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Enhancement of long-term memory expression by a single trial during consolidation

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ABSTRACT

Before the memory trace is stored long term, it must undergo a phase of consolidation during which it remains susceptible to modifications. It has previously been proposed that during consolidation, memories are kept from being stored long term, and can therefore be modified with additional information resulting from ongoing behavior. The *Chasmagnathus* associative memory model is used here to test whether it is possible during consolidation to modify the long-term expression of a memory generated by a weak training procedure. In this memory model, long-term memory expression is achieved after strong training protocols, a 15-spaced trial procedure. After a weak training protocol (WTP, six spaced trials), crabs do not show memory retention when tested in the long term. Nevertheless, the WTP builds a long-term memory that it is indeed consolidated, but remains unexpressed. Here we show that memory can be modified by experience during this short period after learning: memory expression can be enhanced by a *Single Trial Session*, on the condition that this session takes place contingent upon the consolidation period. We also found that during this time, the memory built by the WTP is behaviorally expressed, in contrast with what occurs at long term. Our results support the idea that during consolidation memories can be evaluated in the background of concurrent experiences. In particular, we propose that during the consolidation period it is possible for crabs to assess which experiences, among those stored long term, will be expressed long term.

Memory formation is not a straightforward and rigid process. Instead, the memory trace is not only stored according to the conditions in which it was acquired, but must also undergo a phase of consolidation during which it remains susceptible to modifications, such as strengthening by the action of endogenous modulators systems [15]. It has been proposed that during consolidation, memories are kept from being fixed, and can thus be evaluated with additional information resulting from ongoing behavior [2,8,11,15,18]. Evidence of this hypothesis is the fact that after weak training procedures, the resulting memories that are present only in the short term can be enhanced to long-term memory by presenting one or more training trials shortly after learning [3,4,19,29,33]. In *Chasmagnathus*, a WTP builds a long-term memory that can be retrieved but is not behaviorally expressed [10]. Hence, we used the *Chasmagnathus* memory model to investigate whether a reminder treatment during consolidation can modify the long-term expression of a memory generated by a WTP.

The *Chasmagnathus* context-signal memory (CSM) model is based on the defensive response of the crabs to a visual danger stimulus (VDS): a plastic screen that moves horizontally above the animal, triggering an escape response. The experimental device, the actometer [14], referred to as the training context (context A), consisted of a bowl-shaped opaque container with a steep concave 12 cm-high wall (23 cm top diameter and 9 cm floor diameter) covered to a depth of 0.5 cm with artificial sea water, where the crab was lodged before each experimental session. After the iterative spaced presentation of the VDS, the initial escape response is replaced by a freezing-to-VDS response. After a strong training (42 min, 15 spaced trials consisting of a 9 s presentation of the VDS) a long-term memory mediated by an association between the learning context and the VDS, i.e. a freezing response to the VDS, at least up to five days after training, can be observed [14,34].

After a weak training protocol (WTP, six spaced trials, total time = 15 min), crabs do not show memory retention when tested in the long term [6,7,9,26]. Nevertheless, the WTP builds a long-term memory that it is indeed consolidated, but remains unexpressed [10]. This long-term memory, which depends on mRNA transcription and translation (Frenkel et al. Ph.D. Thesis, 2009), can be unveiled by enhancing it during its reconsolidation [10]. Thus, in this study we used a WTP to evaluate whether a single post training reminder trial could alter the long-term expression of this memory.

Intermolt adult male crabs of the species *Chasmagnathus granulatus*, 2.7–3.0 cm across carapace and weighing 17 ± 0.2 g, were

