Effects of early environmental conditions on the development of behaviour in a jumping spider

Dissertation

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Use of English in the thesis authored by Jannis Liedtke

To whom it may concern,

This is to affirm that I am a native speaker of English, and that the English used in the thesis entitled “Effects of early environmental conditions on the development of behaviour in a jumping spider" by Jannis Liedtke is clear, coherent, and of university level quality.

Yours sincerely,

Tamar Marcus

Contents

Zusammenfassung

Natürliche Selektion bevorzugt Lebewesen, die optimal an ihre Umwelt angepasst sind. Damit sich Tiere flexibel an Veränderungen ihrer Umwelt anpassen können, müssen sie Informationen aus ihrem Umfeld aufnehmen und verarbeiten. Das dafür benötigte neuronale System ist jedoch in seiner Entwicklung und durch seinen hohen Metabolismus sehr energieaufwendig. Man kann daher annehmen, dass nur so viel in ein Nervensystem investiert wird, wie unbedingt erforderlich ist, um mit der Komplexität der Umwelt umgehen zu können. Es wird seit langem darüber diskutiert, welche Umwelteinflüsse die Evolution und Ontogenese von vergrößerten bzw. kompetenteren Gehirnen vorantreibt. Dabei werden häufig die „sozialen“ und „physikalischen“ Umweltaspekte gegenüber gestellt. „Sozial“ bezieht sich in diesem Zusammenhang auf alle Interaktionen zwischen Artgenossen; dies beinhaltet daher auch antagonistische Auseinandersetzungen. Unter „physikalisch“ werden alle nicht-sozialen Komponenten der Umwelt zusammengefasst. Eine Möglichkeit, um die wichtigsten Faktoren für die Entwicklung von leistungsstärkeren Gehirnen zu bestimmen ist, die Umweltbedingungen während der Entwicklung eines Tieres experimentell zu manipulieren. In meiner Doktorarbeit habe ich daher Geschwister aus unterschiedlichen Familien einer Springspinnenart (*Marpissa muscosa*) unter verschiedenen Umweltbedingungen aufgezogen. Dabei wurden jeweils die Aspekte der „sozialen“ und die der „physikalischen“ Umwelt manipuliert. In einer Versuchsgruppe wurden Geschwister gemeinsam in einer ansonsten einfachen Umwelt aufgezogen. Dem gegenüber standen Versuchstiere, die zwar einzeln, aber dafür in einer physikalisch komplexen Umwelt aufwuchsen, die unter anderem mit Steinen, Rinde und Blättern angereichert wurde. Als Kontrolle gab es eine Versuchsgruppe, in der einzelne Tiere in einer einfachen Umwelt aufwuchsen, die weder sozial noch physikalisch angereichert war. Das Verhalten der Spinnen wurde daraufhin in unterschiedlichen Experimenten untersucht. In einem Versuch sollten die Spinnen in einem einfachen Labyrinth eine Futterbelohnung finden und es wurde geprüft, ob sie assoziativ lernen und das gelernte Muster umlernen können. In einem anderen Test wurden die Spinnen mit ihrem Spiegelbild konfrontiert, um so ihr Sozialverhalten zu studieren. Um ihr Explorationsverhalten zu untersuchen, wurden die Spinnen in eine neue, zunächst leere, später mit einem für die Spinnen unbekannten Objekt versehene Versuchsarena gesetzt und ihre Aktivität aufgezeichnet. Des Weiteren wurde untersucht, ob das Explorationsverhalten konsistent ist und die Tiere daher eine sogenannte „Persönlichkeit“ aufweisen. Dafür wurden die Spinnen ein zweites Mal in einem Abstand von einer Woche mit demselben Versuchsaufbau getestet. Die Ergebnisse bestätigen die Annahme, dass die Entwicklung des Verhaltens durch Umweltbedingungen stark beeinflusst wird. Bemerkenswerterweise zeigten dabei die in Gruppen aufgewachsenen Spinnen die höchsten Leistungen, sowohl in dem Lernversuch, als auch in ihrem Verhalten im sozialen Kontext. Dieses Ergebnis lässt vermuten, dass Investitionen in diese beiden Fähigkeiten, die zu unterschiedlichen Aspekten der Umwelt zu zählen sind, womöglich nicht in einem Trade-off zueinander stehen. Des Weiteren zeigten Individuen, die in einer physikalisch angereicherten Umwelt aufwuchsen, konsistent erhöhte Explorationstendenzen. Dieses Ergebnis zeigt, dass auch die Entwicklung einer „Persönlichkeit“ von den Umweltbedingungen beeinflusst werden kann. Ebenso wurde die

Annahme bestätigt, dass Spinnen, die ohne Anreicherung in ihrer Umwelt aufwuchsen, insgesamt die geringsten Leistungen in dem untersuchten Verhalten zeigten. Zusammengenommen lassen die Ergebnisse darauf schließen, dass die plastische Entwicklung verschiedener Verhaltensweisen, sowie möglicherweise auch der physiologischen Merkmale, ganzheitlich stattfindet und so zu einem integrativen Phänotyp führt, der bestmöglich an die individuellen Umweltbedingungen angepasst ist.

Summary

Natural selection favours individuals that are well adapted to their environment and thereby increase their reproductive success. In order to respond plastically to changes and thus remain optimally adapted, animals must be able to perceive and process information from their environment. The underlying sensory and neuronal systems are metabolically and developmentally costly. Thus, we can expect that animals will invest just enough in these traits to handle the complexity of their surroundings. There has been an ongoing discussion which environmental aspects may be particularly cognitively demanding and thus drive the evolution and development of competent neuronal systems. Traditionally, two aspects of the environment are emphasised. On the one hand, the so called "social" aspect refers to all cognitively demanding processes caused by interactions between individuals. These also include antagonistic and potentially harmful interactions. On the other hand, the "physical" aspect refers to all other features of the environment, favouring, for example, foraging and navigation skills. One way to disentangle these driving forces is to experimentally manipulate the rearing conditions in which animals are raised. In my doctoral thesis, I used a split-brood design to investigate the impact of "social" and "physical" environmental conditions on the development of behaviour in the jumping spider *Marpissa muscosa*. I reared spiderlings in three different environments. In the "social" treatment, spiders were reared in groups and had contact with their siblings in an otherwise unenriched box. In the "physical" treatment, spiders were reared solitarily in a box enriched with physical objects, for example, a piece of bark, leaves and stones. As a control, I used solitarily reared spiders, which obtained no enrichment at all. In order to elucidate rearing effects on behaviour, spiders had to participate in different tasks. In one task, I aimed to investigate the spiders` ability of associative learning. For this purpose, I used a simple t-maze with a hidden food-reward on one side of the maze, which was relocated after four trials to induce reversal learning. In another task, I observed the social behaviour of spiders when being confronted with their own mirror image. Moreover, exploration tendencies were tested in an open-field and by presenting a novel-object to the spiders. Both exploration tests were repeated a week later in order to find out if the exploratory behaviour was consistent, meaning that these animals express so-called "personalities". Results obtained from my thesis confirm that environmental conditions strongly affect the development of behaviour. Interestingly, socially reared spiders performed better in both the social and the learning task than spiders from the deprived treatment. This suggests that the two underlying skills, associated with different environmental domains, are not traded off against each other. The finding that physically enriched spiders were consistently more explorative corroborates the assumption that the development of "personalities" is also influenced by environmental conditions. Furthermore, the results confirm the hypothesis that deprived spiders overall showed the lowest performance in the behaviour tested. Taken together, these findings suggest that plastic responses to environmental conditions lead to a coherent phenotype which integrates different aspects of behaviour and possibly also physiological traits, thereby allowing individuals to adapt optimally to their specific local conditions.

General Introduction

Evolution by natural selection can produce genetic adaptations enabling animals to cope with new environmental conditions. However, this process is rather slow and usually requires many generations. Crucially, it does not allow adaptations within the life time of an individual. Yet, evolution has led to different mechanisms permitting more rapid responses. Maternal effects, for example, may allow parents to adjust adaptation of their offspring by altering their developmental trajectory, e.g. via bet-hatching or epigenetic manipulations (reviewed in e.g. Uller 2008; Botero et al. 2015). There are also different ways for individuals themselves to respond to changes during their lifetime. Animals can either stay as they are but change their environment, for example by selecting the environment best suited to their phenotype by niche picking or migration (Stamps & Groothuis 2010; Hensley et al. 2012; Wolf & Weissing 2012; Mettke-Hofmann 2014), or they may actively alter the local environment through niche construction (Sterelny 2007; Smith et al. 2008; Rendell et al. 2011). Alternatively, individuals can change themselves, e.g. their physiology or behaviour, in order to adapt to local conditions, which means being plastic.

Plasticity is defined as the ability of a genotype to produce different phenotypes (West-Eberhard 2003). It has been argued that individuals may become better equipped for future environmental conditions by altering their developmental trajectory (Bateson et al. 2014). Recently, two kinds of plasticity which are of interest here have been defined as developmental and activational plasticity (Snell-Rood 2013; for a similar distinction see Nettle & Bateson 2015). Developmental plasticity refers to changes during early ontogeny in response to early environmental conditions leading to different phenotypes. Via maternal effects, these adaptations may even be transgenerational (Uller 2008; Curley et al. 2009; Burton & Metcalfe 2014). These changes are typically long-lasting and often permanent (reviewed in Snell-Rood 2013). Irreversible developmental changes anticipating future conditions bear a risk of error, i.e. if the conditions turn out to be different than expected. Therefore, developmental changes can be maladaptive (Bateson et al. 2004). Activational plasticity, on the other hand, refers to changes throughout the lifetime of an animal and is based on reversible alteration of physiological states, such as hibernation, change of coat, etc. and/or behavioural changes, e.g. altering foraging activity or learning new paths (Snell-Rood 2013). Activational plasticity is therefore a very flexible mechanism to handle new or changing environmental conditions.

However, in order to respond appropriately to the environmental conditions, animals must record information (i.e. possess sensory machinery) from their environment and be able to use them (e.g. potent neuronal system processing them). Both requirements are metabolically and developmentally costly (reviewed e.g. in Deacon 1990; Dukas 2004; Mery & Burns 2010; Shettleworth 2010; Buchanan et al. 2013). Additional costs arise from the fact that sensitive systems need time to adjust to local conditions and likely include suboptimal responses, e.g. in processes based on learning (e.g. Dall et al. 2004; Mery & Burns 2010). Whether the benefits of plasticity outweigh the costs depend on the animals' ecology including its life-history characteristics, e.g. pace of life, environmental stability and its predictability (e.g. Dall et al. 2004; Sih et al. 2004a; Réale et al. 2007; Mettke-Hofmann 2014; Botero et al. 2015; Nettle & Bateson 2015). Furthermore, particularly in cases involving learning, the trade-offs between costs and benefits are critically influenced by the environmental complexity. The more complex relevant aspects of the animals' environment become, the higher are the costs of the sensory and neuronal system, meaning that it is getting more difficult to perceive and to distinguish all relevant cues (sensory) and more information needs to be processed (neuronal) (reviewed e.g. in Godfrey-Smith 2002; Mettke-Hofmann 2014).

It has been long debated which specific aspects of the environment may be cognitively demanding and therefore drive the evolution and development of an enhanced cognitive system (i.e. increase in nervous system). Traditionally, two aspects have been emphasised and confronted: the social and the physical domain. Here, "social" refers to all cognitively demanding interactions with conspecifics, including not only peaceful and cooperative but also agnostic and harmful encounters (see e.g. Jolly 1966; Humphrey 1976; Byrne & Whiten 1988; Dunbar 1998; Whiten & van Schaik 2007). Byrne and Bates (2010) argue that "...all competition that is based on knowledge of the behavior of animate entities should be seen as affecting "social" cognition...", since interactions with "animate entities" might be different from interactions with "inanimate entities" and inherently cognitively more demanding. This difference may be caused by the "...nearly infinite degrees of freedom..." of feedback in the social domain (Taborsky & Oliveira 2012). Smith and colleagues (2010) emphasise that the cognitive demand of social interactions depend on the mechanism underlying it and that increased sensory stimuli of social interactions rather than sociality per se might be the cognitively challenging aspect (see also Molina et al. 2009). "Physical" normally refers to all other aspects of the environment that potentially create cognitive challenges for individuals and is sometimes referred to as "technical intelligence" or "technical skills" (reviewed e.g. in Byrne 1997; Overington et al. 2009; Heyes 2012). Prominent examples are tool-use (Boesch & Boesch 1990), food-caching (Clayton & Dickinson 1998), or navigation (Wittlinger et al. 2006). There is evidence for both aspects in driving the evolution of cognition (reviewed e.g. in Godfrey-Smith 2002; Emery & Clayton 2004; Whiten & van Schaik 2007). On the one hand, tool-use (Seed & Byrne 2010), invasion-ability (Sol et al. 2005), feeding-opportunism (Overington et al. 2009), or habitat complexity (Clarin et al. 2013), have been linked among other factors to an increase in cognitive abilities and/or brain size (reviewed e.g. in Reader & Laland 2002; Sol 2009). On the other hand, positive correlations between group size and brain size (Dunbar 1992; Kudo & Dunbar 2001; but see Holekamp 2007; Finarelli & Flynn 2009) and between brain size and the quality of pair-bonds (Emery et al. 2007; Shultz & Dunbar 2010) have been shown. Furthermore, since social interactions may involve learning and may be cognitively demanding (see Taborsky & Oliveira 2012 and references in the preceding sentence), it has been suggested that individuals within populations differ in their social skills (e.g. Wolf & McNamara 2013) and that these skills may be traded off against other skills (but see Taborsky et al. 2012).

Since energy resources are generally limited, the question whether cognitive skills are traded off against each other is interesting and important in order to understand the evolution of animal intelligence. For example, it is possible that an increase in brain compartments in response to demands of the social domain (e.g. song nuclei for vocal learning in passerine birds) may lead to a reduction of brain parts needed in the physical domain (e.g. hippocampus for food-caching). Such adaptations to specific cognitive skills may have led to what is termed "mosaic brain" evolution (e.g. Macphail & Bolhuis 2001; Dechmann & Safi 2009), resulting in a brain composed of specialised centres (or modules) for specific cognitive challenges. Alternatively, it has been proposed that evolution has led to a rather generalistic brain, which is able to handle multiple aspects of the environment (reviewed e.g. in Reader & Laland 2002; Heyes 2012). Thereby, an increase in cognitive abilities in response to the needs of one domain may lead to increased performance in the other domain (Byrne & Bates 2007). The question of mosaic or generalist brain evolution is similar and probably interlinked with the question of whether social or physical environmental aspects are the driving force behind the evolution of cognitive abilities in general. Answers to the driving forces behind the evolution of animal cognition and whether the brain is mosaic-like or generalistic may depend on the precise ecology of the species in question, e.g. on the complexity and predictability of its environment.

However, as noted above, individuals of the same species face different environmental conditions and have different physiological characteristics. It is therefore not surprising that individuals of the same population also differ in their behaviour. Indeed, consistent behavioural variation between individuals has recently received increasing attention and is termed "personality", or "behavioural type". One crucial aspect of personality is that individuals behave consistently in different contexts or over time even if conditions have changed, which can lead to suboptimal responses (see e.g. Stamps & Groothuis 2010). Various explanations for the adaptive value of consistent behaviour have been suggested, such as benefits in the context of information use, life-history, sexual selection, and social interactions (reviewed e.g. in Dall et al. 2004; Nettle 2006; Réale et al. 2007; Dingemanse & Wolf 2010; Schuett et al. 2010). Another explanation is that personality is a mechanism to respond plastically to fine-scale local conditions. These may include physical aspects, e.g. living at the edge or in the middle of a forest, or social aspects, e.g. the position within socially structured groups. It has been suggested that behaviour develops in accordance with physiology in response to early environmental conditions (e.g. Sachser et al. 2011; Kasumovic 2013). Since developmental plasticity is often irreversible, behavioural plasticity (i.e. activational plasticity) might be constrained in order to fit to the individual physiology. For example, an individual may grow up under poor nutritional conditions and has therefore developed a small body, which lowers its competitive strength. A matching behavioural type may be a relatively inactive or "shy" profile that saves energy by avoiding unprofitable searches for food and harmful conflicts with conspecifics and other animals as predicted by the state-dependent safety model (Luttbeg & Sih 2010). If food is getting more abundant later in life, increasing foraging-activity might become profitable. However, since adult body size in many species does not change (or only very slowly) the individual may remain poor in competitive strength and should therefore still avoid direct competition with conspecifics. If these contest costs outweigh the benefits of higher food-intake it becomes adaptive for that individual to stick to a rather inactive behavioural type, i.e. to behave consistently across context and time (compare Luttbeg & Sih 2010). In this way the adaptive behavioural plasticity may be constrained by physiology plasticity. Furthermore, it may also be more beneficial to adhere to a once adopted behavioural routine since changing it may involve learning, which itself is associated with cost such as time, suboptimal responses, and cost of metabolism (see references above).

Research questions

Taken together, animals are constantly interacting with their environment and, to a certain degree, are able to respond plastically to the precise conditions which they are facing. However, despite the large number of studies investigating various aspects of evolution and plasticity in response to environmental challenges, the mechanisms behind it remain largely unclear (see e.g. Kasumovic 2013). This short-coming has several causes. One of them is that many studies are purely correlational, such as most investigations of brain size and environmental complexity, or purely theoretical (especially for personality). Another reason is that in experimental approaches only one aspect of the environment is generally manipulated. Therefore, comparisons of the different environmental aspects, which may shape adaptive responses are hindered. Another important limitation is that the different theoretical concepts such as “animal personality”, “animal cognition”, “social competence” and “environmental complexity” (both socially and physically) are rarely considered in conjunction and, to the best of my knowledge, have never been controlled for in a single study.

Therefore, the aim of my doctoral thesis was to investigate these different aspects simultaneously in a single species in order to understand their interplay in response to different environmental conditions. To do so, I reared spiderlings of the jumping spider *Marpissa muscosa* Clerck, 1757 in three different environments (socially enriched, physically enriched and, as control, a deprived treatment) under a food-restricted regime (limited access to food might be crucial to reveal trade-offs; compare Mery & Kawecki 2003; Fisher et al. 2006). Since these spiders are active hunters with well-developed eyes and regular interactions with their conspecifics, it is likely that their development is crucially influenced by the physical and social environment. Spiders were presented with different tasks in order to investigate their learning abilities, social competence, exploration tendency, and whether these were repeatable over time (i.e. a personality trait). I further investigated the genetic background (i.e. family effects) and the influence of sex on the behaviour.

Following questions and predictions were raised:

I) Chapter 1: Are spiders of the species *Marpissa muscosa* able to learn? Prediction: yes, since they are living in a complex and changing environment.

II) Chapter 2: Does the rearing environment affect the learning abilities? Prediction: an increase in environmental complexity will lead to an increase in learning performance, i.e. socially and physically enriched spiders will outperform deprived spiders in the learning task.

III) Chapter 3: Does the rearing environment affect the social competence? Prediction: since social competence is influenced by experience, socially reared spiders will be more competent than solitary reared individuals.

IV) Chapter 4: Do individuals possess a personality and if so, does it differ between the treatments? Prediction: individuals have personalities as found in most species tested to date. Furthermore, the exploratory tendencies will differ between the treatments with physically enriched spiders being most active.

Together, these studies will shed light as to whether animals show plastic responses to environmental conditions, and whether enhanced skills in one domain will be traded off against skills in the other domain. Furthermore, this thesis will help to elucidate if the development of personality is affected by specific environmental conditions and if it is in accordance with the plastic response in other behavioural traits (e.g. learning and social competence).

Chapter One

Association and reversal learning abilities in a jumping spider

by
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Contribution of authors:
Jannis Liedtke & Jutta M. Schneider conceived the research question and wrote the manuscript. J.L. developed and designed the experiments. J.L conducted the experiments, analysed the video material and performed the statistical analyses.

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.

Keywords: Arachnid; arthropod; cognition; salticid; t-maze; reversal learning

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, Davidowitz, and Papaj 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, Dudley, and Whiskin 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 ref. 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, Skow, and Long 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 (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, Kelty, and Jakob 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. Material and Methods

2.1. Test Subjects

Spiders (*Marpissa 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 x 110 x 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.

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 one hour, 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.

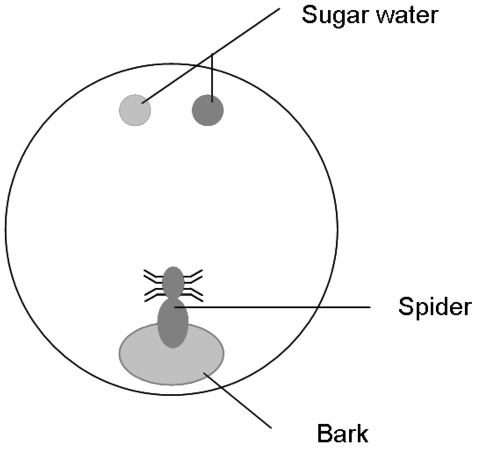

Figure 1: Schematic drawing of test arena used in task 1.

