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## Kurzfassung

Die zentralamerikanische Jagdspinne *Cupiennius salei*, ein nachtaktiver Jäger, ist bekannt für ihr hoch entwickeltes mechanosensorisches System. Aktuelle Studien konnten zeigen, dass auch ihre visuellen Fähigkeiten sehr gut entwickelt sind. In einem simultanen Wahlexperiment zeigten die Tiere keine Präferenz zwischen zwei identischen Targets (2-dimensionale schwarze Streifen, 100cm hoch und 48cm breit). Mussten die Tiere jedoch zwischen einem vertikal und einem geneigten Target unterscheiden, so zeigten sie eine deutliche Präferenz für das vertikal ausgerichtete Target. Das Ziel dieser Studie war herauszufinden, wie das visuelle System von *Cupiennius salei* „Vertikalität“ verarbeitet. Dahingehend wurde untersucht, ob die Spinnen die Gravitation oder einen sichtbaren Horizont als Bezugswert heranziehen. Die Ergebnisse zeigten, dass ein sichtbarer Horizont keinen Einfluss auf die Unterscheidungsfähigkeit zwischen zwei unterschiedlich ausgerichteten Targets darstellt. In Experimenten auf einer geneigten Arena, präferierten die Spinnen signifikant Targets welche bezüglich der Gravitation vertikal ausgerichtet waren bei Neigungen von 12° und 22° aber interessanterweise nicht mehr bei 32°. Dieses Ergebnis führt zu der Annahme, dass die Ausrichtung der Körperstellung auf geneigtem Untergrund der entscheidende intrinsische Faktor für die Verarbeitung von „Vertikalität“ darstellen könnte. Dahingehend wurden Photos von Spinnen auf einer Arena bei unterschiedlichen Neigungswinkeln gemacht, welche dann bezüglich ihrer Körperstellung analysiert worden sind. Die Ergebnisse zeigten, dass die Spinnen mittels ihrer Körperstellung einen schrägen Untergrund weitgehend kompensieren, aber das Ausmaß der Kompensationsfähigkeit sinkt bei steigender Neigung und erreicht eine Art Sättigung. Diese unzureichende Kompensation scheint der Grund für die Unfähigkeit zur Unterscheidung von vertikalen und geneigten Objekten bei einer Neigung der Arena von 32° zu sein, da die Körperstellung der intrinsische Faktor zur Verarbeitung von Vertikalität zu sein scheint.

## Abstract

The Central American wandering-spider *Cupiennius salei*, a nocturnal hunter, is known to have a very good mechanosensory system. Recent studies showed that also their visual capabilities are highly developed. In a twofold simultaneous-choice experiment the animals showed no preference between two identical targets (2 dimensional black bars, 100cm high and 48cm wide). But if the animals have to choose between two targets that differ only in their vertical orientation, they strongly preferred a vertical to a sloped bar. The aim of this study was to examine how the visual system processes “verticality”. Therefore it was tested whether the spiders use either gravity or a visible horizon as a possible reference. The results showed that an artificial horizon had no influence on the animals’ choice. In experiments with an inclined arena the animals significantly preferred the vertical bar with respect to gravity at 12° and 22° but interestingly not at 32°. These results suggest that the alignment of the spider’s body posture on an inclined arena could be the crucial intrinsic factor for the perception of verticality. Therefore photos of spiders sitting on an arena with different inclinations were taken and their body posture with respect to the ground was measured. The results show that the spiders compensate an inclination with respect to gravity but the amount of the compensation decreases with increasing inclination and reaches a kind of saturation. This probably incomplete compensation evidently supports the insufficient discrimination ability of vertical and sloped bars at an arena inclination of 32°, because the body posture seems to be the intrinsic factor for calculating verticality.

Keywords: verticality, spider, *Cupiennius salei*, vision, target discrimination.

## Introduction

This study tries to gain insight into the world of the visual perception of a spider and tries to ask questions to the spiders and to find an adequate approach to receive answers. An important point for doing so is to recognise that the spider's world and the human's world are two different abstractions of the cues an environment allocates. Due to quite different evolutionary pressures, there is no doubt that there is a great difference between the human and the spiders' adaptations which ends in a different tuning of sense organs. So the important and simultaneously very difficult task is to avoid "humanising" the spiders' perception and therefore always to keep in mind these differently adopted sense organs which result in a different perception of the same environment. But what we (*Homo sapiens* and *Cupiennius salei*) have in common is that we are both very successful species, especially the spiders evolutionary history is even much longer than ours. Spiders are a very successful group of animals, with about 30,000 described species they are close in number to bony fishes and protists and crustaceans (Barth 2002). Although most spiders formerly were known just to have highly developed mechanical senses (Barth 1993), the overall importance of the visual sense of arthropods in behavioural contexts has been outlined many times in different groups. Anyhow a great amount of researchers have recently found proper "channels" and gained an impressive amount of information of the capability of the visual system of spiders and in particular for *Cupiennius salei* Keyserling which was the model organism for this investigation. In this thesis it is explained how one of this "channels" has been designed and what the received answer could mean.

### 1. Basic facts about *Cupiennius salei*

#### 1.1 Habitat, behaviour and ecology

The wandering spider *Cupiennius salei* belongs to the family of comb spiders (Ctenidae) and occurs in tropical rain forests in Central America. Having its habitat situated in a tropical rain forest means that the animals have to handle a very high

biodiversity, which results in a serious competition about food and hiding places. Due to this evolutionary pressure and their physiological circumstances *C. salei* has evolved a nocturnal lifestyle. As an ectothermic life-form *C. salei* is not able to regulate its temperature and water content. Their quite large surface-to-volume ratio could be a serious problem for a terrestrial arthropod (Pulz 1987). Thus, the spiders have to handle this task behaviourally. *Cupiennius* typically spends the day hidden in retreats on the plants on which it hunts during night time, courts a partner or molts (Barth 2002). The spiders leave their retreat after sunset and avoid the heat of the day and low humidity outside the retreat (Barth and Seyfarth, 1979). The preferred retreats investigated by Mitter (1994) are monocotyledons like bromeliads and banana plants which provide an optimal micro-climate and good shelters for preventing predation (e.g. between the bases of two neighbouring leaves). Besides the accessible hiding places of monocotyledons they are also good conductors of the vibrations that are so important for the pursuit of prey and mating (Barth 2002). Obviously it is very important for *Cupiennius salei* to choose the right hiding place to enhance their probability of survival.

The question which emerges is which criteria are used to choose between plants or in other words which cues makes a plant attractive to the spiders. Erich Mitter (1994) has done a lot of behavioural studies in the laboratory as well as in the field facing this topic. He found out that the spiders significantly preferred monocots with hiding places over those without hiding places. The spiders also preferred plants with prey than plants without prey. The most astonishing finding was that the spiders also significantly preferred plants with both prey and hiding places than plants with either one advantage but not the other, which leads to the conclusion that the spiders not only use one environmental parameter for their choice behaviour but they are able to take several independent factors in account.

The most likely sensing modality for detecting an optimal dwelling plant for hunting and mating is the visual one rather than mechano-receptive or olfactoric senses which seem to be quite unlikely to perform this task. Following this assumption the interesting question is to solve which crucial optical features a superior dwelling plant should have.

Schmid (1998) tested a bromeliad and a black target shaped like a bromeliad in combination with a rectangular target of equal area and in both tests the spiders were not able to discriminate these objects. These results suggested that the attractiveness is rather determined by general parameters of an object than certain features presented by the silhouette of a plant.

Regarding to this general features Thill (1998) found out that *C. salei* significantly show a preference for ground touching objects against elevated objects. With respect to the presented study the most important finding was discovered again by Schmid (1998), which is that the spiders show a high preference for a vertical against a sloped object. This interesting preference is the basis of this study.

## 1.2 Morphology of the eyes of *Cupiennius salei*

As already mentioned, *Cupiennius salei* is a nocturnal hunter and therefore its eyes are adapted to very low light intensities. Barth and colleagues (1993) found out that the absolute illuminance threshold is clearly below 0.01lx which enables the spiders to use their visual sense also at night under very poor light conditions as provided by moonlight. *C. salei* has eight eyes arranged in two rows which differ in size. The largest are the postero-median (PM) eyes, then there are the two slightly smaller antero-median (AM) eyes which lack a tapetum followed by the postero-lateral (PL), and the smallest antero-lateral (AL) eyes (Fig. 1A). While the AM eyes are understood as principal, all other eye types could be summarized as secondary eyes. The PM and PL eyes cover nearly the whole upper hemisphere and 40° below the equator. In both animals tested by Barth and Land (1992) a gap of 5-20° was found between the visual fields of the PM and PL eyes, and they presumed that this is not an artefact of the method, because no such gap was found between the two PM fields at the frontal section. A second small gap was found at the rear of the animal where the abdomen is situated. The PM eyes seem to have an elongated field while the field of the PL eyes is rather orbital. The small visual field of the AL eyes overlapped fractionally both the PM and the PL visual fields and is projecting downward, looking at the region of the spider's chelicerae. Referring AM eye's field it should be recognised that the retinae of these principal eyes can be moved actively by two muscles (Kaps and Schmid 1996) which could move the field by a few degrees and overlap to a great amount with the visual field of the PM eyes (Fig. 1B) (Barth and Land 1992).