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collected from the narrow coastal inlets of San Clemente del Tuyú, Argentina, and maintained in the laboratory as previously described [9]. All the experiments were conducted in accordance with the Ethics Reference Frame for Biomedical Investigations of the CONICET, equivalent to the standard procedures for animal care and use of the NIH, USA. All efforts were made to minimize the number of animals used. Experiments included three sessions: a *Training Session* (Day 1), a *Single Trial Session* (Day 1; 0.5, 4 or 8 h after the *Training Session*), and a *Testing Session* (Day 2). The experimental design involved one or two pairs of groups of crabs, where each pair had a trained group (TR) and an untrained group (UN). TR and UN groups differed only in the *Training Session*. Throughout the rest of the experiment, both groups underwent the same treatments. Thus, the UN groups served as retention control for their respective TR groups. Each UN or TR group comprised 30–40 crabs. For each experiment, experimental procedures were applied simultaneously to all groups. During the *Training Session* (Day 1), the TR group first spent 10 min in the experimental container (adaptation time), and then received six training trials (six VDS presentations, WTP), while the UN groups remained for the same time in the experimental container, without any VDS presentation. Immediately after the *Training Session*, both UN and TR crabs were moved from the experimental container to be housed individually in the resting containers. On Day 1, at 0.5 h, 4 h or 8 h after the *Training Session*, all groups spent 10 min in the experimental container (adaptation time), and then received one VDS presentation (*Single Trial Session*). Immediately afterwards, crabs were moved from the experimental container to be housed individually in the resting containers. On Day 2, during the *Testing Session*, crabs spent 10 min in the experimental context and were then tested for memory expression with a VDS presentation. The response of crabs was measured by integrating the vibrations in the container produced by the animals during a VDS presentation, collected by four microphones in the base of the containers [14]. Memory retention was assessed by focusing data analysis on test trial scores, i.e. by estimating the difference between the response levels of the TR group and that of the respective untrained UN group at the *Testing Session* (long-term memory) or at the *Single Trial Session* (short-term memory) [14,34]. A TR-group is said to show memory retention when its mean response level at the test trial is statistically lower than the respective UN-group. In Experiments of Fig. 2, a cylindrical (15 cm in diameter and 15 cm in height) plastic container with black and white striped walls was used as a different context (context B). This context is arranged to fit inside the experimental container, and thus the vibrations caused by the motor activity of the animal cannot be registered properly. Consequently, context A is the only one in which the activity of the crab can be measured. Thus, experiments were designed in such a way that any test occurs in context A. These contexts have been used as reactivation control and as context-dependence control in a number of works, proving that animals recognize them as different contexts [10,23,31]. As the variance of activity scores increases with the mean, thus violating the homogeneity of variance assumption of the analysis of variance (ANOVA), the data were $\log_2$ transformed. Because of this, the values resulting from the integration for 9 s of the vibrations measured by the four microphones were transformed to their $\log_2$ and this value was used as a measure of crabs' response ($\log_2$ response). In experiments that involved two pairs of groups, results were analyzed using ANOVA and a priori planned comparisons. Three types of contrasts per experiment were carried out: the first, between the two UN groups of each pair; the second, between the UN and TR groups of one pair; and the third, between the UN and TR groups of the other pair. In experiments that involved only one pair of groups, comparisons between the TR and UN groups were statistically analyzed using a *t*-test. All response scores were represented as the mean ± standard error. We analyzed data using STATISTICA (StatSoft, version 6.0).

On Day 1, one pair of groups, consisting of a trained (TR) group and an untrained (UN) group, underwent a *Weak Training Session* (the TR group received six trials in the experimental container, while the UN group remained in the container without stimulation). Thirty minutes after training, both groups received a single trial (*Single Trial Session*). On Day 2, all groups were tested for memory retention (*Testing Session*) (Fig. 1, upper panel). Activity scores at the *Single Trial Session* (Fig. 1, bottom panel) revealed memory retention (*t*-test; $t(70) = 2.57$, UN-0.5 h > TR-0.5 h; $p < 0.02$). Thus, WTP generates a short-term memory that can be revealed by a VDS presentation at least 30 min after training, in contrast to what is observed after 24 h [7,10,27,28]. At the *Testing Session* (Day 2), a *t*-test also revealed memory retention ($t(68) = 2.80$, UN-0.5 h > TR-0.5 h; $p < 0.006$). Therefore, a single trial given 30 min after weak training is sufficient to enhance long-term memory expression.