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 randomize the sequences in order to avoid serial presentation on one site. Consecutive trials were either presented 2-3 hours later on the same day or in the following days with at least 20 hours 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 x 58 x 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 (38 mm diameter) white plastic cap (starting zone) into which the spiders were put at the beginning of each trial. Spiders could see the conditional stimulus (hereafter CS) only after they climbed out of this cap. In this task only one (uncoloured) drop (20 µl) of sugar water was used as a reward. This drop was placed behind one of the two Lego obstacles so that, in contrast to task 1, spiders could not see it from the beginning but only from a position on top of or near the obstacles. There were essentially three ways for the spiders to get into the position from where they could first see the reward; (1) they could walk between the two obstacles and turn left or right; (2) they could climb over one of the two obstacles; (3) or they could walk on the test box's ceiling (hanging upside down) until they were positioned above the reward. We noted where the spider was, when it first could have seen the

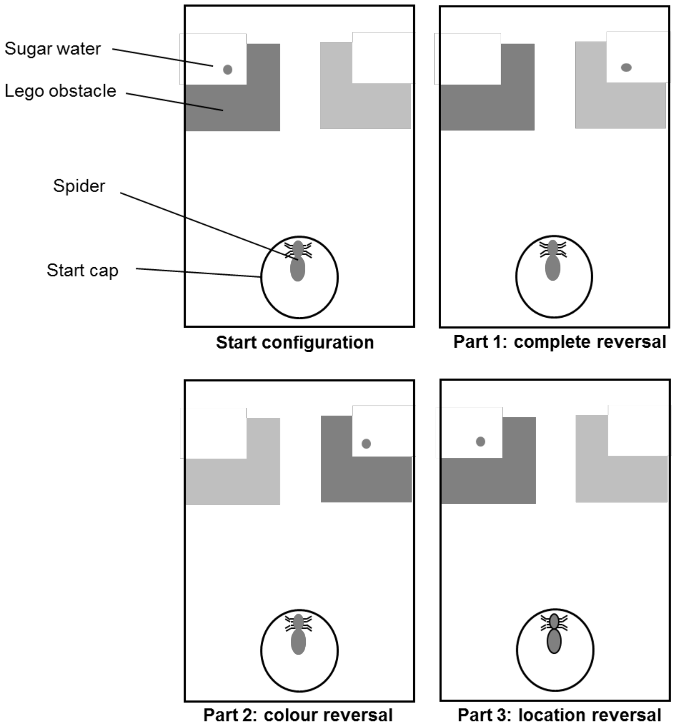

Figure 2: Schematic drawing of test arena used in task 2. After the start configurations the reversal tasks were implemented that i) in part 1 both the location and the colour cues were reversed ii) in part 2 the colour cue and iii) in part 3 the location

reward, namely when it was by the left or right obstacle, and used it to define the spider's first choice. Similar to task 1, spiders could move freely within the test arena for one hour and had the opportunity to access the reward repeatedly.

We recorded the following durations: time until they first touched an obstacle (if spiders were walking on the ceiling we recorded the time when they were positioned above one obstacle); time until they made the first choice as defined above; and finally the time until they touched the reward. To check for attractiveness of the reward, we calculated the duration between "first choice" (i.e. the time they potentially could see the reward) and "time they touched the reward".

Part 1: complete reversal

The complete reversal set-up was the first of three parts of task 2 and consisted of 9 trials. For the first four trials in part 1, the reward was placed behind the right-hand obstacle which was either constantly blue (7 spiders) or yellow (5 spiders). Thereby, both the colour (blue/yellow) and the location (right) could have served as a CS which predicts the reward. On the fifth to the 9th trial we presented a complete reversal of the CSs (colour of the obstacles and location of the reward were changed) (Fig. 2). After this complete reversal task we intended to gain further insight in the predictor-stimulus the spiders rely on. Therefore, we conducted another two reversal tasks (part 2 and 3) in which only one cue was reversed (i.e. location or colour).

Part 2: colour reversal

After a four-day break, we conducted the 2nd reversal task with a total of 6 trials. We started with three trials under the most recent configuration (i.e. colour and location were the same for each individual as in the last five trials of part 1) and then the reversal trial followed. This time, however, only the colour was reversed whereas the location was held constant (Fig. 2). After the reversal trial only two further trials were conducted to prevent loss of interest by the animals.

Part 3: location reversal

To ensure a balanced diet and maintain the spiders' motivation to feed on sugar water, we gave the spiders five *Drosophila* flies each and stopped testing for eight days. To ensure that the spiders reached a certain accuracy before presenting the reversal trial after this long break, we conducted seven trials with the same configurations as in the last three trials of part 2. Then the reversal trial followed and this time only the location was reversed (from left to right) but the colour (yellow or blue) stayed the same (Fig. 2). Hereafter two trials followed until the end of testing.

2.4. Definition of voluntary choices

In both tasks (1 and 2) most individuals repeatedly touched the drops. To assign learning success we focussed on the first choice of each individual per trial only. A voluntary choice was counted when the spiders touched the drops with their anterior two pairs of legs or their chelicerae. Cases in which spiders either touched a drop by chance (e.g. by falling off the ceiling) or not at all were excluded from analyses. All trials were recorded with a digital camcorder (Panasonic HC-V500). By mistake, data of trial three (task1) were deleted and only data for two individuals could be recovered.

3. Analyses

Statistical analyses were done using R version 2.15.0 (R Development Core Team 2012). We used a one sided binomial test to determine whether the spiders performed better than expected by chance in both tasks. The expected mean was set to 0.5.

To determine the spiders' ability of reversal learning in the second task (part 1) we performed a binomial test with the trials before the reversal and a separate binomial test for the four trials after the reversal. Similarly, we ran separated binomial tests before and after the reversal trials in part 2 and part 3 respectively. The reversal trials were excluded from the analyses of these parts. Additionally, we ran a binomial test on the performance of the spiders on the sixth trial of part1 (the first after the reversal) in order to test whether a significant part of the spiders learned the reversed conditions after a single trial.

To analyse possible influences of explanatory variables, we conducted a generalized linear mixed model (GLMM) fitted by Laplace approximation. We defined the ID of individual spiders as a random factor to correct for repeated measurements. The response of the spiders in each trial (correct or incorrect) was the dependent variable (error structure = binomial and loglink function was used).

In task 1 the maximum model contained the following explanatory variables: 1) colour of the negative stimulus; 2) position of the negative stimulus; 3) individual preference for one colour (as defined above); 4) first or second trial on the same day and 5) no. of trial (2-9). Four interactions were included in the full model: "variable 5: variable 2"; "variable 5: variable 4"; "variable 2: variable 4"; and "variable 2: variable 1". We considered these interactions to be the most likely to have non-additive effects on the dependent variable. We did not include further interactions because we did not want to further complicate the model and lose degrees of freedom unnecessarily.

In task 2 the maximum model contained the following explanatory variables: 1) time until touching an obstacle; 2) trial no.; 3) duration between potentially seeing and touching the reward measured in three categories (less than 1 min., between 1 and 3 min., and more than 3 min.); 4) location of reward (left/right); and finally 5) colour (yellow/blue). No interactions were included this time because we did not expect non-additive effects of the explanatory variables and we did not want to reduce the degrees of freedom unnecessarily.

Models were reduced starting with the least significant interaction. After all non-significant interactions had been removed, reduction of main effects started with the least significant. Models were compared using ANOVA and treated as significantly different with p-values smaller than 0.05. All p-values presented here are derived from ANOVA (χ^2) model comparisons between one model containing the focus variable and one model having the variable removed (p-values listed in Tab. 1 and 2).

To check if motivation of spiders decreased with time, we conducted another GLMM (with ID as random factor) for task 2. Participation defined as touching the reward within the duration of each trial (one hour) or not, was used as the binomial dependent variable. The explanatory variable was part 1, 2, 3 of this task.

Table 1: Variables of GLMM of task 1.

Generalized linear mixed model (GLMM: binomial error structure and loglink function) fitted by Laplace approximation on the response of spiders in each trial (correct or incorrect). IDs of individual spiders were included as a random factor. The maximum model was reduced until only significant variables remained in the final model. The table shows χ^2, DF, p-values of each variable by the time it was excluded from the model.

Explanatory Variable	χ^2	DF	p values
colour of negative stimulus (Var. 1)	0.004	1	0.953
position of neg. stimulus (Var. 2)	1.267	1	0.26
preference (Var. 3)	1.617	1	0.204
first or second trial of a day (Var. 4)	9.187	1	0.002
total no. of trials (Var. 5)	0.148	1	0.701
Variable 5 : Variable 2	0.292	1	0.589
Variable 5 : Variable 4	3.336	1	0.068
Variable 2 : Variable 4	0.385	1	0.535
Variable 2 : Variable 1	0.034	1	0.853

Table 2: Variables of GLMM of task 2.

Generalized linear mixed model (GLMM: binomial error structure and loglink function) fitted by Laplace approximation on the response of spiders in each trial (correct or incorrect). IDs of individual spiders were included as a random factor. The maximum model was reduced until only significant variables remained in the final model. The table shows χ^2, DF, p-values of each variable by the time it was excluded from the model.

Explanatory Variable	χ^2	DF	p values
time until touching an obstacle (Var. 1)	0.0001	1	0.994
trial no. (Var. 2)	1.447	1	0.229
duration between seeing and touching the reward (Var. 3)	39.374	2	<0.0001
location of reward (Var. 4)	0.001	1	0.977
colour (Var. 5)	0.483	1	0.487

4. Results

4.1. Task 1

In order to test for associative learning abilities, we presented the spiders with a choice of two differently coloured sugar water drops. One of these drops contained citric acid to make it a negative stimulus.

Learning success: Spiders chose the correct colour significantly more often than expected by chance (n = 89, p = 0.003) (see Fig. 3). At the individual level, we observed differences in the accuracy (see Fig. 4).

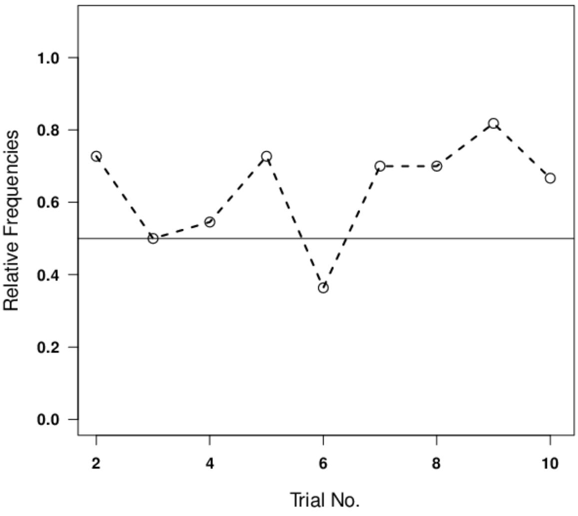

Figure 3: Task 1: Circles combined by dashed line show relative frequencies of correct choices per trial across all individuals. The solid line shows expected level of chance. The first trial, in which solely the negative CS was presented, is not shown.

On the first trial after the introduction of the aversive stimulus (sugar water drop with citric acid), 73 % of spiders did respond correctly. According to the GLMM the percentage of correct responses did not increase significantly with the no. of trials (see Tab. 1).

Furthermore, the percentage of correct responses were higher when spiders were tested twice on the same day (χ^2=9.187, DF=1, p= 0.002). However, there was no clear pattern across all spiders. Some individuals became more accurate, while others became less accurate when tested a second time on the same day.

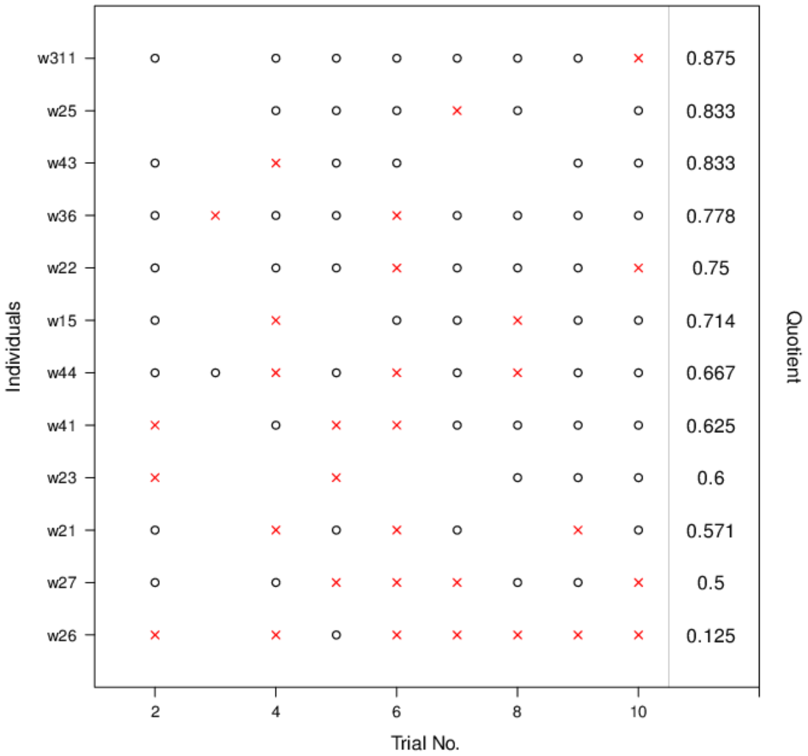

Figure 4: Task 1: The response (o= correct; x= incorrect) of each individual per trial and the quotient over all trials. Blank spaces indicate that the spider did not respond.

4.2. Task 2

A simplified t-maze was used to test reversal learning abilities. Spiders had to choose between a yellow and blue plastic Lego obstacle behind which a sugar water reward was placed on one side. The task was divided into three parts in which colour and location, colour only and location only were reversed.

Learning success: In part1 spiders chose correctly more often than predicted by chance before the presentation of the reversal trial ($n = 32$, $p = 0.01$). After the reversal trial spider chose correctly more often than predicted by chance again ($n = 43$, $p < 0.001$) (see Fig. 5). Furthermore, 10 out of 12 spiders chose correctly already during the first trial after the reversal (trial no.6) ($n = 12$, $p = 0.02$). In part 2 spiders chose correctly more often than predicted by chance before ($n = 31$, $p = 0.035$) but not after ($n =19$, $p = 0.084$) the presentation of the reversal trial. A similar pattern was observed for part 3 in which spiders chose correctly more often than predicted by chance before ($n = 66$, $p = 0.009$) but not after ($n =13$, $p = 0.5$) the presentation of the reversal trial.

Similar to task 1 the individuals differed strongly in their performance (see Fig 6). As expected, the group level performance in the complete reversal trial (trial 5) dropped dramatically. In the colour reversal trial (trial 13) the performance did not follow this pattern. In the location reversal trial (trial 23) the performance even increased. Unfortunately, only four individuals participated in this trial.

According to the GLMM on the responses of the spiders, the only significant explanatory variable was the time interval between potentially seeing and touching the reward (Tab. 2). We interpreted this latency as an indicator of the spider's motivation to obtain the food-reward. In trials in which spiders had short time delays (< 1min) between seeing and taking the reward, the percentage of correct choices was 87 %. In trials in which spiders needed longer (> 1 min) the percentage of correct choices dropped to 44 %.

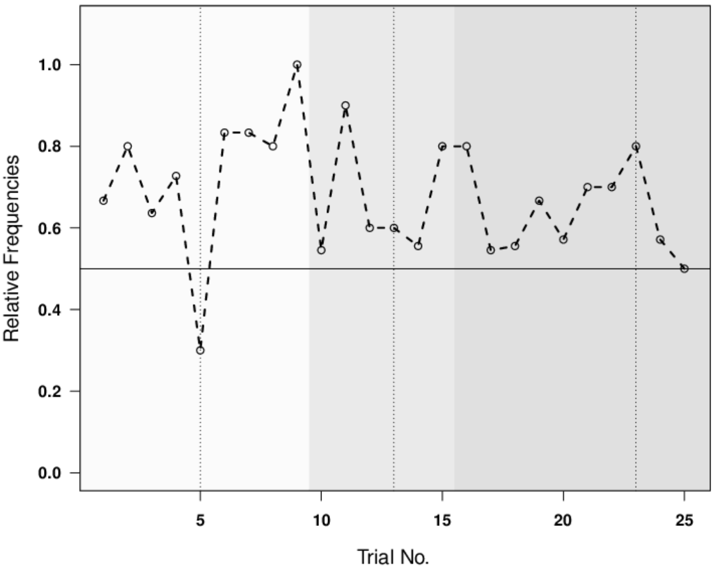

Figure 5: Task 2: Circles connected by dashed line show relative frequencies of correct choices per trial across all individuals. The solid line depicts the level of chance. Light, medium, and dark grey indicate part 1, 2, and 3 (complete reversal, colour

In the first trial after the complete reversal, spiders responded correctly in 10 out of 12 cases. Furthermore, overall variation in performance did not differ with successive trial numbers (χ^2=1.447, DF= 1, p =0.229).

Finally, a GLMM with the spiders' motivation to participate (i.e. touching the food reward) as the dependent variable, revealed that the motivation significantly decreased from Parts 1-3 of task 2 ($\chi^2 = 11.327$, DF=1, p=0.0008). The number of trials in which spiders did not touch the reward started with one out of 95 trials in the first part, increased to eight out of 70 in the second part, and ended with 14 out of 99 trials in the third part.

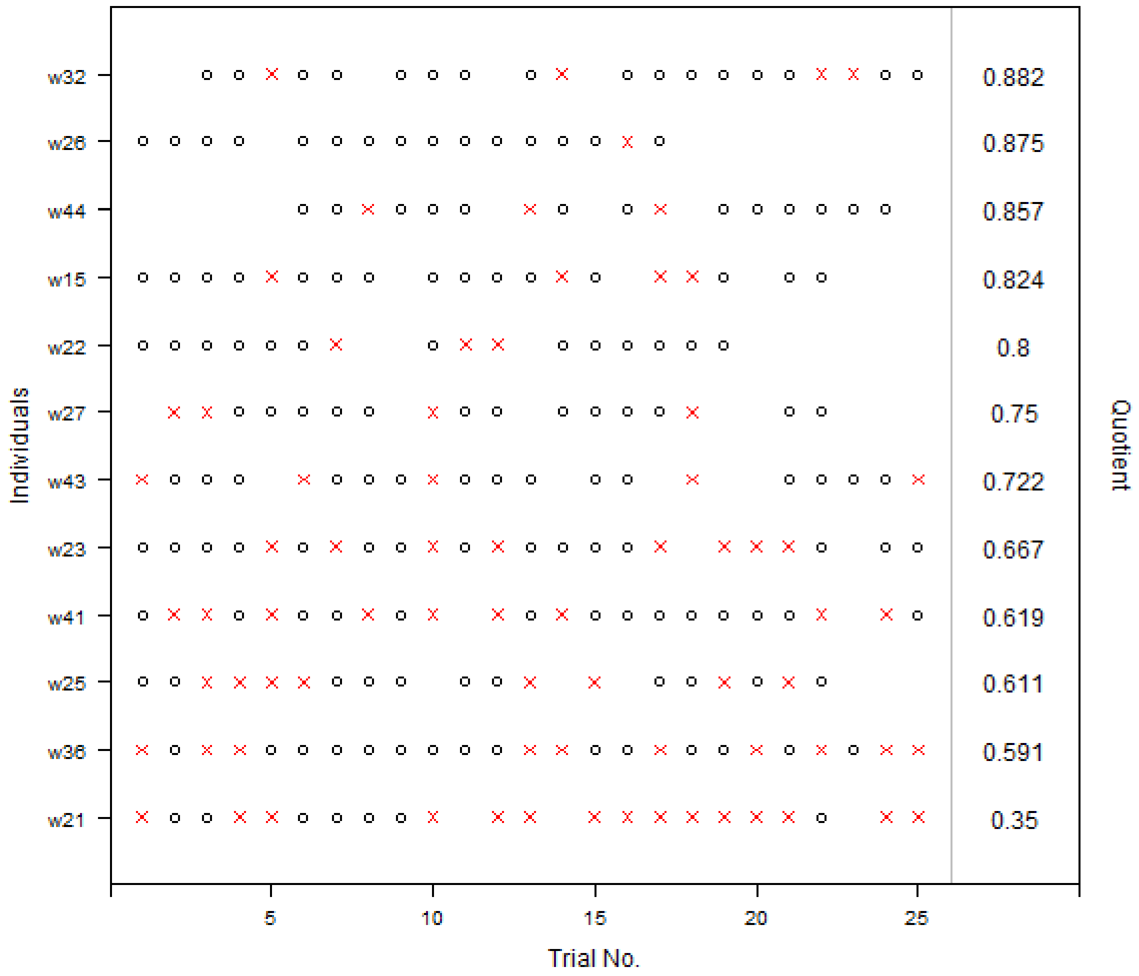

Figure 6: Task 2: The response (o= correct; x= incorrect) of each individual per trial and the quotient over all trials. Blank spaces indicate that the spider did not respond.

5. Discussion

Marpissa muscosa performed above chance level in two different discrimination tasks and were surprisingly quick in reversal learning. Most of the spiders did relearn the conditional stimuli of colour and location in a simple t-maze after one reversal trial. Interestingly, we observed strong individual differences in performance.

From an evolutionary perspective, it might not be surprising that this active hunter did learn and was able to reverse the learned associations in a foraging context quickly. The prey which *M. muscosa* encounters in real life will frequently differ in type and in location. Therefore, hardwired solutions seem inappropriate. Nevertheless, a small brain will likely impose constraints on the degree of neural plasticity and learning ability. Therefore, small animals likely benefit from solutions that require as little neuronal capacity as possible. Extracting and categorising information has been suggested as a potential mechanism for saving storage room (Srinivasan 2006; Chittka and Niven 2009). Furthermore, limited storage may constrain the memorising of individual solutions to any given problem in life and hence favour plastic solutions such as the ability of reversal learning. Larger brained animals face different constraints on their neuronal system (reviewed e.g. in Eberhard and Wcislo 2011; Chittka and Niven 2009) such as the velocity of longer axons and may handle reversal tasks differently as some findings suggest. Our test-spiders performed with an average accuracy of around 70 % across all trials. This is a low accuracy in comparison to studies on other arthropods. For example, reversal learning in honey bees (*Apis mellifica*) started with accuracies of up to 90 % in the beginning of the task which, however, decreased with time (Menzel 1969) and thereby lowered the average accuracy. Decreasing performance in multiple reversal tasks may be a general property of Hymenopterans (see Mota and Giurfa 2010; Chittka 1998; Menzel 1969) and our observations match this pattern. In contrast, vertebrates seem to get better with time (e.g.Bond, Kamil, and Balda 2007 and ref. therein). It might be worthwhile to investigate and compare how large and small brained animals process reversal tasks on a neuronal level and look for mechanistic differences.