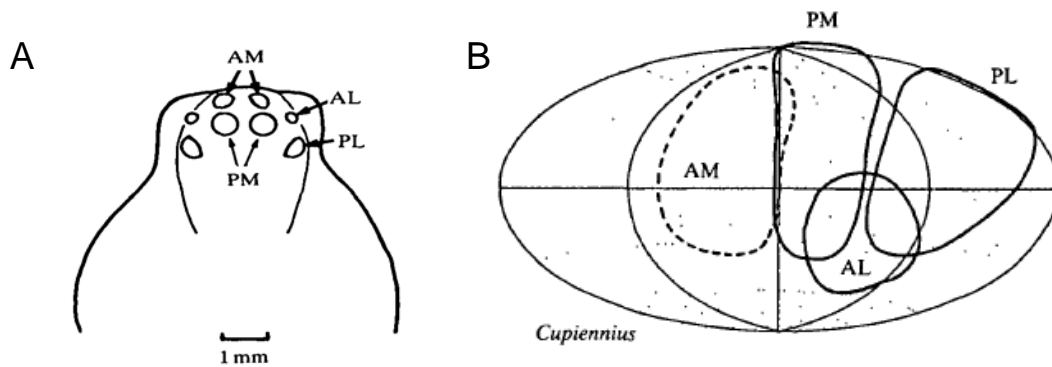


Fig. 1: A Arrangement and proportion of the different eye types. B Visual fields of the principal eyes (AM) and the secondary eyes (PM); (PL) and (AL) measured with a goniometer. The fields are plotted onto a globe with the spider at the centre, and the projection used depicts the whole of that globe, marked off at 90°, 30° and 5° intervals (after Land and Barth 1992).

It seems to be quite illogical that two different eyes have their visual field nearly completely overlapped, which results in a twofold representation of the same area of the environment. Kaps and Schmid (1996) suggested that there are different adaptations for this two eye types. The AM eyes seem to be important for the detection of stationary objects, because this ability was highly detracted after blinding them. Furthermore the retina movement could evidently be understood as mechanism against neural adaptation when the spider is not moving (Land and Barth 1992). As it is true that *C. salei* spends hours without moving in its natural habitat, this seems to be the required mechanism to detect stationary objects. Whereas the PM eyes are understood for keeping track of moving objects.

Regarding to the spectral sensitivity all eyes have a prominent peak at 520 or 540 nm and a shoulder in the ultraviolet range between 340 and 380 nm, the entire range is situated between 300 and 680 nm (Barth et al. 1993). For a spider which is understood to rely mainly on his mechanosensory senses the spatial solution of its eyes is incredibly good. The inter-receptor angles are about 1° in the PM and PL eyes (similar to many insects), 2.9° in the AM and 9.3° in the AL eyes (Land and Barth 1992).

## 2. Taxes

While conducting the experiments, taxes emerged to be an important behavioural component to deal with. Therefore a short introduction is given explaining what a taxis is, and which types exist (Table 1). A taxis is understood as an innate behavioural response (orienting) towards a directional stimulus (positive taxis) or away from this stimulus (negative taxis). The stimulus has to be constantly present, otherwise the behaviour vanishes. Besides classifying taxes based on their stimuli, they could be distinguished with the performed direction of the behavioural response. Telotaxis describes the direct orientation to the stimulus and menotaxis means migration with a certain angle respective to the stimulus direction. The symmetric alignment towards a stimulus is called tropotaxis. Tropotaxis requires two spatial isolated sense organs and the alignment happens in the same angle towards both organs. Mnemotaxis sets a landmark based memory in account with the primary taxisrelated stimulus.

Tab. 1: Types of taxes determined by their relevant stimuli.

Name of taxis	Tactic stimulus
Phototaxis	Light
<i>Geotaxis</i>	<i>Gravity</i>
Chemotaxis	Odour
Anemotaxis	Wind
Rheotaxis	Water current
Astrotaxis	Sun or moon
Polarotaxis	Polarized light
Magnetotaxis	Magnetic field
<i>Scototaxis</i>	<i>Low reflecting areas</i>
Perigrammotaxis	Vertical contrasted edges
Hypsotaxis	Highest silhouettes
Photohorotaxis	Contrasted lines underneath

Taxes are considered as elementary components of behaviour, because they are simple and appear earliest in ontogeny (Smith, 1993; Menzel et al., 1993). Campan (1997) argues that taxes often constitute the first steps in the ontogeny of orientation, and that taxes are determined by a flexible balance between genetic and epigenetic factors. Taxes are assisting the ecological adaptations to the repression a habitat burdens and they are often part of complex behaviours. They may be involved as tactic components

of an innate releasing mechanism (Lorenz and Tinbergen 1938). Taxes are possibly included in the perceptive responses of innately attractive signals or play an appetitive function to certain animals (Campan 1997).

*C. salei* shows a tendency to run towards low reflecting areas which is described as scototaxis. A scototactic stimulus is a local orienting source, it does not act by its intensity and is thus distinct from negative phototaxis (Campan et al. 1987). Michieli (1959) suggests that the attractiveness of a low reflecting object is mainly provided by the contrast perceived at the edges (perigrammotaxis). Scototaxis seems to be intermediate between negative phototaxis and response to contrast (Bui Huy and Campan 1982). Campan (1997) also argues that scototaxis is mainly effective in combination with other taxes. Scototaxis has been outlined several times to be a basic factor in the ontogeny of orientational behaviour. Papi and Tongiorgi (1963) have shown that the wolf spider *Artosa varianna* is directed towards vegetation outlines along banks in the habitat and they learn to associate the dark signal of the bank with a sun compass direction and use this information to return to a familiar bank (mnemotaxis). However in this study the scototactic tendency of *C. salei* is not understood as a high developed behaviour and it is not linked with any idea of learning. The highly reproducible preference to run towards black targets is the fundamental basis of the accomplished behavioural experiments and is therefore associated with scototaxis in the form of a telotaxis. Since scototactic cues are based on optical features of an object the visual sense is the crucial modality of this type of taxis.

The second taxis which emerged during conducting the experiments with an inclined ground was geotaxis. Geotaxis is performed by locomotion which is gravitationally influenced. Positive geotaxis is spoken when the locomotion is directed towards the gravitation (down) and negative geotaxis when the animals migrate away from the gravitation (up). Brown and Odendaal (1994) inferred from observations on isopod species of the genus *Tylos* that geotaxis is also an innate behavioural pattern. The gravity as reference is characterized by its constancy for both the direction and the intensity. The gravity receptive sense organs in invertebrates are mostly statocysts. Statocysts are mainly formed by a fluidfilled sac in which a solid grain (statoconium) lies. The statocyst wall is lined with numerous sensory hairs. By altering the position of the statocyst in space the mechanical stimulus induced by the movement of the

statoconium deflects the sensory hairs. In *Cupiennius salei* such structures are not developed. Like insects they have to rely on other mechanisms to perceive the vector of the gravitational pull. Referring to insects, they may use, as known from ants, their antennae with a geo-receptor which is possibly a Johnston's organ (Vowles 1954), like in ants and in some hymenoptera their hair plates are situated at joints (Markl 1962), or the head/body position such as in dragon flies (Mittelstaedt 1950). Spiders lack all of these mechanisms, however, the slit organs distributed all over the body, are a good candidate for this perceptual task (Barth 2002; Fink 1982).

As in this study two taxis (geo- and scototaxis) appeared simultaneously it was important to understand how this taxes are interacting in *C. salei* while exceeding the experiments. The attractiveness of vertical against sloped objects is already proven (Schmid 1998) but how is this verticality processed?

## Materials and methods

### 1. *Experimental animals*

Adult males (N=12) of the species *Cupiennius salei* Keys (Ctenidae) were used in all experiments. They were bred at the Department of Neurobiology, Vienna, Austria, under natural daylight conditions and fed once per week on flies (*Calliphora* sp.). With respect to their natural habitat, the Central American forest, the conditions were regulated to a temperature between 22 and 28 °C and a relative humidity about 80 to 95 %. All animals were kept individually in jar glasses.

### 2. *Experimental setups*

Two weeks prior the experiments the animals were adapted to an artificial photoperiod (12h:12h L:D). The experiments were carried out in a room without windows and air-conditioning in order to avoid distracting vibrations transmitted through the floor. The experiments were conducted during the artificial day with an illumination of 60lx (Pocket Light Meter AZ Instrument Model 8581; Laesent International Co. Limited, Guang Dong, China), which is quite similar to the remaining illumination on the ground of the rain forest. During the artificial night the animals were kept in complete darkness.

#### 2.1 Running experiments

The experimental setup consisted of an arena, sized 2m x 1.70m enclosed by white walls of 2.5m height. The arena was placed in the middle of the room touching the front wall. On the front wall targets made of black cardboard were presented. The arena was placed horizontal to gravity which was ensured with a water level. Also the mounting of the targets set vertical with respect to the gravity was proven with a water level.

The animals were released in 1.80m distance from the wall out of a plastic cap facing the targets. In order to exclude any effects of side preference the targets were placed

alternately at both positions (left or right) in simultaneous-choice experiments. A run was evaluated as successful, if the animal touched (with at least one leg) or climbed onto one of the targets. An undirected run was counted, if they did not touch one of the targets but touched the artificial horizon between the targets (Fig. 3AE; 4B). In the experiment with the reduced horizon (Fig. 3B) and with both stimuli at the same height (Fig. 3C) a run was counted as successful when the spiders touched the wall underneath the elevated stimulus. If the spider left the arena or did not move, the trial was repeated. The number of all successful runs towards the targets and all undirected runs were recorded. For each experiment at least 40 runs were accomplished except in the control experiment for side preferences where only 20 runs were conducted because the side preference was also excluded with alternately changing the position of the targets accomplished in all experiments. A twotailed paired-sign test was used to test for significances.

### 2.1.1 Preliminary experiments

The arena was laminated with a white d-c-fix® film. At the front wall two targets were placed in a distance of 122cm measured from their low inner edges. The size of the targets was 24cm in width and 50cm in height. The vertical targets were built as rectangles and the sloped targets as a parallelogram. The area of all used targets was kept constant.

### Control experiments

Two identical targets were tested, to investigate if a significant side preference exists. To control if the preference for vertical objects against sloped objects is reproducible three different sloping angles ( $12^\circ$ ,  $22^\circ$  and  $32^\circ$ ) were tested against a vertical target (Fig. 2).