In order to test whether this enhancing effect is restricted to the consolidation period (up to 4 h but not 6 h after training, in *Chasmagnathus* [21,22]), the same procedure was performed but varying the delay of the *Single Trial Session* to the *Training Session*. Two pairs of groups, each one consisting of a TR and an UN group, underwent a *Weak Training Session*. One pair received the *Single Trial Session* 4 h after training (4 h pair) while the other received it 8 h after training (8 h pair). On Day 2, all groups were tested for memory expression (Fig. 1, upper panel). Activity scores at the *Single Trial Session* (Fig. 1, bottom panel) revealed memory retention for the 4 h pair (*t*-test, $t(70) = 2.61$; UN-4 h > TR-4 h; $p < 0.02$) but not for the 8 h pair ($t(68) = 1.34$; $p = 0.20$). At the *Testing Session*, planned comparison [ANOVA, $F(3,142) = 3.04$; $p < 0.05$] for the 4 h and 8 h pairs disclosed memory retention between UN and TR groups for the 4 h pair (UN-4 h > TR-4 h; $p < 0.005$), but not between those of the 8 h pair ($p = 0.96$), nor between the UN groups ($p = 0.39$). Memory after a WTP is therefore expressed at least up to 4 h, whereas at 8 h memory is no longer expressed. A single trial in a short period after training (less than 8 h) is sufficient to modify the long-term expression of the acquired memory.

To test whether this enhancement of memory expression may be achieved by the sole exposure to the training context, or whether it necessarily involves a retraining process, the following experiment was performed. On Day 1, two pairs of groups underwent a *Weak Training Session*. Four hours after training one pair received one trial (single trial pair) during the *Single Trial Session*, while at the same time the other pair was exposed to the training container but was not stimulated (No trial pair). On Day 2, all groups were tested for memory retention (Fig. 2A, left panel). As expected, during the *Single Trial Session* (Fig. 2A, right panel) a *t*-test on activity scores showed memory expression for the single trial pair ($t(56) = 2.18$; UN-single trial > TR-single trial; $p < 0.05$). At the *Testing Session*, planned comparison [ANOVA, $F(3,120) = 4.51$; $p = 0.01$] disclosed a significant difference on activity scores between the UN and TR groups for the single trial pair (UN-single trial > TR-single trial; $p < 0.05$), but not between those of the No trial pair ($p = 0.53$), nor between the UN groups ($p = 0.66$). A context reminder lacking VDS presentation is therefore not sufficient to achieve the enhancement of memory expression.

To test whether the presentation of the US is sufficient to enhance memory after a WTP, animals were re-exposed to de VDS on the *Single Trial Session* in a context (CS) different from that used in the *Training Session*. On Day 1, a pair of UN–TR groups underwent a *Weak Training Session* in the same containers used in the previous experiments (context A). Four hours after training, both groups received a single trial in a different context (context B). On Day 2, both groups were tested (Fig. 2B, left panel, ABA pair); a *t*-test on activity scores revealed no memory expression ($t(68) = 1.26$; $p = 0.26$). Thus, a single US presentation was not suf-