It is well established that species differ in their abilities to solve spatial versus visual reversal tasks (reviewed by Bond and colleagues (2007). Reasons for such differences are likely to be found in the species' ecologies. In our study the spiders seemed to rely most on colour cues and less on spatial cues. This may reflect sensory properties of jumping spiders which have excellent colour vision (Foelix 2011). Jumping spiders are known to rely on visual cues in the contexts of e.g. foraging (reviewed in Jackson and Pollard 1996), navigation (Hoefler and Jakob 2006), and communication (e.g. Jackson et al. 1990).

Another important and universal issue in learning tasks is the motivation of participants. We cannot completely control for differences in motivation of animals. Even if the subjects have formed correct associations they still might choose the "wrong" stimulus for reasons of e.g. curiosity. This might be especially true in situations in which the incorrect choice comes at no or low cost. In the first task of this study the negative stimulus was a distasteful food item. This may not prevent curious individuals from trying that stimulus again - which actually had been a positive stimulus in the pre-testing phase. Indeed, curiosity may facilitate reversal learning abilities (for further discussion on personality and cognition see Sih and Del Giudice 2012). Our data suggest that individual differences in motivation and personality traits such as curiosity likely account for some of the variation in performance and not learning ability alone. Indeed, in trials in which motivation of spiders was high (i.e. short time delays between seeing and taking the reward), the percentage of correct choices was up to 90%. In trials in which motivation was apparently low, the performance was at the level of chance.

Moreover, it has been argued that penalization (rather than only absence of a positive stimulus) of incorrect choices increases attention of honey bees and thereby learning and discrimination abilities (Avargues-Weber et al. 2010). Our spiders learned fast in the first task which had an aversive stimulus but they performed just as well in the second task without an aversive stimulus. Therefore, the question how much an aversive stimulus will promote learning in *Marpissa* is left unanswered.

A closer look at individual differences in performing learning tasks reveals an interesting pattern. In both tasks we had individuals with average learning success rates of over 80 % and individuals which were only slightly above chance (success rate around 60%). Noteworthy, two spiders performed remarkably poor in one task each (success rates 12.5 and 35 % respectively). This may indicate that they used inadequate learning rules. Especially the performance of one individual (w26) is best (and most parsimoniously) explained by the usage of a win-stay, lose-shift strategy. In the first task, the location (but not the colour) was changed from trial to trial and this individual was wrong all but one time (accuracy of 12.5 %). In the second task in which location was changed only in the reversal trials, the same individual reached an accuracy of 87.5% which was the second highest of all spiders. Apparently this individual chose the side where the reward was located in the preceding trial.

In general, different performances of individuals in reversal learning tasks have been reported for other species as well (e.g. Leal and Powell 2012; Mota and Giurfa 2010; Bond, Kamil, and Balda 2007) and indicate that such differences are common. The individual differences in the usage of certain types of predictors and in forming learning (or association) rules highlight the potential existence of variation in learning abilities within species. Natural (MacLean et al. 2012) and possibly sexual selection (Boogert, Fawcett, and Lefebvre 2011; Verzijden et al. 2012) can act on such variation potentially leading to directional changes in learning abilities at the population level.

As mentioned above, it has been shown previously that spiders can learn (e.g. Bays 1962; Jackson and Nelson 2011; Punzo and Ludwig 2002; Jakob et al. 2007; Nakata 2013) including learning from negative feedback (Bednarski, Taylor, and Jakob 2012; Jackson, Cross, and Carter 2006; Hénaut, Machkour-M'Rabet, and Lachaud 2013). Especially jumping spiders are well known for their complex foraging behaviour which apparently relies on learning (Jackson and Cross 2011). However, not every attempt to train jumping spiders in a simple associative task resulted in rapid learning. For example, *Phidippus princeps* that were trained on a food-colour association in a t-maze did not show any evidence of learning the association within the first four trials (Jakob et al. 2007). However, test groups of trained and untrained individuals differed significantly after eight training trials which clearly demonstrate their ability to learn. Other studies found no evidence of learning in spiders at all. For example, Schneider and Polat did not find any learning in an orb-web spider (*Nephila senegalensis*) in response to pleasant und unpleasant food rewards combined with different vibration frequencies as a predictor (Schneider J.M. and Polat S., unpublished data). These observations stress the relevance of methodological differences such as the task design and nature of the reward on the outcome. Even small differences in the timing of the conditional and unconditional stimulus might have an influence on the performance of individuals. Furthermore, differences in the ecology of species under study (active hunter versus sit-and-wait predator) might be similarly relevant for the outcome of a given test design (see e.g.

Bond, Kamil, and Balda 2007; Day, Crews, and Wilczynski 1999). Unfortunately, all these points make direct comparisons of learning abilities between different study setups, even within same or closely related species, difficult. In general, to get a clearer impression of what species are capable of, we need to conduct (and ideally repeat) more experiments and publish not only positive but also negative results.

Taken together, our findings not only show that spiders with their limited nervous systems are able to learn and relearn quickly. They also raise questions of how much individuals (and species) vary in these abilities and how they differ in the usage of reliable predictor types and learning strategies. Finally, as an indication of intelligence and/or flexible behaviour in general, it might be worth considering not only the ability of reversal learning per se but also taking into account the ability to use and switch between different strategies and predictors.

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Chapter Two

Social makes smart: Rearing conditions affect learning in jumping spiders

by

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under review

Contribution of authors:
Jannis Liedtke & Jutta M. Schneider conceived the research question and wrote the manuscript. J.L. developed and designed the experiments. J.L conducted the experiments, analysed the video material and performed the statistical analyses.

Abstract

There is a long-standing debate as to whether social or physical environmental aspects drive the evolution and development of cognitive abilities. There is increasing evidence that environmental conditions affect the development of cognitive abilities and its underlying neuronal system. Surprisingly few studies capitalised on developmental plasticity to compare the effects of these two domains during development on cognitive abilities later in life. One critical, but rarely met requirement is to avoid confounding effects such as stress induced by isolated upbringing of individuals needed for a necessary control group. Jumping spiders are ideally suited in this context because they can be reared in groups but also in isolation and they possess cognitive abilities enabling learning. We split broods of spiders and reared them either in a physically or in a socially enriched environment as well as under completely deprived conditions which served as a 'no-enrichment' control. Spiders reared in groups significantly outperformed deprived spiders in an associative learning task, suggesting that social interactions confront animals with cognitive challenges that enhance learning ability. Physical enrichment did not have such a strong effect with success-ratios between the average responses of socially enriched and of deprived spiders. By demonstrating improved performance of socially reared spiders in a non-social task we raise the question of domain generality of cognitive abilities in these small animals.

Keywords: domain general cognition; operant conditioning; reversal learning; Salticids; Salticidae, t-maze

1. Introduction

In its broadest definition, the term cognition includes all forms of learning as well as causal understanding, planning, reasoning, and deception (Shettleworth 2010). Cognitive abilities require the development and maintenance of costly neuronal tissue (reviewed e.g. in Mery & Burns 2010; Buchanan et al. 2013), and experimental approaches demonstrated that increased investment in cognition is traded off against larval competitive ability (Mery & Kawecki 2003), gut size (Kotrschal et al. 2013), fecundity (Snell-Rood et al. 2011), and longevity (Burger et al. 2008). Hence, we expect that cognitive abilities are strongly favoured by selection under certain environmental circumstances that remain largely unknown.

A long-standing debate contrasts benefits of solving *physical* challenges (technical-brain hypothesis) with mastering *social* challenges (social-brain hypothesis). In this context, *social* refers to all interactions with conspecifics, including antagonistic and potentially harmful competitive relations (Jolly 1966; Humphrey 1976; Byrne & Whiten 1988; Dunbar 1998). Potential selective factors in the social context include cooperative breeding (Burkart & van Schaik 2010), pair-bonding (Emery et al. 2007), and group living (Shultz & Dunbar 2010a; Shultz & Dunbar 2010b). *Physical* generally refers to all other aspects of the environment, and may favour cognitive skills such as navigation and food-caching (reviewed e.g. in Byrne 1997; Overington et al. 2009; Heyes 2012). Recent meta-analyses support selection for increased brain size due to tool-use (Lefebvre et al. 2004) or to innovation (e.g. Sol et al. 2005; Overington et al. 2009).

While the above studies provide support for both hypotheses, most of the evidence is derived from positive correlations between relative brain sizes and cognition. To date, few studies, mostly on rodents and hymenoptera, provide experimental evidence for an increase of cognitive abilities or brain volume in response to either the social or the physical environment (reviewed in Rosenzweig & Bennett 1996; van Praag et al. 2000; Kihslinger & Nevitt 2006; Maleszka et al. 2009; see also Smith et al. 2010). However, these studies rarely test social and physical challenges simultaneously but focus on a single aspect (but see Rosenzweig et al. 1978; Schrijver et al. 2004). Hence, a direct comparison of social or physical aspects on the development or on the evolution of increased cognitive abilities is not possible. Another aggravation is that many of the tested species may have been negatively affected by stress due to social isolation (reviewed in e.g. Cacioppo & Hawkey 2009; Sachser et al. 2011) or overcrowding (Gonda et al. 2009; Brockmark et al. 2010).

Here we present an experimental study in which we manipulated the social and physical environments simultaneously to compare their influences on the development of learning abilities in a jumping spider (Salticidae). Salticids are ideal to address these questions for two main reasons. Firstly, recent studies have demonstrated that comparatively small animals like insects and spiders possess astonishing cognitive abilities (Chittka & Niven 2009; Jackson & Cross 2011; Jakob et al. 2011) ranging from simple associative learning (Liedtke & Schneider 2014), over detour (Tarsitano & Jackson 1997), to social learning (reviewed in Leadbeater & Chittka 2007). Secondly, jumping spiders are active hunters with acute eyesight, and they interact with conspecifics using complex displays (e.g. Clark & Morjan 2001; McGinley et al. 2015; Tedore & Johnsen 2015). It is not clear how cognitively demanding social interactions for jumping spiders are, but minimum of information must be processed (see e.g. Fawcett & Mowles 2013) with the associated costs. In addition to metabolic costs of neuronal tissue, small animals face space problems which may limit the expansion of brain tissue. Such constraints may have favoured more generalistic (domain-general) instead of specialised brains with cognitive abilities suited for multiple tasks (compare Srinivasan 2006; Chittka & Niven 2009). Alternatively, we may assume domain-specific abilities with separately underlying neuronal compartments or modules (Macphail & Bolhuis 2001; Shettleworth 2012). According to this hypothesis, investment in social skills may require trade-offs against investments in other skills such as associative learning abilities in the context of foraging. While there is evidence that both social and physical enrichment can affect the development of behaviour in spiders (Carducci & Jakob 2000; Punzo & Alvarez 2002; Punzo & Ludwig 2002; Clark et al. 2015), no study has assessed both aspects simultaneously. Our study species (*Marpissa muscosa*, Clerck, 1757) is well suited for manipulating the social environment because cannibalism is rare unless the spiders are starved. Therefore, the spiders can be held in groups as well as in isolation without showing signs of stress such as reduced activity or growth. In this study "social enrichment" refers to the observation that individuals living in groups were regularly interacting with one another, thereby increasing the environmental complexity to be computed.

We tested the cognitive ability of *M. muscosa* by assessing their associative learning abilities using an established t-maze paradigm (Liedtke & Schneider 2014). We selected a foraging context as a non-social task to answer the question whether enrichment per-se increases cognition or whether specific experiences cause the development of specific skills. If enrichment per-se increases learning abilities, then we predict that both physically and socially enriched spiders will outperform their conspecifics from the no-enrichment control. If specific experiences are needed, we predict that physically enriched spiders will perform best since they grew up in constantly changing environments which may favour associative and reversal learning abilities.

2. Material and Methods

2.1 Rearing conditions

For the experiments we used F1 offspring derived from 22 wild caught females (*M. muscosa*). Two weeks after oviposition, egg-sacs were separated from the females to prevent any post-hatching maternal effects. After hatching, we split the broods and distributed juveniles across the three treatment groups pseudo-randomly to ensure an even representation of families across the treatments. At that time, the spiderlings were very small with a body length of roughly 2 mm. Adult spider sizes typically ranges from 7-9 mm for males and 9-11 mm for females. All spiders were raised in transparent plastic boxes with white tissue covering the bottom. To ensure ventilation, the boxes had gauze-covered holes. In the 'deprived' treatment (treatment: 'd') spiders were kept isolated without visual contact to conspecifics in a small box (98x58x35mm) with no further enrichment except for a single small ball out of white tissue to provide some cover. In the 'physically enriched' treatment (treatment: 'p') spiders were kept isolated in boxes (145x110x68mm) that were enriched with natural and artificial objects (e.g. Lego® bricks, bottle cap, wooden plateau, bark, leaves, and stones; for more details about the enrichment protocol see supplementary Tab. S1). Objects were rearranged every other week, and enrichment was increased until the spiderlings were 46 weeks old. In treatments 'd' and 'p', visual contact with conspecifics was prevented by wooden barriers. In the 'socially enriched' group treatment (treatment: 'g') siblings were raised together in groups of five to 15 (Mean ± SE = 8 ± 2.98) individuals per box. The size of boxes was adjusted according to group size (see Tab. S2) so that the per-capita surface area (ranging from 173 – 358cm^2) was similar to spiders of the deprived treatment (223 cm^2). Per capita surface area in the 'd' and 'g' treatment was always considerably smaller than in the physically enriched treatment (899 cm^2, including the surface of the wooden plateau). A few paper balls (one for every second spider) were included to provide shelter. In the group treatment, spiders were separated when they reached the subadult instar (instar before the moult to maturity; recognised by visibility of sexual organs) to prevent mating. From then on, individuals were kept in small transparent boxes (98x58x35mm) that were put in close vicinity (< 3 cm apart) to facilitate visual contact with conspecifics. A total of 7 cannibalistic acts were observed, each in a different social group.

Spiders were raised in four age-cohorts per treatment. Cohort A, B, and C derived from females spiders caught in 2012. Spiders from cohort A and B hatched in July and August

2012. Spiders from cohort C hatched between December 2012 and January 2013. For cohort D, new spiders were collected in 2013 and their offspring which hatched in July 2013 were used for the experiment. Cohort A, C and D were raised similarly. Spiders from cohort B were kept in large groups of 11-35 spiderlings in a physically deprived environment for the first two months after hatching. Only after this period were they assigned pseudo-randomly to the three treatments. In total, spiderlings were from 21 maternal lines (cohorts: A =8, B= 5, C= 9, D =5). One matriline was represented in cohort A, B, C and two in cohort A and B (taken from different egg-sacs produced by the same mother). We included these spiders to compensate for a reduction of sample size caused by unplanned loss of spiderlings in cohort A due to unsuccessful moulting or to escapes (both independent of treatments: Generalized Linear Model (GLM) χ^2= -0.745; p = 0.689 and GLM χ^2= -4.368; p = 0.113 respectively). We evaluated the strength of the rearing effect in the first two months by comparing the performance of cohort B with spiders of the other three cohorts, which were assigned to the treatments immediately after hatching. We did not detect any differences in their learning abilities (see Tab. 1). All spiders were raised in the same laboratory room with a 17:7 hour light:dark cycle. Temperature ranged between 22-24°C and humidity between 30-60%, with higher humidity inside the boxes due to regular spraying. To induce trade-offs in investment (compare Mery & Kawecki 2003), spiders received a limited amount of food. Depending on the spiders’ age, they were fed 3 -15 *Drosophila* spec. per individual per week (for more details see Tab. S3). Flies were bred on an enriched died (Drosophila Instant III; Dr. D. Bretz) including vitamins, trace elements, and amino acids. The diet is rich enough to allow weight gain and growth, but not rich enough to allow rapid weight gain. A total of 158 individuals participated in the experiment (treatments: d = 47, p = 59, g = 52; cohorts: A =42, B= 33, C= 41, D = 42) aged eight to 15 months.

Table 1: Rearing effects on learning performance. Model output (GLMM) indicating effects on the mean level of learning and reversal learning behaviour in the t-maze. P-values stem from the step when a variable was dropped from the model (Crawley 2002). Number of observations 586; from 158 individuals; from 21 maternal lines. Significance is indicated in **bold**. Colour of CS: colour of conditional stimulus; treat: treatment; LeanRev: a two level factor indicating learning and reversal learning task

Explanatory Variable	**P-value**	**DF**	χ^2
Colour of CS:treat	0.9767	2	0.0471
Colour of CS:sex	0.6529	1	0.2023
Treat:cohort	0.5948	6	4.6093
LearnRev:treat	**0.0156**	2	8.3203
LearnRev:sex	**<0.001**	1	10.919
Cohort	0.4867	3	2.4374
Frequency of drinking	0.3521	1	0.8657
Colour of CS	**0.0184**	1	5.5558

2.2. Experimental procedure

We used a simplified t-maze to test the learning abilities of the spiders. The t-mazes consisted of small Perspex boxes (98mm×58mm×35 mm) containing two obstacles (31mm max length, 24mm max width) made of three plastic bricks (Lego®). These obstacles were placed at one end 13mm away from the wall (Fig. 1) with a gap of 12mm width between them. The two obstacles were blue and yellow, and their position on the right or the left hand side of the box was alternated between test spiders. The colour and the location severed as conditional stimulus (CS). *Hasarius adansoni* jumping spiders are known to have colour-vision, and both colours are within their visible spectrum (Nakamura & Yamashita 2000). In a preceding study, we were able to show associative learning abilities in *M. muscosa* with the same setup used in the present study (Liedtke & Schneider 2014). Before the trials spiders were transferred from their home-boxes into a white plastic cap (37 mm diameter, 12mm high, Fig. 1) which was covered with the bottom part of a plastic petri dish to prevent spiders from escaping. At the beginning of each trial, the spider was placed within this covered cap on the opposite end of the experimental box with the cap touching its wall, where it served as start zone. The distance between the start cap and the Lego® obstacles was 20 mm. After the transfer, we removed the petri dish and closed the box with its lid and the trial started. Spiders were able to see the obstacles only after they had climbed out of this cap. In cases where the spiders tried to climb out of the start cap before the box was closed, we prevented them from moving in the box by gently forcing them back with the tip of a brush. In rare cases (seven trials, in total) in which spiders were too quick and ran or jumped to the obstacles, we allowed them to stay in the experimental box for the complete hour, but the trials were excluded from analyses. In one case, the experimental box was not closed properly and the spider escaped never to be seen again. A drop of sugar water (20 µl) was used as a reward, and placed out of sight behind one of the Lego® obstacles. All trials were video recorded, and the experimenter left the room during testing to avoid any disturbances. Each individual was tested on four consecutive days, with two trials per day. During trials one to four, spiders were able to learn a colour and/or location as a predictor. During trial five we rearranged the setting by putting the reward behind the other coloured brick on the other side of the maze, thereby creating a complete reversal task. Spiders were allowed to relearn these configurations until trial 8, after which testing was terminated. Each trial lasted one hour in which individuals could move freely within the maze and had the opportunity to access the reward repeatedly. We recorded behind

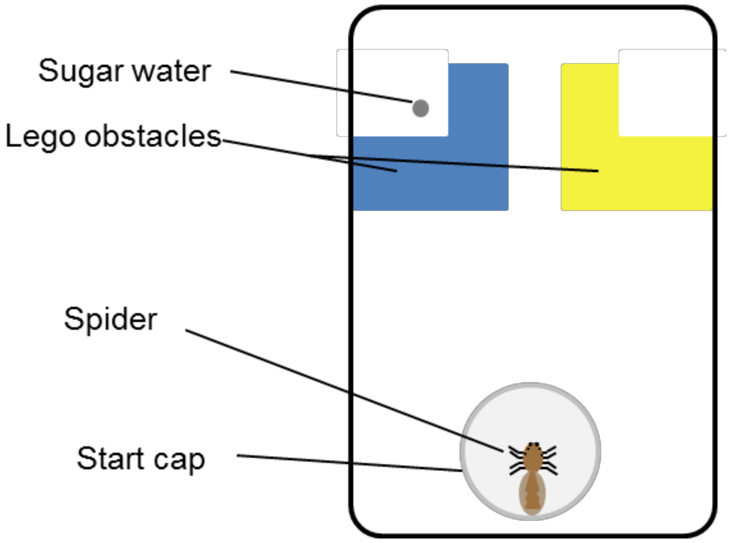

Figure 1: Schematic drawing of t-maze used for the learning task. Colour and position (left, right) of the Lego® obstacle served as conditional stimuli. In the beginning of each trial a spider was carefully placed into the opaque start cap. Reversal task was implemented by placing the food reward (sugar water drop) behind the other Lego® obstacle.

which obstacle a spider first walked as the first choice, the time it took to do so, the time of when and how often the spiders touched the reward.

3. Analyses

All analyses were done using R 3.1.0, (RCoreTeam 2014). We used mixed models and backwards variable selection. All models were reduced stepwise by excluding non-significant terms starting with least significant interactions (Crawley 2002). The maximal model was kept as simple as possible, and interactions were included based on preceding data exploration. Therefore, not all models included the same interactions.

We used a generalized linear mixed effect model (GLMM) fitted by Laplace approximation to estimate the effects of treatments, cohorts, sex, and motivation (frequency of drinking from the reward during the preceding trial) of spiders, as well as colour of the obstacle i.e. the conditional stimulus (CS) on learning performance. Although the significant effect of colour was independent of treatment (spiders performed better with a blue CS), we included this predictor variable to account for a better overall fit of the model. The dependent variable was the response of spiders in each trial (correct or incorrect) with binomial error structure and a loglink function. We analysed learning and reversal learning tasks together in one model, but included an explanatory variable with two levels: one indicating learning trials (trial 2-5), the other reversal learning trials (trial 6-8). We were thereby able to separate the effects of learning and reversal learning abilities. We included two random factors: identity of the individuals to account for repeated measurements, and identity of the mother to account for potential dependencies between siblings. In the maximal model we included five interactions: treatment x cohort, learning task x treatment, learning task x sex, treatment x colour of CS, and sex x colour of CS. We only included data from trials in which spiders actually fed on the reward to ensure that they were motivated.

