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Review

Molecular mechanisms of memory in imprinting

Revaz O. Solomonia[a,b], Brian J. McCabe[c,*]

[a] Institute of Chemical Biology, Ilia State University, 3/5 K Cholokashvili Av, Tbilisi 0162, Georgia
[b] I. Beritashvili Centre of Experimental Biomedicine, Tbilisi, Georgia
[c] University of Cambridge, Department of Zoology, Sub-Department of Animal Behaviour, Madingley, Cambridge CB23 8AA, United Kingdom

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ABSTRACT

Converging evidence implicates the intermediate and medial mesopallium (IMM) of the domestic chick forebrain in memory for a visual imprinting stimulus. During and after imprinting training, neuronal responsiveness in the IMM to the familiar stimulus exhibits a distinct temporal profile, suggesting several memory phases. We discuss the temporal progression of learning-related biochemical changes in the IMM, relative to the start of this electrophysiological profile. *c-fos* gene expression increases <15 min after training onset, followed by a learning-related increase in Fos expression, in neurons immunopositive for GABA, taurine and parvalbumin (not calbindin). Approximately simultaneously or shortly after, there are increases in phosphorylation level of glutamate (AMPA) receptor subunits and in releasable neurotransmitter pools of GABA and taurine. Later, the mean area of spine synapse post-synaptic densities, N-methyl-D-aspartate receptor number and phosphorylation level of further synaptic proteins are elevated. After ~15 h, learning-related changes in amounts of several synaptic proteins are observed. The results indicate progression from transient/labile to trophic synaptic modification, culminating in stable recognition memory.

Contents

* Corresponding author. Tel.: +44 1223 741801; fax: +44 1223 741802.
E-mail addresses: revaz_solomonia@iliauni.edu.ge (R.O. Solomonia), bjm1@cam.ac.uk (B.J. McCabe).

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1. Introduction

Over the past few decades, there has been substantial progress in understanding the mechanisms of learning and memory. This progress continues to depend on a combination of complementary experimental approaches on a variety of experimental animals. The domestic chick is one such animal and offers a number of important advantages. First, a region of the chick forebrain has been identified as being of crucial importance for the learning process of filial imprinting, the available evidence indicating that it is a site of storage of information about a visual stimulus to which a chick has become imprinted. This region is the intermediate and medial mesopallium (IMM), formerly known as the intermediate and medial hyperstriatum ventrale (IMHV) (Reiner et al., 2004). The IMM is a bilateral structure adjacent to the lateral wall of the lateral ventricle (Fig. 1) and makes up approximately 3% of the telencephalon by volume. The evidence implicating the IMM as a memory system for imprinting is summarized extensively elsewhere (see e.g. Horn, 1985, 2004; McCabe, 2013). The IMM is sufficiently localized to be targeted by lesion experiments, to be probed with microelectrodes (see Nicol and Moorman, in this issue) and to be subjected to quantitative histological (Bradley et al., 1981; Horn, 1985; McCabe and Horn, 1994; Suge et al., 2010; Suge and McCabe, 2004) and biochemical analysis (Horn, 2004; Solomonia et al., 1997, 1998, 2003, 2005, 2008, 2011, 2013). The IMM also plays an essential role in single-trial passive avoidance learning in the chick (see e.g. Rose, 2000). Here, we focus on imprinting.

In addition to the availability of the IMM as a memory system for study, research into neural mechanisms of imprinting is aided by the fact that behavioural aspects of imprinting and the neurobiology of the avian brain have been extensively documented. It is also an important advantage that the visual experience of the recently hatched chick has been minimal and can be controlled, facilitating the detection and analysis of learning-related changes in the brain. The fact that the chick does not require food or water for the early part of the typically three- to four-day sensitive period for filial imprinting removes a complication inherent in animals that must be fed. Newly-hatched chicks are very active and vocalize extensively, offering abundant behavioural read-out from which learning and memory-related behaviour may be inferred. Imprinting is a powerful and rapid form of learning, associated with processes having the characteristics of recognition memory observed in a range of animals (Bateson, 1990). Features of imprinting memory closely resemble recognition memory in mammals, suggesting that mechanisms revealed in the chick may exist in other vertebrates.

This review will concentrate on biochemical changes occurring in the IMM at various times in the first day after imprinting training. Concomitant electrophysiological changes in the IMM are described and discussed elsewhere (Nicol and Moorman, in this issue). We shall attempt to keep these two sets of observations in register and comment on ways in which they might be connected. Where the opportunity arises, we shall attempt to relate neural changes observed in studies of imprinting to changes arising from learning and neural modifications observed in other species.

The accumulated evidence strongly indicates that formation of the recognition memory of imprinting involves a time-dependent chain of biochemical processes in the IMM. Such processes are clearly expressed in the left side of this region. Changes in the right IMM after training, though resembling events in the left in some respects, have a different temporal pattern, as might be expected from the functional lateralization of the IMM (McCabe, 1991, 2013; Nicol and Moorman, in this issue; Rose, 2000). Research on biochemical learning-related changes has focussed mainly on the first day after training, and this may conveniently be divided into three parts: (1) Early changes (detected up to ~7 h after the start of training); (2) Intermediate changes (detected ~7–15 h after the start of training) and (3) Late changes (detected >15 h after the start of training).

All results described here employed an artificial training stimulus of the type that was also used for the electrophysiological experiments mentioned above. That is, chicks were trained by exposing them to either a rotating, internally-illuminated red box or to a rotating, internally illuminated blue cylinder as described, for example, by Bolhuis et al. (2000).

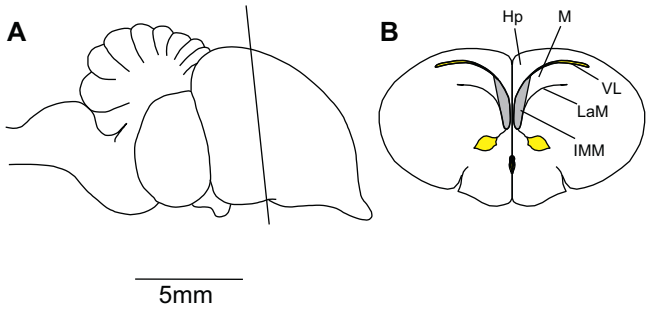

Fig. 1. Position of the IMM. A, side view of the chick brain, indicating the plane of section for B. B, coronal section; Hp, hippocampus; IMM, intermediate medial mesopallium; LaM, lamina mesopallialis; M, mesopallium; VL, lateral ventricle.

2. Early changes (up to ~7 h after the start of training)

2.1. c-fos

The expression of the immediate-early gene *c-fos* can be induced in some neurons on stimulation (Herdegen and Leah, 1998; Herrera and Robertson, 1996). Expression of this gene and its product Fos have accordingly been used extensively as neural activity markers.

Training for 60 min with a visual stimulus accompanied by the maternal call of a hen typically results in strong visual imprinting in some chicks but less strong imprinting in others, permitting correlations to be run between a behavioural measure of the strength of learning and a physiological variable potentially involved in learning or memory. An appropriate measure of learning strength is the preference score, derived from a test in which a chick, previously trained by exposure to an imprinting stimulus, is exposed

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