



# Natural variation in long-term memory formation among *Nasonia* parasitic wasp species

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## ABSTRACT

Closely related species of parasitic wasps can differ substantially in memory dynamics. In this study we demonstrate differences in the number of conditioning trials required to form long-term memory between the closely related parasitic wasp species *Nasonia vitripennis* and *Nasonia giraulti* (Hymenoptera: Pteromalidae). A single conditioning trial, in which a female wasp associates an odour with the reward of finding a host, results in the formation of transcription-dependent long-term memory in *N. vitripennis*, whereas *N. giraulti* requires spaced training to do so. Memory formation does not depend on the type of reward: oviposition, which was hypothesized to be a 'larger' reward results in similar memory retention as host feeding in both *Nasonia* species. There are several genetic and genomic tools available for *Nasonia* species to identify genetic mechanisms that underlie the observed variation in the number of trials required to form long-term memory.

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## 1. Introduction

The ability to learn and form memories is universal across the Animal Kingdom and both behavioural and cellular properties of memory formation are conserved among distant animal phyla (Dubnau, 2003). This makes insects relevant model species for memory research and a diverse group of insect species have been studied intensively for this reason (Margulies et al., 2005; Eisenhardt, 2006; Hoedjes et al., 2011). During an associative learning experience, an insect will associate a specific cue or behaviour with a rewarding or punishing stimulus. As a result, the insect will demonstrate, respectively, an increased or decreased preference towards that cue or tendency to perform the specific behaviour. Associative learning can thereby optimize behaviour aimed at finding food, hosts or mates (Lavery and Plowright, 1988; Papaj and Vet, 1990; Raine and Chittka, 2008).

After a learning experience, different types of memory can be formed which differ in their characteristics, as well as in cellular pathways that are involved in the formation of these memory types. Comparable classifications of memory types were made for *Drosophila melanogaster*, *Apis mellifera* and a number of parasitic wasp species (Eisenhardt, 2006; Margulies et al., 2005; Hoedjes et al., 2011). Immediately after conditioning, short term memory

(STM) is present. This type of memory lasts, depending on the investigated species, several minutes up to a few hours (Menzel, 1999; van den Berg et al., 2011). STM is sensitive to disruption with anaesthesia and is, therefore, also known as a form of anaesthesia-sensitive memory (ASM) (Xia et al., 1999). Hours to days after conditioning, longer-lasting memory types will be formed. This is a process called memory consolidation and two main types of memory are distinguished: anaesthesia-resistant memory (ARM) and long-term memory (LTM). LTM is the most stable and durable type of memory and requires protein synthesis, in contrast to ARM, which is resistant to anaesthesia but does not require protein synthesis (Tully et al., 1994; Smid et al., 2007). Generally, single or massed conditioning trials, i.e. without or with a short inter-trial interval, will result in the formation of ASM and ARM. Many animal species will only form LTM after spaced conditioning, i.e. multiple trials with a longer inter-trial interval (e.g. Margulies et al., 2005; Eisenhardt, 2006). There is, however, variation in the number of conditioning trials required to form LTM: some insect species will form LTM after only a single conditioning trial.

LTM formation after a single trial has been demonstrated in a number of parasitic wasp species, including *Cotesia glomerata*, *Trichogramma evanescens* and *Lariophagus distinguendus* (Smid et al., 2007; Huigens et al., 2009; Collatz et al., 2006). Interestingly, closely related species of these parasitic wasps, for example *Cotesia rubucula*, do require spaced conditioning trials to form LTM. Additionally, the number of trials depends on the reinforcing

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stimulus that is experienced during conditioning. For example, fruit flies will form LTM after a single appetitive conditioning trial, but not after a single aversive conditioning trial (Krashes and Waddell, 2008). Memory formation in bumble bees depends on nectar concentration of the flowers and memory dynamics of parasitic wasps may depend on the value of the host (Cnaani et al., 2006; Kruidhof et al., 2012). Both the inter- and intraspecific variation in the number of trials required to form LTM are high among parasitic wasps species, which are, therefore, considered model species to study both ultimate and proximate factors involved (Hoedjes et al., 2011).

Parasitic wasps learn cues to find their inconspicuous insect hosts in which they lay their eggs and most studies have focussed on this so-called oviposition learning (Hoedjes et al., 2011). Variation in LTM formation is thought to depend on the ecology of both the parasitic wasp species and its host species: Factors such as the variability of the host environment, whether hosts occur gregariously or solitary, the quality of the host, and the number of hosts that a parasitic wasp will parasitize have been hypothesized to be important (Hoedjes et al., 2011; Kruidhof et al., 2012). In addition, different stimuli that are encountered during oviposition can also affect the formation of LTM. Although, oviposition is generally considered the reinforcing stimulus in oviposition learning, there are also other aspects of the rewarding stimulus. These include contact of antennae, mouth parts or ovipositor of a female wasp with host faeces, host haemolymph or other chemosensory cues that are present on the host (Takasu and Lewis, 2003; Collatz et al., 2006; Schurmann et al., 2012). Contact with host traces or host haemolymph alone can be sufficient to form a short-term memory, but oviposition was required to form a long-lasting memory in the parasitic wasp species *Microplitis croceipes* (Takasu and Lewis, 2003). A strain derived from a German population of *Nasonia vitripennis* was observed to form ARM after contact with host haemolymph, but LTM when it was also allowed to feed from this host haemolymph (Schurmann et al., 2009, 2012).

