



universität  
wien

# MASTERARBEIT

Titel der Masterarbeit

„Visually elicited prey capture behaviour  
and speed recognition of *C. salei* “

verfasst von

BSc. Reithofer Christina

angestrebter akademischer Grad

Master of Science (MSc)

Wien, 2014

Studienkennzahl lt. Studienblatt:

A 066 878

Studienrichtung lt. Studienblatt:

Verhaltens-, Neuro- und Kognitionsbiologie

Betreut von:

ao. Univ.-Prof. Dipl.-Biol. Dr. Axel Schmid



<b>1. Abstract.....</b>	<b>2</b>
<b>2. Introduction .....</b>	<b>3</b>
<b>3. Material and Methods .....</b>	<b>6</b>
<b>3.1. Animals.....</b>	<b>6</b>
<b>3.2. Experimental setup and technical devices .....</b>	<b>6</b>
<b>3.3. Experimental process .....</b>	<b>7</b>
<b>3.4. Visual Stimulation.....</b>	<b>8</b>
3.4.1. Dot size and dot speed .....	9
3.4.2. Pre-tests and Control-test.....	10
3.4.3. Speed Tests.....	11
3.4.4. Dot appearance .....	12
<b>3.5. Data-analysis and calculations .....</b>	<b>13</b>
3.5.1. Behavioural patterns .....	14
3.5.2. Latency .....	14
<b>3.6. Valid and invalid runs .....</b>	<b>15</b>
<b>4. Results.....</b>	<b>16</b>
<b>4.1. Pre-tests.....</b>	<b>16</b>
<b>4.2. Control test.....</b>	<b>17</b>
<b>4.3. Speed tests .....</b>	<b>17</b>
4.3.1. Reaction rate .....	17
4.3.2. First behavioural response.....	24
4.3.3. Position of dot .....	31
4.3.4. All reactions.....	37
<b>4.4. Dot appearance.....</b>	<b>39</b>
<b>5. Discussion .....</b>	<b>42</b>
<b>6. Summary.....</b>	<b>49</b>
<b>7. Zusammenfassung .....</b>	<b>50</b>
<b>8. Literature .....</b>	<b>51</b>
<b>9. Acknowledge.....</b>	<b>53</b>

# 1. Abstract

*Cupennius salei* is a nocturnal hunting spider, that captures its prey as a wait-and sit predator out of ambush (Barth and Seyfarth, 1979). Its mechano-sensory sense is very well developed and is responsible as the main information source about environment and prey (Barth, 2002). But *C. salei* shows good visual ability as well. Its eight eyes differ in position, function and anatomy. While the Principal eyes (anterior-median eyes) are responsible for object discrimination, the Secondary eyes (posterior-median, posterior-lateral, anterior-median eyes) are responsible for detecting objects (Schmid 1998, Neuhofer et al, 2009).

This study is interested in the visual abilities of the spider. It focuses on the prey capture behaviour and studies the differences in reaction rate and behavioural patterns due to speed variation of the presented computer-generated stimulus. It could be shown that *C. salei* has good abilities for detecting stimuli that are moving very slowly. Even when a stimulus moves with a speed of  $0.013^{\circ}/s$ , the spider reacts to it. The maximum reaction rate was found to be a speed of  $0.49^{\circ}/s$  and the upper limit of speed recognition was  $81.9^{\circ}/s$ . Furthermore, the first shown behavioural patterns are orientation and attack behaviour, following and threatening behaviour are rarely shown at first, but very often shown during a series of behaviours while capturing prey.

## 2. Introduction

*Cupennius salei* is a nocturnal hunting spider living throughout Central America. The climate there presents a moderate daytime temperature of about 25° and a high degree of humidity (Barth and Seyfarth, 1979). *C. salei* lives well hidden on and behind leaves of banana stems or at the base of agaves as well as on bromeliads. These plants serve as substrate for prey capturing at night (Barth and Seyfarth, 1979). Through the day, *C. salei* shows low total activity. The active phase of the spider immediately starts after the onset of darkness (Schmitt et al., 1990).

The most evolved sense in *C. salei* for hunting and other behaviours is the vibratory sense. Extremely sensitive vibration receptors are located on the legs. The metatarsal organ is a lyriform organ and a very good detector of vibrations of the substrate (Barth, 2002). The vibratory sense was tested by presenting a flying blowfly as prey and analysing the reaction rate of the spider depending on the initiated airflow (Klopsch et al., 2012). Just the airflow of the prey can be detected by *C. salei* as a vibratory cue for attacking the fly (Klopsch et al., 2012).

In respect of these studies the question arose, why a nocturnal spider has eight eyes when the vibratory sense is so well developed. Like most spiders, *C. salei* has four pairs of eyes. They are arranged in a specific way and named after their position: Anterior-median (AM), anterior-lateral (AL), posterior-median (PM) and posterior-lateral (PL) eyes (Barth, 2002). In addition, the eyes can be differed by their morphology and function. The AM eyes are the principal and the six others are the secondary eyes. This system of nomenclature is based on the morphological structures of the eyes (Barth, 2002). The principal eyes differ from the secondary eyes by lacking a reflecting tapetum and by receptors that are differently structured. In addition, the principal eyes are evers. Evers eyes are orientated with the photosensitive rhabdomers towards the light. The secondary eyes are invers, what means that the rhabdomers are orientated to the tapetum (Grusch et al, 1997; Land

und Barth, 1992). Another difference is the moveable retina of the AM eyes (Land and Barth, 1991).

Intracellular recordings from photoreceptor cells showed, that *C. salei* has three groups of photoreceptors in the retina with spectral sensitivity maxima at wavelengths of 340nm, 480nm and 520nm (Walla et al., 1996). These features allow the spider to see UV-light, blue and green. These results were proven in behavioural tests as well (Zopf et al., 2013).

The different types of eyes are specialised in their function (Schmid, 1998). In behavioural experiments was found, that both, AM and PM eyes, are responsible for detecting targets. Target-discrimination of stationary objects is only possible with intact AM eyes (Schmid, 1998). This specialisation of the eyes can be very useful for capturing prey and detecting predators. For detecting stimuli of the environment like prey or predators, the visual perception of motion is indispensable, too. In general, motion of objects is detected as a change in retinal image. There is a continuous image flow on the retina, the so-called optic flow. Changes in the retinal image leads to changes in the optical flow that is perceived and analysed in the brain. This optic flow is a rich source of information about the locomotion of the subject itself and the motion of stimuli in the environment (Egelhaaf and Warzecha, 1999).

The mechanism of movement perception in *C. salei* was studied by measuring the eye muscle activity of spiders. Tethered female spiders were positioned in a white arena and presented to a computer-generated moving stimulus. It was found, that the secondary eyes are responsible for movement detection (Neuhofer et al., 2009). When the principal eyes were covered, the activity of the eye muscle was not influenced. But masking the secondary eyes and presenting the moving stimulus lead to a decrease of the eye muscle activity (Neuhofer et al., 2009).

Other experiments showed that vision is a necessary sense for capturing prey. Just visual cues could elicit attack behaviour similarly to substrate vibrations or airflow stimuli (Fenk et al., 2010). The different qualities of the stimulus enormously influence the reaction rate. Several studies were done at the University of Vienna to search for a stimulus that s to the highest reaction rate. In these visual studies, it was found, that the larger the dot, the more spiders reacted to the stimulus (Lindner, 2013 unpublished). Additionally, it was

shown, that differences in the latency to the reaction are related to the position of the dot and its moving direction (Schützinger, 2014 unpublished). The angle of the moving direction plays an important role for the release of attack behaviour in *C. salei* as well. The spiders do not react to horizontally moving dots. The highest reaction rate was generated at a stimulus moving upwards with an angle of 55° (Schützinger, 2014 unpublished).

All this information was gathered and gave reason for further tests to find out about the influence of stimulus speed. The current study tries to identify visual cues that elicit the highest amount of attack behaviour to artificially generated stimuli. Especially the speed of the presented stimuli is the centre of interest in this study. The main question is about differences in behavioural responses and differences in latencies when the visual stimuli are presented under different speed conditions. Furthermore, the limits of speed recognition should be analysed, that means which speed is too slow or too fast and does not elicit prey capture behaviour anymore.

Through these careful considerations, two hypotheses can be raised:

- a) The reaction rate of *C. salei* differs due to speed variation. Through diverse speeds even the composition of behavioural patterns and their latencies differ.
- b) There is an optimum speed, where the most reactions are shown, and limits of speed recognition. *C. salei* is not able to detect stimuli with very fast and very slow speeds. These speed limits prevent behavioural response of the spiders.

### **3. Material and Methods**

#### **3.1. Animals**

In this study the nocturnal wandering spider *Cupennius salei* (Ctenidae) was tested for its attack behaviour. The animals are reared in adequate animal housing at the Department of Neurobiology of the University of Vienna and were used to a circadian cycle of 12 hours light and 12 hours darkness from 8 am to 8 pm. The animals live individually in glass jars with crumble peat and a water bin inside. The animals were fed once a week and provided with water ad libitum.

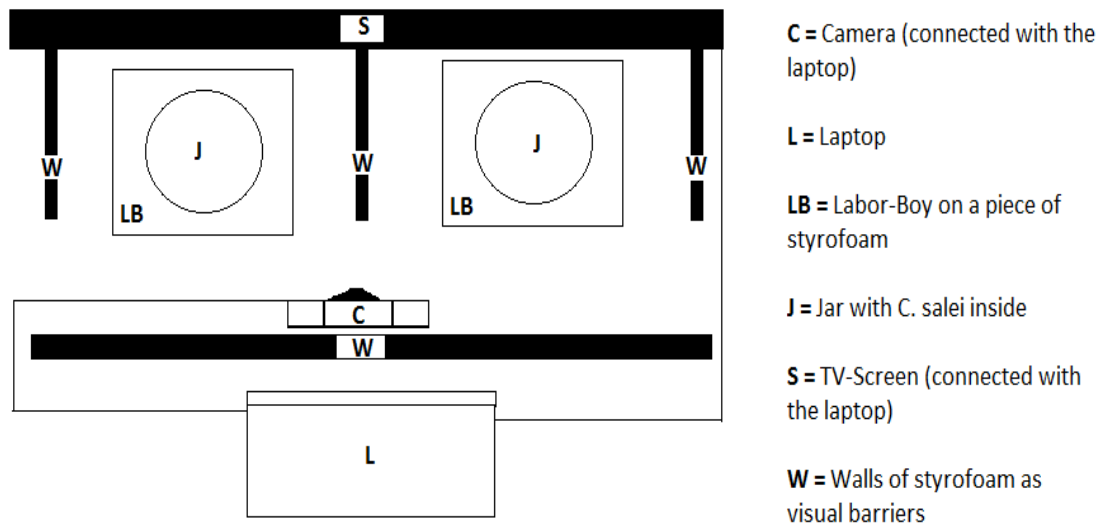
All in all, 64 pre-adult (4-12 months old) female spiders were used in the experiments with visual stimulation of hunting behaviour. Not all animals were tested in each trial because of ecdysis in certain individual intervals. If *C. salei* is shortly before or after a moult, it will react less or even not to stimuli, because of the high amount of energy needed for ecdysis. If a spider was tested and moult itself a few days afterwards, the data from three days before and after the ecdysis were deleted.

#### **3.2. Experimental setup and technical devices**

The spiders were positioned in front of a 30 cm high LCD-Screen (SamsungSyncMaster T220, Samsung Electronics, Daegu, Korea), where a presentation was shown. The spiders were visually separated from the environment by walls of Styrofoam. The jars with the spiders inside were put on Styrofoam to exclude vibratory stimuli. A Labor-Boy was positioned beneath to adjust the starting position of the spider, so that every spider was in the centre of the jars back wall (30 cm distance from the screen) when the presentation started. The experiments were recorded with a webcam (Logitech Pro 9000, Logitech, Apples, Switzerland). The webcam and the LCD-screens were connected to a laptop (HP 6730b, Hewlett-Packard Company, Wilmington, USA), that was positioned behind a wall of styrofoam, so that the presentation and the cameras could be controlled behind the visual barrier to



the spiders (Figure 1). The experimental setup was available twice, so that four spiders could have been tested at once.



**Figure 1, Schematic top view of the experimental Setup.** A laptop (L) was connected to a LCD-Screen (S), where the presentation was shown. For analysis afterwards, the run was recorded with a video camera (C), which was connected to the laptop as well. With walls of Styrofoam (W) the spiders were visually separated from the environment and from the position of the experimenter, who controlled the experiment with the laptop (L). The spiders within their jars (J) were positioned on the Labor-Boy (LB), so that their position in the jar could be adjusted.

The experiments were recorded with a resolution of 30 frames/second (software: AVS-Video Editor, Online Media Technologies Ltd., London, United Kingdom). The videos were analysed in the program Solomon Coder (Solomon Coder, András Péter, Milano, Italy). Data about behavioural reactions, positions of spiders, stimuli, and latencies of the behaviour were collected.

### 3.3. Experimental process

Each spider was tested twice a day at most with a minimal pause of three hours between the runs. *C. salei* was put 30 cm in front of the screen. The jar was positioned in a way, so that the spider sat on the back wall of the jar and looked directly to the screen with its posterior-median eyes. The spiders are used to position themselves with their head downwards – it is the resting

position of these animals. Through the labour boy the starting position central to the screen was determined.

After putting the spiders in front of the screens, there was a pause of ten minutes to get the spiders used to the green screen and to rehab from tremors that occurred through positioning. Afterwards, the presentations were started.

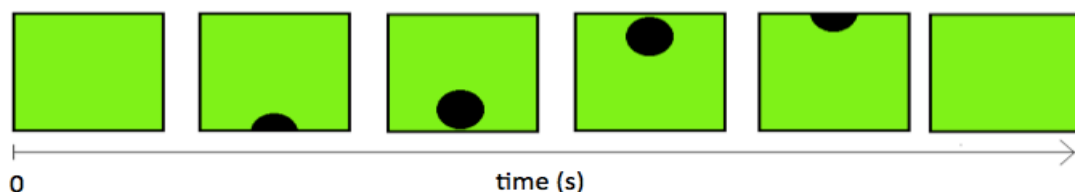
### Testing Conditions

The temperature ranged from 21° to 29°. The relative humidity varied between 50% and 65%. To exclude vibratory disturbances and to provide a calm environment for the spiders, the experiments were done mainly during the summer holidays.

The light intensity could be regulated and was dimmed to 35.2 lx. This intensity was chosen to keep the same test condition as introduced in prior studies (Lindner, 2013 and Schützinger, 2014).

### 3.4. Visual Stimulation

All presentations were illustrated in Microsoft Powerpoint. The presentation consisted of a black dot that appeared on a green background (Figure 2). The green background was used because of the high spectral sensitivity of *C. salei* in this range of wavelengths (Walla et al., 1996). *C. salei* reacts to shapes with prey capture behaviour which look unlike their natural prey (Fenk et al, 2010). Choosing black dots as stimuli created the maximum contrast of stimuli to the background. This maximum contrast ensures the best perception by the spider.

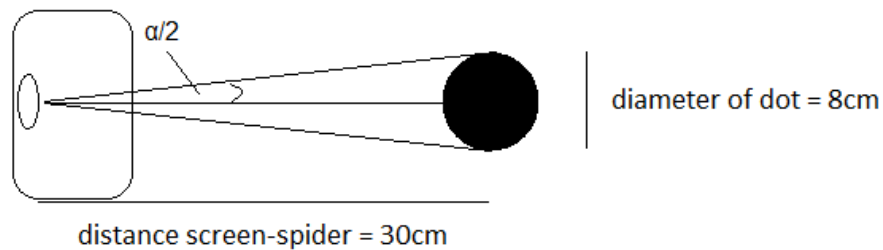


**Figure 2, Schematic timeline of the visual stimulation.** The black dot moved through the screen with a certain speed and disappeared at the top. Afterwards it slid in there again to move down with the same speed (not shown here). This presentation led to visual caused prey capture behaviour of *C. salei*.