We built an additional model to explore potential differences between treatments on overall participation in the task, which we defined as whether the spiders touched the reward or not. We ran a GLMM with participation as the dependent variable with a binomial error structure and a loglink function. Explanatory variables were: treatment, cohort, colour of CS, sex, and trial number, in addition to the interaction between treatment and cohort.

Using a linear mixed model we checked if the latency between seeing the reward and touching it differed between treatments. The dependant variable 'latency' was transformed using the R package 'car' in order to approximate a normal distribution. We included treatment, cohort, sex, trial number, and frequency of drinking from the reward per trial, in addition to the interaction between treatment and cohort as explanatory variables.

P-values given in tables were obtained from likelihood ratio tests comparing the models with and without the explanatory variable (or interaction) (Crawley 2002). Interactions were analysed using the R package 'phia' (De Rosario-Martinez 2015). P-values for differences between levels of the explanatory factor 'treatment' (i.e. 'd', 'g', and 'p') were obtained from likelihood ratio tests comparing a model with all three levels and a model in which the two focus levels were combined.

4. Results

We found significant interactions between success in the learning tasks and treatment (Generalized Linear Mixed Model (GLMM): χ^2=8.320; df= 2; p=0.016; Tab. 1). Further analyses of the interaction showed that spiders reared in a socially enriched environment (treatment ‘g’) outperformed deprived spiders (treatment ‘d’) in the learning trials (trials 2-5) (see Fig. 2; χ^2= 6.193; df=1; p=0.013; Tab. 2). The performance of physically enriched spiders (treatment ‘p’) was not significantly different from socially enriched ones (χ^2= 0.975; df=1; p=0.324; Tab. 2) nor from deprived spiders (χ^2= 2.696; df=1; p=0.101; Tab. 2). Their success ratios were in between the ratios of the other two treatments. In the reversal task (trials 6-8) we found no differences between the treatments (see Tab. 2). Although the spiders from the deprived treatment had the highest scores, their performance did not differ from chance (binomial test; n=56, p=0.141; see also Tab. S4 for binomial tests of the other treatments).

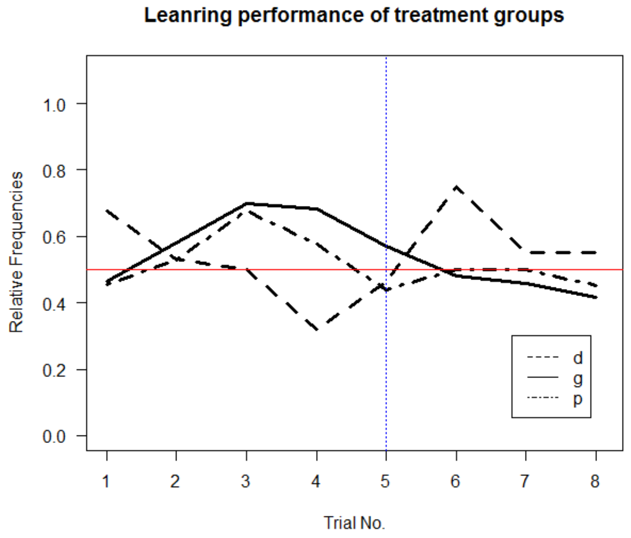

Figure 2: Learning (trials 2-5) and reversal learning (trials 6-8) performance of spiders raised under different environments. Lines show relative frequencies of correct choices per trial across individuals per treatments. Dashed for deprived treatment (‘d’); solid line group treatment (‘g’), and dashed line with dots physically enriched treatment (‘p’). Slender horizontal line indicates level of chance and dotted vertical line start of reversal task.

We also found an interaction between learning task and sex (see Fig. 3; GLMM:χ^2=10.919; df= 1; p<0.001; Tab. 1). Females performed better than chance in the learning trials while males did not (binomial test: females n=193, p=0.031; males n= 160; p= 1). Female success rate, however, did not differ significantly from that of males (58% in females versus 50% in males; χ^2=1.9141; df=1; p=0.167). In the reversal task, males were better than predicted by chance (binomial test: males n= 103; p= 0.03) and more successful than females (χ^2= 8.906; df=1; p=0.003). Females showed a tendency towards performing significantly lower than chance (binomial test: females n=131, p=0.08).

Table 2: Posthoc analysis of interactions between treatments and learning task. P-values were obtained from χ^2 – tests done with r package 'phia' (De Rosario-Martinez 2015). 'd': deprived, 'g': socially enriched, and 'p': physically enriched treatment Number of observations 586; from 158 Individuals; from 21 maternal lines. Significance is indicated in **bold**.

Comparing Treatments	**Task**	**P-value**	**DF**	χ^2
d-g	Learning	**0.013**	1	6.193
d-p	Learning	0.101	1	2.696
g-p	Learning	0.324	1	0.975
d-g	Reversal Learning	0.169	1	1.893
d-p	Reversal Learning	0.089	1	2.892
g-p	Reversal Learning	0.808	1	0.059

The latency between seeing the reward and touching it did not differ between treatments (Linear Mixed Model: χ^2= =1.562; df=2; p=0.458; Tab. 3). However, participation, defined as touching the reward or not, did (GLMM: χ^2= 9.922; df=2; p=0.007; Tab. 4). Spiders that grew up in a physically enriched treatment were more likely to touch the reward (predicted probability 61.9 %) than deprived spiders (43.3 %; χ^2= 9.818; df=1; p=0.002), while socially reared spiders (51.0 %) did not significantly differ to any of the other two treatments (respectively: χ^2= 1.436; df=1; p=0.231 and χ^2= 3.059; df=1; p=0.08).

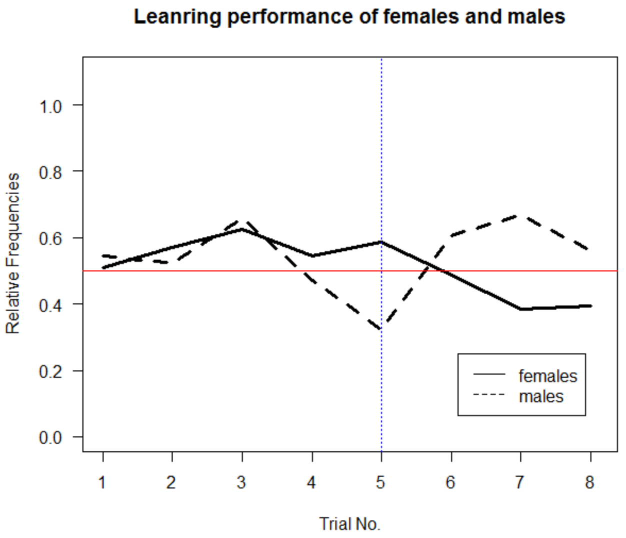

Figure 3: Learning (trials 2-5) and reversal learning (trials 6-8) performance of spiders. Lines show relative frequencies of correct choices per trial across individuals for females (solid line) and males (dashed line). Slender horizontal line indicates level of chance and dotted vertical lines start of reversal task.

Table 3: Latency of touching the sugar reward. Model output (LMM) indicating effects on the latency between seeing and touching the reward. P-values stem from the step when a variable was dropped from the model (Crawley 2002). Number of observations 586; from 158 Individuals; from 21 maternal lines. Significance is indicated in **bold**. Colour of CS: colour of conditional stimulus; Treat: treatment; Tnr: trial number.

Explanatory Variable	**P-value**	**DF**	χ^2
Treat:cohort	0.475	6	5.553
Sex	0.079	1	3.078
Frequency of drinking	**0.003**	1	8.885
Treat	0.458	2	1.562
Cohort	0.066	3	7.191
Tnr	0.487	1	0.484

Table 4: Participation in learning tasks. Model output (GLMM) indicating effects on the likelihood of participation in the t-maze (i.e. feeding on the reward or not). P-values stem from the step when a variable was dropped from the model (Crawley 2002). Number of observations 1320; from 175 Individuals; from 22 maternal lines. Significance is indicated in **bold**. Colour of CS: colour of conditional stimulus; Treat: treatment; Tnr: trial number.

Explanatory Variable	**P-value**	**DF**	χ^2
Treat:cohort	0.893	6	2.272
Colour of CS	0.755	1	0.098
Cohort	0.543	3	2.145
Sex	0.501	1	0.452
Tnr	0.117	1	2.456
Treat	**0.007**	2	9.922

5. Discussion

Enrichment during development resulted in an improved learning performance in our study animals. However, only spiders reared in a socially enriched environment outperformed deprived spiders in learning trials. Success scores of physically enriched spiders lay between the scores of socially enriched and deprived spiders, but neither difference was statistically significant. In the reversal task we found no differences between the treatments. This suggests that none of the treatments groups reversed their learned response in the given time but rather retained their preference adopted in the first task. The relatively high scores of the control spiders are explained by their poor performance in the learning task (one cannot reverse something that was not learned).

Interestingly, we found an interaction between success in the learning task and sex. While only females performed better than chance in the learning trials, their success rate did not differ significantly from that of males. In the reversal task, however, males were better than predicted by chance and more successful than females, which even showed a tendency towards performing significant lower than chance. These findings suggest that females had greater difficulties in overwriting the learned association than males. These sex differences may be related to differing cognitive needs of males and females. For example, in the context of mating, male spiders are the searching sex and thus may have the greater need to reverse the value of locations than females. In many taxa, including jumping spiders, female reproductive success increases with size and body condition, so fecundity selection (Head 1995; Prenter et al. 1999) may render females more vulnerable to trade-offs between investments (Kuntner & Elgar 2014). Such sex-specific trade-offs are generally thought to explain reversed sexual size dimorphism in spiders and in insects or of patterns of sex change in fish (Fairbairn et al. 2007). Sex-specific trade-offs between investment in cognition and in other fitness-relevant traits such as fecundity, may also explain the sex differences we found in learning performance. Studies in rodents have shown that learning and reversal learning rely on different neuronal mechanisms (Schrijver et al. 2004; Codita et al. 2011), implying that external factors can affect these abilities differently and potentially independently. Provided that similar physiological differences may exist in jumping spiders, selection on male reversal learning abilities would not affect their 'normal' associative learning abilities and vice versa for females. However, these possibilities have not been studied in spiders and as such the above explanations are purely speculative.

One possible explanation for the relatively good performance of socially enriched spiders may be that they had an increased motivation to feed due to resource competition in groups. We do not however think this is the case. The frequency of spiders feeding on the reward per trial did not affect the learning process, which contradicts the existence of a connection between motivation to feed and learning performance. We further explored potential differences in motivation, e.g. by increased hunger or competition, by analysing the latency until a spider saw the reward and touched it and found that it did not differ between treatments. However, spiders that grew up in a physically enriched treatment were more likely to touch the reward than deprived spiders, while socially reared spiders were in between the deprived and physically enriched spiders.

Another potential explanation for the treatment effects is that increased motor activity of spiders in groups may have induced neuronal growth and thereby affected learning abilities (van Praag et al. 2000; Freund et al. 2013). However, in a parallel study we tested differences in exploratory behaviour, and found that physically enriched spiders were the most active (Liedtke, J.; Redekop. D.; Schneider, J.M.; Schuett W.; unpublished manuscript). If this increased motor activity would be a driver for improved learning, physically enriched spiders should have performed best in the present learning study. Although the difference between social and physical enrichment was not statistically significant, the data show the reverse pattern. Overall, we consider it unlikely that motor activity per-se accounts for the success of the socially enriched spiders in this study.

We suggest that in the case of *M. muscosa,* socially reared spiders might have been confronted with cognitively more challenging tasks than their conspecific reared in isolation. Interactions with conspecifics may require remembering the location of conspecifics (and their retreats), assessing their fighting abilities (dominance), their sex, and developmental stage. Furthermore, conflicts with conspecifics may force submissive individuals to change their paths or resting places, consequently inducing involuntary movements. However, as mentioned in the introduction, the precise cognitive demands of social interactions in jumping spiders are still unclear (Elwood & Arnott 2013; Fawcett & Mowles 2013). Studies on hymenoptera suggest that the cognitive demands of social interactions depend on the underlying sensory mechanisms, with pheromone mediated dominance structures being less demanding than those based on direct behavioural interactions (Molina et al. 2009; Smith et al. 2010). Interestingly, a study on the nematode *Caenorhabditis elegans* showed that artificial mechanosensory stimulation can reverse negative effects of isolation on behaviour (Rose et al. 2005). We regularly observed interactions between spiders in the social treatment. Spiders showed a typical display involving waving with their raised frontal legs and moving side-ways in a zig-zag pattern without physical contact. While such visual displays were frequent, physical interactions were rarely observed making it unlikely that the latter explains the better performance of spiders raised in groups. Indeed the complex visual displays may be an important aspect of the social domain, which increases the amount of environmental information that has to be perceived and processed by group living spiders. Furthermore, spiders in all three treatments were fed with living flies that moved around freely, providing a source of physical and visual stimulation making it less likely that the presence of actively moving entities caused the detected differences.

In general, our results show that the environment in which an individual lives has an impact on the development of cognitive abilities. In line with theory and earlier findings, an increase in environmental complexity seems to generate challenges for the animal which lead to a better performance in learning abilities (Rosenzweig & Bennett 1996; van Praag et al. 2000; but see Durisko & Dukas 2013), and may lead to the maintenance (i.e. 'use it or lose it' (Swaab 1991; Pettmann & Henderson 1998)) and to even growth of the underlying neuronal tissue (Clayton 1995). Our results indicate that cognitive abilities can be domain general, and that adaptations to one aspect of the environment may facilitate increased abilities in other domains.

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Supplemental Materials

Table S1: Sizes of boxes used for socially reared spiders. Depending on group size (left column) spiders were reared in different sized boxes. For large groups two box-types were used due to logistic reasons. Smaller groups resulted either from removal of subadult individuals (see manuscript) or from death of group members.

Group size	Sizes in mm (l x w x h)	Surface in mm^2
2-4	145 x 110 x 68	7168
5-9	235 x 175 x 90	15600
10-15	355 x 235 x 130	32025
10-15	350 x 240 x 140	33332

Table S2: Enrichment protocol for physical treatment. Novel physical enrichment objects were added as the spiders aged. Due to logistic reasons not all boxes could be handled at the same time. Within cohorts changes were arranged within a single week. The larger ranges are due to the different cohorts. Since cohorts were included as explanatory variable in the analyses, potential effects of these differences were statistical accounted for. Objects were rearranged every other week and every two months Lego bricks were exchanged by a different colour. The colours used in the learning tasks (i.e. yellow and blue) were never used as enrichment.

Spiders age in weeks	Objects
1	piece of bark
	two small stones
	Iceland moss (*Cetraria islandica*)
	wooden plateau
10-13	Lego® bricks in either: dark green, light green, orange, brown, white, black
12-17	leaf of plane tree (*Platanus spec.*)
21-29	orange coloured cords
46	bottle cap

Table S3: Food protocol**.** Depending on the spiders' age they received a certain amount of *Drosophila* fruit flies per week. Spiders of Cohort 3 and 4 additionally got one drop of sugar water in the first week.

Spiders age in weeks	Species	Quantity
1-2	D. *melanogaster*	4
3-9	*D. hydei*	3
10-14	*D. hydei*	5
15-17	*D. hydei*	6
18-22	*D. hydei*	7
23-25	*D. hydei*	10
26-31	*D. hydei*	13
32 ongoing	*D. hydei*	15

Table S4: Success ratios. For each of the three treatments success ratios (correct/total choices) per trial, and the average success over learning (trials 2-5) and reversal learning (trials 6-8) are given. P-values derive from two-sided binomial tests with 0.50 success chance. Significant values ($p<0.05$) are indicated in **bold**.

	“Deprived”			**“Socially enriched”**			**“physically enriched”**		
Trial No.	success ratio	p-value	average success	success ratio	p-value	average success	success ratio	p-value	average success
1	21/31	0.071	-	13/28	0.851	-	21/46	0.659	-
2	17/32	0.860	48/106 p-value = 0.382	18/31	0.473	68/108 p-value = **0.009**	18/34	0.864	76/139 p-value = 0.309
3	10/20	1		21/30	**0.043**		21/31	0.230	
4	9/28	0.087		13/19	0.167		19/33	0.487	
5	12/26	0.845		16/28	0.572		18/41	0.533	
6	12/16	0.077	34/56 p-value = 0.141	12/25	1	33/73 p-value = 0.483	19/38	1	51/105 p-value = 0.845
7	11/20	0.824		11/24	0.839		18/36	1	
8	11/20	0.824		10/24	0.541		14/31	0.72	

Chapter Three

Growing up with siblings enhances social skills in a jumping spider

by

Jannis Liedtke & Jutta M. Schneider

submitted

Contribution of authors:
Jannis Liedtke & Jutta M. Schneider conceived the research question and wrote the manuscript. J.L. developed and designed the experiments. Tomma Dirks and Angelika Taebel-Hellwig conducted the experiments. Constance Lausecker analysed the video material. J.L. performed the statistical analyses.

Abstract

Most animals interact regularly with conspecifics. Such social interactions can be beneficial, but can also be costly, harmful, or even deadly. Therefore, animals should be under selection to optimise behaviour and energy expenditure. Depending on the environment (e.g. how often conflicts with rivals occur), the benefit of investment in social skills may vary. Since environmental conditions are often not fully predictable and may change over time, it should be advantageous to react plastically according to the conditions perceived by the individuals. In particular, developmental plasticity might be a powerful adaptation mechanism to the precise conditions experienced in life. Here we test the hypothesis that the development of social skills depends on early environmental conditions. We confronted spiders reared in different environments with a mirror-image of themselves, and analysed their behavioural response. Since test setting was in a neutral place without any resources to defend, non-aggressive behaviour should have been adequate. As predicted, spiders reared with conspecifics behaved more adequately i.e. less aggressive in front of the mirror than solitary reared siblings. Our findings emphasise the importance of early environment in the development of social behaviour, even in non-social arachnids.

Keywords: arachnids; arthropod; development; salticid; social behaviour; social competence

1. Introduction

Environmental conditions are known to affect the development of social behaviour in animals (reviewed e.g. in Arnold & Taborsky 2010; Sachser et al. 2011), including humans (reviewed in Sheridan & McLaughlin ; Sheridan & McLaughlin 2014). Growing up in contact with conspecifics can strongly influence not only behaviour (reviewed in e.g. Moretz et al. 2007; Taborsky et al. 2012), but also life-history traits and physical condition (reviewed in Cacioppo & Hawkey 2009). In most species, interacting animals face a large variety of social situations, and the ability to respond adequately to these situations (i.e. fitness-increasing) is known as "social competence" (Oliveira 2009). Natural and sexual selection can act upon variation in social skills, i.e. acting adaptively in a certain situation, thereby driving evolution towards more socially competent individuals and possibly even more complex social systems (Taborsky & Oliveira 2012). However, to be able to behave adaptively, individuals need to possess the cognitive abilities to process all relevant information (but see Elwood & Arnott 2013). Neuronal and sensory tissue is metabolically and developmentally costly (Laughlin et al. 1998; Niven & Laughlin 2008), and furthermore, individuals may need to learn an adequate response to a certain situation (Arnold & Taborsky 2010). Therefore, animals need to balance costs and benefits of social competence and weigh the net-gain against trade-offs with other energy demanding processes. Ideally, a system should be developmentally plastic and able to divert resources to this trait depending on specific environmental circumstances. For example, individuals living in low density populations may have few social interactions, lowering the benefits of social competence. As a result, these individuals may invest less in their social skills than conspecifics living in higher density populations (however, overcrowded populations may negatively affect behavioural skills (see e.g. Brockmark et al. 2010)). Hence, developmental plasticity in response to early environmental conditions may play a key role in preparing individuals for their future social life, at least in systems where early conditions reliably predict densities an individual will face later in life (reviewed e.g. in Kasumovic 2013; Snell-Rood 2013).

The effects of early environmental conditions on the development of social behaviour were mainly studied in vertebrates (reviewed in Taborsky & Oliveira 2012). However, if the concept of social competence meets the requirements of generality, we expect similar patterns to occur across a wide range of animal taxa. Invertebrates regularly interact with conspecifics (reviewd e.g. in Sokolowski 2010), and the development of behaviour in arthropods can be affected by social cues (reviewed e.g. in Kasumovic & Brooks 2011). Social isolation during development was found to affect learning, hunting behaviour, and brain morphology in wolf spiders (Punzo & Ludwig 2002). Recently, Clark and colleagues (2015) demonstrated that wolf spiders reared in isolation were impaired in their eavesdropping behaviours later in life.
Due to the small body size of arthropods, their neuronal system may have even stronger investment constraints (Chittka & Niven 2009). One might therefore expect that these miniature neuronal systems need to be more generalistic in order to handle all aspects of the environment (see e.g. Srinivasan 2006) using the same underling neuronal circuits when dealing with information from both the social and the physical domain. Consequently, effects on the neuronal system caused by increased complexity resulting in more information units needed to be processed within one domain may affect the other domain as well.

In this study we investigated if the development of social skills is influenced by early environmental conditions (rearing conditions) in a jumping spider. Jumping spiders are an ideal model system to study the effects of environmental conditions because they regularly interact with conspecifics by showing stereotypic displays with distinctive categories (e.g. Royauté et al. 2013; McGinley et al. 2015; Tedore & Johnsen 2015), are active hunters, possess accurate vision (Foelix 2011), and show flexible behaviour in different contexts such as hunting (Jackson et al. 2002; Jackson & Nelson 2012) and learning (Liedtke & Schneider 2014). Furthermore, in preceding studies we have demonstrated that rearing conditions affect the development of different behavioural aspects, such as exploratory behaviour (Liedtke et al. submitted) and learning (Liedtke and Schneider submitted). Here we tested whether a) spiders reared in groups show different social behaviour in comparison to solitarily reared spiders and 2) if physical enrichment (i.e. increased complexity of the physical environment) alone might induce differences in responses of the social domain. The second question arises from the rationale that i) physically enriched spiders were more exploratory and active (Liedtke et al. submitted) which may have facilitated development of social responsiveness and ii) that physical enrichment may induce the development of a more elaborate neuronal system which may enable spiders to behave more adequately in a social context.