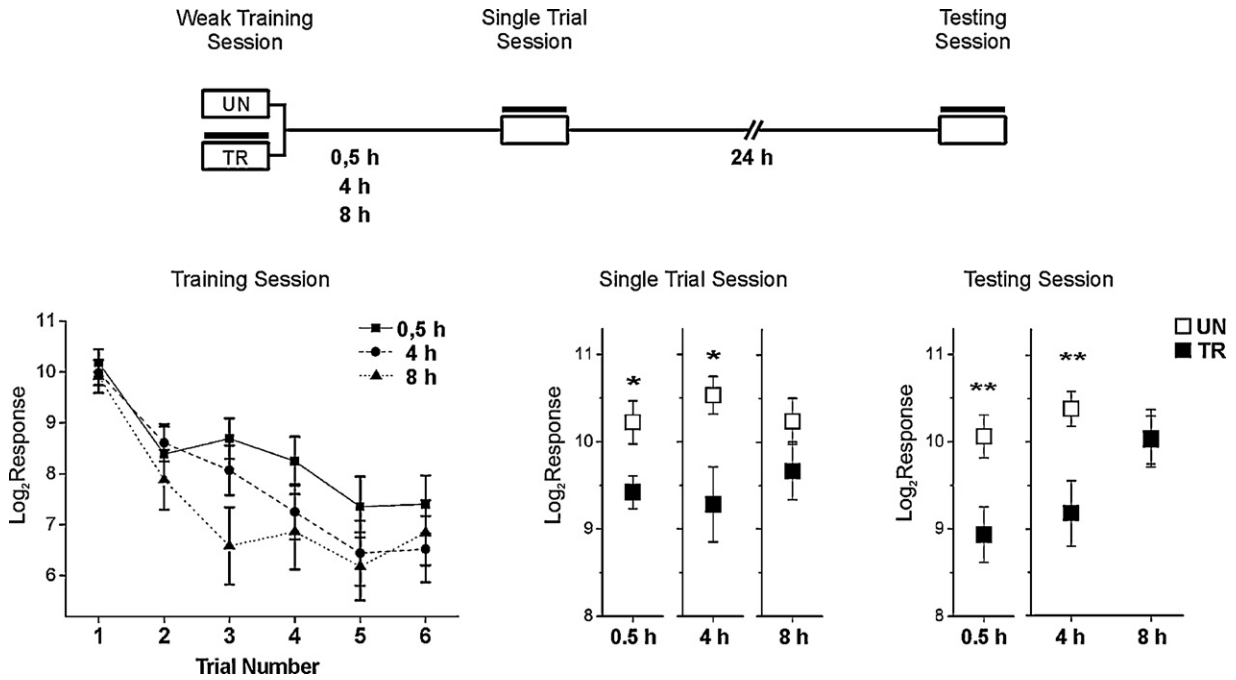

Fig. 1. Enhancement of memory expression by a single trial up to 4 h, but not 8 h, after weak training. Top panel: Experimental designs: White boxes represent context A. A line above a box represents the VDS presentation/s. Bottom panel: Results: Graph ordinates: $\log_2$ response during stimulus presentation (means ± SE); open symbols (□): UN groups, filled symbols (■): TR groups. Significant differences between TR groups and their correspondent UN group: $^{*}p < 0.05$, $^{**}p < 0.01$. *A single trial shortly after a WTP enhances memory expression:* after a WTP memory is expressed at 0.5 h ($^{*}p < 0.05$) and at 4 h ($^{*}p < 0.05$), but not at 8 h. Testing results 24 h after WTP show that a single trial can enhance memory expression if given at 0.5 h ($^{**}p < 0.01$) or at 4 h ($^{**}p < 0.01$), but not at 8 h.

ficient to enhance memory. This result, together with that showed on Fig. 2A, shows that the CS–US association must be presented to enhance memory expression at least at 4 h after a WTP.

As explained before, memory retention cannot be evaluated in context B. In experiments using a strong-training protocol (15 spaced trials) it has been showed that CSM is context specific in the long-term [34] but not in the short-term [31]. To evaluate whether the short-term memory expressed after a WTP is context-specific, a pair of UN–TR groups underwent a *Weak Training Session* in context B and memory retention was evaluated in context A at 4 h (*Single Trial Session*) and on Day 2 (Fig. 2B, left panel, BAA pair). At the *Single Trial Session*, a *t*-test on activity scores disclosed significant differences between the UN and TR groups ($t(68) = 2.08$; UN-BAA > TR-BAA; $p < 0.05$). At the *Testing Session*, no differences were observed between the UN and TR groups ($t(68) = 1.22$; $p = 0.23$). Therefore, the short-term memory triggered by a WTP differs from the long-term memory not only in its expression but also in its context specificity.

After learning, memories can be modified by new experiences [13,19,20,31–33] or by several agents [16]. In this study, we showed that a memory can be modified by a subsequent learning experience. After weak training, which builds a memory that is not expressed long term [10], a single reinforced context presentation can enhance memory expression. This modification has an acute temporal dynamics: enhancement of memory expression occurs if a single trial is presented at up to 4 h after weak training, but not if the stimulus is presented at 8 h (Fig. 1) or at 24–72 h [10].