Earlier studies showed a significant preference to vertical moving stimuli by *C. salei* (Schützinger, 2014). The stimulus in these experiments had a horizontal path and a permanent size. The dot slid into the screen and moved straight vertically to the top and disappeared there by sliding out of the screen. Afterwards, the dot slid in at the top again and moved downwards. This motion was repeated in certain quantity and was the visual cue for the spiders and should lead to a behavioural response by *C. salei* (Figure 2).

### 3.4.1. Dot size and dot speed

The absolute dot size was measured in cm and afterwards, the apparent magnitude was calculated. The apparent magnitude is the angle through which an object is perceived by an observer. The distance from spider to the screen was 30 cm, the dot had an diameter of 8 cm (Figure 3).



**Figure 3, Scheme for the calculation of the visual angle.** The dot had an absolute size of 8 cm and the distance from the spider to the screen was 30 cm. The angle  $\alpha$  is the apparent magnitude of the dot and was calculated to be  $15^\circ$ .

Through conversion of the formula for the apparent magnitude  $\tan(\alpha/2) = g/2r$ , where  $g$  is the size of the dot and  $r$  the distance from the spider to the object. The dot size by a diameter of 8cm was calculated to be  $15^\circ$  (Figure 3). This size was used for all speed tests.

The same formula was needed when speed had to be measured in  $^\circ/\text{s}$ . The dot slid through a way of 38 cm. This distance was measured by the height of the screen (30cm) plus the dot size (8 cm), that means the distance of the points, where the dot appeared first on the screen with any fraction to the point, where the dot disappeared completely.

Therefore, the apparent magnitude of the screen was  $\alpha = 64^\circ$ . This angle had to be passed by the dot in different speeds, so for instance if the dot needed 20 seconds to pass the screen, the speed was  $64^\circ/20s = 3.2^\circ/s$ . The speeds used in the experiment are given in Table 1 and Table 2.

### 3.4.2. Pre-tests and Control-test

Four different tests were used to find out the optimal stimulus conditions for testing the behavioural reactions to speed. In the speed tests size and starting direction of the dot should be presented in a way that most behavioural responses could be elicited. The pre-tests differed in size and in starting position of the dot. The speed in all three pre-tests was chosen as  $49.8^\circ/s$  (Table 1). This speed corresponded to a similar experiment (Schützinger, 2014), where this speed condition elicited the most behavioural responses in *C. salei*. All other qualities, like colour of dot or background colour, did not vary.

**Table 1, Parameters of stimuli in pre-tests.** The presented stimuli in the pre-tests differed in size ( $^\circ$ ) and starting position of the dot. “Top” means that the dot slid in at the top of the screen and moved downwards. “Bottom” means that the dot slid in at the bottom and moved upwards.

pre-test	dot size ( $^\circ$ )	starting position	speed ( $^\circ/s$ )	repetitions
1	11	top	49.8	5
2	11	bottom	49.8	5
3	15	top	49.8	5
4	15	bottom	49.8	5

When the pre-tests were done and analysed, it was decided to work with the dot parameters of pre-test 2, because the most reactions were elicited there (Results, Table 3).

A control test was done to support the hypothesis that speed is the main quality of the stimulus that leads to prey capture behaviour. It should show, that a stationary stimulus with the same parameters as in the speed tests does not lead to behavioural responses by *C. salei*. The control test consisted of 10 min pauses for the spiders in front of the screen and a stationary dot

afterwards. First, the screen showed just a green background with no visible dot. After these 10 minutes, the control-presentation was started, where a stationary black dot was presented on the green background for 15 minutes in the center of the screen. The dot size was  $15^\circ$  and equal to the dot size in the speed tests.

### 3.4.3. Speed Tests

For testing the behavioural reactions to speed, eleven different speeds were set. All presentations contained the same dot size ( $15^\circ$ ) and the same direction, so that the dot started to slide in from the bottom of the screen and moved vertically upwards. The speeds were tested in the range of 0.013-81.9°/s. The parameters of the different speed tests are shown in Table 2. Each test differed in duration of the presentation, which was an unavoidable result of the different speeds.

**Table 2, Parameters of the presentations in the speed tests.** Speeds between 0°/s (Control-test) and 81.9°/s were studied. The presentations differed greatly in duration because of the different speeds. To get longer total durations in the faster speed conditions, the presentations were repeated for a certain time. For analysing the latency, the points of time, when the dot was fully visible and was disappeared afterwards were measured as well.

test	speed [°/s]	total duration [s]	dot fully visible after [s]	dot disappeared after [s]	repetitions
Test 1	81.9	15	0.19	0.8	4
Test 2	42.6	20	0.35	1.5	4
Test 3	30.1	25	0.50	2.1	4
Test 4	17.3	60	0.86	3.7	4
Test 5	6.1	70	2.5	10.5	3
Test 6	2.9	170	5.4	22.2	3
Test 7	0.98	200	15.4	65.6	3
Test 8	0.49	280	30.7	130.8	1
Test 9	0.118	545	127.9	545.2	0
Test 10	0.059	1093	256.4	1093.0	0
Test 11	0.013	4685	1099.8	4685.7	0
Control	0	900	-	-	-

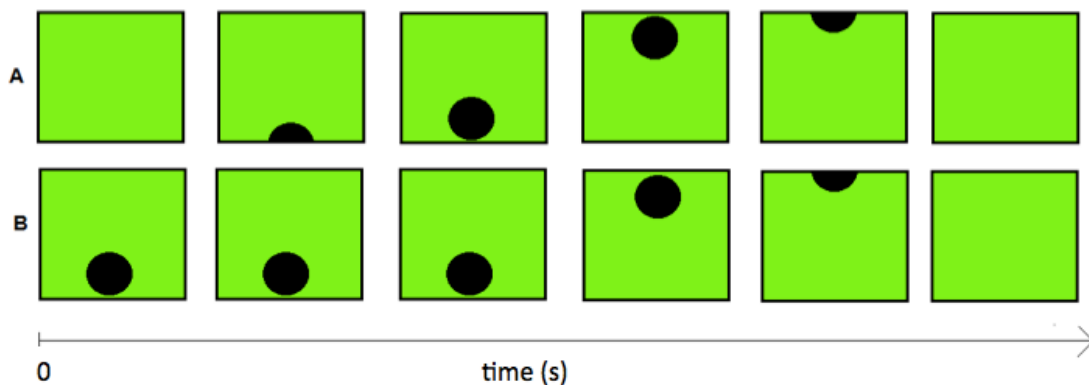
For instance, the fastest presentation (Test 1, see Table 2) lasted for about 15 seconds, and the dot needed 0.19s to appear fully on the screen, but the dot

with a speed of  $2.9^\circ/\text{s}$  needed 5.4s. To get a longer presentation at the faster speeds, the presentation was repeated for at most four times (Table 2).

#### 3.4.4. Dot appearance

Furthermore, a series of experiments was done to test the influence of an appearing dot on the screen in comparison to a visible dot that starts to move. After a series of experimental runs, it was observed, that many behavioural reactions were shown when the dot slid in the screen and was not even fully visible. Hence, the question arose, if the appearance of the dot had an influence to the reaction rate of *C. salei*.

For studying this question, an additional test was done with the speed condition from test 9 and 10. These speeds ( $0.059^\circ/\text{s}$  and  $0.118^\circ/\text{s}$ ) were used because there were the most behavioural responses in the speed tests (see Results, Figure 6).



**Figure 4, Schematic time-line of test condition A and B.** In test condition A, the dot slid into the screen. In test condition B, the dot appeared stationary, and started to move upwards at the same time as the dot in test condition A was fully visible. Presentations A and B just differed in the appearance of the dot, but not in the duration.

In both speed conditions about 30 runs each were done with two different presentations. Presentation A was the defined test where the dot moved in the screen after a 10-minute pause. Presentation B already showed the whole dot at the bottom section of the screen when the spiders were positioned in front of the screen. After the 10 minutes pause, the dot was stationary as well until the point of time was reached, where the dot of presentation A was fully visible. Then, the dot of presentation B started to move upwards too, so that the dots

of the presentations reached the top of the screen at the same time. This temporal configuration ensured same total durations of the presentations (Figure 4).

### 3.5. Data-analysis and calculations

The recorded videos were analysed in Solomon Coder (Solomon Coder, András Péter, Milano, Italy). The behavioural patterns **attack**, **orientation**, **following** and **threatening behaviour** were observed. The temporal resolution of the videos were 30 frames/s. This allowed a precise analysis of time with 33 ms/frame. In addition to the shown behaviour, latency, the position of dot and spider were noticed as well. Starting time of measuring latency was defined as one frame (33 ms) before the moving dot started to appear at the screen.

The data were analysed in the software program IBM SPSS Statistics 22.0.0.0 (IBM Statistics, Armonk, USA) on a laptop (MacBook Air, Apple Inc., Cupertino, USA). The differences in reaction rate and composition of behavioural patterns in different speed conditions were analysed with the  $\chi^2$ -Test. The  $\chi^2$ -Test ensured logical comparison of the behavioural patterns and gave information if the composition of behaviour in the tests differed significantly to each other or not. To find out about that, each test was compared to all other slower speed tests, until a significant difference was found.

The declaration of the significance in figures and tables are the following: \*\*\* for high significant differences ( $p \leq 0.001$ ), \*\* for  $0.001 < p \leq 0.01$  and \* for  $0.01 < p < 0.05$ .

### **3.5.1. Behavioural patterns**

#### **Attack behaviour**

A behavioural reaction was referred to an attack, when the spider immediately jumps towards the dot or to the ground. An attack always contains a jump that lasts for less than a second. More than one attack can be shown in one trial of behaviour.

#### **Following behaviour**

Following behaviour is defined as a quick locomotion to the dot. The movement contains no jump, so the spider just runs in the direction of the dot. The spider can be sitting on the walls of the jar, when following behaviour occurs. But this quick run can be on the ground as well, so that the following behaviour is subsequent to the attack behaviour. There can be more than one following behaviours in one test run.

#### **Orientation behaviour**

Orientation behaviour is a movement of the spider towards the dot without changing its position in the jar. This means, that orientation does not contain locomotion, just orienting the body to it. There can be several orientation behaviours in one test.

#### **Threatening behaviour**

Threatening behaviour can be described as a movement of the forelegs. The spider does not change its position in the jar. The spider bends its forelegs together and moves them towards the dot.

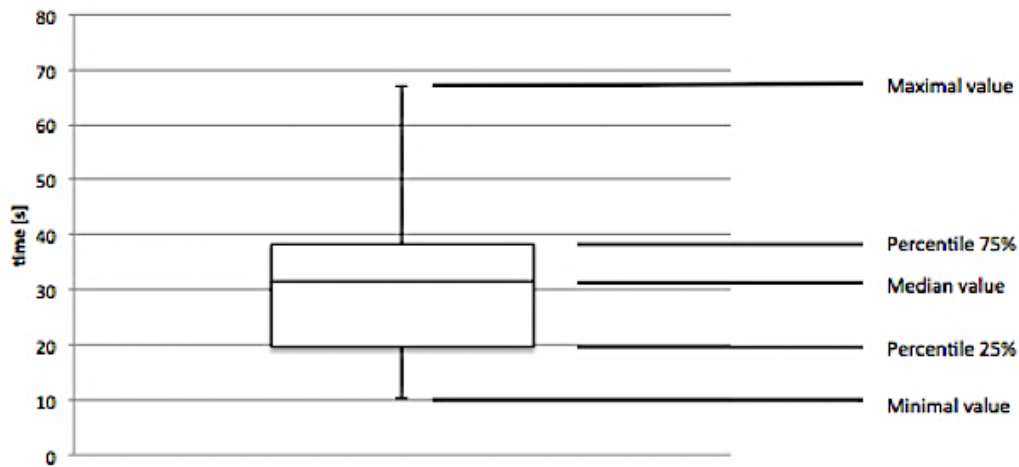
### **3.5.2. Latency**

The latency was measured from the point of time where the dot started to slide into the screen. For that reason, the starting point for any analysis is 33ms before the dot started to move into the screen.

The latencies for each speed condition are shown as typical boxplots in the results. The minimal and maximum value is shown as the endpoint of the vertical line. The box gives information about 50% of the data points that are



distributed regularly around the median value. The median value is the horizontal line in the box (Figure 5).



**Figure 5, Schematic overview of a boxplot to present the latencies.** All data are shown in a boxplot. The edges of the vertical line represent the minimal and maximum value of latency. The box encloses the central 50% of data around the median value.

The latencies were compared through the Wilcoxon-Test. The Wilcoxon-Test compares two sample-sizes and gives information about their differences. This allows comparing the latencies of each test to all other speed conditions. Each test was compared to the next slower test until a significant difference was found.

### 3.6. Valid and invalid runs

Each test started with a ten minutes pause for the spiders in front of the screen. If any interruption occurred during that time, the run was counted as invalid. These interruptions could have been any kind of noise or vibrations, like a slamming door outside. The interruption could also be a visual cue, like any movement of the experimenter or a motion cue when the spider was positioned in front of the screen.

## 4. Results

### 4.1. Pre-tests

All in all, 720 runs were done with 30 spiders in the pre-tests. The highest reaction rate (26.3%) was elicited in test condition 4, where the dot size was 15° and the dot slid in from the bottom (Table 3). The lowest reaction rate (10.7%) was observed in pre-test 1, where the dot appeared at the top and had a size of 11°.

**Table 3, Parameters, sample size (n) and reaction rate of the four pre-tests.** Pre-test 1 had the lowest reaction rate compared to the three other pre-tests. In only 10.7% of the test-runs 1 any reaction was shown to the downwards moving smaller dot. The most reactions occurred in pre-test condition 4, where the larger dot moved upwards.

Pre-test	Dot size	Starting position	n	Reactions
1	●	↓	206	10.7%
2	●	↑	168	24.4%
3	●	↓	171	23.3%
4	●	↑	175	26.3%
total			720	20.7%

Pre-test 1 differed highly significant to the other pre-tests. Between the pre-tests 2, 3 and 4 no differences were found (Table 4).

**Table 4, Sample size (n),  $\chi^2$ -values and significances for the different pre-test conditions.** The reaction rate differed significantly in pre-test 1 compared to all other pre-tests. The reaction rates in pre-tests 2,3 and 4 did not vary to each other.

pre-tests	n	$\chi^2$	p	
1-2	374	12.445	0	***
1-3	377	10.989	0.001	***
1-4	381	15.717	0	***
2-3	339	0.048	0.464	no sign.
2-4	343	0.16	0.391	no sign.
3-4	346	0.388	0.309	no sign.

The highest reaction rate was shown in pre-test 4, therefore the parameters of the dot in pre-test 4 were chosen to be presented in the speed tests.

## **4.2. Control test**

In total, 76 spiders were confronted in the control test with a central stationary dot. But only 11 spiders showed any reaction to it. This led to a reaction rate of 14.3%. These 11 reactions consisted of two following behaviours, and nine orientation behaviours as first reaction.

All in all, 24 behavioural patterns were shown in those 11 positive runs. Orientation behaviour was shown for 14 times (58%) and following behaviour occurred ten times (42%). Either attack behaviour or threatening behaviour occurred at any time through the presentation of the control stimulus.

