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# Association and reversal learning abilities in a jumping spider

Jannis Liedtke*, Jutta M. Schneider

*Zoological Institute, University of Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany*

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ABSTRACT

The ability to learn and overwrite learned associations allows animals to respond adaptively to changes in their environment. However, such behavioural plasticity is presumed to be costly and the question arises to which extent animals with restricted neuronal capacity are capable of such flexible behaviour. In this study, we investigated the learning and reversal learning abilities of a jumping spider (*Marpissa muscosa*). In two discrimination tasks spiders had to associate colour in the first task and colour *or* location in the second task as a predictor of a food reward. Results show that spiders were able to quickly form and reverse associations. Individuals show differences in their learning success and in their preference of which cues they used (colour vs. location) as a reward's predictor. These results highlight the potential for flexible behaviour in species with small neuronal capacities and short life spans.

## 1. Introduction

Learning can be defined as the ability to modify behaviour based on experience (Shettleworth, 2010). It allows an animal to adapt (within its own lifetime) to its environment and to respond to changes within it. This form of phenotypic plasticity, however, does not come for free (Snell-Rood, 2013). The high metabolism of the nervous system is often referred to as a likely candidate of such costs, i.e. in terms of energy consumption (e.g. Dunbar and Shultz, 2007; Butler, 2008; Niven and Laughlin, 2008). An increase of cognitive abilities will then be traded off against other functions and there is indeed evidence that butterflies with higher learning abilities have reduced reproductive success (Snell-Rood et al., 2011). Similarly, an elegant selection experiment with guppies revealed that selection on smaller brain-size leads to higher fecundity (Kotrschal et al., 2013). Thus, animals should be under selection to reduce investment into learning capacities to an adaptive minimum and we might expect to find differences in learning abilities between and within species.

Previous research has led to evidence that learning abilities are not restricted to big brained mammals and birds (reviewed in Chittka and Niven, 2009). Investigations of smaller animals, including fish (e.g. Schuster et al., 2006; Salwiczek and Bshary, 2011), rodents (e.g. du Toit et al., 2012; Galef et al., 2008) and reptiles (e.g. Leal and Powell, 2012; Wilkinson et al., 2010), but also insects (reviewed e.g. in Webb, 2012), molluscs (Alves et al., 2007; Fiorito and Scotto, 1992), and nematodes (reviewed e.g. in Sasakura and Mori, 2013), have revealed that learning abilities are apparently widespread in the animal kingdom. Hence, the question arises how small brains deal with cognitive challenges and how flexible the process can be in comparison with large-brained animals.

Despite its enormous adaptive potential (see e.g. Dukas, 2013), behavioural flexibility (as an expression of phenotypic plasticity) has received only limited attention for many years (West-Eberhard, 2003). Especially in unpredictable environments, the ability to quickly react to changes adequately may outweigh the costs and increase the fitness of individuals. A particularly flexible manifestation of learning has been named reversal learning (e.g. Menzel, 1969 and references therein). Here, an individual first learns that a conditional stimulus A and not B predicts an unconditional stimulus C and after a certain time the predictors are reversed; i.e. stimulus B and not A predicts C. The abilities, and more precisely the time needed to respond correctly to such a reversal, can be used to determine the behavioural flexibility in the context of learning.

However, tests of reversal learning abilities in arthropods have been largely limited to social Hymenoptera (e.g. Menzel, 1969; Chittka, 1998; Mota and Giurfa, 2010). Spiders, as another large group of arthropods, have received less attention regarding their learning abilities (but see e.g. Jackson and Cross, 2011; Jakob et al., 2011). Indeed, we are unaware of any study which investigates reversal learning ability in arachnids. Spiders, however, with species numbering about 40,000, are a highly diverse and widespread group. Its members live in very different environments and developed a large variety of lifestyles ranging from rather opportunistic orb-web spiders to more agile families of active hunters such as wolf spiders (Lycosidae) and jumping spiders

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* Corresponding author. Tel.: +49 40 42838 7894.
*E-mail address:* jannisliedtke@gmx.de (J. Liedtke).

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(Salticidae) (Foelix, 2011). In contrast with the majority of spider families, jumping spiders have exquisite eyesight with two principal eyes supporting colour and binocular vision and high visual acuity. The three pairs of secondary eyes are mostly used for motion detection (reviewed in Foelix, 2011). It has been experimentally shown that they use visual cues as predictors for positive and negative rewards (Jakob et al., 2007; Nakamura and Yamashita, 2000) and to navigate across open space (Baker et al., 2009). Furthermore, as prey type and location are likely to change frequently in the spiders' natural habitat, reversal learning should be favoured by natural selection. Thus, at least in the context of foraging behaviour, reversal learning abilities are expected to be adaptive.

To understand the evolution of cognitive abilities and behavioural plasticity in general, it is desirable to test and compare species from multiple taxa using tasks that test for similar abilities despite species specific behavioural and morphological differences. While such an approach is often called for (e.g. Giurfa, 2013), there are numerous practical difficulties. Indeed, associative learning and reversal learning tasks in the context of foraging are particularly suited for this purpose and are useful paradigms for larger scale comparisons. In this paper we investigated the learning and reversal learning abilities of *Marpissa muscosa* (Salticidae) by presenting wild caught individuals with two different discrimination tasks.