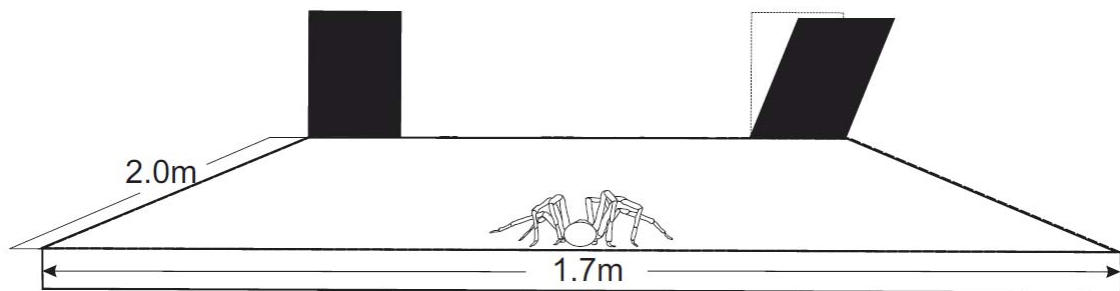


Fig. 2: View from behind on the experimental set-up. The spiders were set close to the frontal side of the arena to maximize the decision-time and to allow to orientate themselves. Two identical targets were presented to test for side preferences. It was documented if the spiders run towards the left or to the right target. Furthermore two targets which only differ in their vertical orientation were tested. It was documented if the spiders run towards the vertical or to the sloped target. The differently orientated targets were changed alternately during the test procedure to exclude side preferences.

### Experimental fine-tuning

To find out if a visible horizon serves as a referential structure for the discrimination of verticality, an artificial horizon made of black cardboard was used. The horizon was built as a right angled triangle and was placed on the front wall. The measurement of the horizon with an acute angle of  $22^\circ$  was calculated with the formula:  $\text{adjacent leg}(x) = \tan \alpha \times \text{arenawidth} (1.7\text{ m})$ . One target was set vertical with respect to gravity and the other perpendicular on the artificial horizon. Setting the target perpendicular to the horizon results in the sloping angle  $\alpha$  of the target with respect to gravity, while the target which was set perpendicular to the gravitation is sloped with the angle  $\alpha$  with respect to the horizon. An angle of  $\alpha=22^\circ$  was tested (Fig. 3A).

Due to exclude an emerged scototactic side preference, caused by the much bigger overall black area, the horizon was reduced to a stripe with 2cm thickness in an additional experiment. The tested angle was  $\alpha=22^\circ$  (Fig. 3B).

While conducting this experiment a significant preference for the ground touching stimulus emerged. In order to avoid a preference for the ground touching stimulus the targets were presented at the same height with an angle of  $\alpha=22^\circ$  (Fig. 3C).

Furthermore the arena was inclined in its horizontal adjustment to investigate if gravity is the basic reference for calculating verticality. One side of the arena was raised and this resulted in an inclined ground on which the spiders had to orientate towards the targets. With a bonded iron chain, which was attached to a trolley stand, the preferred inclination of the arena was achieved. For calculating the amount of the necessary elevation(x) of one side of the arena, the following formula was used:  $elevation(x) = \sin \alpha \times arenawidth$  (1.7m). One target was set vertical with respect to gravity and the other perpendicular to the inclined arena which results in the same inclination angle  $\alpha$  for the arena and the target. Inclinations of  $\alpha=12^\circ$  and  $22^\circ$  were tested (Fig. 3D).

The inclination might cause a preference for running upwards (to the elevated side). This could be described as negative geotaxis. For setting geotaxis and scototaxis in competition, an experiment was designed where the arena was inclined and simultaneously a triangular horizon was presented. For setting up this experiment the same procedure was used as described above. The angle  $\alpha=12^\circ$  both the arena inclination and the horizon was tested. In the setup the inclination angle was kept equal to the angle of the horizon (Fig. 3E).



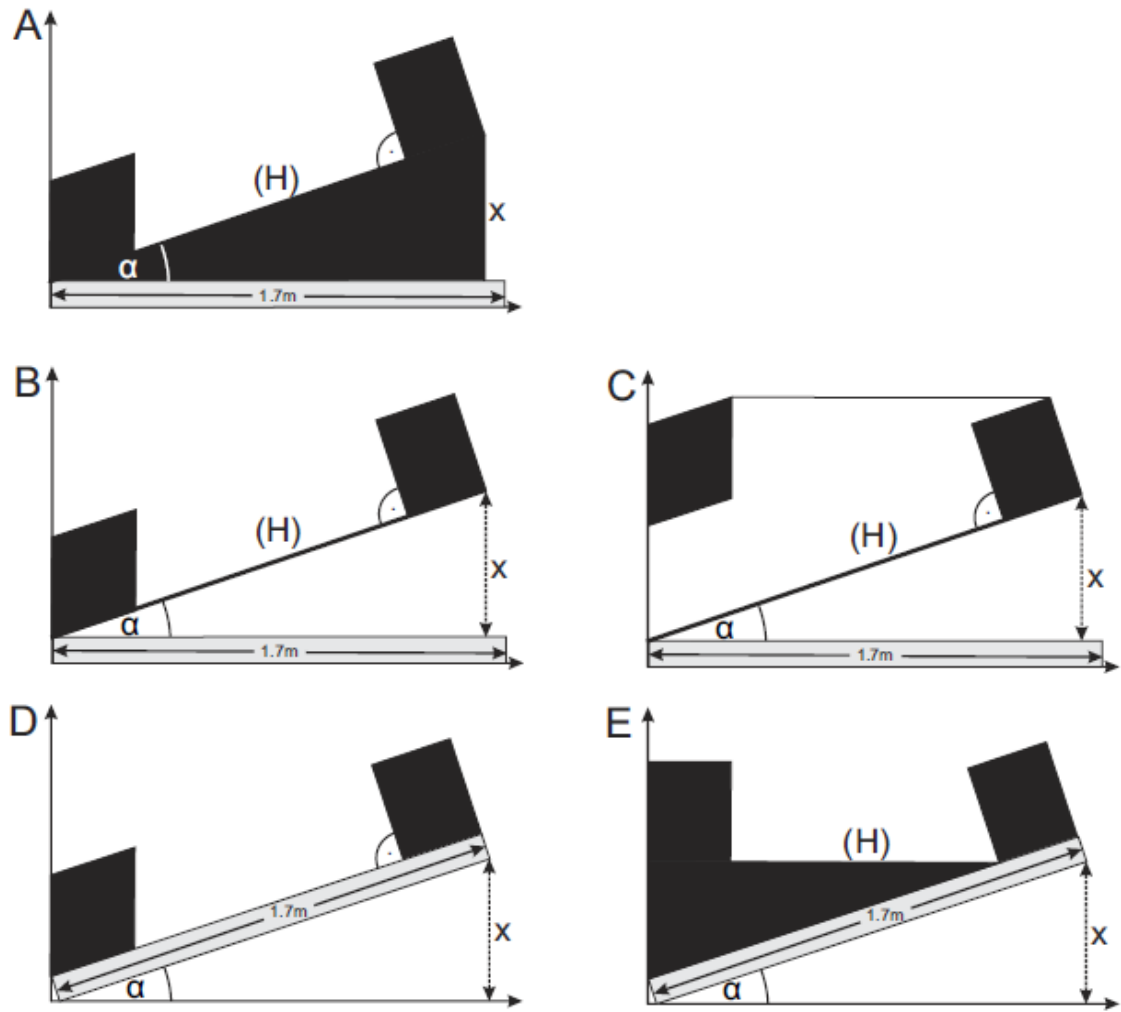


Fig. 3: Schematic drawings of the arena with the experimental setups for the 5 different preliminary experiments. The targets are 24cm in width and 50cm in height. ABC Artificial horizon experiments: The artificial horizon (H) is build as a right angled triangle with the desired acute angle  $\alpha$ . The measurements were calculated with the formula:  $adjacent\ leg(x) = \tan \alpha \times arenawidth(1.7m)$ . One Target is set vertical with respect to gravity and the other perpendicular to the horizon. A The overall area of the horizon is kept in black. B The horizon is reduced to a black stripe of 2cm thickness. C The ground touching stimulus is elevated to the same height as the stimulus situated at the upper side of the reduced horizon. D Inclined arena experiment: One side of the arena is raised up to achieve the desired inclination angel  $\alpha$ . One target is set perpendicular to the arena and the other vertical to gravity. E The horizon is combined with the inclined arena. One target is set perpendicular to the horizon and the other perpendicular to the arena.

### 2.1.2 Main experiments

In order to counter the geotactic problems (inclined arena) and the scototactic problems (artificial horizon) some changes on the basis of the preliminary experiments were necessary. The scototactic problems caused by a right angled triangle horizon were decreased by using an isosceles triangle and the area of the targets was quadrupled to 48cm width and 100cm height. The reason for doing so was to ensure that the area of each target is significantly higher than the area of the horizon with the largest black area ( $\alpha=32^\circ$ ). An isosceles triangle eliminates the scototactic side effect, which was caused by a right-angled triangle horizon (Fig. 4B). The second advantage of quadrupling the target area was that the geotaxis also diminished in the experiments with an inclined arena (Fig. 4CDE). Additionally the arena was covered with a black sheet. This provided a better grip, because some spiders seemed to slip on the previously used arena and secondly the optic impression of a visible horizon is more lifelike, when no boarder between the horizon and the arena is available. To control if the preference for vertical objects is still existent, two targets with different vertical orientations were tested (Fig. 4A). Furthermore the inclined arena covered with a white sheet was tested at an inclination angle of  $22^\circ$  (Fig. 4E), to find out if the black sheet influenced the geotactic tendency. In the experiments shown in Figure 4A-C the angles  $\alpha$  of  $12^\circ$ ,  $22^\circ$  and  $32^\circ$  were tested. In the other experiments (Figure 4DE) only the angle  $\alpha$  of  $22^\circ$  was tested.