We used *Marpissa muscosa* as study species, which is socially tolerant and often lives in close proximity to conspecifics in nature (personal observation). The spiders can easily be kept in groups although cannibalism can occur, especially when animals are starved. We tested spiders' social behaviour by confronting them with their own mirror image, which is known to evoke typical display behaviour like a real conspecific (reviewed in Foelix 2011). The test arena was a neutral place without any resources, representing a situation in which non-aggressive behaviour should be adequate. We predicted that group living spiders should behave less aggressive than solitarily reared spiders reflecting their better social skills. For physically enriched spiders, three principle scenarios were possible: (a) under the hypothesis of a generalistic neuronal system, we predicted that physically enriched spiders may have social skills similar to the group living individuals and behave more adequately than deprived spiders (i.e. reared without enrichment in both the social and physical domain). (b) Alternatively, investment in neuronal tissue as a response to increased complexity in the physical domain may be traded off against investment in neuronal tissue for the social domain. This hypothesis predicts reduced social skills for these spiders in comparison to the social group and (to a lesser extent) to the control group. (c) Finally, there might be no (relevant) trade-off between the abilities of the two domains, and thus social skills of physically enriched spiders may be unaffected by the physical enrichment. In this scenario we predicted to find no differences in the behaviour in comparison to the control group.

2. Material and Methods

2.1. Rearing conditions

For the experiments we used spiderlings derived from 20 females collected in northern Germany in spring 2012 and 2013. These females were individually housed in plastic boxes with white paper tissue covering the ground and enriched with dry leaves and a piece of bark. We separated females from their egg sacs two weeks after they had laid eggs to prevent any post-hatching maternal effects. We split broods and randomly allocated siblings in equal numbers to three rearing treatments (i) deprived, ii) socially enriched , iii) physically enriched). In the deprived treatment spiders were reared solitarily in a small plastic box (98 x 58 x 35mm) with only white paper tissue covering the ground and a small ball of paper tissue to provide some shelter. In the physically enriched treatment spiders were reared solitarily as well, but in larger plastic boxes (145 x 110 x 68mm) which were enriched with a range of artificial and natural objects (e.g. bark, leaves, stones, Lego bricks, and bottle caps). Enrichment increased over the course of the experiment until the 46th week, by which most spiders reached maturity. Objects were rearranged every other week. In both of these treatments spiders were prevented from visual and tactile contact with conspecifics. In the socially enriched treatment spiders were raised in groups with up to 15 siblings in a box. The bottom of these boxes was covered with white paper tissue and paper balls were included to provide shelter. The size of the boxes were matched to the actual group size with roughly 222cm^2 per capita, which was approximately the surface size provided in the deprived treatment and substantially smaller than in the physically enriched treatment. When reaching subadulthood, group-living spiders were separated from their siblings to prevent mating. These spiders were then housed solitarily in the same translucent boxes used for the deprived treatment. However, in this case boxes were put in close proximity to each other to facilitate visual interactions with conspecifics. According to the spiders' age they were fed fruit flies once per week (3-15 *Drosophila* spec). The average per capita amount was the same in all three treatments but we did not control for actual feedings events. In the group treatment spiders may have fed on flies that were rationed for their siblings.

2.2. Experimental design

Prior to the experiment, each spider was carefully placed into a white opaque plastic cap (55 mm diameter, 12 mm high), which was covered with a plastic Petri dish to prevent spiders from escaping. A spider was then transferred into the experimental box (145 x 110 x 68 mm) inside this cap. A mirror (79 x 55 mm) was attached to one side of the experimental box (see Fig. 1) which was otherwise empty. Then the cover was removed from the start cap and the spider had one hour to freely explore the box and interact with its own mirror image. For the individuals from the two solitary treatment groups, this was their first encounter a 'conspecific'. Our primary goal was to test spiders of all three treatments under as similar conditions as possible. We therefore used a mirror instead of a real conspecific to ensure that each individual met an "opponent" of exactly the same size, thereby excluded the possibility of different responses induced by individuals facing a smaller or a larger rival (e.g. Tedore & Johnsen 2015). However, we had to sacrifice the analysis of contact phases in more detail (e.g. its duration) (see McGinley et al. 2015) because we assume that physical contact with the mirror is dramatically different from being in contact with a real conspecific, and thus induces artificial behaviour. We therefore did not analyse the duration of contact but rather concentrated on whether the spiders engaged in physical contact or not. The experiments were videotaped, and experimenters did not interfere with or interrupt the trials. We conducted three experiments simultaneously with one representative of each treatment if possible. However, due to differences in sample size this was not always the case. In total we tested 140 spiders (44 from deprived, 53 form physically enriched, and 43 from socially enriched treatment).

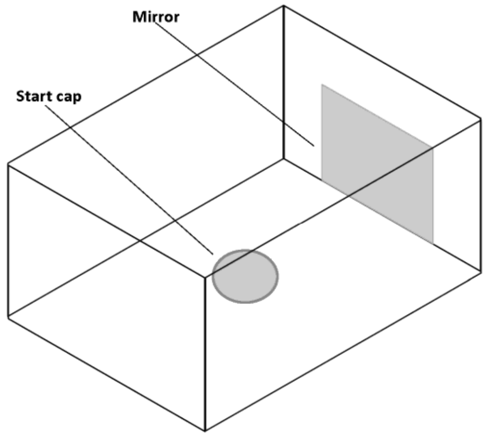

Figure 1: Schematic drawing of the test arena (not to scale).

During a pilot study with 13 laboratory raised and nine wild caught spiders, we defined 9 distinct behavioural categories and classified them as aggressive, neutral, or submissive reactions (see Tab. 1). We used these categories in the present study. When analysing the videos, we determined whether spiders reacted to the mirror image, the kind of behaviour category displayed, and its duration. Each reaction was categorised as aggressive, neutral, or submissive according to the relative duration of behavioural categories shown during this reaction. For example, if a spider spends 60% of the time submissive and 20% aggressive or neutral, the reaction was categorised as submissive. If, however, a spider touched the mirror or jumped at it during the reaction, it was classified as aggressive independently of additional neutral or submissive behaviours it may have shown during this interaction. This was done to account for the dramatic increase of aggressive behaviour and the potential harmful outcome of physical combat with real opponents (see e.g. Taylor & Elwood 2003). To estimate the overall performance of an individual, we summed up each reaction it displayed during the one hour trial, and classified the spider accordingly (i.e. if the majority of reactions were classified as aggressive the spiders` overall performance was classified as such). Video analysis was performed by a person naïve to the spiders' origin (i.e. treatment).

Table 1: Behavioural categories defined and classified as neutral, aggressive or submissive.

Behavioural Category	**Description**	**Classification**
Posturing	Individual is posturing in front of the mirror without any movement (sometimes it squats down)	Neutral
Approach	Individual approaches really slowly with few stops (of 1 or 2 seconds duration)	Neutral
Zig Zag	Individual walks sideways in front of the mirror (mostly with first pair of legs uplifted)	Aggressive
Jump	Individual attacks its own reflection by jumping on the mirror	Aggressive
Contact	Individual touches the mirror with the tarsi of the first pair of legs (often many times)	Aggressive
Quick approach	Individual approaches the mirror quickly without stops	Aggressive
Jump Back	Individual jumps backwards when it is in front of the mirror	Submissive
Retreat	Individual retreats from the mirror by running back	Submissive
Walk Back	Individual walks back with first pair of leg uplifted (more or less slowly)	Submissive

2.3. Statistical Analysis

All analyses were done using R 3.1.0 (RCoreTeam 2014). We applied generalised estimating equation models (GEEs) to investigate the potential effect of treatment, sex, and age (adult or not) and an interaction between sex and age on the dependent variables. We used maternal line as grouping variable and an "exchangeable" correlation structure to account for potential dependencies between siblings. We also included the variable "start time" in order to control for differences in the actual time spiders spent in the test arena outside of the start cap. For variables comprising durations we used the "powerTransform" function of the "car" package (Fox & Weisberg 2011) to transform data to normality if necessary. For other variables, appropriate error structures were used (i.e. binomial or Poisson family, see Tab. 2). We used stepwise model reduction, starting with the interaction before least significant single terms were removed, resulting in minimal models containing significant terms only. P-values given in the results derive from Wald statistics obtained by comparing a model without an explanatory variable with a model including this variable (Zuur et al. 2009). In the analyses, we focused on the behaviour shown in the very first reaction a spider displayed in front the mirror as well as behaviour during the whole trial (i.e. one hour) in order to determine the overall performance of each individual. We analysed eight response variables: if spiders reacted to the mirror ("React"), whether the first reaction was classified as aggressive or not ("First reaction aggressive"), whether the overall behaviour was classified as aggressive or not ("Total reaction aggressive"), total duration of reaction to the mirror reflection ("Total duration of reaction"), percent of total display time defined as aggressive ("Percent aggressive"), percent of total display time defined as submissive ("Percent submissive"), if a spider touched the mirror with the tarsi of the first pair of legs ("Contact with mirror"), and number of separate reactions during the whole trial ("Number of Reactions"). For the analysis of percentage-based data we used the function "cbind" in R to create a new vector which includes e.g. the total time of aggressive and non-aggressive display. This approach is recommended (Crawley 2005) because it computes not only plain percentages, but also weights the individuals according to their total display duration.

3. Results

Regardless of rearing conditions, all spiders showed stereotypic behaviours (see Tab. 1) identical to those shown in a pilot study by spiders caught from the wild. However, rearing condition, sex, and age influenced the frequencies and likelihood of these behaviours displayed in front of the mirror (see Tab. 2). In total, the likelihood of whether a spider reacted to its mirror reflection or not was influenced by the spiders' sex, as females were more reactive than males (Tab. 2). Moreover, rearing conditions significantly influenced the aggressiveness of spiders' performance over the entire test duration, as individuals reared in groups were less aggressive and had a lower probability of touching the mirror than deprived and physically enriched spiders. Individuals of both solitary treatments did not significantly differ from each other in these two categories (see Fig. 2 and Tab. 3). Physically enriched spiders were the most active individuals, showing significantly longer total display durations than socially reared spiders (see Fig. 2 and Tab. 3). Although the total display duration of deprived spiders was shorter compared with physically enriched spiders (although not significant), the proportion of aggressive behaviour was significantly higher in this treatment. The proportion of aggressive behaviour in physically and socially enriched spiders did not differ significantly from each other (see Fig. 2 and Tab. 3). Developmental stage also influenced the spiders' behaviour, as adult spiders were more aggressive in their first reaction and in their proportion of showing aggressive behaviour than immature spiders (Tab. 2). Finally, neither the total number of reactions nor the relative amount of submissive behaviour was influenced by any of the investigated variables (Tab. 2). None of the interactions between sex and developmental stage were significant (Tab. 2).

Table 2: P-values for main effects derive from Wald tests comparing generalised estimating equation models (GEEs) with and without the explanatory variable (Zuur et al. 2009). Letter indicate treatments ("d"= deprived; "g"= group; "p"= physical enriched), sex ("f"=female; "m"= male), and developmental stage ("ad"=adult; "im"= immature). Significant main effects are indicated in "**bold**" and significant effects between treatments are indicated by ">" (larger as) or "<" (smaller as), and "=" (not significant difference). N=sample size.

Response variable	**N**	**Error Structure**	**Treatment**	**Sex**	**Adult**	**Sex:Adult**
Reaction	129	Binomial	p= 0.14 (χ^2_2=4.0)	p= **0.015** (χ^2_1=5.87) **w>m**	p= 0.57 (χ^2_1=0. 325)	p=0.29 (χ^2_1=1.12)
First reaction aggressive	115	Binomial	p= 0.2 (χ^2_2=3.2)	p= 0.27 (χ^2_1=1.22)	p= **0.017** (χ^2_1=5.71) **ad>im**	p=0.76 (χ^2_1=1.12)
Total reaction aggressive	115	Binomial	p= **0.031** (χ^2_2=6.96) **g<p=d**	p= 0.15 (χ^2_1=2.1)	p= 0.3 (χ^2_1=1.08)	p= 0.39 (χ^2_1=0.75)
Total duration of reaction	115	Gaussian	p= **0.0091** (χ^2_2=9.41) **g=d<p**	p= 0.42 (χ^2_1=0.656)	p= 0.17 (χ^2_1=1.87)	p= 0. 96 (χ^2_1=1.12)
Percent aggressive	115	Binomial	p= **0.022** (χ^2_2=7.64) **g=p<d**	p= 0.58 (χ^2_1=0.302)	p= **0.0091** (χ^2_1=6.79) **ad>im**	p= 0.419 (χ^2_1=1.12)
Percent submissive	115	Binomial	p= 0.73 (χ^2_2=0.634)	p= 0.21 (χ^2_1=1.6)	p= 0.3 (χ^2_1=1.07)	p= 0. 157 (χ^2_1=1.12)
Contact with mirror	115	Binomial	p= **0.0049** (χ^2_2=7.93) **g<p=d**	p= 0.67 (χ^2_1=0.181)	p= 0.37 (χ^2_1=0.794)	p= 0.15 (χ^2_1=1.12)
Number of Reactions	115	Poisson	p= 0.93 (χ^2_2=0.142)	p= 0.92 (χ^2_1=0.011)	p= 0.21 (χ^2_1=1.57)	p= 0.58 (χ^2_1=1.12)

Table 3: Model outputs (GEEs) testing for behavioural differences between treatments displayed in front of the mirror. The letters in the columns for explanatory variables symbolize the treatments (d= deprived; g= group living; p= physically enriched). Sample size was 115 for all variables. Significance is indicated in **bold**.

Response variable	**Explanatory variables**		
	Treatment: d;g	Treatment: d;p	Treatment: g;p
Total reaction aggressive	**p=0.014** ($\div^{2}_{1}$=6.09)	p=0.702 ($\div^{2}_{1}$=0.15)	**p=0.029** ($\div^{2}_{1}$=4.77)
Total duration of reaction	p=0.072 ($\div^{2}_{1}$=3.24)	p=0.270 ($\div^{2}_{1}$=1.22)	**p=0.005** ($\div^{2}_{1}$=7.75)
Percent aggressive	**p=0.009** ($\div^{2}_{1}$=6.78)	**p=0.009** ($\div^{2}_{1}$=6.92)	p=0.076 ($\div^{2}_{1}$=3.16)
Contact with mirror	**p=0.031** ($\div^{2}_{1}$=4.66)	p=0.117 ($\div^{2}_{1}$=2.46)	**p<0.001** ($\div^{2}_{1}$=14.23)

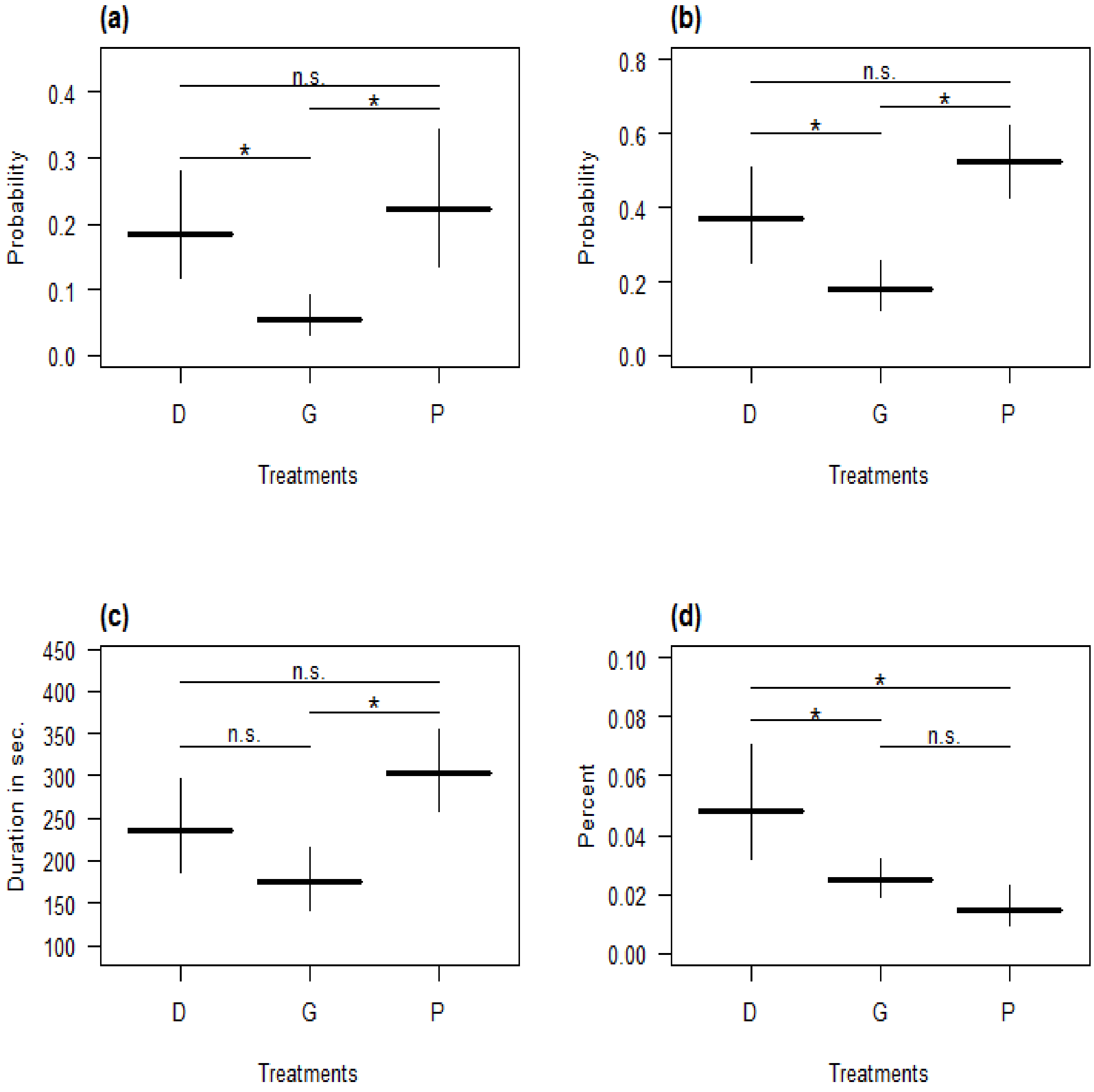

Figure 2: Panels show predictions for four different behavioural categories shown by spiders in front of a mirror (a-d). Spiders were reared in three different treatments: “D”= deprived; “G” = group living; “P” = physically enriched. Predictions derive from generalised estimating equations models (GEEs) with n= 115. a) Probability of being classified as aggressive b) Probability of contacting the mirror image. c) Total duration of display. d) Percent of display duration spent with aggressive behaviour.

4. Discussion

We found that the development of social behaviour in arachnids is affected by early environmental conditions, which is in line with findings from various vertebrate taxa (reviewed in Taborsky & Oliveira 2012). Jumping spiders raised with their siblings responded differently and more adequately when confronted with their own mirror image compared to individuals raised in isolation. We also found a sex difference in response behaviour, with females behaving more responsive to their own mirror image than males. Furthermore, adult spiders were more aggressive than immature spiders.

Jumping spiders raised without contact to conspecifics were more aggressive, which is in accordance with the common finding that isolation increases aggressive behaviour (reviewed in e.g. Sokolowski 2010; Sachser et al. 2011). Aggressive behaviour is moreover promoted when animals need to defend a certain resource from conspecifics (Sundstrom et al. 2003; and references within). In our study, however, spiders were tested in a neutral context, i.e. inside an empty box only containing a mirror and the start cap, and thus did not have any resources to defend. Accordingly, we consider non-aggressive behaviour as the adequate response to the mirror image. In line with our hypothesis, individuals raised in groups were less aggressive, and were less likely to touch their mirror image. Touching an opponent is considered to be a particularly important and aggressive step in a contest due to the risk of harmful physical interactions with a potentially deadly outcome (McGinley et al. 2015). Therefore, we conclude that socially reared spiders possess better social skills than spiders reared in isolation. It is of note that there were no differences in reaction towards the mirror (i.e. the likelihood to react; or in the total amount of reactions shown) between any of the three treatments. This suggests that differences between treatments were indeed caused by differences in social competence (Taborsky & Oliveira 2013), and not due to differences in social responsiveness (Wolf & McNamara 2013).

Comparing the results of the overall performance of the two socially deprived treatments does not allow clear conclusions to be drawn as to potential positive or negative effects of physical enrichment on social skills. Both treatment groups were found to be equally often aggressive and had the same likelihood of contacting the mirror. Physically enriched spiders showed the longest total duration of display. However, on a percentage basis they did not spend more time being aggressive compared with spiders raised in groups, and they were less aggressive than deprived spiders. It seems likely that their prolonged display derived from the generally increased motor activity which has been found in exploration tests conducted in a preceding study (Liedtke et al. submitted).

Interestingly, when accounting for the first interaction with the mirror image only, there was no difference in aggressive behaviour between the spiders from any of the three treatments (neither in the likelihood to contact the mirror, nor in the behavioural category). However, spiders raised in groups had the lowest likelihood to be categorized as aggressive in the first ‘contest’, although this result was not significant (socially enriched: 8.6 %; deprived: 16.8% and physically enriched: 19.9 %). Solitary spiders reacted less often while spiders raised in groups were slightly more aggressive in comparison to their overall performance. Similarly, the duration of displays during subsequent reactions increased in both solitary treatments, while it decreased in spiders raised in groups. We speculate that these patterns may be caused by different hormone responses (Cushing & Kramer 2005; Oliveira 2009; Sachser et al. 2011), or alternatively may be due to differences in learning abilities. In rats, for example, maternal deprivation led to reduced performance in social learning tasks: e.g. deprived rats did not distinguish between known and new opponents, whereas individuals being reared with mothers investigated known conspecifics less (Levy 2003). Indeed, in another study we have shown advanced learning abilities for socially reared spiders in a feeding context (Liedtke and Schneider, submitted). It remains to be tested if improved learning skills in a social context may cause the behavioural differences found in the present study (compare Clark et al. 2015) or if cognitively less demanding mechanisms may sufficiently explain the observed pattern (see e.g. Elwood and Arnold 2013).