## **4.3. Speed tests**

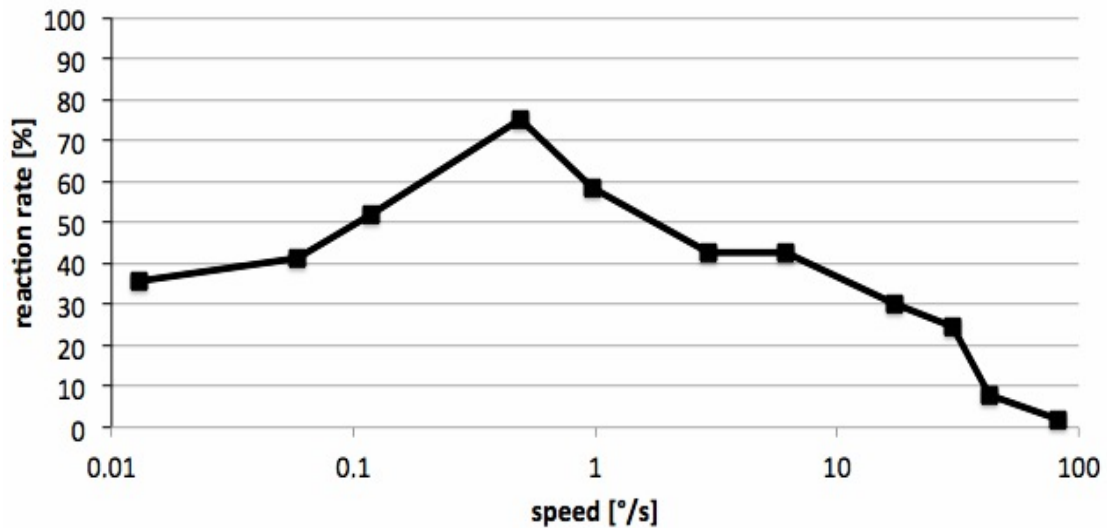
### **4.3.1. Reaction rate**

Eleven different speeds were tested in the range of 0.013-81.9°/s. All in all, 1891 runs were done with 58 female *C. salei*. The sample sizes in the speed tests varied and are shown in Table 5.

From 1891 runs, 681 were counted as positive, so any behavioural pattern was shown in 36.5% of the runs (Table 5). The fewest reactions were shown in test 1, where the fastest stimulus (81.9°/s) was presented. In this test condition the reaction rate was only 2.0%. The highest behavioural reaction rate was observed when the dot moved with a speed of 0.49°/s. 75% of the spiders showed a reaction to the moving dot in this test condition (Table 5). The extinction of behavioural response could not be reached in the slow speed conditions. Even with the slowest test (Test 11, 0.013°/s) more than 30% of the runs were positive (Figure 6, Table 5).

**Table 5, Reaction rate [%], and sample size (n) of *C. salei* to 11 different speed-conditions.** The reaction rates in different speed conditions vary enormously from 2% in the fastest speed condition (81.9°/s) to 75% at a speed of 0.49°/s.

test	speed [°/s]	n (total)	reaction rate			
			no reactions (n)	%	reactions (n)	%
1	81.9	199	195	98.0	4	2.0
2	42.6	214	197	92.1	19	7.9
3	30.1	218	164	75.2	28	24.8
4	17.3	242	169	69.8	150	30.2
5	6.1	219	126	57.5	145	42.5
6	2.9	205	117	57.1	88	42.9
7	0.98	247	102	41.3	93	58.7
8	0.49	200	50	25.0	73	75.0
9	0.118	62	34	54.8	54	45.2
10	0.059	57	38	66.7	17	33.3
11	0.013	28	18	64.3	4	35.7
Total		1891	1210	63.5	681	36.5



**Figure 6, Reaction rate to different speeds.** The reactions of *C. salei* to different speeds from 0.013°/s to 81.9°/s were studied in the speed tests. The highest reaction rate was shown with a speed of 0.49°/s. In the range from 0.118°/s to 6.1°/s, the reaction rate is above 40%. With increasing speed the reaction rate sinks and nearly erases with the highest speed of 81.9°/s. For data see table 6.

Figure 6 shows the reaction rates under the different speed conditions. There is an upper limitation of behavioural response, when the dot moved with a speed of about 81.9°/s. The behavioural reaction rate increased continuously to a maximum of 75%, when the speed was decreased to a speed of 0.49°/s. If the dot decreased in speed furthermore, the spiders reacted less to it again. In

the range of 0.013°/s to 17.3°/s, more than 30% of the spiders reacted to the stimulus.

The  $\chi^2$ -tests shows highly significant differences between most of the tested speeds. These results are shown in Table 6a and 6b. In the speed conditions 81.9°/s and 42.6°/s significantly less reactions were shown than in all the other tests. From the speed 30.1°/s to 17.3°/s, no difference was identifiable. The same case was in the speed range from 6.1°/s to 2.9°/s, and in the three slowest speed tests (0.118°/s – 0.013°/s). For data, see Table 6a and 6b.

**Table 6 (a, b), Significant differences between the several speed tests.** The results of the  $\chi^2$ -test are shown. For all  $\chi^2$ -tests there are certain sample sizes (N),  $\chi^2$ -values and significances (p). Table 6a shows the results, where a significant difference is given. Table 6b shows the insignificant results. There is no difference between the three slowest speeds, between 30.1°/s and 17.34 °/s and 6.1°/s and 2.9°/s.

**Table 6(a)**

speed 1	speed 2	n (total)	$\chi^2$	p	
81.9	42.6	413	7.523	0.005	**
81.9	30.1	417	45.008	0.000	***
81.9	17.3	441	60.067	0.000	***
81.9	6.1	418	95.754	0.000	***
81.9	2.9	404	96.128	0.000	***
81.9	0.98	446	159.229	0.000	***
81.9	0.49	399	224.231	0.000	***
81.9	0.118	261	81.825	0.000	***
81.9	0.059	256	53.164	0.000	***
81.9	0.013	227	48.183	0.000	***
42.6	30.1	432	22.263	0.000	***
42.6	17.3	456	35.401	0.000	***
42.6	6.1	433	68.067	0.000	***
42.6	2.9	419	68.230	0.000	***
42.6	0.98	461	129.622	0.000	***
42.6	0.49	414	193.155	0.000	***
42.6	0.118	276	48.796	0.000	***
42.6	0.059	271	25.188	0.000	***
42.6	0.013	242	19.264	0.000	***
30.1	6.1	437	15.324	0.000	***
30.1	2.9	423	15.617	0.000	***
30.1	0.98	465	54.467	0.000	***
30.1	0.49	418	105.326	0.000	***
30.1	0.118	280	9.691	0.002	**
17.3	6.1	461	7.549	0.004	**
17.3	2.9	447	7.843	0.003	**
17.3	0.98	489	40.297	0.000	***
17.3	0.49	442	88.054	0.000	***
17.3	0.118	304	5.003	0.020	*
6.1	0.98	466	12.249	0.000	***
6.1	0.49	419	45.420	0.000	***
2.9	0.98	452	11.165	0.001	***
2.9	0.49	405	42.976	0.000	***
2.9	0.118	267	0.097	0.000	***
0.98	0.49	447	13.077	0.000	***
0.98	0.059	304	11.999	0.000	***
0.49	0.118	262	19.346	0.000	***
0.49	0.059	257	34.202	0.000	***
0.49	0.013	228	18.112	0.000	***

Table 6 (b)

speed 1	speed 2	n (total)	$\chi^2$	p
30.1	17.3	460	1.670	0.117
30.1	0.059	275	1.699	0.129
30.1	0.013	246	1.544	0.155
17.3	0.059	299	0.227	0.375
17.3	0.013	270	0.363	0.343
6.1	2.9	424	0.009	0.501
6.1	0.118	281	0.143	0.407
6.1	0.059	276	1.564	0.136
6.1	0.013	247	0.465	0.319
2.9	0.059	262	1.699	0.124
2.9	0.013	233	0.526	0.304
0.98	0.118	309	3.689	0.380
0.98	0.013	275	5.405	0.170
0.118	0.059	119	1.739	0.129
0.118	0.013	90	0.706	0.272
0.059	0.013	85	0.047	0.507

### Latencies to first reaction

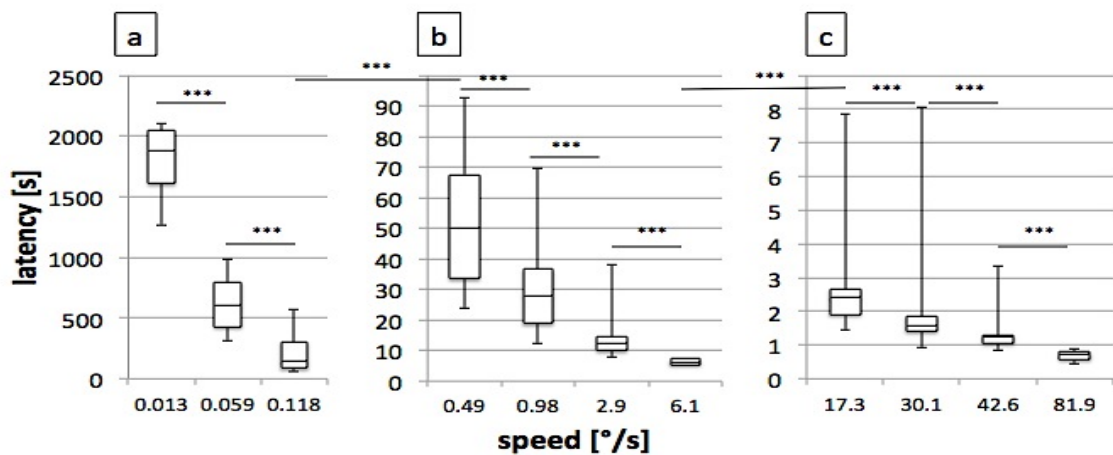
The latencies to the first reaction in the different speed tests are a central question in this study, because it represents the ability of the visual system of *C. salei*.

The faster the dot moved, the faster the spiders reacted to it. The highest latencies occurred at a speed of 0.013°/s. There, the maximum latency was 2100s (=35 min). The median latency was 1877s (=31 min). The spiders reacted much more faster when the speed was raised just up to 0.059°/s. In this test condition the mean latency decreased to 610s and the maximum latency was 988s (Table 7, Figure 7a-c). All speeds faster than 17.3°/s induced mean and median latencies shorter than 3s until the speed of 81.9°/s was reached and the latency was at the minimum of median 0.71s and mean 0.69s. The fastest reaction was shown in the fastest speed condition (Test 1, 0.81°/s). There a spider just reacted after 0.43s to the moving dot (Table 7, Figure 7a-c).

**Table 7, Minimum, median, mean and maximum latencies to different speed conditions.** The table shows the sample size of the positive runs (n) and the latencies to the first reactions. With decreasing speed, the latencies got shorter as well.

speed [°/s]	sample size (n)	latency [s]			
		minimum	median	mean	maximum
81.9	4	0.43	0.71	0.69	0.89
42.6	17	0.83	1.2	1.4	3.3
30.1	52	0.92	1.6	2.0	8.1
17.3	69	1.5	2.4	2.5	7.9
6.1	93	3.2	6.3	7.1	31
2.9	86	3.4	12	14	48
0.98	141	9,1	28	29	62
0.49	141	14	50	54	198
0.118	26	60	143	216	576
0.059	17	311	603	610	988
0.013	6	1266	1877	1791	2100

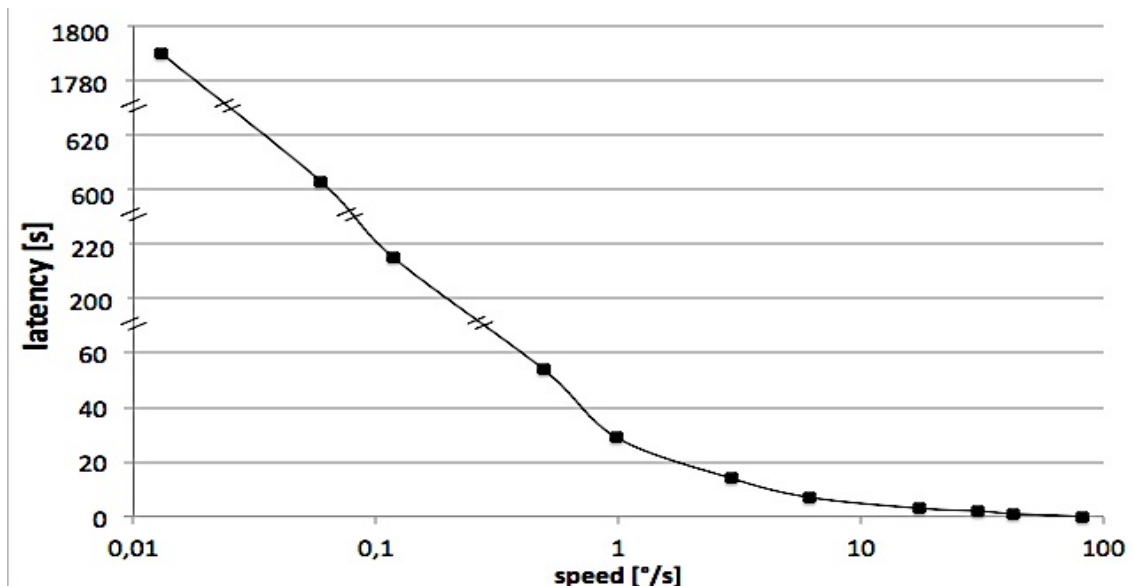
Additionally, the range from minimal to maximum latency got smaller and smaller the faster the dot moved. The widest range of latency occurred in the slowest speed condition (Test 11, 0.013°/s). The longer the presentation lasted - the slower the dot moved across the screen - the more variation appeared in the range of the latency (Table 7, Figure 7a-c).



**Figure 7 (a-c), Latency of all reactions until the first reaction was shown.** The faster the dot moved, the faster the spiders responded to the stimulus. There were many outliers based on the different duration of the presentation. The latency was measured in seconds from the moment, when the dot started to appear. For data, see Table 7.



The curve of the mean latencies in varying speed is shown in Figure 8. The curve decreases rapidly from 1791s to 216s when the speed is increased from 0.01°/s to 0.1°/s. Afterwards, the mean latency decreases towards 0.69s when the speed reaches 81.9°/s - the highest speed level that was tested in this experiment (Figure 8). This decrease of latency due to increase of speed is significant (Table 8).



**Figure 8, Mean latency to the first reaction in different speed conditions.** The faster the dot moved, the faster the spider *C. salei* reacted to it. The mean latency drops constantly from 1791s in the slowest speed test to 0.69s in the fastest speed test. With increasing the speed just from 0.013°/s to 0.059°/s and 0.018°/s, the mean latency reduced from 1791s to 610s and 216s. Increasing furthermore, the latencies got shorter than one minute. The speed conditions faster than 17,3°/s led to latencies shorter 2.5s and a minimal mean latency 0.69s at the fastest speed condition (81.9°/s). For data, see Table 7.

The latencies in every tested speed differed highly significantly to the latencies in the neighboured speed test (Table 8). The latencies vary continuously, that means that the latencies differ not only to the neighboured speed condition but to all other tests as well (Table 8).

