



Review Paper

Memory beyond expression

A. Delorenzi^{a,*}, F.J. Maza^a, L.D. Suárez^a, K. Barreiro^a, V.A. Molina^b, J. Stehberg^c^a Laboratorio de Neurobiología de la Memoria, Departamento de Fisiología y Biología Molecular, IFIByNE-CONICET, Pabellón II, FCEyN, Universidad de Buenos Aires, Ciudad Universitaria (C1428EHA), Argentina^b Departamento de Farmacología, Facultad de Ciencias Químicas, Universidad Nacional de Córdoba, IFEC-CONICET (X5000HUA), Argentina^c Laboratorio de Neurobiología, Departamento de Ciencias Biológicas, Universidad Andrés Bello, Chile

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ABSTRACT

The idea that memories are not invariable after the consolidation process has led to new perspectives about several mnemonic processes. In this framework, we review our studies on the modulation of memory expression during reconsolidation. We propose that during both memory consolidation and reconsolidation, neuromodulators can determine the probability of the memory trace to guide behavior, i.e. they can either increase or decrease its behavioral expressibility without affecting the potential of persistent memories to be activated and become labile. Our hypothesis is based on the findings that positive modulation of memory expression during reconsolidation occurs even if memories are behaviorally unexpressed. This review discusses the original approach taken in the studies of the crab *Neohelice (Chasmagnathus) granulata*, which was then successfully applied to test the hypothesis in rodent fear memory. Data presented offers a new way of thinking about both weak trainings and experimental amnesia: memory retrieval can be dissociated from memory expression. Furthermore, the strategy presented here allowed us to show in human declarative memory that the periods in which long-term memory can be activated and become labile during reconsolidation exceeds the periods in which that memory is expressed, providing direct evidence that conscious access to memory is not needed for reconsolidation. Specific controls based on the constraints of reminders to trigger reconsolidation allow us to distinguish between obliterated and unexpressed but activated long-term memories after amnesic treatments, weak trainings and forgetting. In the hypothesis discussed, memory expressibility – the outcome of experience-dependent changes in the potential to behave – is considered as a flexible and modifiable attribute of long-term memories. Expression seems to be just one of the possible fates of re-activated memories.

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* Corresponding author. Tel.: +54 11 4576 3348; fax: +54 11 4576 3447.

E-mail addresses: delorenzi@fbmc.fcen.uba.ar (A. Delorenzi), fjmaza@fbmc.fcen.uba.ar (F.J. Maza), lsuarez@fbmc.fcen.uba.ar (L.D. Suárez), kbarreiro@gmail.com (K. Barreiro), vmolina@fcq.unc.edu.ar (V.A. Molina), jstehberg@unab.cl (J. Stehberg).

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1. Introduction

How do we select from recent experiences those that will be stored as memories in the long term? The theory of the endogenous modulation of memory consolidation posits that – during the process by which a memory turns from short term into long term – neuromodulatory systems activated by relevant experiences modulate the storage of long-term memory (LTM) (McGaugh, 1989). The experimental approaches that have guided much of the research on the cellular and systemic mechanisms of memory have been based on an operational definition of memory: a change in behavior as a result of previous experience. However, recent studies concerning the action of neuromodulators during memory reconsolidation (Frenkel et al., 2005a) have led us to rethink certain central notions: can unexpressed memories be re-activated and become labile again? Are memory expression and memory reactivation dissociable processes? Are retrieval and memory expression interchangeable concepts?

1.1. Reconsolidation hypothesis

The reconsolidation hypothesis proposes that a previously consolidated memory can enter an unstable state when recalled (memory labilization), becoming transiently sensitive again to disruption by interfering agents (Lewis, 1979; Misanin et al., 1968; Przybyslawski and Sara, 1997; Sara, 2000). Today, the cumulative evidence based on hundreds of studies on reconsolidation challenges once more the traditional view of memory consolidation, principally the notion that new memories are fixed after being consolidated (Dudai, 2012; Nader and Einarsson, 2010; Reichelt and Lee, 2013). This new view has led to novel perspectives about several mnemonic processes (Alberini et al., 2013; Baratti et al., 2009; Dudai and Eisenberg, 2004; Dudai and Morris, 2013; Frenkel et al., 2010b; Gold, 2006; Hupbach et al., 2007; Nader and Wang, 2006; Sara and Hars, 2006; Sierra et al., 2013). In this framework, we review our studies on the positive modulation of memory expression during reconsolidation. Hereafter, the term “memory expression” is referred to as the expression of a representation in behavior (Schacter, 2007).