Another interesting finding was that females were more likely to react to their mirror image than males. A possible explanation could be that males wander around searching for females and may avoid interactions with other males as they walk (if this is the case, we would predict a dramatic change in male behaviour when females are present so the males must compete for them). Females, on the other hand, may be more locally bound (to suitable retreats which provide shelter for egg sacs) and thus may be in greater need to know their social surrounding and interact with their neighbours. Sex differences in response to environmental circumstances have been reported across a wide range of species and on a proximate level are often explained by differences in hormonal systems (reviewed in e.g. Sachser et al. 2011; Hofmann et al. 2014). Finally, both males and females were more aggressive as adults. This is likely caused by increased interspecific competition for mating opportunities when entering a reproductive state.

Overall, our findings indicate that the development of social skills can be plastic in spiders, (but see Bengston et al. 2014) even in non-social species (see also Clark et al. 2015).It is of note that cannibalism can occur in this species, especially when spiders are starved (personal observation). Thus, responding adequately when being faced with conspecifics and thereby avoiding unnecessary and potentially deadly conflicts should increase fitness. The finding that spiders reared in isolation showed more aggression and thus are more susceptible to potentially harmful behaviours can be interpreted in multiple ways. One explanation is that individuals must interact with conspecifics early in life in order to develop social skills, which allows them to learn adequate responses and to form the required underlying neuronal and hormonal systems (reviewed in Cushing & Kramer 2005). A downside of such plastic systems could be that lack of social input may cause maladaptive development (see e.g. Branchi et al. 2006; Cacioppo & Hawkey 2009). However, this explanation prompts the question why pre-adjusted stereotypic response rules did not develop in the place of plastic systems. Indeed, the displays shown by spiders in this study were stereotypic and not flexible. Differences only occurred in the degree to which spiders showed aggressive behaviour. On the other hand, the apparently reduced social skills of individuals reared in isolation might be adaptive under specific circumstances. As stated above, the ability to respond adequately in social situations likely comes at some cost, such as the acquisition and maintenance of the neuronal system required by these skills (Niven & Laughlin 2008; but see Elwood & Arnott 2013). Thus, in environments where encounters with conspecific are infrequent, the advantage of being socially competent diminishes (all other things being equal) and may be traded off against other fitness related traits (e.g. longevity or fecundity). Therefore, plastic systems which sensitively respond to environmental conditions may be beneficial. The developmental plasticity found in this study may indicate such a system, which relies on adequate input (i.e. social interactions in the early environment) in order to develop social skills with the underlying neuronal and hormonal machinery. It would be interesting to investigate if social competence is density-dependent in the field and if increased social skills promote group cohesion, which may facilitate a positive feedback loop potentially leading to sociality (as suggested by Taborsky & Oliveira 2012).

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Chapter Four

Early environmental conditions shape personality differences in a jumping spider

by

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under review

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Jannis Liedtke, Daniel Redekop, Jutta M. Schneider & Wiebke Schuett developed the ideas and methods and wrote the manuscript. D.R. conducted the experiments and analysed the video material. J.L. & W.S. performed the statistical analyses.

Abstract

Individuals of many species across the animal kingdom are found to be less plastic than expected, even in behavioral traits. The existence of consistent behavioral differences between individuals, termed personality differences, is puzzling, since plastic behavior is considered ideal to enable animals to adaptively respond to changes in environmental conditions. In order to elucidate which mechanisms are important for the evolution of personality differences, it is crucial to understand which aspects of the environment are important for the development of personality differences. Here, we tested whether physical or social aspects of the environment during development influences individual differentiation using the jumping spider *Marpissa muscosa*. We applied a split-brood design and raised spider siblings in three different environments: a deprived environment with no enrichment, a socially and a physically enriched environment. We focused on exploratory behavior and repeatedly assessed individual behavior in a novel environment and a novel object test. Results show that the environment during development influenced spiders' exploratory tendencies: spiders raised in enriched environments tended to be more exploratory. Most investigated behaviors were repeatable (i.e. personality differences existed) across all individuals tested, whereas only few behaviors were also repeatable across individuals that had experienced the same environmental condition. Taken together, our results indicate that external stimuli can influence the development of personality traits in a jumping spider. We also found family by environment interactions on behavioral traits potentially suggesting genetic variation in developmental plasticity.

Keywords: animal personality; arachnids; arthropod; behavioral syndromes; exploration; rearing; salticid; temperament

1. Introduction

Consistent behavioral differences among individuals of the same population are widespread across various taxa in the animal kingdom (reviewed in e.g. Gosling, 2001; Bell et al., 2009; Kralj-Fišer and Schuett, 2014). This means individuals differ in their mean level of behavior (inter-individual behavioral variation) while being (more or less) consistent in their behavior over time and/or different contexts (intra-individual consistency). The existence of such personality differences is puzzling, given that it would seem sensible for individuals to be plastic and to adjust their behavior adaptively to changes in the environmental conditions (e.g. Sih et al., 2004).

Hypotheses that explain the adaptive value of animal personalities are linked to information use (McElreath and Strimling, 2006; Wolf et al., 2008), life-history (McElreath et al., 2007; Wolf et al., 2007), sexual selection (Schuett et al., 2010), and social interactions (McNamara et al., 2009) amongst others (Mangel, 1991; Dall et al., 2004; Nettle, 2006; Dingemanse and Wolf, 2010) yet empirical tests of these hypotheses remain scarce (but see e.g. Schuett et al., 2011b; Kralj-Fišer and Schneider, 2012; Nicolaus et al., 2012; Schuett et al., 2015). In order to understand the evolution of personality differences, it is also crucial to elucidate the development of personality differences. There is a general consensus that across species, on average about 30% of inter-individual variation in behavior is genetically inherited (e.g. Stirling et al., 2002; van Oers et al., 2005; Quinn et al., 2009; van Oers and Sinn, 2011), while the remaining variation originates from environmental sources (Buss and Greiling, 1999). In particular, environmental conditions experienced during early life may contribute to the development of personality differences by directing individuals into different life-history strategies and personalities ("early experiential calibration", Buss and Greiling, 1999; see also Carere et al., 2005). It has been proposed that similar to life-history traits, personality traits can adjust within a genetically predetermined reaction norm (see e.g. Dingemanse et al., 2010; Groothuis and Trillmich, 2011). As for developmental behavioral plasticity in general, the potential for these plastic responses might be restricted to sensitive periods during ontogenesis (e.g. Groothuis and Trillmich, 2011, or "developmental windows" Luttbeg and Sih, 2010; Faulk and Dolinoy, 2011;), since changing an once adopted behavioral phenotype is associated with cost (reviewed in Snell-Rood, 2013). These processes can therefore lead to consistently different phenotypes even with similar genotypes (see Sih et al., 2004; Luttbeg and Sih, 2010) and these differences may be under frequency dependent selection (Lichtenstein and Pruitt, 2015).

To truly understand the evolution of personality differences, we need a comprehensive understanding of the specific environmental aspects shaping the development of personality difference (see Duckworth, 2010; Stamps and Groothuis, 2010). Previous studies have already shown developmental effects on mean behavioral levels such as social interactions (Iba et al., 1995; Arnold and Taborsky, 2010; Ballen et al., 2014; Liebgold, 2014), motor activity (Carducci and Jakob, 2000; Buchsbaum and Morse, 2012), or parental care (Margulis et al., 2005; Branchi et al., 2006). More studies are now desirable that investigate whether behavioral differences induced by developmental effects are consistent and stable, i.e. whether environmental conditions experienced influence animal personalities. Indeed, there is an increasing number of studies focusing on the development of animal personality (e.g. Sinn et al., 2008; Brodin, 2009; Schuett et al., 2011a; Gyuris et al., 2012; Hedrick and Kortet, 2012; Niemelä et al., 2012b; Petelle et al., 2013; Sweeney et al., 2013; Tremmel and Müller, 2013; Guenther et al., 2014; Johnson et al., 2015). To clearly identify underlying processes, experimental studies in which environmental conditions are manipulated are needed. The majority of studies that measured personality development in an experimental setting manipulated either food availability (e.g. Carere et al., 2005; Edenbrow and Croft, 2013), or stress by inducing immune challenge (e.g. Butler et al., 2012; DiRienzo et al., 2015), by increasing antipredator pressure (e.g. Bell and Sih, 2007; Niemelä et al., 2012a; Edenbrow and Croft, 2013), or by preventing access to shelter (Bengston et al., 2014).

Another aspect (potentially overlapping with above mentioned environmental aspects), which might influence the development of personality, is the complexity of the environment itself. Studies on animal intelligence have shown that increasing complexity in the social and/or in the physical environment induces behavioural and neural responses across different taxa (see e.g. Renner and Rosenzweig, 1987; Schrijver et al., 2004; Gonda et al., 2009; Brockmark et al., 2010; Kotrschal et al., 2012). This suggests that an increase in complexity directs animals to develop enhanced cognitive abilities allowing them to cope with increased information. Increased cognitive abilities (i.e. the ability to perceive and compute information) may itself lead to changes in individual behaviour and life-history strategies (reviewed e.g. in Mettke-Hofmann, 2014; Trompf and Brown, 2014). Therefore, we assume that exploratory behavior, for example, should be generally positively linked to the amount of information (i.e. the complexity) available in the environment because knowledge of the environment allows behaving adaptively (at least up to a certain point; compare e.g. Niemelä et al., 2013). If, however, information gathering is potentially harmful individuals may show less exploratory tendencies. Such potentially harmful situations might be predation risk or risky interactions with conspecifics. To date, only few studies have investigated the effect of environmental complexity on personality either by increasing the social (Carere et al., 2005; DiRienzo et al., 2012) or the physical complexity (Bolhuis et al., 2005; Fox and Millam, 2007). Also, it remains unclear whether both aspects induce similar or different responses as these two aspects have rarely been manipulated in conjunction (but compare Carere et al., 2005; Bengston et al., 2014). A better understanding of these aspects is essential for elucidating which mechanisms are important for generating and maintaining personality.

In this study we investigated the effects of the social and the environmental complexity as well as genetic effects on the development of personality differences using the jumping spider *Marpissa muscosa*. Jumping spiders are active hunters, have highly developed eyes and are sensitive to multiple aspects of their environment (Foelix, 2011). Therefore, we expect their personality development to be strongly influenced by external stimuli (see for an example Royauté et al., 2013), including environmental complexity. Furthermore, we expect exploratory behavior to be a highly relevant behavior for jumping spiders because, among others, they need to search for prey, shelter, and mates. Carducci and Jakob (2000) showed indeed that jumping spiders reared in a physically enriched environment were on average more exploratory later in life. Here we also added a social component to compare potential effects of the physical environment with effects of the social enrichment (see above).

We used a split-brood design and raised jumping spider siblings in three different environments: a deprived environment with no enrichment, a socially and a physically enriched environment. This design allowed us to test for family, environmental effect and their interaction on personality (mean level of behavior; behavioral repeatability within and among treatment groups) and plasticity. We repeatedly measured individual exploratory behavior in a novel environment and towards a novel object. We predicted that enrichment, both physical and social, would lead to the development of more exploratory personalities (mean level of exploratory behavior) because information gathering in complex environments should be more advantageous than in less complex or deprived environments. However, we predicted that on average group living spiders might be less exploratory than physically enriched spiders due to the risk of harmful interactions with conspecifics. Even though *M. muscosa* are not considered social animals, they repeatedly interact with conspecifics in their natural environment (on and beneath the bark of trees). Furthermore, we assessed whether, beside those predicted effects on the mean behavioral level, behavior was also repeatable among and within treatment groups, i.e. whether there were personality differences present in the investigated traits. Finally, by presenting two different analytical approaches (i.e. analyzing repeatability over the whole data set versus within each treatment separately) we want to highlight the possibility of obtaining different results when ignoring potential effects of developmental background on behavior. For example, the characteristics of the study area (from which individuals are sampled), such as the area's size, might influence the likelihood to detect personality differences: with increasing area the environmental heterogeneity often increases, too, and with it maybe also the potential of detecting (environmentally-induced) personality differences.

2. Methods

2.1. Rearing conditions

In June-July 2012 we collected in total 18 adult and 17 subadult females and 18 males in northern Germany. Those females, which did not produce eggsacs in captivity (i.e. had probably not yet successfully mated in the field), were mated in the laboratory (by placing the female with a male in a box over night; males were used only once). Females were held solitary in plastic boxes (145x110x68mm) enriched with some dry leaves, bark and white tissue paper. For the experiments we used spiderlings derived from the 9 females, which were first to produce offspring. Eggsacs were separated from these females two weeks after they had been built to prevent any post-hatching maternal effects. After hatching juvenile siblings were assigned to one of three treatments pseudo-randomly (to ensure a balanced number of siblings in all treatments): a "deprived", a "physically enriched" or a "socially enriched" treatment.

In all three treatments, spiders were held in translucent plastic boxes with holes that were covered with blue gauze to ensure air circulation. We raised spiders in the "deprived" treatment (treatment: "d") alone and without visual contact to conspecifics in boxes of 98x58x35mm size. The bottom of the box was covered with white tissue paper and a small ball of the same material was included to give the spiders the opportunity to hide. Spiders in the "physically enriched" treatment (treatment: "p") were raised alone and without visual contact to conspecifics in boxes of 145x110x68mm size. These boxes were enriched with both natural and artificial objects (such as bark, Iceland moss (*Cetraria islandica*), dry leaves, orange colored cords, Lego© bricks, bottle cap). We increased the degree of enrichment over the weeks until an age of 46 weeks (by which most spiders had reached maturity) and we altered the arrangement of objects every other week. Also a wooden plateau was included to increase the surface and structure of the box. The bottom of the box was covered with white tissue paper. In the "socially enriched", group treatment (treatment: "g") siblings were held together in groups of five to 15 individuals in one box (Mean ± SE = 8.1 ± 3.3). The actual number of individuals per group depended on the total clutch size from which the siblings were allocated to the treatments, i.e. only siblings from large clutches reached the maximum size of 15 group members. The size of the box was matched to the actual group size so that on average each spider had a surface area of roughly 222cm^2, which is similar to the area in the deprived treatment. The bottom of the box was covered with white tissue paper and a few paper balls were included to provide cover. In the socially enriched treatment, we separated spiders from their group when they reached subadulthood (at mean ± SE = 44 ± 8.4 weeks) to prevent uncontrolled matings. The new boxes had the same size and content as in treatment "d" but were put in close proximity to facilitate visual contact among conspecifics.

All animals were kept in the same laboratory room under constant conditions with a 17:7 hour light:dark regime and temperatures between 22-24°C. Humidity was between 30-60% in the room (higher in boxes due to regular spraying into boxes). Depending on its age we fed each spider with 3-15 *Drosophila* spec. per week. Because spiders were held in groups in the social treatment the number of flies consumed by individual spiders might have varied. A total of five cannibalistic acts were observed in four out of twelve social groups. Every other week we monitored the developmental stage of each spider (juvenile, subadult, or maturity) by inspecting the reproductive organs. At maturity the pedipalps of males are differentiated and turn dark and the epigyne of females becomes more pronounced and turns dark.

In 2012 we lost 56 of 142 spiderlings through unsuccessful moulting or escapes (equally distributed across treatments: unsuccessful moulting: GLM, $\chi^2 = 0.745$; $p = 0.689$; escapes: GLM, $\chi^2 = 4.368$; $p = 0.113$). To compensate for the reduction in sample size we also included individuals from family groups in which spiderlings had been raised together in a physically deprived environment for two months after hatching within larger groups (11-35 spiderlings per group). We pseudo-randomly assigned these spiders into the three treatments groups as described above. In the following we will refer to the original spiders as "cohort 1", to the spiders that were included later to compensate for the loss of individuals as "cohort 2".

In June 2013 we collected additional 23 adult, and presumably mated, females from the field. The offspring of five of those females were used to create cohort 3. These spiderlings were raised in similar ways to cohort 1 with some minor variations: we constantly provided small plastic tubes filled with wet cotton wool to prevent dehydration problems. Secondly, in the first week hatchlings received a sugar water drop in addition to the three flies. Finally, to prevent hatchlings from escaping their boxes (in the deprived treatment) they were held in plastic cylindrical containers (5.5 cm diameter). After ten weeks they were transferred to the standard boxes described above for the deprived treatment.

A total of 160 individuals of 14 maternal lines participated in the experiment (treatments: d: N = 51, p: N = 58, g: N = 51). Cohort 1 and 2 consisted of 44 individuals each, cohort 3 consisted of 72 individuals.

2.2. Behavioral tests

We tested all individuals twice each for their behavior in an open field and towards a novel object. In total, we recorded eight different behaviors during these tests (see Tab. 1). Behavioral tests took place in a soundproof room with no windows between 16.7.2013 and 10.8.2013 for cohort 1 and 2 when spiderlings were 51.0 (±0.85 SD) and 52.2 (±1.9 SD) weeks of age, respectively. Spiders of cohort 3 were tested between 27.02.2014 and 26.03.2014 aged 35.1 (±0.97 SD) weeks. All individuals were retested after seven days to determine behavioral consistency. We tested three individuals simultaneously, if possible one from each (49 %) or at least from two (40%) treatments. All spiders were tested in visual isolation from one another.

Table 1: Variables recorded from the open field (OF) and novel object (NO) test as measures of exploratory behavior.

Variable name	Description	Test
Latency to emerge OF	latency to leave the start cap	Open field
Percentage of total area visited OF	percent of fields visited	Open field
Visitation central area OF	whether (yes/no) the individual entered the central area in the last 7.5 min	Open field
Activity in central area OF	duration of being active in the central area relative to the total exploration time i.e. after leaving the start cap	Open field
Resting OF	total duration of resting once the spider had left the start cap (> 3 sec. without movement)	Open field
Touched NO	whether (yes/no) the spider touched the novel object or not	Novel object
Latency NO	latency to touch the object (of those who did touch the NO)	Novel object

The open-field test started after a 30 minutes acclimatization phase to the test room. In a similar approach to Carducci & Jakob (2000) we divided the arena (a plastic box 145x110x68mm) into 30 small quadratic fields (2.80 x 2.90 cm) with a central and an edge area to quantify activity (see Fig. 1). Acclimatization started after the spider was put into a white opaque plastic cap (5.5 cm diameter, 1.2 cm high, Fig. 1). The cap was half-covered with grey plastic foil to generate cover for the spiders. The rationale was that the cap would function as a safe retreat that the spiders would only leave when motivated to explore the open field. Spiders were given a total of 60 minutes to climb out of the start cap and to explore the arena. If spiders did not leave the start cap we removed them from analyses for that trial (in the first trial: d: N = 3, g: N = 6, p: N = 4 and in the second trial d: N = 3, g: N = 2, p: N = 2).

After the open field test we transferred spiders back into the plastic cap, which was covered to prevent spiders from climbing out. A novel object (a greenish wooden barrel: 1.5cm diameter, 1 cm high) was placed at the opposite end of the arena (Fig. 1). After removal of the cover of the cap the spiders were allowed to explore the arena and the novel object for 30 minutes.

We videotaped the behavior and the experimenter (D.R.) left the room for the duration of the tests. After each test the arenas and novel objects were cleaned with water.

2.3. Video analysis

All video clips were anonymized and randomized by a third person before being analyzed (by D.R.). For the open field test we analyzed the first 7.5 minutes and minute 22.5 -30 of each trial (15 min total). The remaining fifteen minutes were not included in order to reduce time of analyzing. For the novel object test all 30 minutes were analyzed.

2.4. Data analyses

All analyses were done using R 3.1.0, (RCoreTeam, 2014) except calculations using the rptR package (Schielzeth and Nakagawa, 2011) for which we used R.2.15.1, (RCoreTeam, 2012) because this package was not yet implemented for latest R versions.

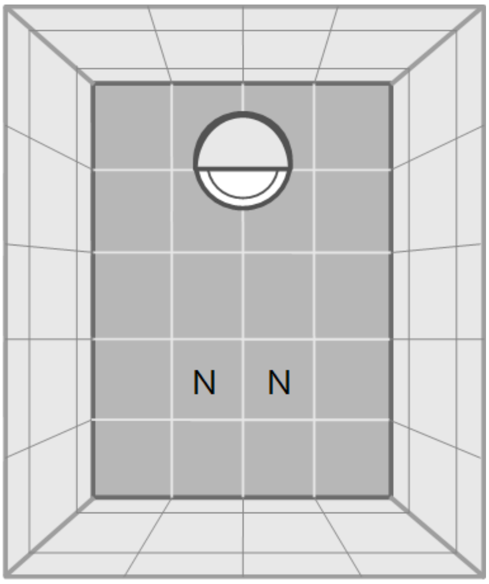

Figure 1: Schematic drawing of test arena for both, the open field and the novel object test. Dark grey fields indicate ground, light grey fields indicate walls. In one end of the arena a white opaque plastic cap is shown which functioned as start point. The cap was half-covered with grey plastic foil to generate shelter for the spiders. The letters "N" indicate the two possible positions in which the novel object was introduced at the beginning of the novel object test. The drawing is not to scale.

In order to explore whether different behavioral variables correlate with one another we ran Spearman rank correlations with data obtained from the first trial. To avoid duplication of results we excluded the total number of fields visited during the open field test (visits and revisits) which correlated strongly with the percentage of total area visited in the open field ("percentage of area visited OF"; $r_s = 0.606$; $p< 0.001$). All other variable combinations correlated only moderately or less ($r_s < 0.42$) and thus a total of seven variables were included in further analyses. We also ran a principal component analysis to reduce the number of variables. However, sufficient principal components together should account for 90 % of the total variation (Crawley, 2013). In our case this would have meant to use nearly as many components as original variables. We therefore only used the original variables which are easy to interpret and facilitate comparison with other studies.