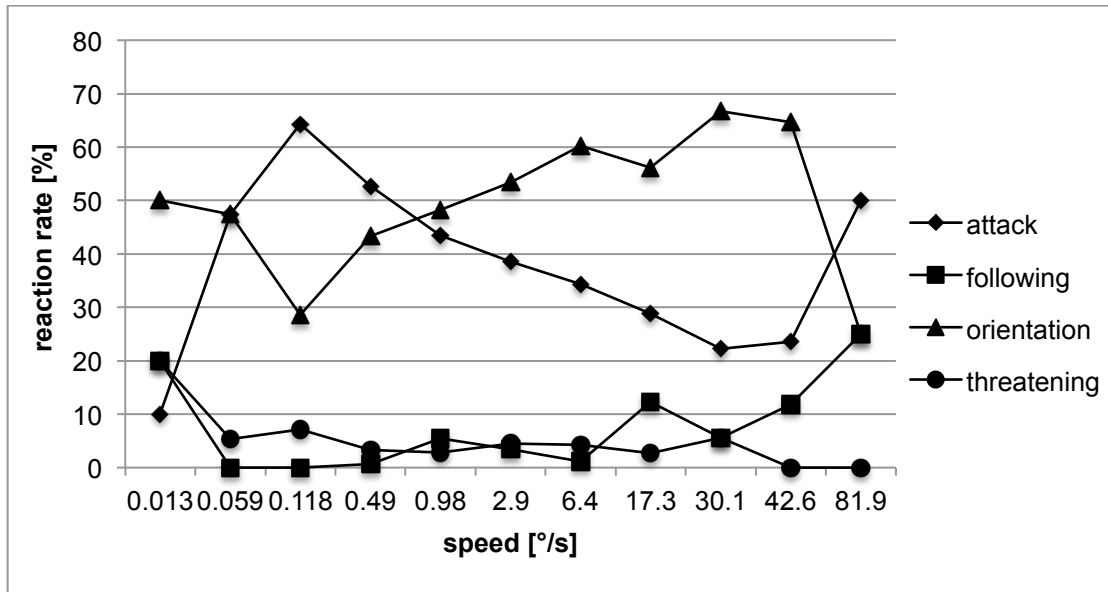
The faster the dot moved, the faster the first reaction was shown by the spiders. When the dot moved more slowly so that the duration of the presentation increased, the reaction to the dot occurred significantly later (Table 8, Figure 7a-c).

**Table 8, Sample sizes (n) and significant differences in the latencies to first behavioural response due to different speeds.** For all speed tests, there are certain sample sizes (n), Wilcoxon-values (W) and significances (p). Each tested speed differs significantly to the neighboured speeds. It is significant, that the latencies decrease with increasing speed from the slowest speed condition.

speed 1 [°/s]	speed 2 [°/s]	n (speed 1)	n (speed 2)	n (total)	W	p	
81.9	42.6	4	17	21	11.0	0.003	***
42.6	30.1	17	52	69	363.5	0.001	***
30.1	17.3	52	69	121	2020.0	0.000	***
17.3	6.1	69	93	162	2576.0	0.000	***
6.1	2.9	93	88	181	5226.0	0.000	***
2.9	0.98	88	145	233	5207.0	0.000	***
0.98	0.49	145	150	295	14594.5	0.000	***
0.049	0.118	150	28	178	12026.0	0.000	***
0.118	0.059	28	19	47	466.0	0.000	***
0.059	0.013	19	10	29	238.0	0.031	***

#### 4.3.2. First behavioural response

The first behavioural response was another focus of interest in this study. All together, 681 runs were positive and a difference of the behavioural pattern in the first reactions could be observed. Figure 9 indicates that orientation or attack behaviour was shown mostly as first behavioural reactions in any speed test (Figure 9). Following behaviour and threatening behaviour were the least first responses in every test. Threatening behaviour as first behavioural response never reached a reaction rate of more than 10%, except in test 11 (speed=0.013°/s). There, a fifth of the first reactions were threatening behaviour to the moving dot (Figure 9). The spiders orientated themselves firstly to the dot in more than 50% in the range of speed from 2.9°/s to 42.6°/s. The highest reaction rate of orientation behaviour was shown in speed condition 30.1°/s. There, 67% of the first behavioural responses were orientation behaviour. The most attacks were shown when the dot moved with a speed of 0.118°/s, the fewest attacks as first reaction were in test 11, where the dot was presented under the slowest speed condition (Figure 9).



**Figure 9, Reaction rate of the first shown behavioural pattern at different speed conditions.** In every speed test, either attack behaviour or orientation was shown as first response to the dot. In the speed conditions 0.98°/s to 42.6°/s the spiders showed more orientation behaviour instead of attack behaviour. Attack behaviour was the preferred first behavioural response in the fastest speed test (test 1) and in the range from 0.059°/s to 0.49°/s.

The first behavioural responses due to different speeds were analysed with the  $\chi^2$ -test and showed highly significant differences ( $\chi^2 = 73.245$ ,  $df=30$ ,  $n=681$ ,  $p=0.000$ ).

With a closer look at each speed condition and the slower contiguous speed condition, there are a few significant differences. The analyse of each speed test compared to all others was the following: Starting with speed condition 1 (81.9°/s), each speed condition was compared to the next slower ones until a significant difference was found.

The distribution of the first shown behavioural pattern from 81.9°/s with decreasing speed did not significantly vary until the speed reached 6.1°/s. The distribution in the speeds 2.9°/s to 0.059°/s did not differ significantly to each other but differed significantly to the distribution of the speed condition 0.013°/s. Detailed data are shown in Table 9.

**Table 9, Significant differences in the first behavioural patterns due to different speed conditions.**

The results of the  $\chi^2$ -test are shown. For all tests, there were certain sample sizes (n),  $\chi^2$ -values and significances (p). If the speed varied, there was a significant difference in showing attack behaviour, following behaviour, orientation behaviour or threatening behaviour as a first reaction to the stimulus.

speed 1 [°/s]	speed 2 [°/s]	n (speed 1)	n (speed 2)	n (total)	$\chi^2$	p	
81.9	6.1	4	93	97	11.894	0.008	**
42.6	0.49	17	150	167	15.177	0.002	**
30.1	0.98	54	145	199	8.077	0.44	*
17.3	6.1	73	93	166	9.363	0.024	*
6.1	0.118	93	28	121	9.375	0.025	*
2.9	0.013	88	10	98	10.429	0.015	**
0.98	0.013	145	10	155	12.766	0.005	**
0.49	0.013	150	10	160	28.15	0.000	***
0.118	0.013	28	10	38	12.089	0.007	**
0.059	0.013	19	10	29	7.838	0.049	*

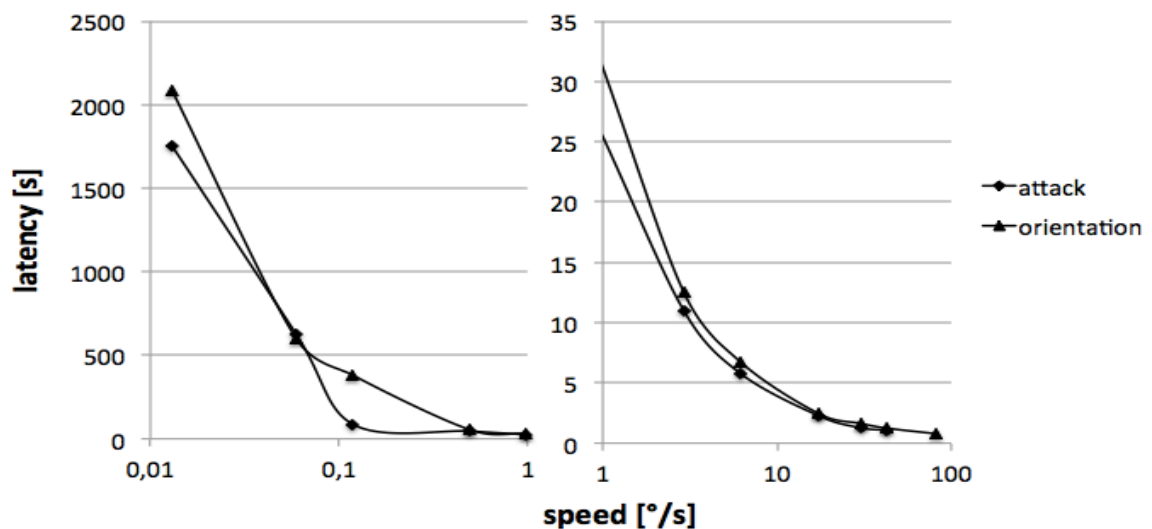
Following behaviour was only slightly observed as first behaviour of *C. salei*, when the spider reacted to the moving dot. All in all, following behaviour was shown only 30 times out of 681 first reactions (4.4%). For this reason, no further analyses with these behavioural patterns were possible. The same situation occurred with threatening behaviour as the first reaction to the stimulus. Only 27 spiders (4.0%) showed threatening behaviour first to the moving dot. Responsible further analyses were not done.

### Latency to first attack- and orientation behaviour

In this part of the results, only data points were statistically analysed and imagined by a boxplot where attack or orientation behaviour was the first behavioural pattern. Test 1 (0.013°/s) and test 11 (81.9°/s) were excluded from the following statistical analysis and the presentation by a boxplot because in these tests less reaction occurred for responsible analysis. For data, see Table 10.

The faster the dot moved, the faster the spiders reacted to it in general. The curves of the latencies to the first attack and orientation behaviour drop extremely when the dot increased in speed from 0.01°/s to 0.1°/s (Figure 10).

Attack behaviour was faster shown than orientation behaviour in every speed test. Long latencies occurred in the slowest speed conditions. When the dot reached a speed of  $0.49^\circ/\text{s}$ , the median and mean latencies to attack and orientation behaviour got shorter than 60s (Figure 10, Table 10). The attack latency curve drops down to a minimal mean latency of 0,53s when the speed reaches  $81.9^\circ/\text{s}$ . The curve of the mean latencies to the first orientation behaviour does not sink that rapidly as the mean attack curve and reaches a minimal mean latency of 0.79s (Figure 10). For detailed data, see Table 10.



**Figure 10, Mean latency to the first attack- and orientation behaviour with increasing speed.** The faster the dot moved, the faster the spiders reacted to the stimulus. Attack behaviour was shown faster than orientation behaviour in every speed condition. In speeds slower than  $0.01^\circ/\text{s}$  the mean attack latencies were higher than 100s, and the orientation latencies were even higher than 380s.

The faster the dot moved, the shorter the latencies to the shown attack and orientation behaviour got. The maximum latency to attack behaviour in the test condition  $0.059^\circ/\text{s}$  was 988s and the minimal latency was 311s (Figure 11a-c, Table 10). The spiders reacted much quicker with just a little increase of speed to  $0.118^\circ/\text{s}$ . When the dot moved with this speed, the mean latency to attack decreased from 629s to 88s with a minimal latency shorter than a minute (Table 10, Figure 10). The fastest attack behaviour was shown at a speed of  $81.9^\circ/\text{s}$ , when the spider attacked the stimulus only after 0.43s. This attack was the fastest reaction ever in all experiments (Table 10). The longest attack behaviour latency occurred in test 11, where the slowest speed was

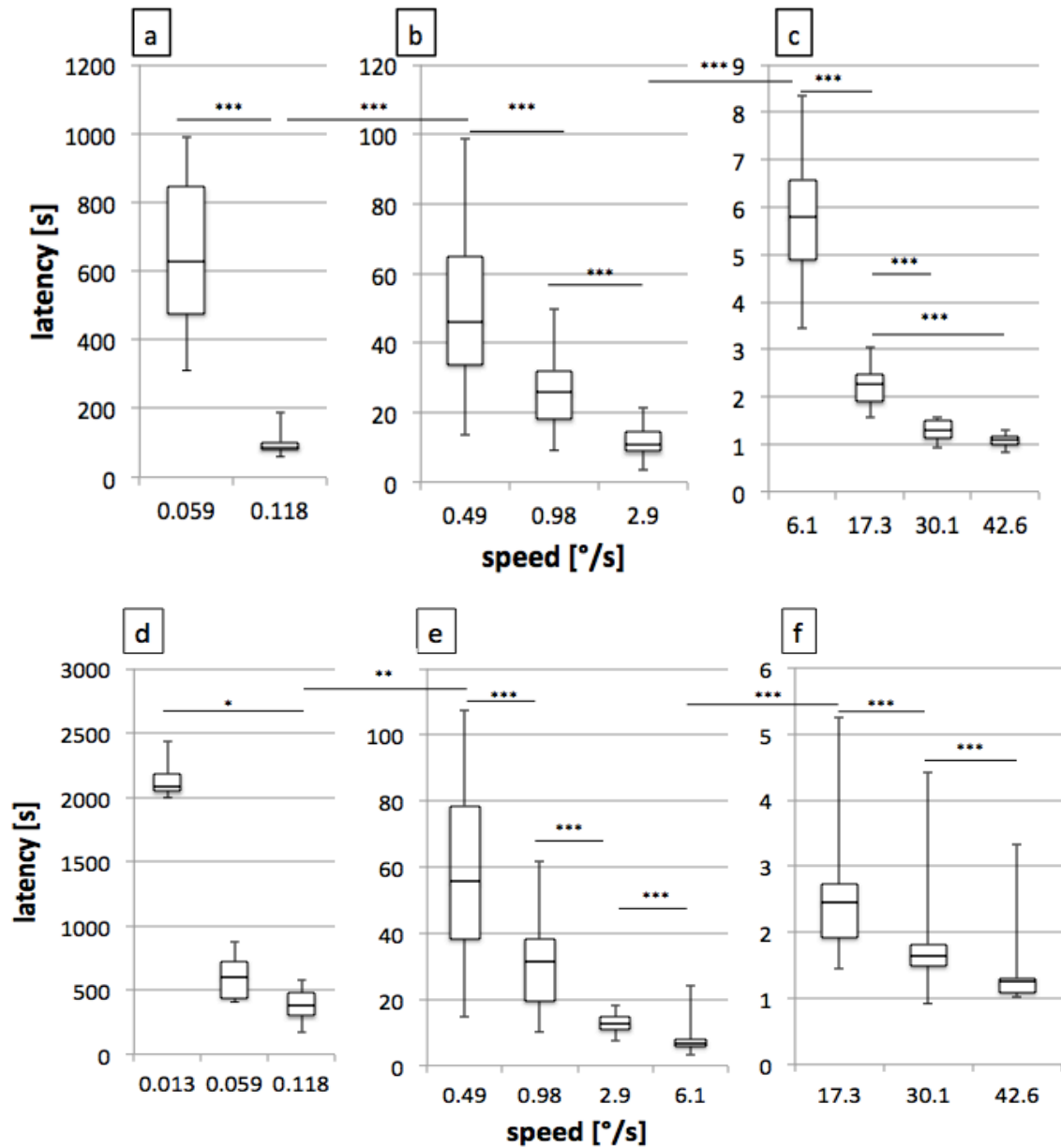
presented. This information is not shown in Figure 11a, 11c because this reaction was the only one in this speed condition.

**Table 10, Overview of the latencies to the first attack behaviour in the different speed conditions.**

The table shows the sample size (n), the minimum, median, mean, and maximum values of latencies in each speed condition. The latencies to first attack or orientation behaviour decreased continuously with increasing speed. Attack behaviour was always faster shown than orientation behaviour.

speed [°/s]	n		latency [s]							
			minimum		median		mean		maximum	
	A	O	A	O	A	O	A	O	A	O
81.9	2	1	0.43	0.79	0.53	0.79	0.53	0.79	0.63	0.79
42.6	4	11	0.83	1.0	1.1	1.3	1.1	1.6	1.3	3.3
30.1	12	33	0.92	0.92	1.3	1.7	1.3	1.8	1.6	4.4
17.3	19	38	1.6	1.5	2.3	2.5	2.2	2.4	3.0	5.3
6.1	31	56	3.4	3.2	5.8	6.8	5.8	7.3	8.4	24
2.9	33	43	3.4	7.5	11	12	12	13	21	18
0.98	63	67	9.1	10	26	32	26	31	50	62
0.49	76	58	13	14	46	56	50	57	99	107
0.118	14	6	59	170	88	382	101	382	188	576
0.059	8	7	311	407	629	603	649	601	988	871
0.013	1	4	1757	1998	1757	2081	1757	2150	1757	2438

The maximum latency to orientation behaviour occurred in the slowest speed condition and was 2438s. This is the longest latency in the entire experiment. The minimal latency in this test condition was 1998s (Table 10). When the speed increased from 0.013°/s to the next speed condition 0.059°/s, the median orientation latency was decreased rapidly from 2081s to 603s (Table 10, Figure 10). The more the speed was increased, the more quickly the spiders responded to the visual stimulus with orientation behaviour (Table 10, Figure 11d-e). The shortest latency where orientation behaviour was shown, was at a speed of 81.9°/s, where the reaction occurred after 0.79s. This information is not shown in figure 11e, because this was the only data point in this speed test.