1.2. Reconsolidation and memory enhancing effects

Although most reconsolidation studies have shown that memory can be disrupted by interfering agents during this phase, memory retention can be increased during reconsolidation by enhancing agents, multiple reactivation sessions and real-life events (Alberini, 2007, 2011; Dudai, 2009; Gordon and Spear, 1973; Lee, 2008; Lewis, 1976; Rodriguez et al., 1999, 1993; Rovee-Collier et al., 1980). Among the earliest studies that reported an enhancing effect specifically during reconsolidation was one in our laboratory with the crab *Chasmagnathus*, now formally known as the *Neohelice, granulata* memory model (Frenkel et al., 2005a).

Here we review our studies that have highlighted that memory re-activation, but not memory expression, of a consolidated trace is necessary for the emergence of reconsolidation. We will discuss

results showing that the periods in which a consolidated LTM can be activated and become labile exceed the periods in which that memory trace is expressed in behavior. In fact, new studies support the view that mechanisms mediating memory re-activation and behavioral expression of memory can indeed be dissociated.

Two other terms require clarification before continuing: ‘persistence’ and ‘(re)activation’. The term persistence (an “alternative term has been commonly used, ‘storage’, which is a misguided metaphor, of the type quite abundant in the science of memory”: page 191 in Roediger et al. (2007)) here refers to the retention over time of the information learned; an experience-dependent internal representation or acquired model of the world, that is only, and only sometimes, expressed in overt behavior (Dudai, 2002b; Eichenbaum, 2007; Roediger et al., 2007). In addition, for the term memory reactivation, we hereafter refer to it as the activation concept, agreeing with Lewis (1979): “Active memory is a subset of inactive memories and contains either newly formed memories or established retrieved memories or both.”

1.3. Reminder environment to induce reconsolidation: the mismatch component

A crucial issue to comprehend the role of reconsolidation is to know the boundary conditions necessary to induce this process (Dudai, 2012; Nader and Einarsson, 2010; Pedreira and Romano, 2013). The duration of the reminder, which should be limited to induce reconsolidation and not extinction (Dudai, 2012; Eisenberg and Dudai, 2004; Pedreira and Maldonado, 2003), is a notable one. Outstandingly, the mismatch requirement is another essential boundary condition to understand the reconsolidation process itself and to elaborate the present discussion. The mismatch component covers the concept of prediction error that arises from discrepancy theories of associative learning (Rescorla and Wagner, 1972); the mismatch between the predicted unconditioned stimulus and the actual unconditioned stimulus is a key condition to generate new learning. Today, it is not surprising that the labilization–reconsolidation process is also triggered by a rupture of the expectations generated by the activated representation of the experience, as was originally demonstrated in *Chasmagnathus* memory model and then in humans by Professor Maldonado’s laboratory (Forcato et al., 2009; Pedreira et al., 2004). In accordance with the general principles of memory organization throughout evolution (Barco et al., 2006; Carew and Sutton, 2001), this boundary condition has been confirmed in several species (Diaz-Mataix et al., 2013; Dudai, 2006, 2009; Forcato et al., 2009; Frenkel et al., 2005a; Morris et al., 2006; Nader et al., 2000; Pedreira et al., 2004; Pedreira and Romano, 2013; Perez-Cuesta and Maldonado, 2009; Rossato et al., 2007; Sevenster et al., 2012, 2013; Winters et al., 2009). To illustrate the point, the effects of some amnesic agents administered after LTM activation will not take place if the brief context presentation is reinforced (i.e. no mismatch condition at reminder session) by the presentation of one training trial at the end of the reminder session in *Chasmagnathus* (Pedreira et al., 2004; Pedreira and Romano, 2013). In consequence, reminder

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