To assess the influence of our treatments and cohorts on the behavioral level of individuals, we used several GEEs (general estimated equations); GEEs are extensions of GLMs and are a robust way for analyzing correlated data (here: data of individuals from the same family) and especially useful when comparing population averages (Liang and Zeger, 1986; Quinn and Keough, 2002; Zuur et al., 2009; Zhang et al., 2012). We used the R package "geepack" (Halekoh et al., 2006) to estimate the effects of rearing conditions (treatment and cohorts) on the mean level of the in Table 1 mentioned seven behavioral variables obtained from the first trial. To account for potential family effects, we included the ID of the mother as cluster variable. In all models we included the two-way interactions between treatment and cohort and between treatment and sex as explanatory variables, as well as their main effects. We also included the variables "latency to emerge OF" and "latency to emerge NO" respectively (see Tab. 1) in the analyses because we wanted to control for differences in the actual duration each individual had spent in the arena outside of the start cap. The "latency to emerge OF" was not included in the analysis of the variable "activity in central area OF" which is a relative estimate. Here, the variation in the time in the arena is already corrected for by different start times. Because many spiders did not touch the novel object (37 of 141) and thus were removed for estimations of the depending variable "latency NO" we excluded the factor "sex" in this analysis as not to overly decrease the sample size (the sex could not be determined for all individuals).

Prior to analysis we excluded missing data so that sample sizes vary for different analyses (see Tab. 2). If required, variables were transformed using the "powerTransform" function of the R package "car" (Fox and Weisberg, 2011) or adequate error structures were used to meet model assumptions (i.e. binomial error structure for binary data; see Tab. 2). Maximal models were simplified step-wise by taking each term out in turn, then excluding the least significant term at each step, starting with interactions first, given the removal of a term did not significantly reduce the explanatory power of the model (Crawley, 2002). We tested whether the explanatory power of the simpler model was significantly reduced compared to the more complex model using Wald statistics (Zuur et al., 2009). Model simplification was continued until the minimal model was found, i.e. the model which included only significant explanatory variables (or main effects which were included in significant interactions). P-values and associated test statistics given for non-significant terms come from the time a term dropped out of the model (see Tab. 2). When the rearing variables (treatment p, d and g and cohorts 1, 2, and 3) were not included in significant interactions but had significant effects on the response variable, we checked for differences between the levels by merging factor levels (compare Crawley, 2002) and compared the explanatory power of the simpler and more complex model. P-values given come from these comparisons (see Tab. 3).

To assess behavioral consistency we estimated behavioral repeatabilities and their 95% confidence intervals from generalized linear mixed effects models using "rptR" package (with 1000 bootstraps and permutations; Nakagawa and Schielzeth, 2010). If confidence intervals did not include zero, repeatability was regarded as significant. We analyzed repeatability over the whole data set (Tab. 4) and within each treatment separately (Tab. 5). For further details on the specific models used, please see Table 4 and Table 5.

In further analyses we investigated genotype by environment interactions. We used the maternal line as a proxy for genotype (but please note that individuals within a family were not genetically identical and that we cannot rule out pre-hatching maternal effects; we therefore use the term "family by environment" interaction). We fitted generalized linear models, GLMs, with our behavioral variables as responses and the interaction between maternal line and treatment as well as their main effects as explanatory variables. We included only families for which we had data from at least two individuals per treatment (total number of individuals per families and test ranged from 10 – 17 across treatments). Only data of the first round of behavioral tests were used in these analyses. In order to meet model assumptions, data were either transformed using the "powerTransform" function of the R package "car" (Fox and Weisberg, 2011)" or adequate error structures were used (see above;

for details see Tab. 6). Significance of interactions was tested with likelihood ratio tests comparing the model with and without this interaction (see Crawley, 2002).

3. Results

3.1. Early environmental effects on inter-individual variation in behavior (mean level differences)

All behavioral variables were affected by the rearing condition with the exception of whether or not spiders touched the novel object ("touched NO"; Tab. 2). Spiders from the deprived treatment tended to be least exploratory: they needed longer to leave the start cap ("latency to emerge OF") than spiders from the physically and socially enriched treatments in the open field test (Fig. 2a & Tab. 3). Spiders from the physically enriched treatment visited more percent of the total area ("percentage of area visited OF") than spiders from the other two treatments (Fig. 2b & Tab. 3). There was a significant effect of treatment on resting duration ("resting OF") depending on the sex of the individual with males resting less in the deprived and physically enriched treatments but more in the social treatment than females (Tab. 2). Furthermore, there were treatment effects on the likelihood for entering the central area ("visitation central area OF"), time spent active in the center ("activity in central area OF"), and in the latency to touch the novel object ("latency NO") but different for the cohorts (cohort x treatment, Tab. 2). Finally, cohort 3 needed less time to climb out the start cap in the open field tests and rested less than spiders from the other two cohorts (Tab. 3).

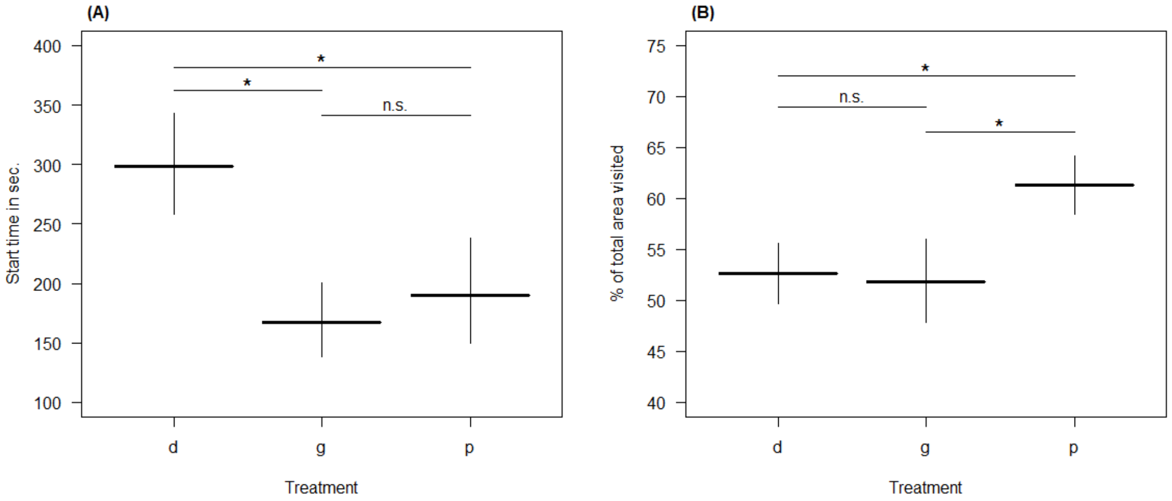

Figure 2: Predicted mean levels (± SE) of behavioral responses in an open field test by spiders raised in one of three different treatment groups (d = "socially and physically deprived"; g = "socially enriched"; p = "physically enriched"). (A) shows the latency to emerge; (B) shows the percentage of area visited i.e. number of fields visited once. All predictions derive from general estimated equations models (GEEs) after stepwise reduction to minimal adequate model including only significant terms. "n.s." indicates non-significant ($p > 0.05$) and "*" significant ($p \leq 0.05$) differences between the mean levels of groups.

Table 2: Model outputs (GEEs) indicating effects on the mean level behavior shown in an open field test (OF) and a novel object test (NO). P-values derived from Wald tests comparing models with and without the explanatory variable (Zuur et al. 2009). P-values for significant terms (indicated in **bold**) derive from minimal adequate models. P-values for non-significant terms derive from models just before the terms were dropped. Coefficients for significant terms derive from minimal adequate models. Coefficients for non-significant terms (in brackets) derive from models just before the terms were dropped. (Please note that estimates of coefficients alter during the model simplification). Reference levels ("Mean") are always treatment = "d", i.e. deprived reared spiders; cohort = "1"; and sex="male". "TreatG" refers to treatment "g", i.e. socially enriched reared spiders; "TreatP" refers to treatment "p", i.e. physically enriched reared spiders. "Cohort2" refers to cohort = "1"; "Cohort3" refers to cohort = "3" and "SexF" refers to female spiders. N = sample size, i.e. number of spiders tested.

Model for response variable	Error Structure	N	Coefficients (of explanatory variable)	Estimate	Std. error	$\chi2$	p-value
Latency to emerge OF	Gaussian	136	Mean	4.788	0.187		
			Treatment x Cohort			χ^2_4=1.52	p=0.82
			TreatG:Cohort2	(-0.363)	(0.602)		
			TreatP:Cohort2	(0.284)	(0.399)		
			TreatG:Cohort3	(-0.157)	(0.468)		
			TreatP:Cohort3	(-0.256)	(0.567)		
			Treatment x Sex			χ^2_2=2.04	p=0.36
			TreatG:SexF	(-0.620)	(0.451)		
			TreatP:SexF	(-0.325)	(0.391)		
			Treatment			χ^2_2=11.5	p=**0.003**
			TreatG	-0.268	0.557		
			TreatP	-0.339	0.532		
			Cohort			χ^2_2=25.0	p**<0.001**
			Cohort2	0.077	0.207		
			Cohort3	-0.858	0.192		
			SexF	(0.231)	(0.189)	χ^2_2=1.5	p=0.22
Percentage of area visited OF	Gaussian	135	Mean	12.391	0.437		
			Treatment x Cohort			χ^2_4=1.67	p=0.8
			TreatG:Cohort2	(-0.816)	(2.252)		
			TreatP:Cohort2	(-0.635)	(1.097)		
			TreatG:Cohort3	(-1.406)	(1.594)		
			TreatP:Cohort3	(-1.129)	(1.099)		
			Treatment x Sex			χ^2_2=1.26	p=0.53
			TreatG:SexF	(-1.524)	(1.439)		
			TreatP:SexF	(-0.281)	(1.055)		
			Treatment			χ^2_2=15.7	p**<0.001**
			TreatG	-0.116	0.616		
			TreatP	1.266	0.400		
			Cohort			χ^2_2=2.22	p=0.33
			Cohort2	(0.328)	(0.563)		

			Cohort3	(1.012)	(0.752)		
			SexF	(0.180)	(0.240)	$\chi^2_1=0.56$	p=0.45
			Latency to emerge OF	-0.005	0.001	$\chi^2_1=40.8$	p**<0.001**
Visitation central area OF	Binomial	135	Mean	0.009	0.796		
			Treatment x cohort			$\chi^2_4=25.6$	p**<0.001**
			TreatG:Cohort2	0.335	0.914		
			TreatP:Cohort2	0.842	1.092		
			TreatG:Cohort3	-1.914	0.347		
			TreatP:Cohort3	1.108	1.159		
			Treatment x Sex			$\chi^2_2=2.08$	p=0.35
			TreatG:SexF	1.513	1.066		
			TreatP:SexF	0.293	0.818		
			Treatment				
			TreatG	1.225	0.288		
			TreatP	0.111	0.760		
			Cohort				
			Cohort2	-0.666	1.080		
			Cohort3	-0.460	0.904		
			SexF	-0.643	0.374	$\chi^2_1=2.95$	p=0.086
			Latency to emerge OF	0.001	0.001	$\chi^2_1=1.0$	p=0.32
Activity in central area OF	Gaussian	114	Mean	0.508	0.050		
			Treatment x Cohort			$\chi^2_4=13.8$	p=**0.008**
			TreatG:Cohort2	0.045	0.054		
			TreatP:Cohort2	-0.098	0.051		
			TreatG:Cohort3	-0.006	0.045		
			TreatP:Cohort3	-0.095	0.053		
			Treatment x Sex			$\chi^2_2=4.22$	p=0.12
			TreatG:SexF	(-0.031)	(0.036)		
			TreatP:SexF	(-0.071)	(0.035)		
			Treatment				
			TreatG	-0.016	0.039		
			TreatP	0.074	0.048		
			Cohort				
			Cohort2	0.015	0.053		
			Cohort3	-0.025	0.059		
			SexF	(-0.008)	(0.015)	$\chi^2_1=0.30$	p=0.59
Resting time OF	Gaussian	132	Mean	0.787	0.041		
			Tratment x Cohort			$\chi^2_4=5.89$	p=0.21
			TreatG:Cohort2	(-0.071)	(0.059)		
			TreatP:Cohort2	(-0.030)	(0.031)		
			TreatG:Cohort3	(-0.088)	(0.039)		
			TreatP:Cohort3	(-0.029)	(0.037)		
			Treatment x Sex			$\chi^2_2=6.5$	p=**0.039**
			TreatG:SexF	-0.041	0.025		
			TreatP:SexF	0.015	0.022		
			Treatment				

			TreatG	0.018	0.015		
			TreatP	-0.055	0.016		
			Cohort			χ^2_2=22.4	p**<0.001**
			Cohort2	-0.020	0.025		
			Cohort3	-0.010	0.024		
			SexF	0.010	0.021		
			Latency to emerge OF	(-0.00003)	(0.00002)	χ^2_1=1.5	p=0.22
Touched NO	Binomial	141	Mean	1.035	0.261		
			Treatment x Cohort			χ^2_4=6.62	p=0.16
			TreatG:Cohort2	(4.50e+15)	(1.45e+06)		
			TreatP:Cohort2	(0.397)	(0.481)		
			TreatG:Cohort3	(-0.986)	(1.13)		
			TreatP:Cohort3	(0.357)	(1.14)		
			Treatment x Sex			χ^2_2=0.68	p=0.71
			TreatG:SexF	(1.590)	(0.644)		
			TreatP:SexF	(-0.346)	(0.834)		
			Treatment			χ^2_2=1.28	p=0.53
			TreatG	(0.345)	(0.537)		
			TreatP	(0.246)	(0.341)		
			Cohort			χ^2_2=0.52	p=0.77
			Cohort2	(-0.123)	(0.601)		
			Cohort3	(0.279)	(0.439)		
			SexF	(-0.217)	(0.364)	χ^2_1=0.36	p=0.55
			Latency to emerge NO	(-0.001)	(0.001)	χ^2_1=0.65	p=0.42
			Resting time OF	(0.287)	(1.213)	χ^2_1=0.06	p=0.81
Latency NO	Gaussian	115	Mean	8.940	0.962		
			Treatment x Cohort			χ^2_4=10.0	p=**0.04**
			TreatG:Cohort2	-3.405	1.451		
			TreatP:Cohort2	-0.551	1.279		
			TreatG:Cohort3	-0.710	1.614		
			TreatP:Cohort3	-0.232	1.647		
			Treatment				
			TreatG	1.473	1.240		
			TreatP	-0.245	0.847		
			Cohort				
			Cohort2	2.054	1.125		
			Cohort3	0.374	1.345		
			Latency to emerge NO	0.005	0.001	χ^2_1=0.65	p**<0.001**
			Resting time OF	(1.929)	(3.159)	χ^2_1=0.373	p=0.54

Table 3: Model outputs (GEEs) testing for behavioral differences among treatments or cohorts in an open field test (first trial). The letters in the columns for explanatory variables symbolize the treatments (d= deprived; g= group living; p= physically enriched) and the cohorts (1, 2, and 3) that were compared. P-values derived from Wald tests comparing models (Zuur et al. 2009) with and without the indicated levels merged together. N = sample size, i.e. number of spiders tested. Significance is indicated in **bold**.

Response variable	N	Explanatory variables					
		Treatment: d;g	Treatment: d;p	Treatment: g;p	Cohort: 1;2	Cohort: 1;3	Cohort: 2;3
Latency to emerge OF	136	**p<0.001** (χ^2_1=11.5)	**p=0.037** (χ^2_1=4.35)	p=0.47 (χ^2_1=0.52)	p=0.71 (χ^2_1=0.14)	**p<0.001** (χ^2_1=20.1)	**p<0.001** (χ^2_1=17.6)
Percentage of area visited OF	135	p=0.85 (χ^2_1=0.04)	**p=0.002** (χ^2_1=10.0)	**p=0.007** (χ^2_1=7.3)	--------	--------	--------
Resting OF	136	--------	--------	--------	p=0.4187 (χ^2_1=0.65)	**p<0.001** (χ^2_1=15.55)	**p<0.001** (χ^2_1=14.8)

3.2. Repeatability

All behavioral measures were repeatable over time, except the latency to touch the novel object (Tab. 4). However, when analyzed separately for each treatment, few behavioral variables remained significantly repeatable (Tab. 5): one in the deprived and three out of seven in the socially and in the physically enriched treatment.

3.3. Family by environment interactions

Family by environment interactions were found on those three behavioral variables that were not repeatable in any of the three treatment groups, namely: whether or not spiders entered the central area of the open field, whether they touched the novel object, and the latency to do so (Tab. 6).

Table 4: Repeatabilities of behavior shown in the open field test (OF) and the novel object test (NO) over all individuals. Estimates derive from models with bootstraps and permutations (each 1000). Variables are listed in the left column and repeatabilities (R), their standard errors (SE) and 95% confidence intervals (given in original scale). "rptR methods" refers to the used method in the analysis (see Nakagawa and Schielzeth 2010). Note: not each individual participated in both test runs therefore number of trials are not twice the size as number of individuals. N Ind. = number of individuals. N Tr. = number of trials. Significance (i.e. confidence interval not including zero) is indicated in **bold**.

Variable	Error Structure	N Ind.	N Tr.	R	SE	Confidence Interval	rptR Method	link function
Latency to emerge OF	Gaussian	158	300	0.33	0.077	**0.183-0.478**	LMM.REML	-
Percentage of area visited OF	Gaussian	159	310	0.264	0.08	**0.105-0.415**	LMM.REML	-
Visitation central area OF	Binomial	159	311	0.278	0.081	**0.07-0.391**	PQL method	logitlink
Activity in central area OF	Gaussian	146	249	0.341	0.089	**0.165-0.507**	LMM.REML	-
Resting OF	Gaussian	155	285	0.477	0.066	**0.332-0.597**	LMM.REML	-
Touched NO	Binomial	160	320	0.203	0.071	**0.085-0.357**	PQL method	logitlink
Latency NO	Gaussian	140	232	0.045	0.076	0-0.247	LMM.REML	-

Table 5: Repeatabilities of behavior shown in the open field test (OF) and the novel object test (NO) tested separately for each treatment. Estimates derive from models with bootstraps and permutations (each 1000). Variables are shown in the left column and repeatabilities (R), their standard errors (SE) and 95% confidence intervals (given in original scale) are given. “rptR methods” refers to the used method in the analysis (see Nakagawa and Schielzeth 2010). Note: not all individuals participated in both test series, so that the numbers of trials are not twice the number of individuals. N Ind. = number of individuals. N Tr. = number of trials. Significance (i.e. confidence interval not including zero) is indicated in **bold**.

		Treatment d					Treatment g					Treatment p				
Variable	Error Structure	N Ind.	N Tr.	R	SE	CI	N Ind.	N Tr.	R	SE	CI	N Ind.	N Tr.	R	SE	CI
Latency to emerge OF	Gaussian	51	96	0.208	0.135	0-0.481	50	94	0.306	0.136	**0.038-0.561**	57	110	0.310	0.120	**0.067-0.540**
Percentage of area visited OF	Gaussian	50	95	0.196	0.133	0-0.465	51	101	0.308	0.124	**0.044-0.520**	58	114	0.227	0.121	0-0.462
Visitation central area OF	Binomial	50	96	0.358	0.144	0-0.574	51	101	0.227	0.134	0-0.488	58	114	0.228	0.124	0-0.440
Activity in central area OF	Gaussian	44	69	0.217	0.167	0-0.572	48	82	0	0.101	0-0.339	54	98	0.678	0.081	**0.499-0.809**
Resting OF	Gaussian	48	87	0.450	0.450	**0.161-0.661**	50	96	0.613	0.093	**0.386-0.759**	57	102	0.355	0.123	**0.107-0.566**
Touched NO	Binomial	51	102	0.176	0.128	0-0.434	51	102	0.139	0.122	0-0.400	58	116	0.263	0.118	0-0.483
Latency NO	Gaussian	44	69	0.154	0.159	0-0.518	47	79	0	0.103	0-0.351	49	84	0.165	0.145	0-0.474

Table 6: Model outputs (GLMs) testing for family x environment interactions fitting an interaction between maternal line and treatment as explanatory variables on behavior shown in the open field test (OF) and the novel object test (NO). We included only families in which we had data from at least two individuals per treatment (five families for "Activity in central area", six families for all other variables). P-values derived from likelihood ratio tests ("F" = F-test; "χ^2" = Chi-square Test) of models with and without the interaction. Significance is indicated in **bold**.

Variable	Error Structure	DF	Test-statistic	P-value
Latency to emerge OF	Gaussian	10,60	F =0.54	0.858
Percentage of area visited OF	Gaussian	10,70	F =0.78	0.648
Visitation central area OF	Binomial	1	χ^2 =18.7	**0.044**
Activity in central area OF	Gaussian	8,48	F =1.69	0.125
Resting OF	Gaussian	10,66	F =1.72	0.326
Touched NO	Binomial	1	χ^2 =19.38	**0.036**
Latency NO	Gaussian	10,52	F =2.14	**0.038**

4. Discussion

The early environment in which spiders were raised significantly affected their exploratory tendencies. Individual differences in the investigated traits were repeatable (at least over the whole study population), hence, we found evidence for personality differences. These findings combined indicate that external stimuli can influence the development of personality traits. We also found suggestive evidence for family by environmental interactions on behavioral traits potentially indicating that plasticity itself might be under selection.

We found differences in the mean level of behaviors in our treatment groups, suggesting that the early environment influenced the development of exploratory behavior in the jumping spiders. In particular, individuals raised in the physically enriched treatment group were more exploratory than their siblings in the deprived treatment. This finding corroborates results from earlier studies on spiders (e.g. Carducci and Jakob, 2000; Buchsbaum and Morse, 2012; Bengston et al., 2014), nematodes (Rose et al., 2005) and vertebrates (e.g. Rosenzweig and Bennett, 1996; van Praag et al., 2000). Exploration, as an information-gathering process, might be more beneficial in an enriched (or generally more complex) than in a deprived (or generally very simple) environment with little to explore. Exploration can be costly (e.g. in terms of increased metabolism, or mortality risk) and thus individuals should not explore if not necessary. We found furthermore a sex-dependent treatment effect on the resting duration with group living males resting more than solitarily reared ones. Sexual size dimorphism is associated with a risk of cannibalism by the larger females (Wilder and Rypstra, 2008; Liedtke, J., personal observation), which may suggest that group living males are less active and thereby reduce encounter rates with females (compare sex-reversed pattern found in mice offspring Heiming et al., 2009; and Hedrick and Kortet, 2012, for sex-dependent consistency over metamorphosis). Accordingly, a plastic response to the (early) environmental condition that an individual experiences seems sensible. Indeed, external influences particularly during development might have long lasting effects (reviewed in e.g. Snell-Rood, 2013).