**Figure 11 (a-e), Latencies in different speed conditions when attack behaviour (a-c) and orientation behaviour (d-f) was shown first.** The faster the dot moved, the faster *C. salei* reacted to the visual stimulus. The attack behaviour occurred faster as the orientation behaviour in every speed condition and reached the minimal latency of the entire experiment series with 0.43s. Attack: n(total)=263, Orientation: n(total)=324; For detailed data see Table 10.

The speed conditions 81.9°/s and 0.013°/s were dropped out of the analysis with Wilcoxon-Test for independent samples because of their small sample size < 4. All analysed speeds in the range of 42.6°/s to 0.059°/s differ significantly in their latencies to the first attack behaviour. The results of the Wilcoxon-tests for each speed are shown in Table 11.

**Table 11, Wilcoxon-test for latencies to first attack behaviour due to different speed conditions.** For all tests there are certain sample sizes (n), Wilcoxon-values (W) and significances (p). Each tested speed differs significantly to the neighboured speeds. Every tested speed differed highly significantly to each other speed.

speed 1	speed 2	n (speed 1)	n (speed 2)	n (total)	W	p	
42.6	17.3	4	20	24	10.000	0.002	**
30.1	17.3	12	20	32	78.500	0.000	***
17.3	6.1	20	32	52	237.000	0.000	***
6.1	2.9	32	34	66	658.000	0.000	***
2.9	0.98	34	63	97	739.000	0.000	***
0.98	0.49	63	79	142	2690.500	0.000	***
0.49	0.118	79	18	97	3277.000	0.000	***
0.118	0.059	18	9	27	174.000	0.000	***

The differences in the speeds from 42.6°/s to 0.059°/s are significant to each other. The results of the analysis with the Wilcoxon-test are shown in table 12, where the different sample sizes for the certain speed tests are listed, too.

**Table 12, Wilcoxon-test for latencies to first orientation behaviour due to different speed conditions.** For all tests there are certain sample sizes (n), Wilcoxon-values (W) and significances (p). Each tested speed differs significantly to the neighboured speeds in their latencies. The differences in the speed range from 42.6°/s to 0.49°/s are significant.

speed 1	speed 2	n (speed 1)	n (speed 2)	n (total)	W	p	
81.9	no analyse because of n=1						
42.6	30.1	11	34	45	146,5	0,005	**
30.1	17.3	34	38	72	791,0	0,000	***
17.3	6.1	38	56	94	748,0	0,000	***
6.1	2.9	56	47	103	1772,0	0,000	***
2.9	0.98	47	70	117	1470,5	0,000	***
0.98	0.49	70	65	135	3399,5	0,000	***
0,049	0.118	65	8	73	2233,0	0,002	**
0.118	0.013	8	5	13	42,0	0,040	*
0.059	0.013	9	5	14	53,0	0,053	no sign.

If a closer look to each speed condition were to be taken, there were significant differences in attack behaviour compared to attack behaviour in certain tests. These results are shown in Table 13. Attack behaviour is significantly faster shown in the speed conditions 30.1°/s, 6.1°/s, 2.9°/s and



0.98°/s. The results at a speed of 30.1°/s are highly significant (Table 13). The median latency to attack behaviour in this condition is 1.29 s, the minimal latency 0.92 s, and maximum latency 1.55s (Table 10). For orientation behaviour there is a median latency of 1.65 s, a minimal latency of 0.92 s and a maximum latency of 2.60s (Table 11). The same relations were true for speeds 6.1°/s, 2.9°/s and 0.98°/s. The spiders attacked the dot significantly earlier in these speeds as they orientated themselves to it (Table 13).

**Table 13, Differences in latencies to attack and orientation behaviour due to different speed conditions.** For all tests there are certain sample sizes (n), Wilcoxon-values (W) and significances (p). Attack behaviour is significantly faster shown in the speed conditions 30.1°/s, 6.1°/s, 2.9°/s and 0.98°/s. The results at a speed of 30.1°/s are highly significant.

speed [°/s]	n (attack)	n (orientation)	W	p	
81.9	2	1	3	0.667	no sig
42.6	4	11	22.5	0.211	no sig
30.1	12	34	133.5	0.000	***
17.3	20	38	529	0.318	no sig
6.1	32	56	1103	0.005	**
2.9	34	47	1170.5	0.032	*
0.98	63	70	3714.5	0.022	*
0.49	79	65	5259	0.06	no sig
0.118	18	8	208	0.052	no sig
0.059	9	9	72	0.258	no sig
0.013	1	5	2	0.38	no sig

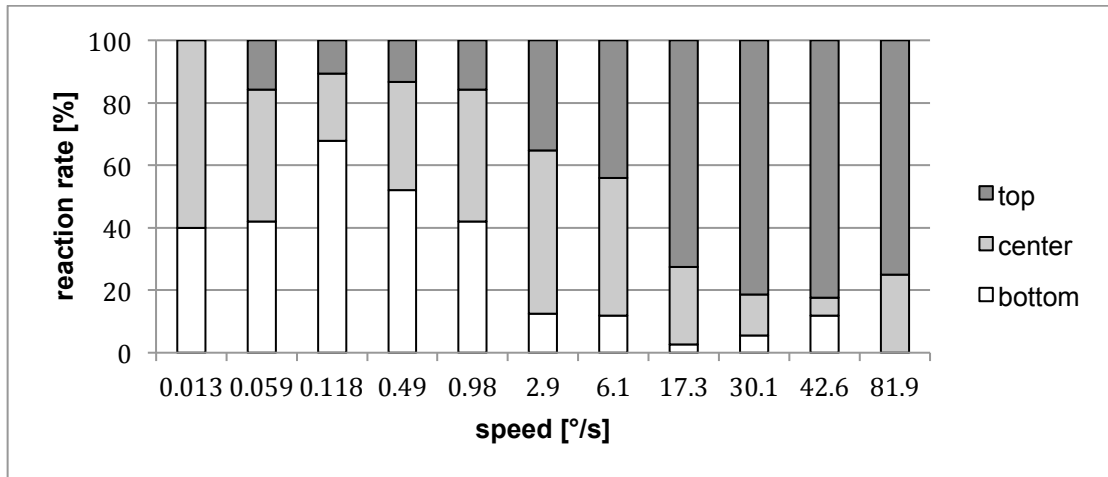
#### 4.3.3. Position of dot

##### All first reactions

In the experiment the spiders were always positioned in a way that they were horizontal to the centre of the screen. In some test runs, the spiders moved to the top or to the bottom of the jar, these data points are not analysed here.

Figure 12 shows the position of the dot, when the first reactions of the spiders occurred. The faster the dot moved, the more the spiders reacted to the dot when it was in the top region of the screen. If the dot was faster than 2.9°/s more than 35% of the first reactions of the spiders occurred when the dot was

in the top third of the screen. If the dot was faster than 17.3°/s, even more than 70 % of all behavioural patterns occurred in the top third of the screen. If the dot was slower than 1°/s more than 40 % of the reactions occurred when the dot appeared in the bottom section of the screen (Figure 12).



**Figure 12, Position of the dot, when the spider reacted the first time to the moving stimulus.** The different colours point out the position of the dot (top, center, bottom). The quicker the dot moved, the more the spiders reacted to the dot when it was in the top region of the screen. The slower the dot moved, the more the spiders reacted to the dot in the bottom region of the screen.

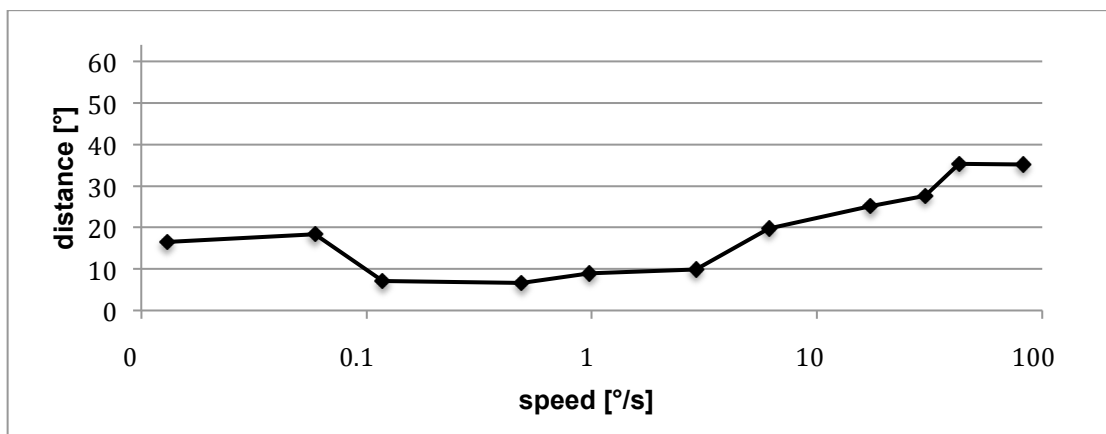
**Table 14, Significant differences in the position of the dot when the first reaction occurred due to variation of speed.** The  $\chi^2$ -test was done with each speed (speed 1) and all the other slower speeds. Speed 2 is the first slower speed, where the difference is significant. The table gives information about the different sample sizes, the  $\chi^2$ -values and the significance (p). The distributions of the position of the dot, when the reaction occurred differed significantly to some slower speeds. There was no significant difference in the four slowest speeds.

speed 1	speed 2	n (total)	n (speed 1)	n (speed 2)	$\chi^2$	p	
81.9	0.98	149	4	145	9.757	0.008	**
42.6	6.1	110	17	93	9.703	0.008	**
30.1	6.1	147	54	93	19.808	0	***
17.3	6.1	166	73	93	14.53	0.001	**
6.1	0.98	238	93	145	33.966	0	***
2.9	0.98	233	88	145	29.752	0	***
0.98	0.118	173	145	28	6.37	0.041	*
0,049	no significant differences to slower speeds						
0.118	no significant differences to slower speeds						
0.059	no significant differences to slower speeds						
0.013	no significant differences to slower speeds						

The differences between the speeds and the distribution of the position of the dot when the behavioural response occurred are significant ( $\chi^2 = 269.295$ ,  $n=681$ ,  $df=30$ ,  $p=0.000$ ). The results of the statistical analysis for each speed are shown in Table 14. The four slowest speeds did not vary in the position of the dot. The position of the dot in the speeds  $81.8^\circ/s$  to  $2.9^\circ/s$  differed to the position of the dot in the speeds  $0.98^\circ/s$  and  $6.1^\circ/s$  (Table 14).

With information about speed and latency, the travelled distance of the dot can be calculated. This was done, to find out about the minimal distance of the dot, when a reaction was elicited in the speed tests. These results are shown in Figure 13 for all first reactions.

The spiders reacted the fastest at a speed of  $0.49^\circ/s$ , there the dot was in the bottom part of the screen and had moved for  $6.7^\circ$ . With decreasing speed from this point, the dot was still in the bottom part of the screen, but moved nearly  $20^\circ$  until the first reaction was shown. Speeds from  $0.98^\circ/s$  to  $81.9^\circ/s$  led to distances of more than  $10^\circ$ . From speed  $17.3^\circ/s$  to  $81.9^\circ/s$  the dot moved more than  $25^\circ$  and released a reaction in the upper edge of the lower section of the screen (Figure 13).

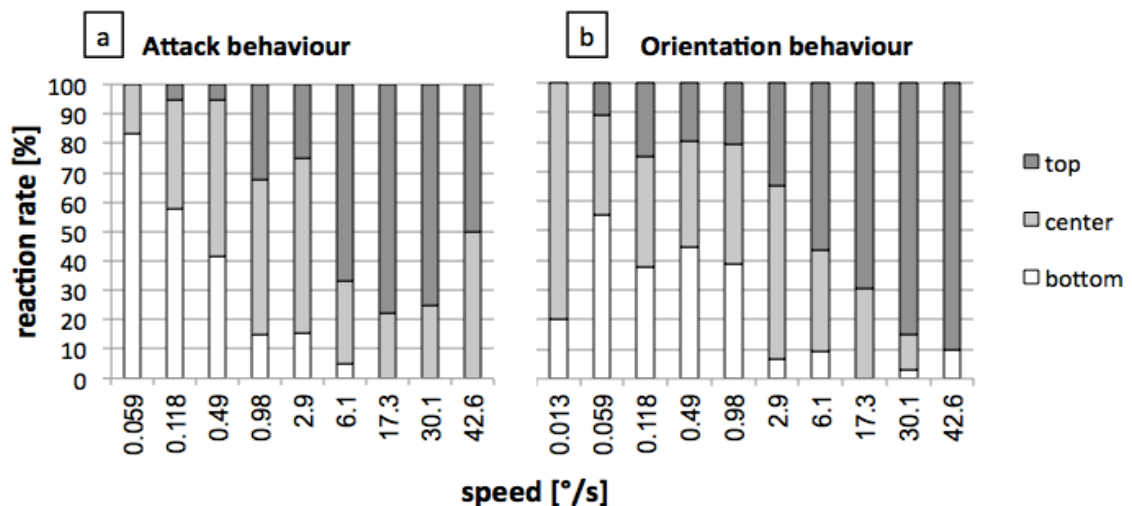


**Figure 13, Minimal distance of dot when reaction was elicited.** The shortest distance was given at a speed of  $0.49^\circ/s$ . With decreasing speed from this point, the dot moved up to nearly  $20^\circ$  until a reaction was elicited. In the faster speed conditions the dot travelled through the screen quite far until the first reaction was shown by *C. saiei*.

## Dot position at first attack- and orientation behaviour

The data for the following analysis are the first reactions, where the spiders were sitting in 90° to the central region of the screen. 263 attacks (39%) were shown as the first reactions of the spiders to the moving dot. Orientation behaviour was shown in 324 first reactions (51%). The distribution of the dot position to first attack and orientation behaviour was statistically analysed with the  $\chi^2$ -test. Only speeds were analysed where the sample size was larger or equal than 4 reactions.

Spiders reacted with attack behaviour to dots in the bottom part of the screen in the slow test conditions 5-10 (speed 6.1-0.059°/s). For the top section, the opposite was true – the faster the dot moved, the more attacks were shown when the dot reached the top section of the screen (Figure 14a).



**Figure 14 (a,b), Position of the dot, when the spider attacks the dot as first reaction or orientated to it.** The amount of attacks to a dot in the bottom part of the screen increases with decreasing speed. No attacks in the bottom part of the screen occurred in the speed range of 6.1°/s-42.6°/s. The most attacks in the top section of the screen occurred at a speed of 30.1°/s. The faster the speeds were, the more orientation behaviour occurred when the dot was in the top section of the screen. For data see table 15, 16.