In *Chasmagnathus*, a WTP does build a long-term memory, which depends on mRNA transcription and translation (Frenkel et al. Ph.D. Thesis) but is not long-term expressed [10]. In this work, we showed that after a WTP, a short-term memory is expressed and is not context-specific. Thus, this is the first evidence of a short-term CSM built after a WTP that can be behaviorally distinguished from the long-term CSM. It has been proposed that behavioral differences between short- and long-term memories reflect the different functional requirements at each period [18]. The findings that behavior is sustained in the short term by a memory distinct from that long-term stored is consistent with the idea of parallel processes of short-term memory and long-term memory consolidation triggered by a WTP [12,18,30]. In this sense, for a short time after weak learning, the best response for an organism would be to express the recently acquired behavior, while during consolidation the recent experience continues being evaluated. This could be true for the case of aversive experiences, because overestimating the relevance of a dangerous stimulus is less costly than underestimating it. It has been shown that weak training builds a CSM trace that is not expressed long term [10]. This consolidated but unexpressed memory could be retrieved and reactivated by the presentation of a specific reminder, returning it to a labile state that is vulnerable to enhancement treatments. Moreover, this unexpressed long-term memory depends on mRNA transcription and translation, a diagnostic characteristic of long-term memory consolidation (Frenkel Ph.D. Thesis).

A single trial after a WTP can change the long-term expression of the acquired response. This change, however, will occur only if the single trial is presented during a short temporal window after training. It is therefore unlikely that the change in behavior observed after 24 h could be explained by the summation of two independent memory traces built after each training session. If a synergistic effect of two memory traces could explain the memory performance on Day 2, then a single trial 8 h after WTP would be expected to have the same effect as a single trial after 4 h or 0.5 h.

A tempting proposition is that a reconsolidation-like process could mediate the modification in long-term memory expression, since the single trial works as a reminder. However, in *Chasmagnathus* it has been demonstrated that not any reminder can trigger reconsolidation at long term. In fact, unlike an unreinforced reminder, a reinforced reminder (a single trial in the training context) as the one used here to modify memory expression cannot induce reconsolidation [10,23–25]. Also, it has been shown that the