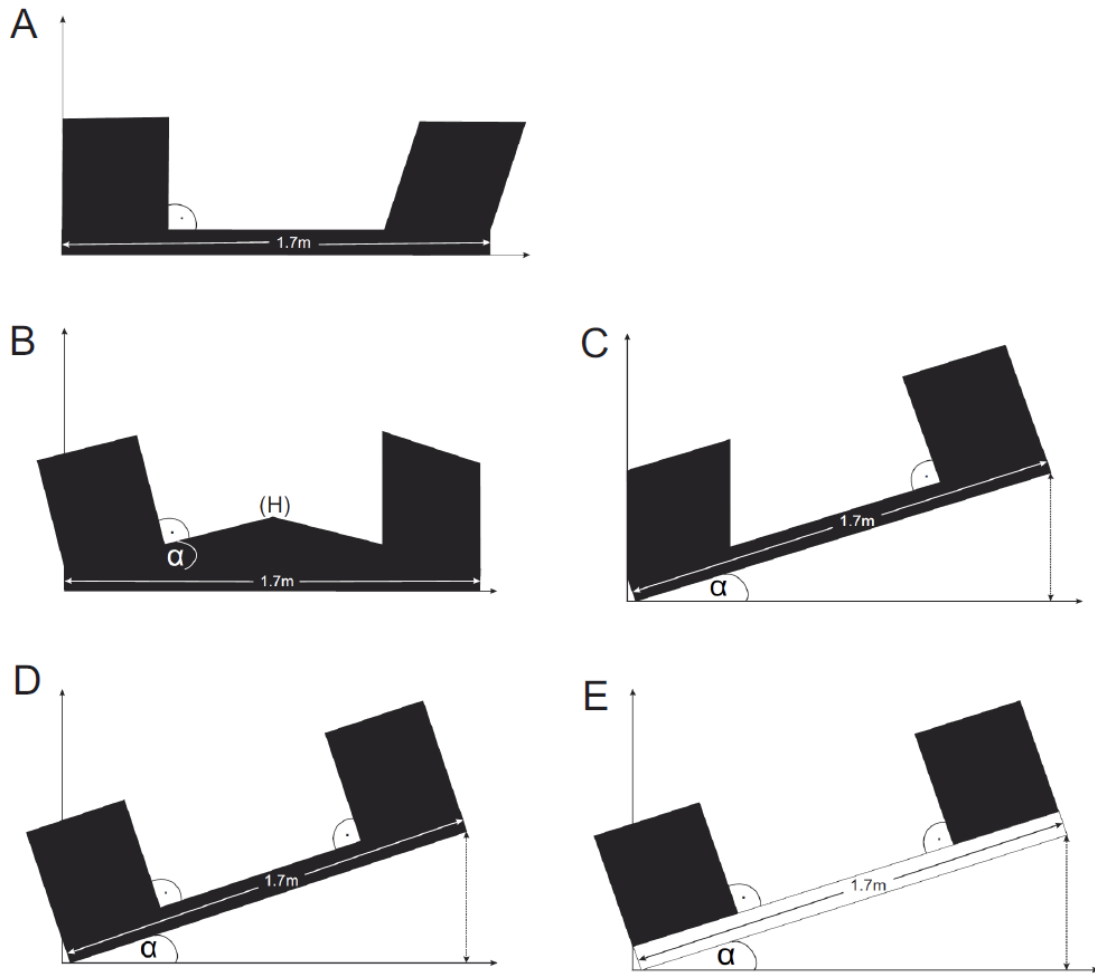


Fig. 4: Main experiments: The arena was covered with a black sheet and the targets were 100cm high and 48cm wide. A Two targets which differ in their vertical orientation were tested. B The horizon (H) is build as an isosceles triangle with the desired angle  $\alpha$ . One target is set perpendicular to the horizon and the other vertical with respect to gravity. CDE Inclined arena experiments: One side of the arena is raised up to achieve the desired inclination angel  $\alpha$ . C One target is set vertical to gravity and the other perpendicular to the inclined arena. D Both targets were set perpendicular to the arena. E Both targets were set perpendicular to the arena and the arena was covered with a white sheet.

## 2.2 Photoanalysis: Compensatory body-posture on an inclined ground

While conducting the running experiments the spiders seemed to adjust their body posture to a given inclination (Fig. 5). To analyse this behaviour in more detail an additional experiment has to be carried out.

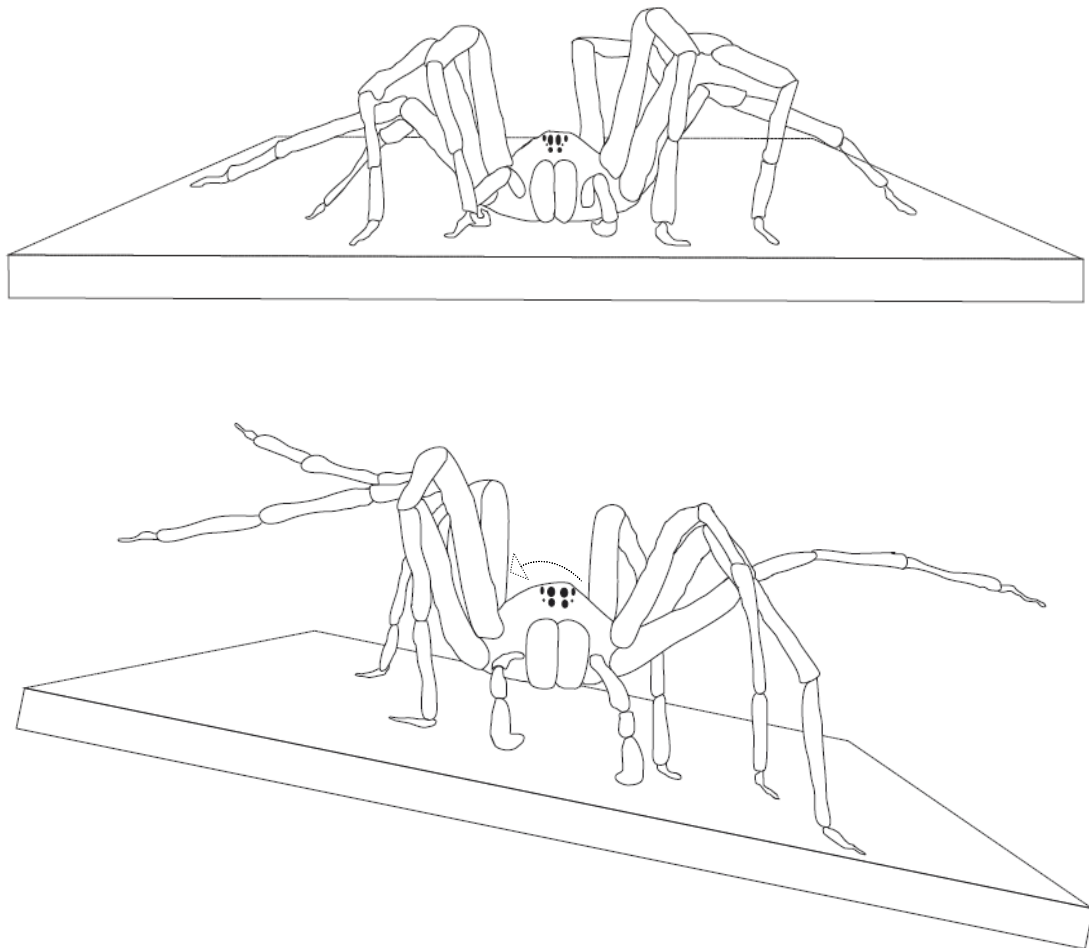


Fig. 5: Trace of original photographs, taken from spiders while sitting on an arena, with and without an inclination. Note the compensatory body-posture from the spider sitting on the inclined arena.

### 2.2.1 Setup & Procedure

A small supported slab (39x39cm) with alterable horizontal adjustment was constructed, which was covered with a white sheet, both to provide enough grip for the spider and to maximise the contrast for the photo analysis. A USB-microscope (Veho Discovery (VMS-001) with 200x magnification; Veho Ltd.; Hampshire, United Kingdom) was mounted on the edge of the slab, to keep the horizon of all photos constant. This was

necessary to have a reference for calculating the body posture with respect to the horizon of the photos (Fig. 6B; Fig. 7). The spiders were set on the slab facing the USB-microscope frontally. The photos were taken when the spiders had their opisthosoma elevated to ensure that the spider is in readiness for an orientation run. On the wall behind this setup a vertical black target (48x100cm) was presented to provide a relevant optical target while taking the photos. Photos of 12 spiders were taken for the inclination angles  $\alpha = 0^\circ, 7^\circ, 12^\circ, 22^\circ, 32^\circ$  and  $37^\circ$ . Additionally a spider with coated eyes was tested at an angle of  $32^\circ$ .