The different responses of the three cohorts in our experiment may be an indication for sensitive phases (e.g. Groothuis and Trillmich, 2011) or “developmental-windows” (Luttbeg and Sih, 2010; Faulk and Dolinoy, 2011) within the developmental process of personality differences. The cohorts experienced different experimental conditions: in contrast to spiders from cohort 1 and 3, spiders from the cohort 2 were raised in groups for the first two months before they were assigned to the three treatments. Therefore, this cohort received an early social enrichment, regardless of later treatment. Results show that individuals from cohort 2 differed from the other two cohorts in several behaviors. Although it is difficult to explain the direction of these effects, these results indicate that, at least for social enrichment, environmental conditions encountered in the first two months seem to have long lasting effects (permanent environmental effects sensu Dochtermann et al., 2015) on the development of behavioral tendencies. These patterns deserve further attention by follow-up studies in order to understand the proximate mechanisms of these apparently sensitive periods and if such effects can be induced by manipulation of the physical environment as well.

Group living also had positive effects on exploratory behavior in non-social contexts. This is in contrast to previous studies showing no effects of group living on behavior in non-social tests (reviewed in Taborsky et al., 2012). Yet, other studies found impairments of social isolation in multiple aspects of behavior (reviewed in e.g. Ballen et al., 2014). Hence, at least in some species contact to conspecifics can induce stable behavioral differences in other than the social realm. This suggests that early environmental conditions can create behavioral differences in a context-general way.

Noteworthy, we found significant family by environmental interactions on three of the investigated behavioral variables. This potentially indicates genetic variation for plasticity and suggests that plasticity itself might be under natural selection (Pigliucci, 2005; Dingemanse et al., 2010). Whether higher or lower plasticity is favored might depend on how stable and predictable environmental conditions are over time, with more stable conditions potentially favoring lower plasticity (see e.g. Dingemanse et al., 2010; Snell-Rood, 2013). But please note that we cannot rule out pre-hatching maternal effects in our study. Further studies are required to provide more insights.

Five behaviors that were repeatable over the whole population were not repeatable in all subpopulations (i.e. treatment groups) when estimated separately. Also, some confidence intervals of repeatabilities overlapped greatly among treatment groups, suggesting repeatability was not necessarily significantly different among groups. Therefore, the extent of repeatability was likely not induced by the environment conditions experienced. The pattern, that behaviors were repeatable across all individuals but not within all treatment groups, could potentially arise if between-individual variation in behavior within treatment groups is rather low (compared to between-individual variation across treatments) and/or if within-individual consistency in behavior is low. In both behavioral tests the average response of the deprived group was lower than that of the two enriched treatment groups, thereby leading to mean-level consistency (i.e. consistent differences between the average responses of each group; sensu Stamps and Groothuis, 2010). These consistent differences between treatment groups may explain why we found significant effects when we tested for repeatability over the whole population. The behavioral consistency of individual spiders within each treatment, on the other hand, may have been rather low, so that we found behavioral repeatability in fewer variables when treatments were assessed separately. This may indicate that for these variables, repeatability is mostly an effect of environmental induction by divergently shifting the mean level of each subpopulation (i.e. deprived group towards lower versus enriched groups towards higher exploratory tendencies). Yet, these interpretations should be viewed with caution, since the absence of repeatable behavior within treatments in the five variables mentioned above could alternatively be an artefact of lower sample sizes within than among treatments. However, sample sizes in each subpopulation were still decent (≥ 38; see Tab. 5) indicating that these patterns might be biological relevant and deserve attention in further studies. For example, studies using samples derived from larger study areas may be more likely to find repeatability even with relative low individual stability because they might include individuals with different environmental backgrounds.

Nevertheless, we also should bear in mind that environmental induction does not necessarily lead to differential consistency but could even lead to the opposite. If individuals have different genotypes they may have different innate levels in behavioral expressions. However, plasticity, i.e. the ability to respond sensitively to the environment, could lead to an approximation of these initial differences according to local conditions. Furthermore, we expect that, with plasticity being costly (see e.g. Dall et al., 2004; Pigliucci, 2005), individuals having an innate behavioral level closer to the local optimum to have an improved fitness (all other things being equal) because they need less modification in their responses. This implies that mean level should be under selection which may explain the differences between families in this study.

Taken together, results found in this study indicate that the development of personality traits, at least one aspect of personality: mean level of behavior, is influenced by the environmental conditions experienced; families may differ in plasticity and thus provide the raw material for natural selection to act upon; and finally, observed patterns of personality distribution found in the field may be crucially influenced by plastic responses of sensitive systems.

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General Discussion

With my thesis, I aimed to identify which environmental factors may affect the development of cognitive abilities in the jumping spider *Marpissa muscosa*. The results of this project confirm that spiders are able to learn and to reverse the learned association (Chapter 1). Furthermore, the overall findings show remarkable influences of rearing conditions on the development of phenotypes in these jumping spiders (Chapter 2 - 4). More specifically, I found, as expected, that socially reared spiders were more skilled in social interactions (Chapter 3), which is in accordance with findings in other species (reviewed in Taborsky & Oliveira 2012), but has rarely been shown in spiders (but see Clark et al. 2015). Interestingly, socially reared spiders also performed better in a learning task in which a food reward was hidden in a t-maze (Chapter 2). Importantly, this task was tested in isolation and social skills were not required to solve it. The fact that socially reared spiders were better in two tasks allocated to different domains may be interpreted in different ways. Below, I will present alternative explanations (non-exhaustive) to interpret the results. These are embedded in two general theories of brain evolution: the domain-specific scenario versus the domain-general scenario (see e.g. Heyes 2012). These different interpretations share the underlying assumption that the tasks tested in this project are cognitively demanding, i.e. involving perception and processing of information. Cognitive processes require neuronal tissue, which is metabolically and developmentally costly (Niven & Laughlin 2008; Mery & Burns 2010; Buchanan et al. 2013). Indeed, it has been shown that investments in cognitive abilities are traded off against other traits, for example competitive ability (Mery & Kawecki 2003), gut size (Kotrschal et al. 2013), or fecundity (Snell-Rood et al. 2011). Furthermore, there is accumulating evidence that neuronal systems need environmental input in order to develop normally. It has been shown that brain development can be influenced by early environmental conditions in a variety of taxa including spiders, fish, amphibians, and humans (Punzo & Ludwig 2002; Kihslinger & Nevitt 2006; Gonda et al. 2009; Gonda et al. 2010; Sheridan & McLaughlin 2014). Yet, the precise mechanisms behind the evolution and development of the brain remain highly disputed.

One interpretation of my findings is based on a modular view of the brain morphology and assumes that the two tested abilities, i.e. learning in a maze and social skills, are governed by independent neuronal compartments (or modules; i.e. the theory of mosaic brain evolution; Macphail & Bolhuis 2001; Shettleworth 2012). Under this assumption, we might expect that abilities are traded off against each other and individuals who are successful in a social task should be less successful in a task of the physical domain and vice versa. However, we did not find such a trade-off between learning and social competence, in fact spiders reared in groups were the best performers in both task types. This begs the question why socially enriched spiders are better than deprived spiders in a non-social task. Furthermore, against my expectations, socially reared spiders even tended to be more successful than physically enriched spiders. One possible explanation could be that physically enriched spiders may have traded off their learning skills against investment in their increased motor activity, as shown in the exploration task (see Chapter 4 and further below in the discussion). Indeed, investigations of brain morphology (Steinhoff, P. O. M; Liedtke, J; Sombke, A; Schneider, J.M. & Uhl, G; unpublished) suggest that physically enriched spiders develop a larger arcuate body, which is likely to be related to motor activity (Homberg 2008; Loesel et al. 2011). At first glance it may seem counterproductive to reduce associative learning abilities in order to enhance exploration activity since the value of exploration should diminish if an individual cannot remember what it has explored. However, there is some evidence that higher exploration tendencies on the cost of accurate learning may be adaptive under certain circumstances, for example under high food abundances, and is often referred to as having a "proactive" personality (reviewed e.g. in Sih et al. 2004b; Réale et al. 2007). While this is one possible explanation, the question remains as to why socially reared spiders are better than the deprived spiders, which did not face trade-offs neither with cognitive nor with motor activity?

An alternative explanation assumes a domain-general ability of the brain, and is somewhat contrary to mosaic brain hypothesis (see e.g. Byrne & Bates 2007; Heyes 2012). Under this hypothesis, neuronal tissue for higher cognitive tasks may be located in one compartment with no clear-cut task-specialisation. On this level, spiders would have a generalistic brain, which is able to handle cognitive processes deriving from different challenges. Consequently, an increase in the computational power caused by one domain should increase abilities in other domains as well. Thus, the increased cognitive abilities of group-living spiders induced by challenges of the social world may allow them to solve non-social tasks such as the t-maze. This could explain why socially reared spiders were better than spiders of both other treatment groups. However, physically enriched spiders were slightly (although not significantly) better than the deprived spiders in the learning task. Following the approach of domain-general abilities, this finding would anticipate a slightly better performance in the social task as well. Unfortunately, the results obtained from that task do not allow a clear conclusion to be drawn. Some behavioural aspects shown by physically enriched spiders may be cautiously interpreted as indicating them to be more socially competent than deprived spiders (see Chapter 3 for more details). The idea of a domain-general brain is attractive because it assumes reduced costs of neuronal tissue and larger brains. Indeed, Srinivasan (2006) pointed out that brains of small animals such as arthropods are under significant size constraints. Limited space may favour generalistic brains, possibly at the cost of accuracy in some functions (Chittka & Niven 2009).

Yet another alternative interpretation is that social competence involves learning, and in order to be socially competent an organism must invest in both neuronal structures that govern learning abilities and in neuronal structures which support abilities needed for social interactions. This approach lays somewhat between the generalistic and the mosaic brain hypotheses. While specialised areas for specific tasks, e.g. for self-assessment, are assumed as in the mosaic hypothesis, neuronal complexes suited for the use in multiple situations, such as associative learning abilities resemble a generalistic approach. Indeed, the mammalian brain might have such an organisation. For example, the human forebrain has highly specialised parts such as the visual cortex, the auditory cortex, and centres for speech (see e.g. Shepherd 2004), but it also includes areas such as the associative cortex, which is activated during tasks of multiple types. Hence, the human brain uses domain-specific but also domain-general capacities (compare Shettleworth 2012). Personally, I favour this intermediate approach since it best explains both neuroanatomical and behavioural findings.

In any case, all of the above explanations suggest that socially reared spiders invested more in neuronal tissue involved in learning and social competence. Unfortunately, I was not able to fully disentangle whether they faced a trade-off or if they were released from investments in other traits. As noted above, socially reared spiders were less active, perhaps to avoid the risk of harmful interactions with conspecifics. 3D reconstructions and size measurements of brains suggest that this reduction in motor-activity is associated with lower investment in the arcuate body, which tends to be smaller than in physically enriched spiders, although not significantly so (Steinhoff et al. unpublished). This reduced investment might have freed resources which then could be allocated to an improvement of abilities such as social competence which required for group living. On the other hand, I cannot rule out that socially reared spiders needed to invest in social competence and therefore could not allocate more energy into exploration and arcuate body accordingly – thus facing a trade-off. Of course, these explanations are not mutually exclusive and both might be partially true. Similarly, I cannot conclusively discern whether physically enriched spiders traded off their learning abilities or if they simply did not need any in their environment as discussed above.

Finally, trade-offs may have occurred with traits other than cognitive ones and their underlying neuronal tissue. Life-history traits such as longevity, body size, or fecundity are influenced by neuronal investment in many animal taxa (see references in Chapter 2 and above). Unfortunately, this has not been tested for *Marpissa muscosa* so far. Since some spiders from this project were still alive by the time of writing, analyses of life-history traits will be the subject of future investigations. Alternative approaches to test the presence and the nature of trade-offs could be to include a fourth treatment with spiders enriched in both domains (here trade-offs might become more clear), or to provide ad libitum food, thus releasing spiders from trade-offs caused by limited access to resources. Furthermore, socially reared spiders could be experimentally forced to move as much as physically enriched spiders, and it could then be recorded whether trade-offs would occur with other traits.

I would now like to shift the focus of the discussion to an integrated view on the development of so-called personalities. As expected, physically enriched spiders were on average the most explorative individuals (Chapter 4). Deprived spiders showed the least explorative tendencies, whereas socially reared spiders showed intermediate responses (Chapter 4). Since the behaviour was repeatable over time, I conclude that rearing conditions affect the development of personality. One explanation as to why animals may consistently differ in their behaviour is that their personalities develop in accordance to the environmental conditions in which they matured (e.g. Sachser et al. 2011; Sheridan & McLaughlin 2014). For example, a forager will easily find food resources under high food abundances and does not need to remember the precise location since its prey can be found everywhere. Under such circumstances, high exploratory tendencies with low learning abilities might constitute an adequate personality. This personality type is sometimes referred to as “proactive” (reviewed in e.g. Sih et al. 2004b; Carere et al. 2005; Réale et al. 2007). However, when food is rare and difficult to access, an animal may benefit from a slow and careful exploration of its environment and from relying on past experience. This alternative and opposing personality type has been called “reactive” (reviewed in e.g. Sih et al. 2004a; Carere et al. 2005; Réale et al. 2007). In general, these types can be described as two extremes of a continuum and, for matter of simplification it is convenient to concentrate on these two types here. While these examples describe mechanisms which fit different environments, theoretically both personality types (reactive and proactive) can coexist in the same environment (reviewed e.g. Sih et al. 2004b; Réale et al. 2010). For example, under negative frequency dependence both personality types may lead to the same payoff and thus could coexist in the same population (Dall et al. 2004; Mathot et al. 2011 see also Wolf & Weissing 2010). The behavioural pattern found in this thesis for physically and socially enriched spiders is in accordance with expectations based on the proactive-reactive continuum. Physically enriched spiders, for example, were more explorative (Chapter 4) but learned less accurately (Chapter 2). This seems to be suitable for their enriched environment, which provides much to explore at low risk (Chapter 2 & 4). Socially enriched spiders, on the other hand, were less active but more accurate at learning. The combination of an unstructured environment and the increased risk of harmful interactions with conspecifics may produce more careful and less exploratory personalities. In addition, the need to remember the location of potential rivals and the ability to show adequate display behaviour may both have confronted spiders raised in a group with cognitive challenges. Consequently, these challenges may have caused these spiders to invest more in learning abilities. Therefore, becoming a less exploratory but more accurate learner may be an adaptive response. Taken together, the findings suggest that personalities may develop in accordance with the environment in which an animal lives, including trade-offs between information gathering and risk-taking.

In contrast to socially or physically enriched spiders, deprived spiders did not fit into the theory of proactive-reactive personalities types as described above. Deprived spiders showed the lowest exploration tendencies (Chapter 4) and performed the worst in the learning task (Chapter 2). There are different possible explanations for these findings. For example, it has been proposed that the lack of sufficient environmental input during ontogeny can lead to the development of maladaptive phenotypes (Bateson et al. 2004; Branchi et al. 2006; Cacioppo & Hawkey 2009), including personalities (e.g. Curley et al. 2009; Ballen et al. 2014). Alternatively, deprived spiders may be adapted to their extreme uniform and constant environment in which neither exploration nor accurate learning generate any payoffs. Thus, they may have invested less into cognitive abilities and more into other traits, for example body size or fecundity. Consequently, I would assume lower fitness for deprived spiders when being placed in enriched environments later in life since they do not seem to have the cognitive abilities to handle the increased complexity. This is also a likely reason why many reintroduction projects, in which animals are raised in deprived conditions and then released into the wild, are often not very successful (McDougall et al. 2006). Furthermore, other studies have shown that the most exploratory individuals may also be the most accurate learners in several vertebrate taxa (reviewed in e.g. Scheid & Noe 2010; Trompf & Brown 2014). Together, this suggests that the reactive-proactive continuum may only exist under specific conditions and that we might find different correlations between exploration and learning abilities in different environments (compare Brydges et al. 2008; Houston 2010). For example, in a risky environment the most exploratory individuals may also be the best learners. If individuals face the risk of predation they need to know their environment well, e.g. remember where potential predators or hiding places are located. Individuals with weaker learning abilities may benefit from avoiding exploration in order to decrease the risk of harmful encounters. This positive correlation between exploration and learning is very different from what we would expect according to the proactive-reactive framework, in which a negative correlation between the two traits is suggested. The latter might be more profitable in environments with less predation. Indeed, there is evidence that predation may positively link exploration and learning in fish (see e.g. Dugatkin & Alfieri 2003; but see Brydges et al. 2008). In light of these considerations, it would be very interesting to look for treatment specific patterns. For example, we might expect that within the group treatment the most exploratory spiders are also the best learners since they face the risk of harmful interaction with their conspecifics. In the physically enriched treatment we might find patterns that resemble the proactive-reactive profile as described above (see e.g. Sih et al. 2004b; Réale et al. 2010). In the deprived treatment on the other hand, such correlations between exploration and learning may not exist due to the lack of environmental input which drive these patterns. Unfortunately, I was unable to investigate the learning performance on an individual level since the learning test was rather short due to time constraints and therefore such a comparison within treatments is not possible with the current data.

One possibility to disentangle whether personalities developed by spiders are adaptive or maladaptive due to the lack of environmental input (e.g. Curley et al. 2009; Ballen et al. 2014) would be to show fitness benefits in the deprived spiders relative to the other two treatments, e.g. in longevity or body size. Moreover, enriched spiders may have relatively lower fecundity when being experimentally transferred to deprived environments since they invested in traits which are unnecessary in deprived environments. Taken together, the results of my thesis suggest that the plastic response is not one-dimensional or rigid, but that the different phenotypes develop in a rather holistic way, integrating behavioural skills, such as learning and social competence with personalities. It remains to be tested whether life-history traits also respond plastically in conjunction with the demonstrated changes (compare Stamps 2007; Edenbrow & Croft 2013), and whether these integrative phenotypes are adaptive in terms of reproductive success. However, there is also a downside of such an integrative adjustment of phenotype. Once developmental plasticity has produced an integrative phenotype well suited to local environmental conditions it becomes difficult to reorganise the whole "package". In other words, it might be relatively simple to change a single behavioural tendency, but to change behaviour in conjunction with all other developed traits might be extremely difficult. Thus, individuals may not be able to respond appropriately if conditions change later in life. This might be one reason why personalities are limited in their plasticity and animals behave consistently despite potential maladaptive responses.

A further interesting finding of this thesis is that the sex of spiders influenced the development of behaviour (Chapter 2 - 4). Most specifically, females tended to be better at learning but performed significantly worse in reversal learning than males (Chapter 2). These differences may correspond to sex-specific selection pressures and trade-offs. For example, males may need to continuously re-evaluate the value of locations when searching for mating partners. Females, on the other hand, may not need reversal-learning abilities as they are more locally bound, and therefore may benefit more from investing in fecundity instead (see Chapter 2 and 4 for more detailed discussions). Another very interesting finding is that maternal lines (as a proxy for genetic effects) differ in their plastic response to the environmental conditions (see Chapter 4). This suggests sufficient genetic variation for selection to act on plasticity. This is important since it has been suggest that plasticity may in turn influence evolutionary processes. Depending on the precise circumstance, the ability of a genotype to respond plastically can both speed up but also hinder evolution (reviewed e.g. Dennett 1995; Huey et al. 2003; Buchanan et al. 2013). The precise mechanism behind these feedback loops, such as the Baldwin effect (Crispo 2007) or Waddington assimilation (Pigliucci et al. 2006), are beyond the scope of my thesis. However, I would like to point out that phenotypic plasticity can positively influence the survival of individuals, and eventually of entire species, when being confronted with new circumstances. In this regard, plasticity also plays a major role in nature conservation, since animals may cope more easily with human-made changes, e.g. due to agriculture, global change, or introduction to new habitats (Sol et al. 2005; McDougall et al. 2006; Sol et al. 2008). Finally, another important implication of enrichment studies extends to the more applied field of animal welfare, a field which in my opinion deserves more attention. In captivity, animals cannot pick a niche that suits their personality, and deprived or overcrowded conditions may often lead to the development of psychotic behaviour (Kihslinger & Nevitt 2006; Brockmark et al. 2010; Mason et al. 2013). My project shows that even in such “simple” organisms like arthropods, housing conditions can strongly affect the animals’ development. In order to allow for a normal development and for the wellbeing of captive animals, they should generally be held under enriched conditions. Yet, optimal enrichment differs between species and depends on individual differences within the species (see e.g. Bolhuis et al. 2005; Fox & Millam 2007) and thus should be properly investigated.

Taken together, environmental enrichment had a positive effect on the social competence and associative learning of spiders in this project. I detected no trade-off between the mean performances in the two different tasks (social skills and learning). However, I was unable to investigate this trade-off on an individual level due to a low per capita trial ratio in the learning task. Thus, it would be worthwhile to investigate if such trade-offs exist on an individual level within treatment groups in a follow-up study. Furthermore, it would be very interesting to search for possible trade-offs between performance and life-history traits, such as developmental time, body size and longevity between treatments and between individuals within treatments. In conclusion, increased social complexity in *Marpissa muscosa* was positively linked to social skills and learning abilities. Thus, it seems that social interactions drive the development of increased cognitive abilities, at least in this species. Deprived spiders, on the other hand, showed the lowest performance in the investigated abilities. However, it remains to be tested if these behavioural skills have been traded off against other traits, such as longevity and fecundity. Alternatively, the lack of environmental input during ontogeny may have led to the development of a maladaptive phenotype.

References for General Introduction and Discussion

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Hamburg, den