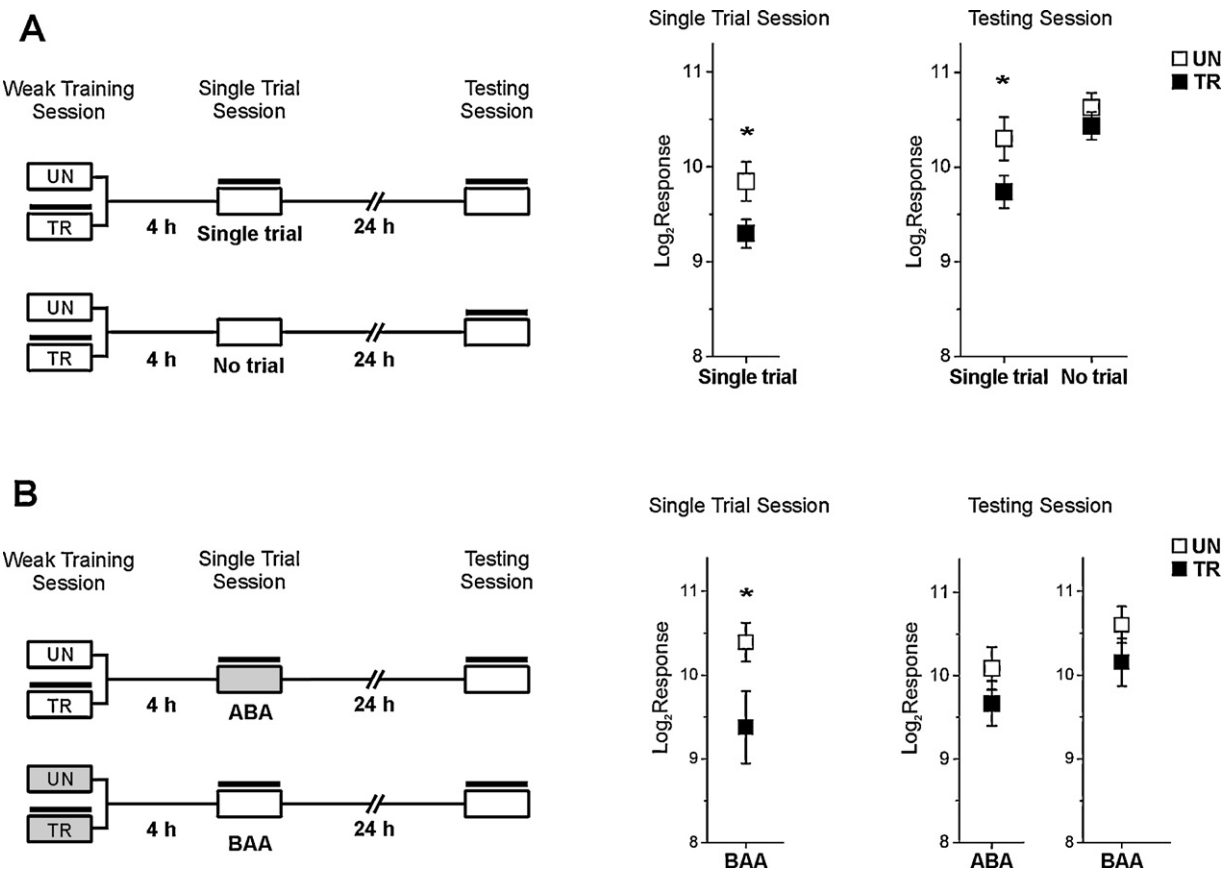

Fig. 2. A single CS–US presentation is necessary to enhance memory expression. Left panel: Experimental designs: white boxes represent context A. A line above a box represents VDS presentation/s. *Single Trial Sessions* were performed 4 h after WTP (six trials) training. *Testing Sessions* were performed 24 h after training. Right panel: Results: Graph ordinates: $\log_2$ response during stimulus presentation (means ± SE); open symbols (□): UN groups, filled symbols (■): TR groups. Significant differences between TR groups and their correspondent UN group: $^*p < 0.05$. (A) *The sole presentation of the training context is not sufficient to enhance memory expression:* a single trial 4 h after weak training enhances memory expression ($^*p < 0.05$). Memory remains unexpressed 24 h after weak training if stimulus is not presented. (B) *The sole presentation of the VDS is not sufficient to enhance memory expression:* a single trial in a novel context 4 h after weak training is not sufficient to enhance memory expression. Memory after six trials is expressed in a different context ($^*p < 0.05$).

unexpressed long-term memory built by a WTP can be reactivated by the presentation of an unreinforced reminder, making it susceptible to enhancing treatments, but that the reactivation *per se* does not induce changes in memory expression [1,10,21,22]. Accordingly, the same unreinforced reminder was used in experiment of Fig. 2A and it was not able to induce a change in the expression of long-term memory.

The temporal window in which the single trial is performed seems to be the main characteristic of this procedure to enhance long-term memory expression. A possible explanation for this memory enhancing effect is that shorter inter-trial intervals produce better acquisition [17]. However, it is noticeably that this temporal window – up to 4 h, but less than 8 h – coincides with the temporal window described for protein synthesis-dependent long-term memory consolidation after strong training in *Chasmagnathus* (up to 4 h, but less than 6 h; [21,22,28]). This feature resembles previous studies in other memory models showing that during consolidation and the short-term memory expression period, it is possible to enhance memory e.g. [5,9,17,20,29,33]. Moreover, memory expression in *Chasmagnathus* can also be enhanced during consolidation by other experiences, such as water deprivation or exposure to a high salinity environment [5,9]. Hence, the results presented in this work support the idea that, during consolidation, memories can be evaluated in the background of concurrent experiences. In particular, we propose that during the consolidation period an assessment is made of which long-term memories are to be expressed.

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