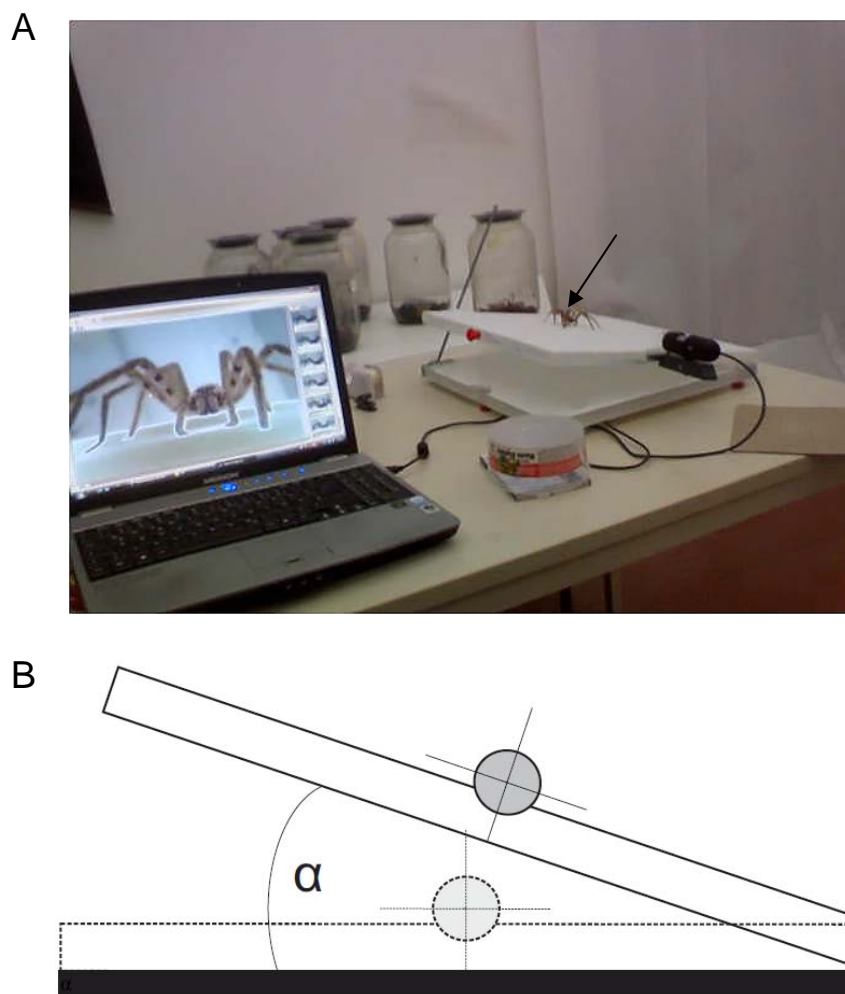


Fig. 6: Experimental setup of the body posture experiment: A The spider was orientated on a small slab (arrow) towards an USB-microscope, and photographs were taken when the spiders had their opisthosoma elevated. The inclination of the slab was altered from  $0^\circ$  to  $37^\circ$  and photographs of 12 spiders were taken at each inclination. B Lateral view of the setup with the USB-microscope placed in the middle. The microscope was mounted in a fixed manner to the slab, in order to ensure that the horizon of the photographs could be used as a referential value for calculating the amount of the compensation.

## 2.2.1 Data Analysis

The photographs were analysed with the freeware ImageJ 1.31k-1 (Wayne Rasband, National Institut of mental constitution, Bethesda, USA), which includes an angle measurement tool. This tool allows to feed a line into the photograph and the angle of this line is calculated. The line was placed between the AM and the PM eyes and between the chelicerae (Fig. 7, Fig. 8). Due to the fact that all photographs were taken with the fixed microscope (Fig. 6B) a vertical line (value of the angle: 90°) drawn between the AM and the PM eyes and the chelicerae means that no compensatory alignment of the body posture was exceeded by the spider. If the line is sloped the spider showed a compensatory alignment behaviour in case the slab is inclined (e.g. Fig. 7). The compensatory angle was calculated with the formula: *compensatory angle* = 90°(no compensation) – *x*(measured angle)

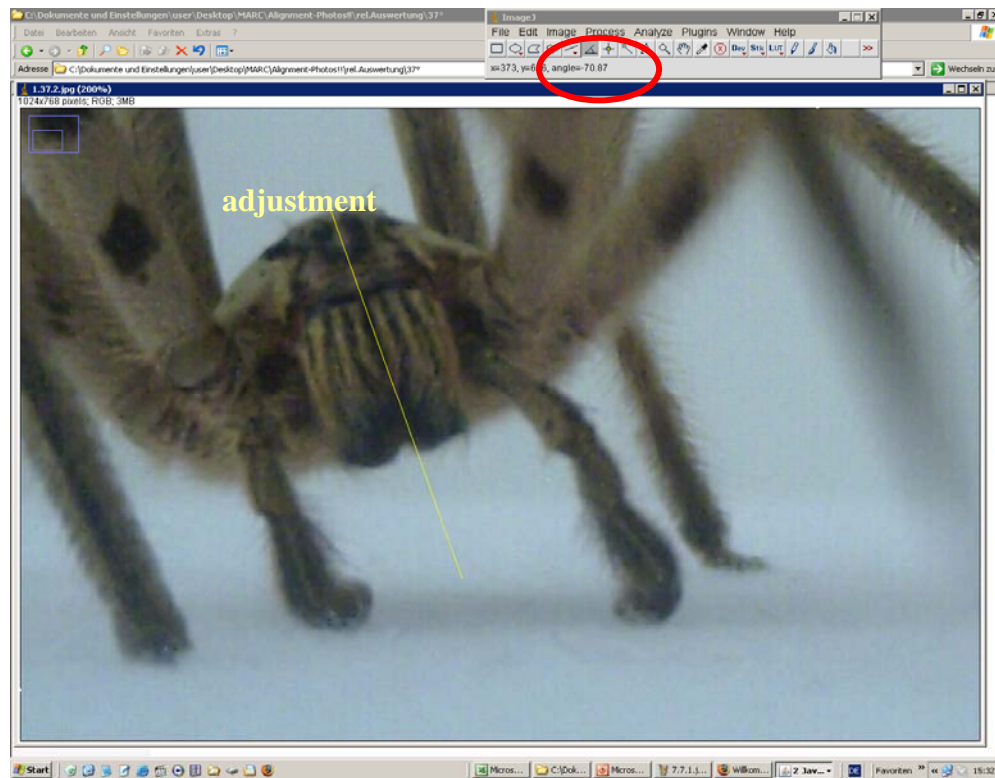


Fig. 7: Sample of an analysis of a compensatory body posture with the angle measurement tool of the software ImageJ. The inclination of the slab was 37°. The value of the measured angle is highlighted in the red ellipse. The yellow line was fed between the AM and the PM eyes and between the chelicerae. It indicates the adjustment angle referring to the inclination. At this example an angle of 70.87° is measured which means that 19.13° of the inclination is compensated by the body adjustment. This compensatory angle was calculated with the formula: compensatory angle = 90° (no compensation) - 70.87° (measured angle).

The compensation of an inclination is done completely when the inclination of the arena is equal to the compensatory adjustment angle. If the adjustment angle was lower than the inclination of the arena, the remaining compensation angle was called error angle (Fig. 8). The error angle was calculated with the formula:

$$\text{error angle} = \text{arena inclination} - \text{compensatory angle} .$$

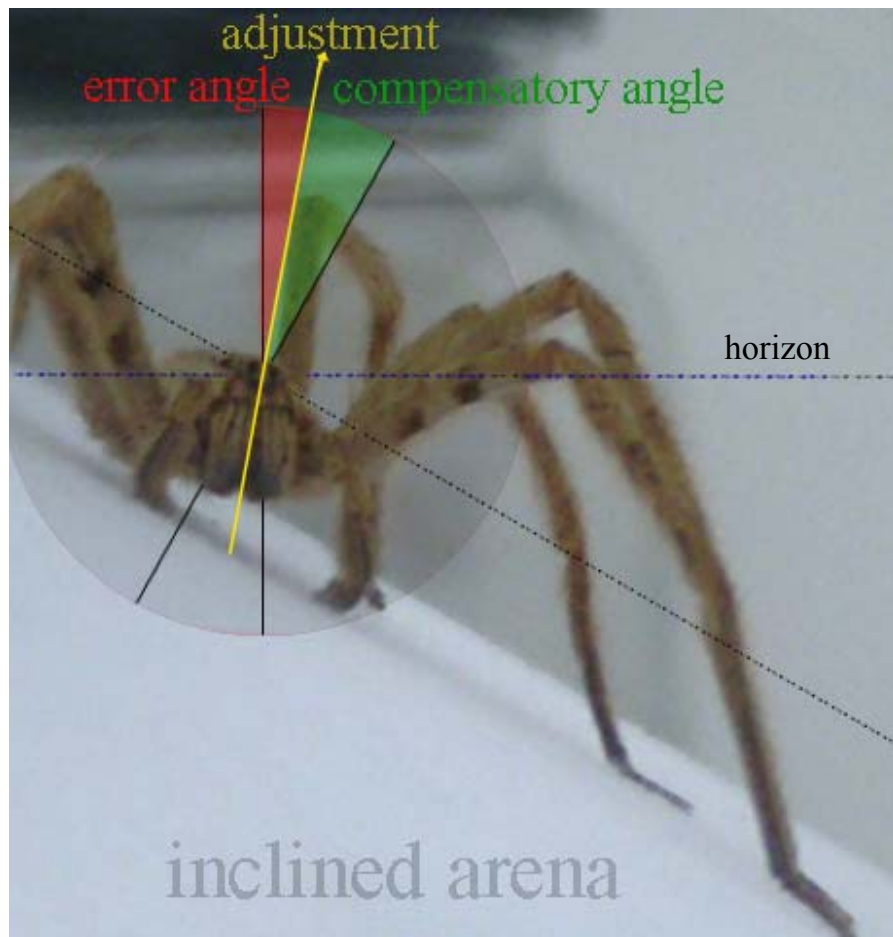


Fig. 8: Photograph of a spider on an inclined arena: The spiders are able to compensate the inclination to a certain amount. The compensatory angle subscribes the amount of the compensation of the inclination done by the spider, while the error angle subscribes the amount of the incompleteness of the horizontal compensatory body posture with respect to the arena inclination.

## Results

### *1. Preliminary Experiments*

The first control experiment with two identical stimuli (Fig. 2) showed no significant side preference. The spiders run 12 times towards the left targets and 8 times towards the right target.

In the second control experiment where a vertical against a sloped target was tested (Fig. 2) all results showed a significant preference for the vertical target. In the experiment with a target with 12° sloping angle the spiders run 27 times towards the vertical target and 13 times towards the sloped target which is a significant preference ( $p<0.05$ ). A 22° sloped target was headed 10 times while the vertical target was chosen 30 times which is a high significant preference at a level of  $p<0.01$ . A 32° sloped target was chosen 9 times while the vertical target was headed 31 times which is again a strong preference for the vertical target at a significance level of  $p<0.01$ .

