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Efference copy: The motoric command for head-bobbing in pigeons

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Introduction

Head-bobbing in birds, is exemplified by two switching phases; the hold and thrust phases. The hold phase is functional in visual perception, while the thrust phase is important for depth information. Head-bobbing is an optokinectic paradigm for perception and action among birds that display it. This is comparable to the saccadic eye movement in higher vertebrates including human beings. In a walking pigeon, when the head is translated horizontally forward in comparative to a static world, the pigeon moves forward synchronising the head translation with other locomotive adjustments. This observable fact raises the question of what motoric information controls head-bobbing? We hypothesise that efferent copy command controls head-bobbing. Our premonition is that the efferent signals drives the neck muscle and instigate head motion. We assume that the command is processed in the nucleus triangularis. The purpose of this study is to investigate our hypothesis using neuroethological, histological and neuropharmacological experiments.

Methods

Prior to surgery, pigeons were trained to walk between two opposite hoppers and peck alternatingly, primarily to display head-bobbing. Thereafter, we bilaterally implanted a pair of guided canullae at the tip of the nucleus Triangularis using stereotaxic calibrations. After recovery, we systemically infused 0.5microlitre of 30micrograms pirenzepine dihydrochloride (the neuropharmacological Muscarinic acetylcholine type I receptor antagonist) and 0.5microlitre saline solutions as the control. After infusions, pigeons were re-introduced into their training arena to perform their learned task. In the second experiments, pigeons were confined inside a box and passively moved on a treadmill after both pirenzepine and saline infusions, to experience heterogeneous optic flow which induces head-bobbing (Frost 1978). All behavioural activities were video-recorded and motion-captured for detailed qualitative and quantitative analysis.

Results

Biomechanical behaviours were prominent and exhibited by the pigeons after pirenzepine infusions. Pitch rotational turning of head and body, vertical translation of head, active visual response and saccades were all feasible. Contrarily, optokinetic horizontal translational head-bobbing was impaired after pirenzepine infusions. Pigeons display perfect head-bobbing after saline infusions, both in the training arena and the treadmill. Evaluation of cannullae positions, reveal that the cannullae were in the right positions at the tip of the triangularis with respect to the predicted diffusion of the drugs into the nucleus triangularis.

Conclusion

The visual system requires non-visual information about the forward motion of the head, this is provided in form of efferent signals of the efference copy commands. It drives the neck muscles to initiate the head motion for the interpretation of the complex field of optic flow that the walking pigeon experiences. Because the visual system also requires information about head motion to compare the forward motion of the head with the anticipated induction of retinal image motion of the pigeon. This is necessary to provide information critical for the relative depths of objects.The triangularis is part of the rotundus which is the largest cellular complex within the thalamus. It selectively contains the muscarinic type 1 acetylcholine receptors different from other parts of the rotundus. Up till now its functions remains unknown. The fact that the blockage of the muscarinic type 1 receptor in the nucleus triangularis impedes head motion and impair head-bobbing confirms our hypothesis that efferent copy certainly controls head-bobbing, and reflect the antagonizing effect of the neuropharmacological drug on the receptors in the triangularis.

References,

Frost, B. J., 1978. The Optokinetic basis of head-bobbing in the pigeon. Journal of Experimental Biology. 74, 187-195.