If the dot moved very quickly (17.3°/s to 42.1°/s) no spider attacked the dot in the bottom region of the screen. The highest attack rate for dots in the bottom section was in test 10, where the dot moved with a speed of 0.059°/s (Figure 14a). The most attacks in the central region of the screen occurred in test 6

(2.9°/s). There, 19 of 32 attacks (59%) were shown in this central section. Attacks in the top region occurred mostly in the fast speeds. The highest attack rate for this section was in test 4 (17.3°/s), where 78% of the spiders attacked the dot (Figure 14a). The differences in the position of the dot are significant and were analysed with a  $\chi^2$ -test. The results are shown in Table 15.

Figure 14b shows the distribution of the position of the dots, when the spiders orientated to them firstly in the different speed conditions. The faster the speed, the more orientation behaviour was shown when the dot slid through the top part of the screen. If the speed decreased, more orientation behaviour was shown when the dot was in the bottom and the central section of the screen (Figure 14b).

**Table 15, Significant differences of the position of the dot when *C. salei* showed attack behaviour first.** The  $\chi^2$ -test was done with each speed (speed 1) and all the other slower speeds. Speed 2 is the first slower speed, where the difference is significant. The table gives information about the different sample sizes, the  $\chi^2$ -values and the probability of error (p).

speed 1	speed 2	n (total)	n (speed 1)	n (speed 2)	$\chi^2$	p	
42.6	0.98	62	4	58	21.095	0	***
30.1	6.1	41	9	32	8.647	0.013	*
17.3	6.1	53	21	32	9.175	0.01	*
6.1	0.98	90	32	58	11.009	0.004	**
2.9	0.98	92	34	58	15.245	0	***
0.98	0.118	76	58	18	9.797	0.007	**
0.118	0.059	26	18	8	9.668	0.008	**

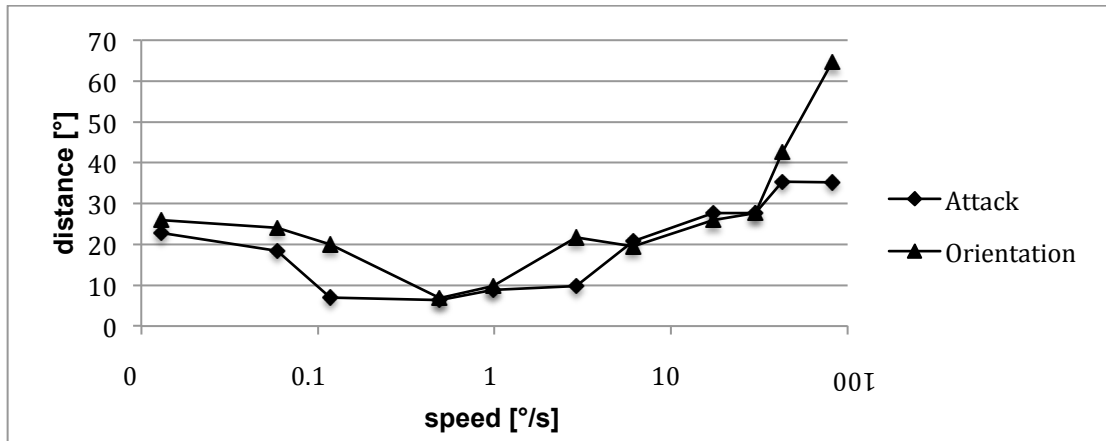
The  $\chi^2$ -test showed no significant differences between slow speed conditions (0.98°/s – 0.059°/s) at the first orientation behaviour (Table 16). The positions in speed condition 2.9°/s differ significantly to speed condition 0.98°/s. When speed decreased from 42.6°/s to 17.3°/s, the spiders reacted much earlier, that means when the dot was in a lower section of the screen. The amount of reactions in the top section decreased from 90% to about 70%, and 30% of the reactions occurred when the dot was in the central section of the screen (Figure 14b). When the speed got more and more slower and reached 2.9°/s, nearly 60% of all first orientations to the dot occurred in the central screen section. When the speed was slowed down to 0.98°/s the orientation rate to

dots in the bottom region increased to 38% and the rates for the top and central region decreased (Figure 14b).

**Table 16, Significant differences of the position of the dot when *C. salei* showed orientation behaviour first.** The  $\chi^2$ -test was done with each speed (speed 1) and all the other slower speeds. Speed 2 is the first slower speed, where the difference is significant. There is no analysis for speed 81.9°/s because *C. salei* showed only one reaction with orientation behaviour in this condition. The table gives information about the different sample sizes, the  $\chi^2$ -values and the probability of error (p).

speed 1 [°/s]	speed 2 [°/s]	n (total)	n (speed 1)	n (speed 2)	$\chi^2$	p	
42.6	17.3	52	11	41	10.82	0.004	**
30.1	6.1	92	56	36	8.52	0.014	**
17.3	2.9	88	41	47	12.806	0.002	**
6.1	2.9	103	56	47	6.822	0.033	**
2.9	0.98	117	47	70	15.288	0	***
0.98	no significant difference with slower speeds						
0.49	no significant difference with slower speeds						
0.118	no significant difference with slower speeds						
0.059	no significant difference with slower speeds						

Attack behaviour was shown faster than orientation behaviour. This difference is also visible in the minimal distance of the moving dot. Attack behaviour led to a minimal distance of 35° in the fastest speed condition, whereas orientation behaviour was first shown, when the dot moved for more than 60° and reaches the top of the screen (Figure 15). With decreasing speed, the distance of dot for attack and orientation behaviour got shorter, but attack behaviour was still shown faster. A remarkable difference is recognisable at a speed of 2.9°/s and 0.118°/s. There, the dot had to move just 10° and 7° to release an attack behaviour, whereas orientation behaviour was not shown until the dot moved for about 20° (Figure 15).



**Figure 15, Minimal distance of the dot through the screen, until the fastest attack and orientation behaviour was shown under several speed conditions.** A moving dot releases attack behaviour faster than orientation behaviour. Both curves have a similar trend with fastest reactions between 0.1°/s and 1°/s. The faster the dot moved from that point, the later the reaction occurred.

#### 4.3.4. All reactions

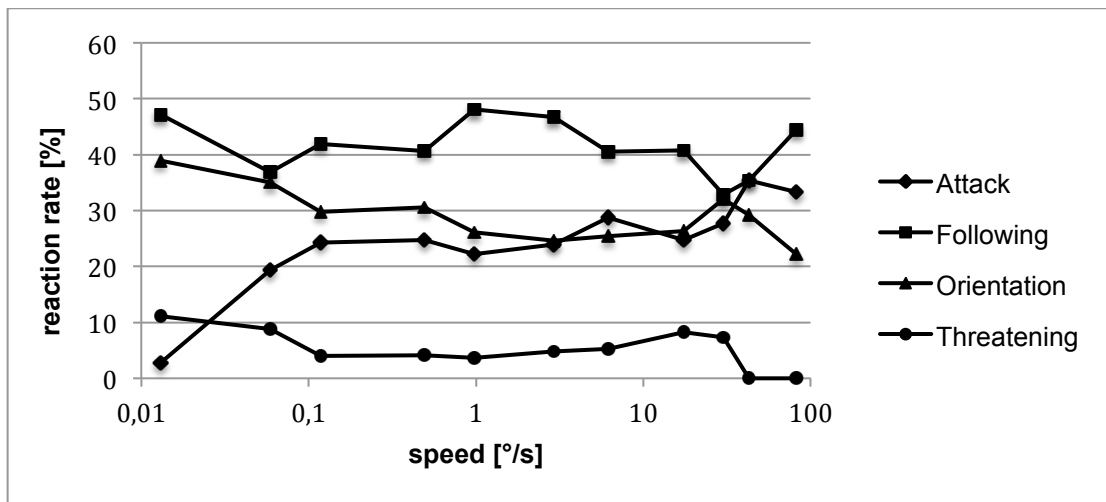
Altogether, 2022 behavioural patterns were shown in 1891 runs. The total numbers and percental rates of the different behavioural patterns in each test are shown in Table 17.

**Table 17, Behavioural patterns in different speed tests.** The most behavioural patterns were shown in test 9, where 490 behaviours were shown. The reaction rate for following behaviour was always more than 30%. Orientation behaviour was also shown for more than 20% in every speed test. Attack and Threatening behaviour were shown at least.

speed [°/s]	attack		following		orientation		threatening		total
	total	%	total	%	total	%	total	%	
0.013	1	3	17	47	14	39	4	11	36
0.059	11	19	21	37	20	35	5	9	57
0.118	18	24	31	42	22	30	3	4	74
0.49	121	25	199	41	150	30	20	4	490
0.98	98	22	212	48	115	26	16	4	441
2.9	65	24	127	47	67	25	13	5	272
6.1	76	29	107	41	67	25	14	5	264
17.3	48	25	79	41	51	26	16	8	194
30.1	38	28	45	33	44	32	10	7	137
42.6	17	35	17	35	14	30	0	0	48
81.9	3	33	4	44	2	23	0	0	9
total	496		859		566		101		2022

In every speed condition, following behaviour was the most shown behaviour with a rate higher than 30% (Table 17, Figure 16).

Figure 16 shows the percental rate of behavioural patterns that occurred, when the test run of a spider was valid. Following was the most shown behavioural pattern by *C. salei*. If the speed of the dot increased, the moving dot was attacked more. Threatening was a rare behavioural response. It was the least shown behaviour in every test condition, except at the slowest speed. Even no threatening behaviour was shown when the dot moved with a speed of 42.6°/s or 81.9°/s. The curve of orientation is developing very smooth, it only increased to nearly 40% when the speed slows down to the slowest speed condition (Figure 16).



**Figure 16, Shown percental rate of following, attack, orientation and threatening behaviour due to speed variation.** Following was the most shown behavioural pattern. The quicker the speed, the more attacks to the moving dot were shown from *C. salei*. Orientation behaviour was always shown for more than 20%. Threatening behaviour was the behavioural pattern that was shown least. For data, see Table 17.

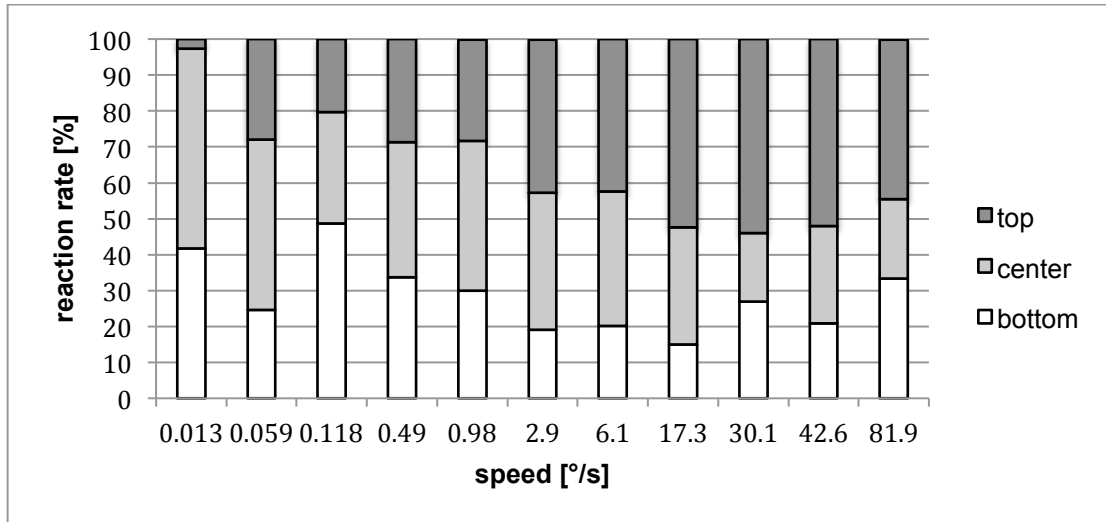
### Dot position

In each test, reactions to dots were observed in each section of the screen. Through the different speed conditions, the spiders reacted significantly different to the moving dots ( $n(\text{total}) = 2023$ ,  $\chi^2 = 138.969$ ,  $p = 0,000$ ).

The most reactions in the top region were shown at a speed of 30.1°/s, the third quickest speed condition. The most reactions in the central section were



shown in the slowest speed, test 11. In no speed condition, the reaction rate for the bottom section reached 50%. The most reactions in the bottom part (48%) occurred at a speed 0.118°/s, a very slow one (Figure 17).



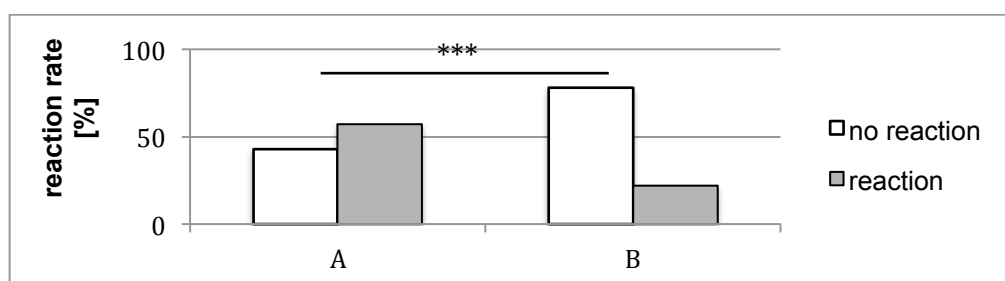
**Figure 17, Location of the stimulus when the reactions were shown.** The location, where the reaction took place differed through the tested speeds significantly.  $n(\text{total})=2023$ ,  $n(81.9)=9$ ,  $n(42.6)=48$ ,  $n(30.1)=137$ ,  $n(17.3)=195$ ,  $n(6.1)=264$ ,  $n(2.9)=272$ ,  $n(0.98)=441$ ,  $n(0.49)=490$ ,  $n(0.118)=74$ ,  $n(0.059)=57$ ,  $n(0.013)=36$ ,  $\chi^2=138,969$ ,  $p=0.000$

#### 4.4. Dot appearance

Further experiments were done to gather information about the influence of dot appearance to the reaction rate. The results of test A, where the dot slid into the screen differed significantly to the results of test B, where the dot was fully visible for the whole presentation and started to move in the same speed as in test condition A when the dot of A was fully visible at the screen (Figure 6).

In test condition A, 57% of the spiders reacted to the appearing dot. Only 22% reacted in test condition B (Figure 18) to it. On the one hand, the amount of reactions in these different test conditions differed highly significantly (A:  $n(\text{reaction})=34$ ,  $n(\text{no reaction})=26$ , B:  $n(\text{reaction})=13$ ,  $n(\text{no reaction})=13$ ;  $\chi^2=14,931$ ,  $df=1$ ,  $p=0,000$ ). But on the other hand, there was no difference in the first shown behavioural patterns. When the dot was not visible at the beginning of the test run, 62% of the spiders showed attack behaviour to the

sliding in dot, in test condition B only 46%. Orientation behaviour was also shown in 46% of the first reactions in test condition B. Neither in test condition A, nor in test condition B was any following behaviour shown as first reaction to the moving stimulus.



**Figure 18, Reaction rate of test 9 and 10 in test condition A and B.** When the dot was appearing at the screen (A), 57% of the spiders reacted to the moving dot. When the dot was stationary visible at the bottom section and started to move as well, only 22% of the spiders reacted to the stimuli (A:  $n(\text{reaction})=34$ ,  $n(\text{no reaction})=26$ , B:  $n(\text{reaction})=13$ ,  $n(\text{no reaction})=13$ ;  $\chi^2=14,931$ ,  $df=1$ ,  $p=0,000$ ).