## 2. Materials and methods

### 2.1. Test subjects

Spiders (*M. muscosa*, Clerck, 1757) were collected in four different parts of northern Germany between 26th of June and 25th of July 2012. All individuals ($n = 13$) were immature at the time of capture. The spiders were kept in Perspex boxes (145 mm × 110 mm × 68 mm) enriched with white paper, pieces of cardboard, dry leaves, and grass stalks. Enrichment improves performance of jumping spiders in experiments (Carducci and Jakob, 2000). The spiders were fed with flies (*Drosophila* sp. or *Calliphora* sp.) and water was regularly sprayed into the cages. To keep motivation high spiders were not fed during testing but received some *Drosophila* flies during the breaks of the second task. Each individual was presented with two different discrimination tasks, the second being subdivided into three different parts. Testing of task 1 took place between January 16th and 23rd and of task 2 between February 20th and 28th 2013. By the time the tests began (16th of January) all but two individuals had moulted to adulthood.

### 2.2. Task 1: Discrimination task with positive and negative stimulus

The rewards used in task 1 were two drops of coloured sugar water. We used food colour (Dr. Oetker Back & Speisefarben) containing glucose syrup, sugar, water, and dye. We used the colours blue and yellow but did not check for spectral characteristics and thus cannot be sure that spiders did actually respond to colour and not alternatively to relative brightness. Before testing, spiders were customised to this new type of food reward by presenting them with uncoloured drops of sugar water in a petri dish. Unfortunately we did not quantify the latency until the individual test spiders fed on the first drop. However, we observed that most wild caught spiders readily fed on the sugar water drops on the first encounter. Feeding times, defined as the time the chelicerae touched the drop, varied from seconds to several minutes throughout the study. We are not aware of any study using sugar water as reward in spiders. However, it has been documented that several spider families do feed on pollen and nectar (Sanders, 2013). It is unknown if *M. muscosa* feeds on nectar or pollen in the wild but Jackson et al. (2001) found nectar feeding in 90 jumping spider species. Hence, we argue that sugar water can be considered a natural food reward. As a negative stimulus we added citric acid (approximately 1/3 of the solution weight) to the sugar water.

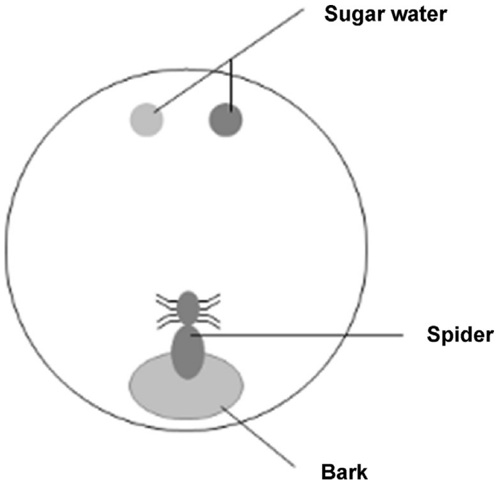

**Fig. 1.** Schematic drawing of test arena used in task 1.

Before the start of the principle tasks, we presented each spider with a translucent and coloured (blue or yellow) drop of sugar water (40 μl) simultaneously. This was done twice. In two more trials, the spiders received a yellow and a blue drop. Each time the first choice of the spider was recorded. This was done to check for colour preferences and we classified an individual to have a preference if it had chosen one colour at least three times (four preferred yellow and one blue).

Eight days after this pre-testing the principal tests were performed. The test arena was a plastic Petri-dish (54 mm diameter wide). The two drops were placed 13 mm apart from each other on the opposite side of the dish where there was a small piece of bark (see Fig. 1). The spiders were carefully placed on the bark in the beginning of each trial. For 1 h, spiders had free access to the sugar water drops. We recorded which drop (yellow or blue) was first touched by each individual and the latency.

In the first trial the spiders were presented with only one drop of the negative stimulus: either the yellow or blue water drop contained citric acid. For the five individuals with a colour preference the preferred colour was assigned to be the negative stimulus in this testing. Therefore, they had to learn against their initially preferred colour. The other individuals were assigned to a colour pseudo-randomly, so one half of the tested animals had blue and the other half yellow as a negative stimulus. During the following nine trials, spiders could choose freely between a yellow or blue drop. We kept the combination of colour and acid constant for each individual. To ensure that spiders learned to associate the colour and not the location (left or right) of the two drops with their taste, location was changed trial by trial. We did not randomise the sequences in order to avoid serial presentation on one site. Consecutive trials were either presented 2–3 h later on the same day or in the following days with at least 20 h in between.

### 2.3. Task 2: Reversal learning in a t-maze with positive stimulus

Reversal learning was tested in a task divided into three parts in which colour and location, colour only and location only were reversed. In this task spiders could choose between two sides of a simplified t-maze (see Fig. 2). Within a small Perspex box (98 mm × 58 mm × 35 mm) two (one blue, the other yellow) plastic Lego obstacles (three Lego bricks stacked into an L-shape) were placed in one end of the box. On the opposite end we placed a small