In the test with the right angled horizon with an overall black area (Fig. 3A), the spiders run 13 times towards the 22° sloped and 18 times towards the vertical target (not significant). 9 runs were undirected (the spiders touched the horizon between the targets). There was no significant preference for a vertical orientation of the targets irrespective the gravitational or the horizontal reference. But there was a significant preference for the side with the bigger overall black area. 30 times this side and only 1 time the side with the acute angle of the horizon was chosen ( $p<0.01$ ) disregarded the vertical orientation of the targets.

In the experiments with the reduced horizon area (Fig. 3B) the spiders run 19 times towards the vertical target and 21 times towards the 22° sloped target (no significance). But 29 times the ground touching target and only 11 times the elevated target was chosen ( $p<0.01$ ) disregarded the vertical orientation.



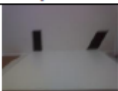





While having both targets mounted at the same height the spiders (Fig. 3C) chose 11 times the vertical and 10 times the 22° sloped target (not significant). 19 runs were counted as undirected, because these spiders touched the wall between the targets.

In the tests with an inclined arena (Fig. 3D) the spider showed no significant preference for the vertical orientations of the targets at angles of 12° and 22°. But there was a significant preference for the elevated side at the angle of 22°. 24 runs were headed towards the lower side while 56 runs were directed towards the elevated side of the arena ( $p<0.01$ ) disregarded the vertical orientation. With an inclination angle of 12°, the spiders run 18 times towards the lower situated targets while 22 runs were headed towards the elevated stimuli disregarded the vertical orientation. In the tests which were conducted 35 days later 18 runs towards the vertical stimulus and 22 towards the sloped target at a sloping angle of 22° were counted. In this experiment 24 spiders run towards the lower side of the arena while 26 had chosen the elevated side, disregarded the vertical adjustment of the targets.

In the experiment with both an inclined arena and a visible horizon (Fig. 3E) the spiders chose 18 times the vertical and 16 times the sloped target at an angle of 12°. 6 runs were counted as undirected. 29 runs were counted towards the side with the adjacent leg of the horizon and 5 runs towards the elevated side of the arena with the acute angle of the horizon which is a high significant preference ( $p<0.01$ ).

The data of all preliminary experiments are summarized in Table 2 to give a better overview.

Tab. 2: Number of choices made by the spiders with different experimental setups. 12 spiders were used in all experiments. The column “Geotaxis d/u” indicates the regression of the runs towards the target placed on the lower (d=down) or the elevated (u=up) side of the arena. The colon “Scototaxis l/r” shows the regression of the runs towards the left (l) and the right (r) side of the horizon (acute angel is situated on the left side and the right angle on the right side). Note that the targets with different vertical orientations were alternately changed in their position left or right.

Experiment	0°/12°	0°/22°	0°/32°	Geotaxis d/u	Scototaxis l/r	Sidepreference 0°/0°
	27*/13	30**/10	31**/9	x	x	12/8
	24/16	40/40		18/22 at 12° 24/56** at 22°	x	
		18/22		14/26* at 22°	x	
		13/18		x	1/30** Nine undirected runs	
	18/16			29**/5 Six undirected runs Negative geotaxis disappeared	29**/5 Six undirected runs	
		19/21		x	29**/11 significance for ground touching stimulus	
		11/10		x	Nineteen undirected runs	

\*Significant at  $p < 0.05$

\*\*Significant at  $p < 0.01$

## 2. Main Experiments

### 2.1. Running experiments

In the experiments testing a vertical against a sloped target on a horizontal arena without horizon (Fig. 4A), the vertical targets were significantly preferred at angles of 12°, 22° and 32°. The spiders run 28 times towards the vertical target and 12 times towards the 12° sloped target ( $p < 0.05$ ). 29 runs were counted towards the vertical target and 11 runs towards the 22° sloped target ( $p < 0.01$ ). 30 runs towards the vertical target were counted while a 32° sloped target was chosen 10 times ( $p < 0.01$ ).

In the experiments with a visible triangle horizon (Fig. 4B) the spiders preferred the vertical targets with respect to gravity in all tested combinations. With an horizon angle of 12° 29 runs were counted towards the vertical target and 11 runs towards the target

which was set perpendicular to the horizon. With an horizon angle of  $22^\circ$  31 runs were directed towards the vertical stimulus and 9 to the target perpendicular to the horizon ( $p<0.01$ ). The vertical stimulus was chosen 30 times and 10 times the target perpendicular to the horizon at an angle of  $32^\circ$  ( $p<0.01$ ).






In the experiments with an inclined arena (Fig. 4C) the spider showed a significant preference for the vertical target at an angle of  $12^\circ$ . 29 runs were directed towards the vertical and 11 to the target set perpendicular to the arena ( $p<0.01$ ). At an inclination of  $22^\circ$  30 runs were directed towards the vertical stimulus and 10 towards the target perpendicular to the horizon ( $p<0.01$ ). At an inclination of  $32^\circ$  21 runs towards the vertical target and 19 runs to the target perpendicular to the horizon were counted, which was no significant preference.

In the test with an inclination of  $22^\circ$  with two identical targets (Fig. 4D), 22 runs were counted to the lower target and 18 runs to the elevated target, which was no significant difference.

Using the  $22^\circ$  inclined arena covered with a white sheet (Fig. 4E) and with two identical targets also no significant side preference could be observed. 17 runs to the elevated and 23 to the lower target were counted which was not significant.

The data of all preliminary experiments are summarized in Table 3 to give a better overview.

Tab. 3: Number of choices made by the spiders with different experimental setups. 12 spiders were used in all experiments. The column “Geotaxis d/u” indicates the regression of the runs to the target placed on the lower (d=down) or the elevated (u=up) side. The column “Scototaxis” indicates the undirected runs towards the artificial horizon between the two targets. Note that the targets with different vertical orientations were alternately changed in their position left or right.

Experiment	0°/12°	0°/22°	0°/32°	Geotaxis d/u	Scototaxis
	28*/12	29**/11	30**/10	x	x
	29**/11	31**/9	30**/10	x	Two undirected runs for 32° Three undirected runs for 22° No undirected run for 12°
	29**/11	31**/9	21/19	21/19 at 12°	x
				21/19 at 22°	
				20/20 at 32°	
				22/18 at 22°	x
				17/23 at 22°	x

\*Significant at  $p < 0.05$

\*\*Significant at  $p < 0.01$

### 3. Body posture experiment:

The body posture of twelve spiders was analysed for each inclination level (0°, 12°, 17°, 22°, 32° and 37° (N=12, n=8x12)). The compensatory angle, of the twelve spiders were averaged and plotted against the respective inclination of the arena. The compensatory angle increases with increasing inclination up to 27° and levels in a kind of saturation at larger inclinations of 32° and 37°. The curve follows a logarithmic function with a reliability of  $R^2=0.9853$  (Fig. 9). At an arena inclination of 12° the mean compensation angle was 8.42° with a standard deviation of 1.38°. At a 22° inclined arena the mean compensation angle was 14.2° with a standard deviation of 2.7°. At 32° the mean compensatory angle was 15.8° with a standard deviation of 4°.

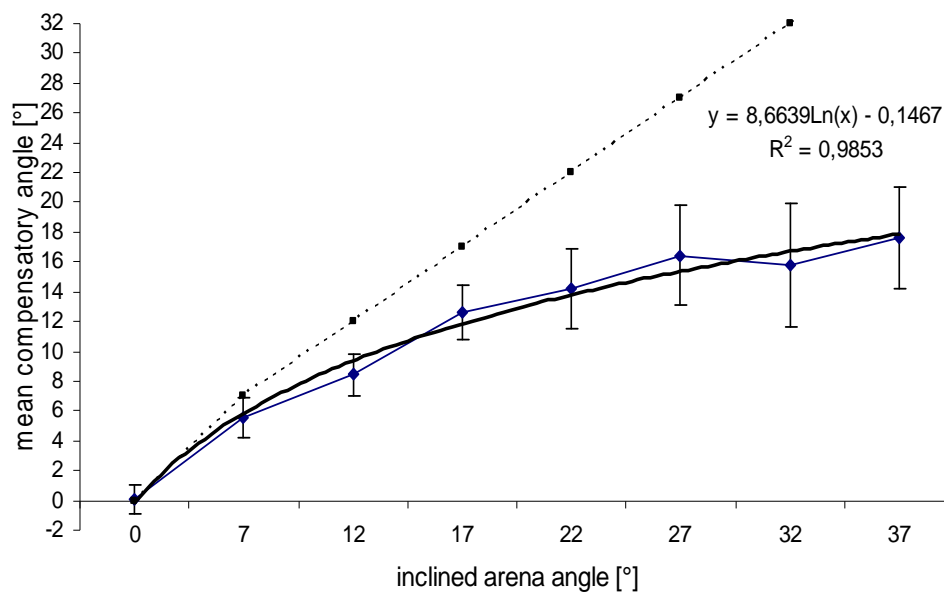


Fig. 9: The mean compensatory body angle on a differently inclined arena. Each data point is the mean of twelve measured compensatory body angles of twelve spiders (N=12, n=8x12). The dotted line indicates a full compensation of the given arena inclination via body posture.

The incompleteness of the compensation (error angle) of 12 spiders was plotted against the particular inclination of the arena. The error angle increases with an increasing inclination of the arena. The curve follows a quadratic function with a reliability of  $R^2=0.9492$  (Fig. 10). On a  $12^\circ$  inclined arena the mean error angle was  $3.58^\circ$  with a standard deviation of  $1.4^\circ$ . For  $22^\circ$  inclination the mean error angle was  $7.8^\circ$  and a standard deviation of  $2.66^\circ$ . For  $32^\circ$  inclination  $16.2^\circ$  mean error angle was measured with a standard deviation of  $4.1^\circ$ .