The genetic mechanisms that are responsible for variation in LTM formation are poorly understood (Hoedjes et al., 2011). Parasitic wasps of the genus *Nasonia* offer unrivalled opportunities to focus on both ecological and genetic aspects of variation in LTM formation. A recent study demonstrated variation in memory retention after a single conditioning trial, which waned within 2 days in *Nasonia giraulti*, but lasted at least 5 days in *N. vitripennis* (Hoedjes et al., 2012). This difference in memory retention between *N. vitripennis* and *N. giraulti* may be explained by differences in ecological factors, as was discussed in Hoedjes et al., 2012. The species of the genus *Nasonia* offer unique opportunities to study the genetic basis of variation in memory formation and genomic and genetic resources are available for these species (Werren et al., 2010). Characterization of differences in long-term memory formation between the *N. vitripennis* and *N. giraulti* strains for which these genetic tools are available is essential to benefit from these opportunities for genetic studies.

The aim of this study was, therefore, to investigate LTM formation in *N. vitripennis* and *N. giraulti* and to investigate the effect of variation in the rewarding stimulus on memory of both species. *N. vitripennis* was expected to form LTM after a single conditioning trial, which was investigated using inhibitors of LTM. The ability of *N. giraulti* to form long-lasting memory after multiple conditioning trials was investigated. In addition, we studied the effect of host feeding and oviposition on memory strength and memory retention in both species. Oviposition was hypothesized to be a 'larger' reward than host feeding, which would result in increased memory retention or a stronger association between the learned cue and the reward.

## 2. Materials and methods

### 2.1. Insects

Inbred strains of *N. vitripennis* (AsymCx) and *N. giraulti* (RV2x(U)) were used. Both strains have a sequenced genome and genetic tools have been developed for these strains (Werren et al., 2010). The wasps were reared on host pupae of *Calliphora vomitoria* at 25 °C and a 16L:8D photoperiod as described by Hoedjes et al., 2012. Pupae of *C. vomitoria* were used also used as host species during all experiments. Wasps were collected on the day of emergence and were allowed access to honey and water ad libitum, unless specified otherwise. Female wasps were used for experiments 1 to 2 days after emergence.

### 2.2. Oviposition behaviour

The aim of this experiment was to determine if oviposition occurs in our strains of *N. vitripennis* and *N. giraulti* during two subsequent periods of contact with a host, before subsequent experiments on oviposition learning were done. Schurmann et al., 2012 demonstrated that their strain of *N. vitripennis* ('Hamburg' strain) will not oviposit, but only drill with their ovipositor to enable host-feeding when allowed access to the hosts for 1 h. Groups of 100 *N. giraulti* and 100 *N. vitripennis* females were individually provided a single host in a well of a 24-well microtiter plate (Greiner Bio-One, Alphen aan den Rijn, The Netherlands) closed with a plastic cap (protection plug, 14.5 mm diameter, Skiffy, Amsterdam, The Netherlands) for 1 h. Wasps that did not initiate drilling into the host within 30 min were afterwards removed from the experiment. Wasps were subsequently kept in a climate cabinet (25 °C) with access to honey and water for 4 h and were then allowed access to another single host for 1 h. The hosts were kept in vials in a climate cabinet (25 °C, 16L:8D) until offspring emerged in order to score the percentage of ovipositing females and the average number of offspring.

### 2.3. Conditioning procedure

Conditioning was done using an olfactory conditioning assay as described by Hoedjes et al., 2012. This is a Pavlovian conditioning assay in which female wasps will associate an odour with the reward of access to a host. Briefly, female wasps were individually allowed access to a host pupa (the unconditioned stimulus, US) for 1 h in the presence of either chocolate or vanilla odour (the conditioned stimulus, CS+). Then, after a 15 min resting period, females were exposed to, respectively, vanilla or chocolate odour (CS-) without a reward present. Two reciprocal groups of 24 wasps were conditioned simultaneously with this procedure.

Memory retention differs between *N. vitripennis* and *N. giraulti* when wasps received a single conditioning trial in which host feeding was the reward (Hoedjes et al., 2012). Oviposition may be perceived as a different and possibly larger reward, than host feeding alone by female parasitic wasps during oviposition learning. This experiment aimed to assess memory retention of both species after a single conditioning trial in which host feeding was the reward (1) vs. a single conditioning trial in which oviposition is the reward (2). In addition, these wasps were compared to wasps that had received two conditioning trials spaced in time by 4 h (3). Female wasps that received a single trial with host feeding as a reward (1) were conditioned as described above. These females perform host feeding, but do generally not oviposit during the conditioning period. Female wasps that received a single trial with oviposition as a reward (2) were allowed to drill into and feed from a single host for 1 h (as described above) without CS+ present. This host feeding before conditioning allows these female wasps

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