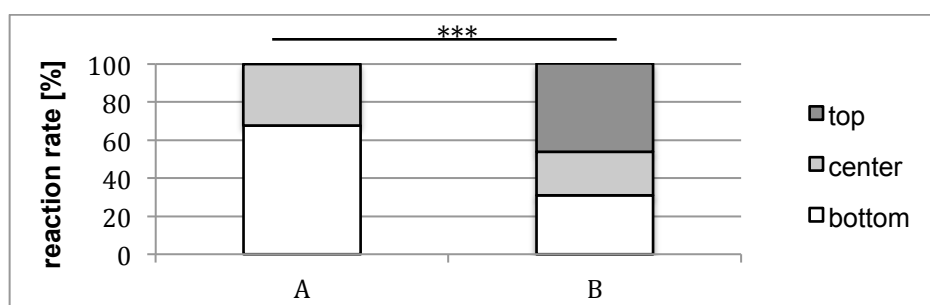
Threatening behaviour reached a rate of first reactions of 6% in test condition A, and 8% in test condition B (Table 18). These results were not significant ( $n(A)=34$ ,  $n(B)=13$ ,  $\chi^2=0,942$ ,  $p=0,624$ ).

**Table 18, First behavioural patterns in test condition A and B in total number (n) and percentage (%).** Attack behaviour was shown most in test condition A with 62%. In test condition B, where the dot was visible all the time for the spider, 46% of the first reactions were attacks. The same amount was shown as orientation behaviour in this test condition. In both test conditions, no following behaviour was shown as first behavioural response to the stimulus.

test condition	behaviour								
	attack		orientation		following		threatening		total
	n	%	n	%	n	%	n	%	n
A	21	62	11	32	0	0	2	6	34
B	6	46	6	46	0	0	1	8	13

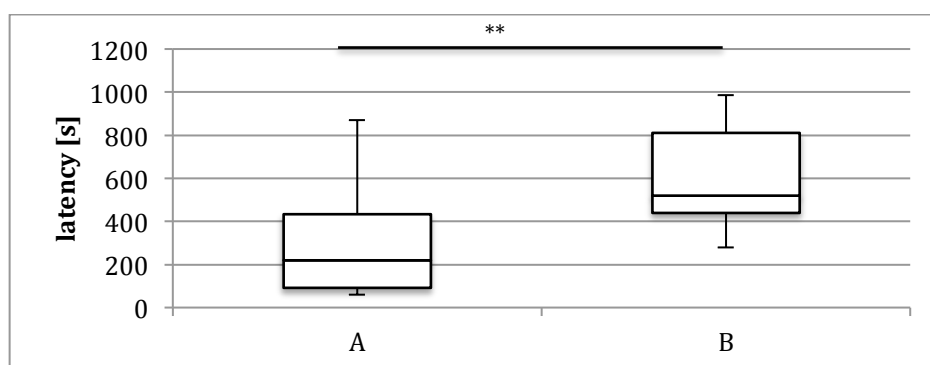
Significant differences could be observed, when the position of the dot was set in relation to the first reaction. In Figure 19, it can be seen that more than two thirds of all first reactions in test condition A occurred, when the dot was in the bottom section of the screen. Only one third of the spiders in test condition B reacted to dots in this section. Additionally, most reactions in test condition B were shown, when the dot slid through the top section of the screen, no spider

in test condition A reacted there (Figure 19). The reaction rate to dots in the central region was in test condition A 32% and in test condition B 23%. These results are significant ( $n(A)=34$ ,  $n(B)=13$ ,  $\chi^2= 18.19$ ,  $p=0,000$ ). These results of the position of the dot go along with the results of the latencies because a reaction in the bottom part occurs earlier than a reaction in the central or top section of the screen.



**Figure 19, Position of the dot in test condition A and B when the first reaction occurred.** The position of the dots varied significantly ( $n(A)=34$ ,  $n(B)=13$ ,  $\chi^2= 18.19$ ,  $p=0,000$ ). When the dot appeared on the screen by sliding in more spiders reacted to the dot in the bottom section of the screen. In test condition B, most spiders did not react to the dot until it reached the top section of the screen.

When the dot was not visible at the beginning of the experiment and slid into the screen, the spiders reacted significantly earlier to the dot as if the dot were fully visible from start. The latencies in test condition A ranged from a minimum of 59.95s to a maximum of 870s. The fastest reaction in test condition B was after 279s and the slowest was after 986s. The median latency was in test condition A 221s and in test condition B with 519s more than twice as long (Figure 20).



**Figure 20, Latencies to first reaction in test condition A and B.** When the dot appeared at the screen (A) the spiders reacted earlier than in test condition B, where the dot was visible the whole time.  $n(A)=34$ ,  $n(B)=13$ ,  $W=704,00$ ,  $U=-2,376$ ,  $p=0,017$

## 5. Discussion

Previous studies showed, that *C. salei* reacts with prey capture behaviour to computer-generated stimuli, and that different qualities of the presented stimuli influence the reaction rate (Lindner, 2013). With respect to this study, more information about the preferred qualities of a visual cue for releasing prey capture behaviour were gathered. It was found, that the elevation of the stimulus path is a main factor for prey detection (Schützinger, 2014).

This study focused on the question of the influence of speed on prey hunting behaviour in *C. salei*. All other qualities of the stimuli, like size or colour, were standardized to get reliable data to analyse the responsibility of speed in visually eliciting prey capture behaviour of the hunting spider.

Movement of visual cues are processed as optic flow. The optic flow is defined as the change of retinal image that is analysed and visually perceived as motion (Egelhaaf and Warzecha, 1999). In the visual system of flies there are direction-selective cells with large receptive fields, which are responsible for encoding time-dependent optic flow.

In behavioural experiments, it was found, that only the secondary eyes of *C. salei* are able to perceive the optic flow (Neuhofer et al., 2009). This result goes along with the structural analysis of the neuronal anatomy of the spiders brain. The eyes of *C. salei* differ in their visual pathways so that the visual information of AM and PM eyes can be processed completely separately (Strausfeld and Barth, 1993; Strausfeld et al., 1993).

### Reaction rate

In this study, the spiders reacted differently to the varying speed conditions of the presented stimuli. First of all, there is a significant difference in the reaction rate due to varying speeds. The visual system of *C. salei* reaches its limit, when the stimulus achieves a speed of more than 81.9°/s. There, the lowest reaction rate was about 2%. If an object is moving faster than this, the retinal image is changing too fast and cannot be perceived by the retinal cells.

Decreasing speed from this point, the spiders improved in the behavioural tests and showed more and more reactions to the moving dot. The slower the dot moved, the more reactions were shown with a maximum reaction rate at a speed of  $0.49^{\circ}/s$ . If the speed decreases again, the reaction rate decreases as well but the limitation of recognition could not be found. Even at a speed of  $0.013^{\circ}/s$ , more than 30% of the spiders reacted to the stimulus.

The main goal of this and previous studies was to find out about different qualities of a stimulus, that release in combination a high rate of prey capture behaviour. It was found, that *C. salei* reacts best to dots of a size of  $15^{\circ}$  (8cm diameter) and a reaction rate of 65% could be reached when the dot moved with a speed of  $56^{\circ}/s$  (Lindner, 2013). These results were repeated and were extended by analysing different slopes of the moving dot. A maximum reaction rate of 44.3 was given with a dot of size  $14.8^{\circ}$  and a speed of  $15.8^{\circ}/s$  (Schützinger, 2014). These maximum rates could be overtopped with decreasing speed and using a vertical slope of the  $15^{\circ}$  large stimuli. A reaction rate of 75% was reached when the dot moved with  $0.49^{\circ}/s$ .

## **Behavioural patterns**

Other predatory spiders that rely on their visual system are jumping spiders (Salticidae). Every action in hunting behaviour is mediated by one or more of the eight eyes (Forster, 1979). There, on the one hand chasing moving objects is described as a function of the secondary eyes, on the other hand the principal eyes (anterior-median) are described as being responsible for stalking stationary prey (Forster, 1979). In another study about prey capture behaviour of jumping spiders, three main hunting behaviours are described: Orientation, Pursuit and Capture (Forster, 1977). Orientation can be defined as a movement or a series of movements that position the spider in a way to watch the prey more effectively (Forster, 1977). Pursuit consists of any following actions to keep the prey in view and to reduce the distance to the object. The most aggressive behavioural pattern in jumping spider's hunting behaviour is capture. Capture is just shown in predictable distances to the prey and is done to catch the prey (Forster, 1977). The prey hunting behaviour of *C.*

*salei* that was analysed in this study can be described likewise. Orientation and following behaviour are shown at a certain distance to the stimulus. Orientation behaviour was one of the most shown behaviours as a first reaction of the spider. Like in the description of Forster, orientation behaviour is a non-aggressive behaviour where the spider leaves its resting position to stalk the object to gather visual information about it. Predators, mates, prey or other environmental cues can lead to orientation behaviour in nature. Afterwards, orientation behaviour can lead to any behavioural response, for instance, escape-, courtship-, agonistic- and certainly hunting behaviour (Forster, 1977).

Pursuit behaviour of jumping spiders is similar to the following behaviour that is described here for *C. salei*. *C. salei* walks or runs towards the stimuli. Following behaviour is the most shown behavioural pattern in each speed condition. As the spider follows the sit and wait- strategy while hunting, it follows its prey for a few steps, holds back and starts moving again (Forster, 1977). Afterwards, it can either lead to an attack or it can just be described as locomotion without any aggressive intention.

Attack behaviour is the most aggressive and fastest behavioural pattern. It just contains a quick jump at the prey and was shown mostly as first reaction in slow speed conditions. The analysed attack behaviour of *C. salei* is analogous to capture in jumping spiders.

### **First behavioural response**

The behavioural patterns at the first behavioural reaction are very interesting. The faster the dot moved, the more orientation behaviour was shown. Maybe, the dot moved that fast, that the spider recognised the dot but did not identify it as prey. If an object in the natural environment moves that fast it could be a predator or anything else as well. So the spider orientates at first to it and watches the object for further information. When the dot appears at the screen again, it can be followed or attacked. If an object moves quite slowly, the spider can stalk it without being at risk of getting discovered. It can watch the object securely without moving and so decreasing risk of being detected. If the

object moves on and can be identified as a prey, the spider stalks it further and waits until the prey gets in a preferred position to be attacked successfully. This theory could be observed in the experiments.

In the control runs, where a stationary dot was shown, the spiders showed no attack or threatening behaviour. Obviously, the spiders recognised the dot because they orientated towards it and followed it to the screen. But body orientation and locomotion towards a stimulus without aggressive behavioural patterns can be interpreted as no prey capture behaviour. Additionally, the reaction rate in the control group was 13,6%, so the spiders reacted significantly less than in the speed tests. AM and PM eyes in *C. salei* perform the perception of the stationary stimulus (Schmid, 1998). It was shown in behavioural experiments that the eyes differ in functions. Target detection is executed by any of the eyes but target discrimination was only possible with uncovered AM eyes (Schmid, 1998). In addition, it was shown, that *C. salei* does not distinguish between shapes. It does not matter, if the spider is presented with shapes of a bromeliad or a rectangle, they show no preference in running to them (Schmid, 1998). This behaviour of running to dark shapes is interpreted as detecting places to hide. The absence of shape discrimination allowed the use of a moving dot as visual stimuli and not prey-like shaped stimuli in this study.

## **Latencies**

In general it must be recognised, that in fact of the different speeds, the duration of presentation of the stimulus varies. That's the reason, why the latencies in the different speed conditions vary so much. *C. salei* is a sit and wait predator. It hides on plants and stalks its prey before capturing. This behaviour can be observed in the experiments as well. The longer the dot was presented (the slower the dot moved), the longer the latency lasted. If prey moves very fast, maybe when the predator was detected and the prey tries to escape, the spider has to make a quick decision to attack the prey successfully. If prey moves very slowly and the spider has time to stalk it and

to wait for the prey getting in a preferred position to attack, the latency to hunting behaviour is longer. The analysis of the position of the dot, when the first response to the stimuli was shown could be another reason for attacking prey at a certain time. It could be observed that most reactions in the fast speed conditions occurred when the dot was already in the top section of the screen. These results support the sit and wait behaviour and the worse perception of very fast moving objects.

The minimal latency was 0.43s. This time best reflects the sensory abilities of *C. salei*. This latency was given at the fastest speed condition (81.9°/s). This very fast reaction and the results gathered about the reaction rate at very slow speeds give reason for the assumption, that *C. salei*'s visual ability is even much more attuned than suspected.

### **Dot appearance**

During the slow speed tests, it was observed, that many reactions occurred for dots that were not even fully visible on the bottom part of the screen. Analysing the dot position led to the idea that the appearing black dot on the green screen, and not just the speed of the dot, is a rich stimulus that elicits hunting behaviour. To exclude this factor, experiments with test conditions A and B were done. The sliding-in dot represents an invisible prey that appears slowly in the visual field of *C. salei*. The visible dot that starts to move represents a non-moving prey that begins moving at a certain point. The results of these tests show, that an appearing object is attacked significantly faster and more often. All behavioural responses in test condition A occurred, when the dot started to appear on the screen or moved through the bottom or the central section of the screen. No reaction was shown when the dot already passed the top third of the screen. If the dot moved with the same speed but was visible all the time at the bottom section and started to move at a certain point of time, nearly 70% of the reactions occurred in the central and top section of the screen. Observations led to the idea that *C. salei* has preferred positions of prey when it attacks it. The moving stimulus is present the whole time in the visual field of *C. salei*, but it is mostly attacked when it is in a horizontal line to



the spider or appearing from a visual barrier. This position must be correlated to high prey capturing success, in fact the spider can perceive the distance of prey and hunt it successfully. These results go along with the sit and wait hunting strategy and indicate a preference of prey position when *C. salei* has the intention to capture prey.

Visual stimulation, eliciting hunting behaviour was also examined with mantis. In several studies, researchers found, that species differ in preferences of stimulus qualities and showed tracking, approaching and striking behaviour (Prete et al., 2011). In addition, Prete et al. (Prete, 1999) describes that an object consists of more than 10 parameters to be detected as prey.

In comparison to *C. salei*, mantises are opportunistic predators and their prey ranges from small arthropods and conspecifics of the same size to small vertebrates, which are even larger as the mantis (Hurd, 1999). For that reason, mantis must have a wide scheme of stimuli qualities to detect objects as prey, and cannot use the simple matching-to-template strategy (Prete et al., 2011). They concluded that stimulus sizes do not relate to the mantis size. If the dot was enlarged, the tracking behaviour was shown at a consistently high amount (Prete et al., 2011). This fact was also observed in the experiments with *C. salei*. In the pre-tests more reactions were shown when a larger stimulus was presented. The stimulus size was 15°, as large as or even larger than the spider itself. Therefore, the question arises why the spiders attack stimuli that are even larger than themselves. *C. salei* hunts cockroaches, crickets, earwigs, moths and small frogs (Barth and Seyfährth, 1979). All these animals have different shapes. This indicates that *C. salei* can not distinguish between shapes well. But these preys are not that large as the visual stimuli that elicit attack behaviour. One possible explanation is that the large dot is an extraordinary stimulus that leads to high capture motivation. The question why *C. salei* attacks that large stimuli and does not show escape behaviour must be answered in further studies.

## Conclusion

To summarize, speed is an important quality of a stimulus to visually elicit prey capture behaviour. The upper limit of speed recognition is at about  $81^{\circ}/s$ . The lower limit of reaction rate due to speed could not be evaluated in this study. *C. salei* shows different reactions to objects moving with different speeds. Obviously, the faster the speed, the more orientation behaviour is initially shown. The slower the speed, the more attack behaviour is displayed first. The latencies to the first behavioural response increase with decreasing speed, and this supports the sit and wait strategy for prey capturing. In addition, *C. salei* reacts more and faster to appearing objects than to constantly shown objects that start to move. There should be further studies to research the influence of appearing objects to the prey capture behaviour of *C. salei*.