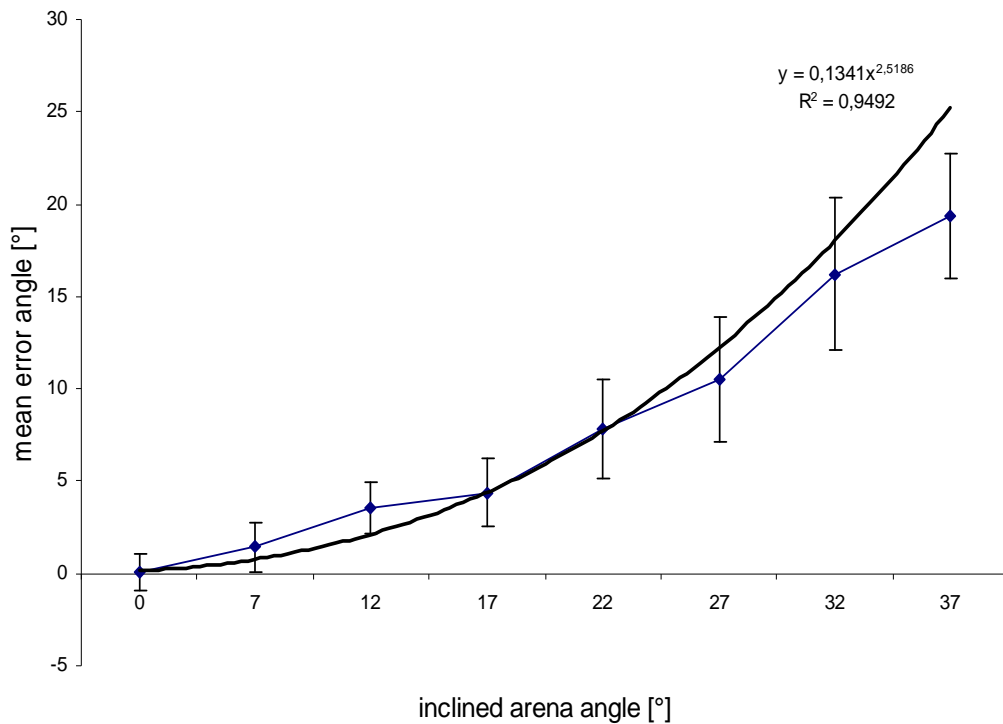


Fig. 10: The mean error angle on a differently inclined arena. Each data point is the mean of twelve measured compensatory body angles of twelve spiders ( $N=12$ ,  $n=8 \times 12$ ).

The spider with coated eyes also showed a compensatory body posture on a 32° inclined arena (Fig. 11).



Fig. 11: A spider sitting on a 32° inclined arena. Although its eyes are coated the spider shows a compensatory body posture.

## Discussion

*Cupiennius salei* is a nocturnal hunter and leaves its retreats at night for hunting, mating and courting. As it is very important for *Cupiennius* to find dwelling plants providing retreats, prey and mates, they have to discriminate them adequately to perform a goal directed orientation towards its retreats. In previous studies, it could be shown that spiders find their dwelling plants visually (Schmid 1998, Thill 1998).

As *Cupiennius* lacks high spatial resolution (inter-receptor angle  $1^{\circ}$ - $3^{\circ}$ ), it seems quite likely that the discrimination of potential targets is led rather by more general optical features than from distinct intricacies. Due to the spatial resolution and the nocturnal lifestyle which allocates a very low light intensity, the stems of the potential dwelling plants appear as black bars. Because of their scototactic behaviour the spiders show an affinity to head towards these low reflecting areas. The areas of the targets seem to be an important feature because *C. salei* strongly prefers bigger targets compared to smaller ones. Besides the area they could alter in shape, their vertical adjustment (sloped or vertical) and in contrast. As shown in Figure 12 the animals are confronted with vertical and sloped targets.

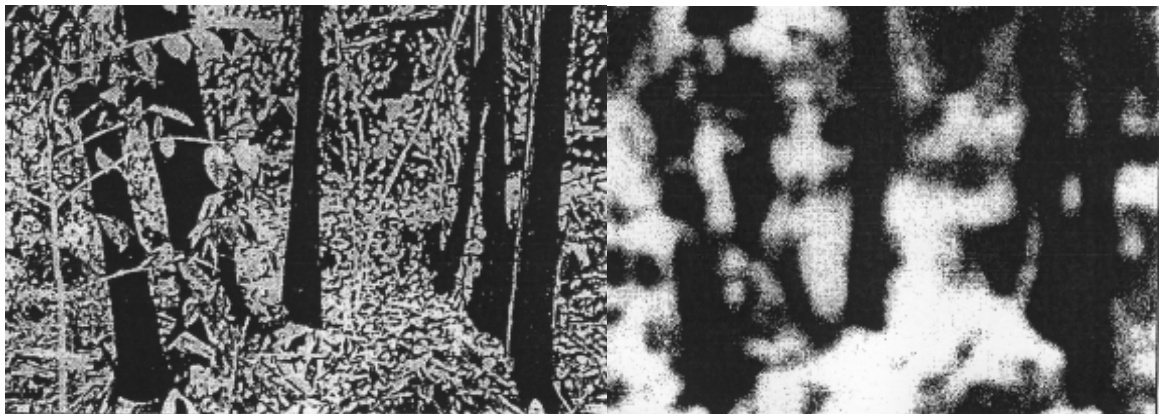


Fig. 12: View into a rain forest with the resolution of a human eye on the left picture compared with the approximated resolution of *C. salei* on the right picture (changed by Thill 1998 after Barth and Seyfarth 1979). Details vanish while vertical and sloped black bars remain at a lower spatial resolution.

Since *Cupiennius* shows a strong preference for vertical against sloped objects, it must be able to discriminate the adjustment of targets. The idea that a visible horizon provides the referential value for this calculation could not be confirmed at least not



with the different types of artificial horizons used in these experiments (Fig. 3ABC, 4B). The horizon was built as a 2 dimensional black triangle. The consideration of this simplification was that an animal of this low height and with its remarkable conoscopic eyes easily sees the ground as an horizon even in relevant distances for approaching possible dwelling plants (Fig. 13AB).



Fig. 13: A Photograph of a forest taken on the ground. The picture roughly shows the sight of an animal at a low level above the ground under a low light intensity. The horizon in this picture appears more or less as a black area with having the trees situated on it. Note this is not a picture of a rain forest and the resolution is much higher than what *Cupiennius* is capable of. B Schematic view of the experimental setup with an artificial horizon and targets situated on it.

Because an optical landmark structure in form of a horizon did not seem to have any influence for calculating verticality, gravity could be considered as a possible referential vector.

In preliminary experiments, the spiders showed a negative geotaxis. In order to have one variable to prove for, it was very important to find a way to exclude geotaxis. Geotaxis seemed to be stress induced because experiments taken with more experimentally accustomed animals showed a weaker geotactic tendency. Furthermore setting scototaxis and geotaxis in competition (Fig. 3E) indicated that the scototactic tendency seemed to be stronger. Presenting bigger structures diminished the geotactic orientation of an animal on an inclined arena. Overall the geotaxis totally disappeared by quadrupling the target area (Fig. 4CDE) and by using experimentally accustomed animals. It seemed that the bigger a vertical target was the more prominent verticality became in the perception of the spiders. The decision where to orientate was probably taken earlier and therefore less influenced by the geotactic tendency, as it is when the first movements are less influenced by an optical stimulus.

Without a geotactic influence the experiments with an inclined arena showed that the spiders preferred the gravity related vertical targets significantly at angles of 12° and 22° but interestingly not at 32°. The results for 12° and 22° strongly indicated that the gravitational input is the crucial referential vector.

Finck (1982) found out that spiders are able to detect the value of gravity. He varnished the legs of the spider *Araneus sericatus* for compromising their lyriform organs especially those located at the patella. He hypothesized the lyriform organ to serve the receptor role in the transduction of gravity related stimuli. Furthermore Finck (1984) showed that the spider *Nuctenea sclopetaria* is able to detect the vector of gravity. Sense organs in the legs which detect body weight are very important for the regulation of posture and locomotion (Noah et. al. 2004). Due to the fact that spiders don't have gravitoreceptive antennae, receptive hairplates near joints or statocysts, the lyriform organs seem to be the adequate candidates for the perception of gravity. There are more than one hundred lyriform organs positioned on the walking legs and pedipalps of *C. salei*, which could be used for this perception task. The compensatory body posture might indicate a compensatory behaviour to level the body load on the eight legs (Fig. 14). Brüssel (1987) has studied this topic on *C. salei* and he argued that horizontally directed forces which act on all eight legs stabilize body posture, and this is valid for spiders standing on a horizontal surface and those standing on a slanted one. According to Barth (2002) the various lyriform organs at least of the tibia are well able to monitor

variable loads and movement states, because of their differing positions and orientations and eminently by their physiological properties. Thus they could be an excellent means of keeping track of the load on the tibia-metatarsus joint.

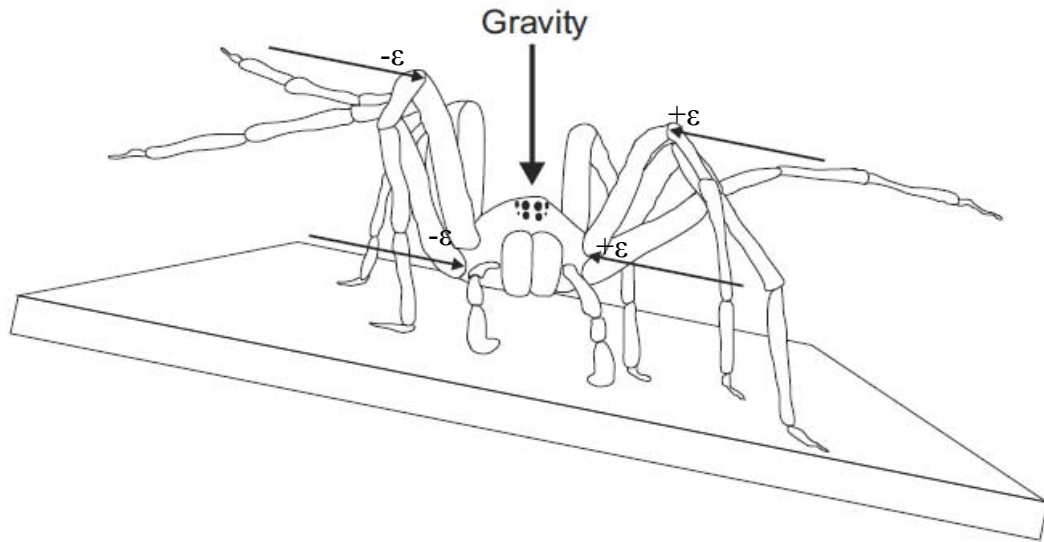


Fig. 14: Spider sitting on an inclined ground. The arrows indicate an example of some possible vectors of the body load force effecting on lyriform organs (extension  $+\epsilon$ ; compression  $-\epsilon$ ) induced by gravity.

