do not exclusively code visual or reward information.

ARTICLE INFO

Article history:
Received 22 June 2016
Received in revised form
29 September 2016
Accepted 1 October 2016
Available online 5 October 2016

Keywords:
NCL
Entopallium
Delay activity
Memory
Differential outcomes

ABSTRACT

We recorded neuronal activity from the nidopallium caudolaterale, the avian equivalent of mammalian prefrontal cortex, and the entopallium, the avian equivalent of the mammalian visual cortex, in four birds trained on a differential outcomes delayed matching-to-sample procedure in which one sample stimulus was followed by reward and the other was not. Despite similar incidence of reward-specific and reward-unspecific delay cell types across the two areas, overall entopallium delay activity occurred following both rewarded and non-rewarded stimuli, whereas nidopallium caudolaterale delay activity tended to occur following the rewarded stimulus but not the non-rewarded stimulus. These findings are consistent with the view that delay activity in entopallium represents a code of the sample stimulus whereas delay activity in nidopallium caudolaterale represents a code of the possibility of an upcoming reward. However, based on the types of delay cells encountered, cells in NCL also code the sample stimulus and cells in ENTO are influenced by reward. We conclude that both areas support the retention of information, but that the activity in each area is differentially modulated by factors such as reward and attentional mechanisms.

1. Introduction

Working memory in humans is a type of memory in which information can be processed and manipulated in order to solve a current task [1]. Nonhuman animals also display all the characteristics of working memory and are often used to study its neural basis [6]. The main working memory procedure adopted across studies using monkeys, rats, and pigeons is the delayed matching-to-sample task (DMS) task. The sequence of events on a typical DMS task is as follows. At the end of an intertrial interval, a sample stimulus is presented to the animal. Following a response to the sample stimulus, the sample is turned off and a delay period is initiated. At the end of the delay period, two comparison stimuli are presented, one the same as the sample stimulus. To obtain a reward, the animal must choose the comparison stimulus that matches the previously-seen sample stimulus. Such a correct response yields a reward, followed by the intertrial interval, effectively signalling the start of the next trial.

To perform accurately on the DMS task the animal must remember the sample stimulus during the delay period. It is well established that cells in the inferior temporal (IT) cortex, a region of extrastriate cortex in the primate visual system, are dedicated to processing the physical characteristics of visual information [7,18]. Such cells, for example, show sustained activation to a stimulus when it is presented as a sample stimulus in a DMS task [13,14]. A number of studies, however, have also shown that some cells in extrastriate cortex exhibit sustained activation during the delay period of a DMS task [5,13,14,40] when no visual information is present. The prevailing view is that the sustained activation in the

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http://dx.doi.org/10.1016/j.bbr.2016.10.003
0166-4328/

delay period reflects a neural correlate of the animal remembering the sample stimulus. Neurons that display sustained activation in the delay period are referred to as delay neurons.

Similar sustained activation in the delay period can also be seen in the activity of neurons in the prefrontal cortex (PFC) of monkeys [12]. Although there have been some reported differences between delay activity in extrastriate cortex and delay activity in PFC, most notably with respect to their susceptibility to intervening interfering stimuli [39], the fact that both areas display sustained activation in the delay period is generally in line with the view that both areas support working memory. However, neurons in the PFC are also known to change their firing rates on tasks that have little, if any, memory component. In particular, PFC neurons strongly code aspects of the impending reward, such as their physical characteristics [58] and the magnitude of the reward [37], and are known to respond differentially to stimuli that predict the presence versus absence of a reward [25], features that extrastriate cortex neurons tend not to process.

Despite notable architectural differences [31], the avian brain similarly consists of regions that parallel the functions of extrastriate cortex and the PFC. Although our understanding of the different visual areas in birds is still emerging, and although there is no certainty yet over what may constitute the equivalent area to primate IT cortex, the entopallium (ENTO) is a pallial area of the avian brain dedicated to the processing of visual information [30,31,44], and may be considered equivalent to a region of the primate extrastriate cortex. In support of this analogy are numerous similarities between the neural characteristics of cells in extrastriate cortex and ENTO. For example, the receptive field sizes of extrastriate and ENTO neurons are relatively large [19,33,46], and unlike earlier visual areas in both species, the receptive fields show little or no retinotopic mapping [20,46]. Similarly, damage to both extrastriate cortex and ENTO result in far greater impairments on pattern discrimination tasks than damage to earlier visual areas in both species [18,26,48,57]. Finally, as in extrastriate cortex [5,13,14,40], neurons in ENTO display sustained activation during the delay period of a DMS task [4].