## 6. Summary

*C. salei* is a nocturnal sit-and-wait predator found throughout Central America (Barth und Seyfarth, 1979). The animals live well hidden and attack their prey from ambush. Therefore, they use their very well developed mechano-sensory sense. The visual sense is well developed as well, but for a long time it was not realized as being important for prey capture.

*C. salei* has four pairs of eyes. They are classified by their position and function in Principal and Secondary eyes. The Principal eyes (anterior-median eyes) are responsible for object discrimination (Schmid, 1998), The Secondary eyes for detection of movement (Neuhofer et al, 2009).

This study wants to consider the question of which factors influence the visual sense of *C. salei* in prey capturing behavior and which qualities a stimulus must have to release a reaction by the spider. To find out that, the stimulus was shown on a screen and all other stimuli like vibrations and airflow were repressed by styrofoam underlayments. In the pre-tests, the size and direction of the stimulus was tested. There was a higher reaction rate to a dot size of  $15.18^\circ$ , but it did not make a difference if the dot slid in from the bottom or the top part of the screen first.

The speed tests showed a different reaction rate to varying speeds of the stimulus. The maximum reaction rate of 75% was reached with a speed of  $0.49^\circ/\text{s}$ . Increasing the speed led to low reaction rates until hardly any reaction was shown at a speed of  $81^\circ/\text{s}$ . Slower speeds still led to reactions. Even with the minimal speed condition of  $0.013^\circ/\text{s}$  the reaction rate was higher than 30%. The latencies were varying due to different speeds too. The faster the dot moved, the faster the reaction occurred. The slower the speed, the longer the latencies. These results support the behaviour of a sit-and-wait predator, as *C. salei* is.

## 7. Zusammenfassung

*C. salei* ist ein nachtaktiver Lauerjäger mit einem Verbreitungsgebiet in Zentralamerika (Barth und Seyfarth, 1979). Die Tiere leben gut versteckt und attackieren ihre Beute aus dem Hinterhalt. *C. salei* nutzt dabei ihren gut ausgebildeten mechano-sensorischen Sinn. Auch ihr visueller Sinn spielt dabei eine erhebliche Rolle, den aber bisher keine tragende Rolle zugesprochen wurde. *C. salei* besitzt vier Augenpaare, die in Haupt- und Nebenaugen eingeteilt werden. Diese Einteilung erfolgt aufgrund der Lage und der Funktion der Augen. Die Hauptaugen (anterior-median Augen) sind verantwortlich für Objektunterscheidungen (Schmid, 1998). Die Nebenaugen (anterior-lateral, posterior-lateral, posterior-median Augen) für die Detektion von Bewegungen (Neuhofer et al, 2009).

Diese Studie geht der Frage nach, in welchem Maße der visuelle Sinn zum Jagdverhalten von *C. salei* beiträgt und wie ein visueller Stimulus gestaltet sein muss um eine Reaktion bei der Spinne auszulösen. Für diesen Zweck wurde der Stimulus auf einem Bildschirm gezeigt und jegliche andere Reize, wie Vibrationen und Luftzüge wurden durch Dämmung mit Styroporunterlagen ausgeschalten.

Bei den Vorversuchen wurde die Reizgröße und Richtung ausgetestet. Die Vorversuche zeigten eine höchste Reaktionsrate bei einer Punktgröße von  $15.18^\circ$ , ob ein Punkt sich von unten oder oben in den Bildschirm bewegte, beeinflusste die Reaktionsrate nicht.

Die anschließenden Versuche zeigten eine unterschiedliche Reaktionsrate zu unterschiedlichen Geschwindigkeiten des Stimulus. Die maximale Reaktionsrate von 75% wurde bei einer Geschwindigkeit von  $0.49^\circ/\text{s}$  erreicht. Bei Erhöhung der Geschwindigkeit sinkt die Reaktionsrate kontinuierlich, bis bei  $81^\circ/\text{s}$  fast keine Reaktionen mehr ausgelöst werden. Langsamere Geschwindigkeit lösen weiterhin Reaktionsraten aus. Sogar bei einer Minimalgeschwindigkeit von  $0.013^\circ/\text{s}$  wurde eine Reaktionsrate von mehr als 30% gemessen. Auch die Latenzzeit bis zur Reaktion variiert stark. Je schneller sich der Reiz bewegt, desto schneller erfolgt die Angriffsreaktion, je langsamer die Geschwindigkeit, desto länger die Latenz. Diese Ergebnisse gehen einher mit der Lauerjagd von *C. salei*.

## 8. Literature

Barth, F. G. (2001): A spider's World: Senses and Behavior; Berlin, Heidelberg, New York; Springer Verlag

Barth, F. G., Seyfarth, E.-A. (1979): *Cupiennius salei* Keys. (Araneae) in the Highlands of Central Guatemala. J. Arachnol. 7(3), 255-263

Engelhaaf, M., Warzecha A.-K. (1999): Encoding of motion in real time by the fly visual system. Curr. Op. Neurobiol. 9, 454-460

Fenk, L. M., Hoinkes, T., Schmid, A. (2010): Vision as a third sensory modality to elicit attack behaviour in a nocturnal spider. J. Comp. Physiol. A. 196, 957-961

Forster, L. M. (1977): A qualitative analysis of hunting behaviour in jumping spiders (Araneae: Salticidae). New Zealand J. Zool. 4(1), 51-62

Forster, L. M. (1979): Visual mechanisms of hunting behaviour in *Trite planiceps*, a jumping spider (Araneae: Salticidae). New Zealand J. Zool. 9, 79-93

Hurd, L. (1999): Ecology of praying mantids. In: Prete, F., Wells, H., Wells, P., Hurd L. (eds): The praying mantids. Johns Hopkins University Press, Baltimore, 43–60

Klopsch, C., Kuhlmann, H. C., Barth, F. G. (2012): Airflow elicits a spider's jump towards airborne prey. I. Airflow around a flying blowfly. J. Royal Society Interface 9(75), 2591-2602

Lindner, P. (2013): Visually elicited prey capture behavior in *Cupiennius salei*. unpublished Diploma-Thesis, University of Vienna

Neuhofer, D., Machan, R., Schmid, A. (2009): Visual perception of motion in a hunting spider. J. Exp. Biol. 212, 2819-2823

Prete, F. R. (1999): Prey Recognition. In: Prete, F., Wells, H., Wells, H., Hurd, L. (eds): The Praying Mantids. Johns Hopkins University Press, Baltimore, 141–179

Prete, F. R., Komito, J. L., Dominguez, S., Senson, G., López, L. Y., Guillen, A., Bogdanivich, N. (2011): Visual stimuli that elicit appetitive behaviors in three morphologically distinct species of praying mantis. J. Comp. Physiol. 197, 877-894

Schmid, A. (1998): Different functions of different eye types in *Cupiennius salei*. J. Exp. Biol. 201, 221-225

Schmitt, A., Schuster, M., Barth, F. G. (1990): Daily locomotor activity patterns in three species of *Cupiennius* (Araneae, Ctenidae): The males are the wandering spiders. J. Arachnol. 18, 249-255

Strausfeld, N. J., Barth F. G. (1993): Two visual systems in one brain: Neuropils serving the secondary eyes of the spider *Cupiennius salei*. J. Comp. Neurol. 328(1), 43-62

Strausfeld, N. J., Weltzien, P., Barth, F. G. (1993): Two visual systems in one brain: Neuropils serving the principal eyes of the spider *Cupiennius salei*. J. Comp. Neurol. 328(1), 63-75

Schützinger, S. (2014): Visually elicited prey capture behavior in *Cupiennius salei*; unpublished Diploma-thesis, University of Vienna

Walla, P., Barth, F. G., Eguchi, E. (1996): Spectral Sensitivity of Single Photoreceptor Cells in the Eyes of the Ctenid Spider *Cupiennius salei* Keys. Zool. Sci. 13, 199-202

Zopf, L. M., Schmid, A., Fredman, D., Eriksson, B. J. (2013): Spectral sensitivity of the ctenid spider *Cupiennius salei*. J. Exp. Biol. 216, 4103-4108

## 9. Acknowledge

First of all, I want to thank my supervisor ao. Univ.-Prof. Dipl.-Biol. Dr. Axel Schmid for his useful comments and his guidance through the process of this master thesis. This study wouldn't be as it is without allocating the thesis and encouraging me in my own ideas. I thank all members of the Department of Neurobiology. It was a pleasure to work there and many friendships were formed. I'd like to bring out Sarah Schützinger for introducing me to the experimental setup and Eva Orlando for her useful remarks.

Last but not least, I want to express my gratitude to my beloved family, front and foremost to my parents, who paved the way for my education. I want to thank my friends and of course, David. The process of finishing this master thesis wouldn't have been so successful and smooth without his encouragement, patience and love.

# Curriculum Vitae

## Angaben zur Person

Nachname(n) / Vorname(n)	<b>Reithofer Christina</b>
Titel	BSc, Bachelor of Science
Adresse	Hippgasse 33/40 1160 Wien (Österreich)
Telefon	043 - 664 89 888 15
E-Mail	christina.reithofer@gmx.at
Staatsangehörigkeit	Österreich
Geburtsdatum und -ort	08/11/1989 in Neunkirchen
Geschlecht	Weiblich

## Schul- und Berufsbildung

<b>September 2014</b>	Abschluss Masterstudium Verhaltens-, Neuro- und Kognitionsbiologie an der Universität Wien
-----------------------	--

<b>Oktober 2011</b>	Abschluss Bachelorstudium Biologie an der Universität Wien
---------------------	--

<b>Zeitraum</b>	<b>1/10/2011- 9/2014</b>
Hauptfächer/berufliche Fähigkeiten	Masterstudium Verhaltens-, Neuro- und Kognitionsbiologie
Ausbildungseinrichtung	Universität Wien Universitätsring 1, 1010 Wien (Österreich)

<b>Zeitraum</b>	<b>seit 01/10/2013</b>
Hauptfächer/berufliche Fähigkeiten	Lehramtsstudium UF Biologie und Umweltkunde, UF Mathematik
Ausbildungseinrichtung	Universität Wien Universitätsring 1, 1010 Wien (Österreich)

<b>Zeitraum</b>	<b>seit 01/10/2011</b>
Hauptfächer/berufliche Fähigkeiten	Bachelorstudium Mathematik
Ausbildungseinrichtung	Universität Wien Universitätsring 1, 1010 Wien (Österreich)

<b>Zeitraum</b>	<b>1/10/2008 – 1/10/2011</b>
erworbenen Qualifikation	Bachelor of Science (BSc)
Hauptfächer/berufliche Fähigkeiten	Bachelorstudium Biologie Wahlbereich: Zoologie
Ausbildungseinrichtung	Universität Wien Universitätsring 1, 1010 Wien (Österreich)



<b>Zeitraum</b>	<b>01/09/2004 - 30/06/2008</b>
erworbenen Qualifikation	Matura
Hauptfächer und Kurse	Biologie, Physik, Chemie, Mathematik, Deutsch, Englisch, Französisch
	Intensivkurs: Biologie
	Begabtenförderung: Französisch, Englisch
	Tutorin der Lernwerkstatt Mathematik (Nachhilfe für jüngere Schüler)
Ausbildungseinrichtung	Bundesoberstufenrealgymnasium Wiener Neustadt Herzog-Leopold-Straße 32, 2700 Wiener Neustadt (Österreich)

<b>Zeitraum</b>	<b>01/09/2000 - 30/06/2004</b>
erworbenen Qualifikation	Hauptschulabschluss
Ausbildungseinrichtung	Hauptschule Zöbern Schulstraße 1, 2871 Zöbern (Österreich)

<b>Zeitraum</b>	<b>01/09/1996 - 30/06/2000</b>
erworbenen Qualifikation	Volksschulabschluss
Ausbildungseinrichtung	Volksschule Zöbern Schulstraße 1, 2871 Zöbern (Österreich)

**Universitäre Praktika im  
Zuge des Bachelor- und  
Masterstudiums**

<b>Zeitraum</b>	<b>Wintersemester 2012</b>
	Neurobiologisches Projektpraktikum
	Selbstständige Aufbereitung einer Studie zum Thema „Spektrale Empfindlichkeit bei Jagdspinnen“ und Abfassen einer wissenschaftlichen Arbeit

<b>Zeitraum</b>	<b>Wintersemester 2011</b>
	Verhaltensbiologisches Projektpraktikum
	Selbstständige Aufbereitung einer Studie zum Thema „Geschlechterunterschiede bei Bewegungen im Schlaf“ und Abfassen einer wissenschaftlichen Arbeit
	Betreuung von Probanden und Durchführung einer Schlafstudie

<b>Zeitraum</b>	<b>September 2011</b>
	Ethologisches Projektpraktikum an der Forschungsstation Grünau
	Selbstständige Aufbereitung einer Studie zum Thema „Käfignutzung bei Rabenvögel“ und Abfassen einer wissenschaftlichen Arbeit
	Mitarbeit auf der Forschungsstation

**Zeitraum****5/7/2011-13/7/2011**

Zoologisches Freilandprojektpraktikum in den Zillertaler Alpen

Selbstständige Aufbereitung einer Studie zum Thema

„Artzusammensetzung und Häufigkeiten von Hummeln im alpinen und subalpinen Raum der Zillertaler Alpen“ und

Abfassen einer wissenschaftlichen Arbeit

Freilandexkursionen

Zoologisches Freilandarbeiten

**Arbeitsverhältnisse****Zeitraum****08/2008 – jetzt****Funktion**

Support-Mitarbeiterin

**Wichtigste Tätigkeiten und Zuständigkeiten**

Gestaltung und Bespielung von Multimedia-Guides für Museen (Nousguides)

Kundenbetreuung vor Ort in den Museen

Erledigung von Behördenwegen

Recherchearbeiten

**Arbeitgeber**

Nous Wissensmanagement GmbH

Ullmannstraße 16, 1150 Wien (Österreich)

**Zeitraum****Sommersemester 2013 – jetzt****Funktion**

Tutorin an der Universität Wien

**Wichtigste Tätigkeiten und Zuständigkeiten**

Betreuung von Bachelor- und Lehramtsstudent/inn/en bei Tierphysiologischen Versuchen

UE Tierphysiologie II

UE Organ- und Kommunikationssysteme

**Arbeitgeber**

Universität Wien

Universitätsring 1, 1010 Wien (Österreich)

**Zeitraum****7/2005, 8/2006, 7/2007****Beruf oder Funktion**

Ferialpraktikum

**Wichtigste Tätigkeiten und Zuständigkeiten**

Zubereiten von Imbissen

Service (Gastronomie)

**Arbeitgeber**

Shell Tankstelle/ A2 Südbahnhof

Raststation A2

2871 Zöbern (Österreich)

**Sonstiges****Sprachen**

Englisch

Fließend in Wort und Schrift

Französisch

Maturaniveau

**IT-Kenntnisse und  
Kompetenzen**

Microsoft, iOS  
souverän im Umgang mit Microsoft Office Programmen  
(Word, Excel, PowerPoint, Outlook)  
sehr gute Kenntnisse und ständiger Umgang mit  
Statistikprogrammen (SPSS)  
Grundkenntnisse in mathematischen Programmen  
(Wolfram Mathematica, Latex, MatLab)  
Programmiersprachen (Java)

**Interessen**

Sport  
Musik (aktives Mitglied des MV Zöbern)  
Reisen (Februar 2014: Zoologische Reise nach Costa  
Rica, geleitet von der Universität Graz)