Why the spiders did not prefer the vertical target at an inclination of  $32^\circ$  remained an open question. Especially because in the experiments on a plain arena it seemed that the more sloped a target was the more it became unattractive.

The correlation between body posture and surface inclination (Fig. 9) showed a decreasing accuracy with increasing inclination, reaching a saturation at  $27^\circ$ . Therefore, the ability to compensate a given inclination via body posture seemed to be limited. Because of this incomplete compensation on higher surface inclinations, errors of processing gravity based verticality could emerge. At an inclination angle of  $32^\circ$  the spiders compensate approximately only half of the inclination. If the body posture is the crucial intrinsic factor, both targets appear equally sloped (Fig. 15).

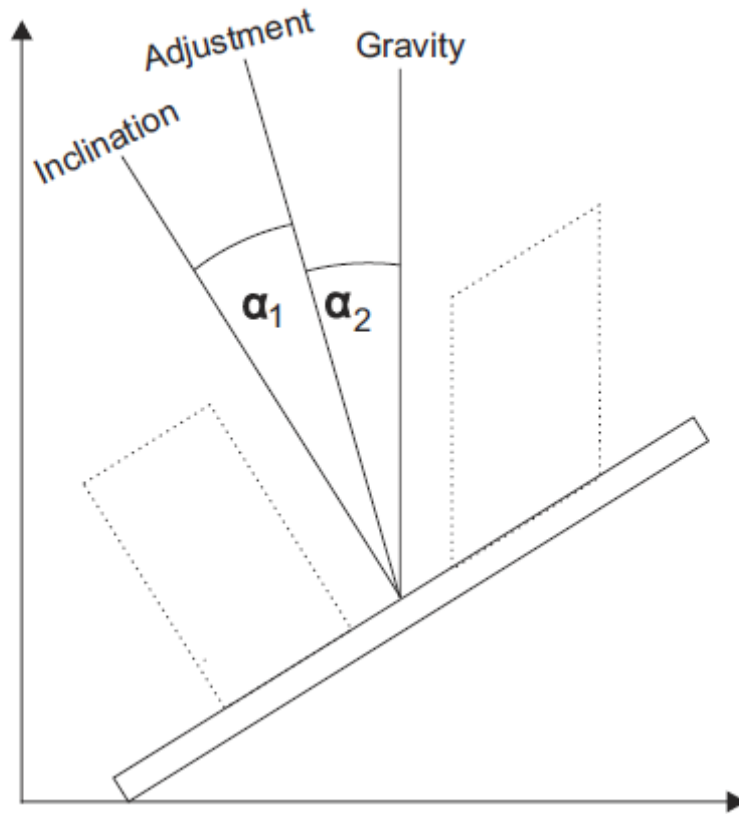


Fig. 15: Schematic view of a 32° inclined arena.  $\alpha_1$ : compensatory angle of the animal,  $\alpha_2$ : error angle remaining to complete compensation. If  $\alpha_1$  and  $\alpha_2$  are equal, both targets (indicated with dotted lines) appear equally sloped.

The emerging hypothesis is that gravity is the crucial referential vector for calculating verticality. But the processing is not calculated directly within a neural based comparing of the visual input against the gravity input received through the lyriform organs. The gravitational input rather modulates the position of the eyes in a compensatory way. The spatial adjustment of the eyes determines the verticality of a target. Hence the adjustment of a visual stimulus and the gravity related adjustment of the retina set in comparison provides the peripheral sensory condition for the perception of verticality on inclined surfaces. The data gained from the photo analysis supports this theory. It's seen that the increasing error in compensating an inclination via body posture (Fig. 10) lead to an insufficient discrimination ability at higher inclinations, which could explain why the spiders haven't been able to discriminate vertical against sloped objects on an 32° inclined arena in the running experiments (Tab. 3).

However, it is very likely that the amount of compensation is in average much higher when the animal is walking. But due to the zig-zag motion and the necessity of

photographing the spiders frontally and the difficulty of focusing a running spider it was only possible to take the photos during the initial phase of an orientation run. The standard deviation increased remarkably with an increasing inclination which indicates a higher ability of compensation than analysed in our experiments. In resting position, the extent of body load supported by a leg depends upon its position relative to the centre of mass (Full et al. 1991), while during walking variations in loading of individual legs act in the cycles of stance and swing (Chang et al. 2000). The compensatory head movements of the cricket *Gryllus bimaculatus* are elicited by cercal and antennal gravity receptors but walking is a necessary condition that these responses occur, which was also seen in the fly *Calliphora erythrocephala* (Horn and Bischof 1983). Furthermore Horn (1982) suggested that in *Calliphora* this relation between walking and the occurrence of compensatory head movements is either caused by a linkage between the peripheral proprioceptors which control walking and gravity receptors, or by a facilitatory effect of central command neurones. Noa and his colleagues (2004) suggested that adjustments made to support body load is based both upon inputs from receptors signalling kinematic variables (muscle length, joint angles) and those receptors which detect the forces that effect the legs. This study was done with cockroaches, which possess campaniform sensilla, which are in their function quite similar to the lyriform organs. Both measure deformations in the exoskeleton, therefore it is quite likely that similar mechanisms may also work in *Cupiennius*. *Cupiennius* must solve this task at least partially with its mechanoreceptive organs, because a compensatory body posture was also seen in spiders with coated eyes (Fig. 11).

*Cupiennius* is able to discriminate vertical against sloped objects. Furthermore the spiders are able to align their body posture to compensate inclinations of the surface. The results of this study strongly indicate that the alignment of the eyes in reference to an object determines the perception of verticality. This finding suggests that the processing of verticality is not done by a true calculation of verticality in the framework of an ecological relevance. In fact the obvious preference emerged from an intrinsic structural neural condition. There is no evolutionary pressure of pure visual processing of verticality. The alignment of the body posture to a given surface inclination is understood as an equilibrate tendency of the centre of mass in order to equally load the walking legs and therefore enhance the stability while walking and not to ensure that verticality is processed adequately.

Preferences for vertical objects are for example also seen in the desert locust *Schistocerca gregaria* (Wallace 1958) and in *Lymantria caterpillars* (Hundertmark 1937) and the most established theory of form discrimination in insects seems to work also in *Cupiennius salei*. This theory says that the operative stimuli are considered as the changes in the intensity of light falling on the retinal cells when an image moves on the retina (Wallace 1958). So when *Cupiennius* perform their zig zag motion in an orientation run the target is moved horizontally on the retina. Thus, as Wallace (1958) said, the vertical contours will be the important ones since they are perpendicular to the direction of the animals motion when they are walking and will produce the greatest number of stimulus changes on the retina per unit time. It seems that the different number of stimulus changes of differently adjusted objects is based on the adjustment of the spiders' neural periphery and determines the discrimination. Hertz (1929) applied the term figure intensity to describe this spontaneous choices based on the stimuli changes per unit time, which she found in bees. Hertz had already argued that this spontaneous choice would be found also in arthropods with different living requirements, and this would reflect the properties of a simple nervous system. This could also be the explanation of the diminishing geotaxis by the enhanced attractiveness of larger vertical contours, because larger vertical contours will led to a greater number of stimuli changes of the retina cells and could trigger a stronger tendency to head these structures than the tendency to follow other sensory inputs. And the more experimental accustomed animals seemed to show more zig zag motion while the less accustomed ones showed more direct approaches to the targets which probably led into fewer stimuli differences. This basic mechanism could possibly also be supported and work without locomotion of the spider by the horizontal active retinal movements which were found by Kaps and Schmid (1996) in the AM eyes, the eye type with the ability of target discrimination. Overall this explanation seems more likely than an evolutionary advantage of evolving a mechanism to adequately discriminate verticality in order to enhance the probability of survival because a more vertical dwelling plant is a better hiding place but rather the perceptive mechanisms of a simple nervous system cause this preference.

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Fig. 13A:

[http://images.google.at/imgres?imgurl=http://www.bescherer.de/zimstern\\_blog/waldboden\\_mittel.jpg&imgrefurl=http://zimstern.wordpress.com/category/top-10-photos/&usg=\\_\\_jiJ7oJJp8tFTIAoJI4CXf-vyIw=&h=778&w=1034&sz=769&hl=de&start=5&um=1&tbnid=1LR\\_fW-oSuePhM:&tbnh=113&tbnw=150&prev=/images%3Fq%3Dboden%2Bwald%26hl%3Dde%26sa%3DN%26um%3D1](http://images.google.at/imgres?imgurl=http://www.bescherer.de/zimstern_blog/waldboden_mittel.jpg&imgrefurl=http://zimstern.wordpress.com/category/top-10-photos/&usg=__jiJ7oJJp8tFTIAoJI4CXf-vyIw=&h=778&w=1034&sz=769&hl=de&start=5&um=1&tbnid=1LR_fW-oSuePhM:&tbnh=113&tbnw=150&prev=/images%3Fq%3Dboden%2Bwald%26hl%3Dde%26sa%3DN%26um%3D1) [4.11.2009, 10:17].

# LEBENS LAUF

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