In contrast to the uncertainty over what primate visual area ENTO may correspond to, there is far greater agreement over which area of the avian brain corresponds to the mammalian PFC. The nidopallium caudolaterale (NCL) is a pallial telencephalic region that, on the basis of behavioural/lesion, neurochemical, and anatomical studies, corresponds to the PFC [9,21–23,35,36,41]. For example, both the NCL and PFC receive projections from different sensory areas, and both project to motor and limbic areas of the brain [27,36]. Furthermore, both are densely innervated by midbrain dopaminergic fibers [8,9,23], and damage to both regions causes difficulties on tasks with delays [16,21,24,41,42].

As in the case for monkeys [12,39], sustained activation during the delay period has also been reported in NCL neurons of both crows [55] and pigeons [3,28,50]. With respect to pigeons, Rose and Colombo [50] recorded neural activity from the NCL during a directed forgetting DMS task, a modification of the standard DMS task in which a sample stimulus is followed by a 2-s cue period. A remember cue (a high-frequency tone) signalled that there would be a test period following a 3-s delay, whereas a forget cue (a low-frequency tone) signalled that there would be no test following the 3-s delay, and hence that no reward was available. Rose and Colombo [50] found high levels of sustained activation in the delay period of NCL neurons following the remember cue but not the forget cue, and thus interpreted the sustained activation to be a neural correlate of the animal remembering the sample stimulus. Similarly, the absence of sustained activation on forget trials was interpreted as evidence that the animal had forgotten the sample stimulus. In this respect, the sustained activation in NCL neurons was interpreted as a neural correlate of the sample stimulus, a suggestion in line with similar views expressed by those working in monkey PFC [12,39].

Although Rose and Colombo [50] interpreted the sustained activation as reflecting a code of the animal either remembering or forgetting the sample stimulus, the fact that activation occurs on remember trials could also be interpreted as a neural correlate of a potential upcoming reward. Similarly, the absence of sustained activation on forget trials could be interpreted as the absence of an upcoming reward. In this respect, the findings with birds parallels those studies with monkeys that argue that PFC neural activity represents a reward based code [58]. To untangle whether NCL activity reflects a sample code or a reward code, Browning, Overmier, and Colombo [3] examined delay activity using a differential-outcomes (DO) version of a directed-forgetting DMS task [52]. As in the Rose and Colombo [50] study, a high-frequency tone indicated that the sample should be remembered, whereas a low-frequency tone indicated that the sample could be forgotten. In contrast to the Rose and Colombo [50] study, however, in a DO procedure correct responses following one sample stimulus are followed by a reward whereas correct responses following the other sample stimulus are not. The key is that on remember trials, the animal must remember the sample to perform correctly, but only one of them is associated with a reward. Using this procedure, Browning et al. [3] were able to show that in NCL sustained activation during the delay period was related more to a reward code than a sample code.

In the current study we used a DO procedure to compare the sustained activation of NCL and ENTO delay neurons. To the extent that sustained activation in NCL represents a reward code, we expected to replicate previous findings that sustained activation occurs after the sample stimulus that predicts the possibility of an upcoming reward and not after the sample stimulus that does not predict a reward. However, if sustained activation also represents a sample code, then we should see examples in which sustained activation occurs after both sample stimuli. More importantly, we compare the sustained activation in NCL to sustained activation in ENTO. To the extent that ENTO represents a region of extrastriate cortex in the avian brain responsible for the retention of visual information, we would expect that, as in the primate brain, sustained activation would represent a sample code and thus we should see sustained activation after both sample stimuli, irrespective of whether or not that particular stimulus is associated with reward.

2. Method

2.1. Subjects

Four experimentally sophisticated pigeons (*Columba livia*) served as the subjects for the current experiment. They had previously served in a study in which they learned to perform a DO DMS task [34]. The pigeons were housed individually in a colony room maintained at 20 °C. The colony room had a light/dark cycle of 12 h with lights on at 7am. The birds were fed a mixture of grain, corn, and peas in a daily amount adjusted to maintain them between 80 and 85% of their free feed body weight. Such levels ensured effective performance during the experiment. Water and grit was available to the pigeons at all times. Animal handling and care were carried out in accordance with the University of Otago Code of Ethical Conduct for the Manipulation of Animals.

2.2. Apparatus and stimuli

An operant chamber measuring 35l × 43w × 39h cm internally was used during both training and electrophysiological testing. At the front of the chamber was a 17-inch monitor, which was used to display the stimuli. A perspex panel with six square holes mea-