A Visually Induced Switch in Mode of Locomotion of a Spider

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The spider *Cupiennius salei* Keys. (Araneae, Ctenidae) is a nocturnal hunter living on monocotyledones. It does not build webs for prey capture. During the day it remains in its retreat and during dusk it begins to hunt for prey or to search for mates. *C. salei* is well equipped with mechanosensory systems to detect air- or substrate- borne vibrations elicited by prey or predators. If none of them produce either air movements or substrate vibrations, and the light intensity is below the threshold (0.1 lx), the animal is virtually "blind". Therefore a hypothetical, additional sensory input should exist, which is used only in complete darkness. The animal was tested on a locomotion compensator were it performs constant walks towards a visual target. Three different light intensities were used (bright 200 lx, dim 0.1 lx, and dark at 950 nm, which is outside the spectral sensitivity range of the animal). At bright and dim illumination the animal walked in the alternating tetrapod gait towards the target. In complete "darkness" the walk was no longer directed and the animal changed its gait and continued walking on only six legs using the first pair as guide-sticks. If the first pair is missing, the second cannot replace this function. This shows a twofold use of the first pair of legs as ordinary walking legs and as guide-sticks or "antennae". Therefore one can assume that visual input causes a behavioral change, which can not be explained by a fixed locomotion pattern but by adaptive changes caused by visual inputs.

Introduction

The Central American wandering spider *Cupiennius salei* belongs to the family of Ctenidae. It is a nocturnal hunter which mainly lives on epiphytic monocotyledons. Being a hunting spider it does not build webs for prey capture but at night it leaves its retreat to hunt for prey or to search for mates.

Cupiennius is well equipped with different mechanosensory systems such as trichobothria (filiform hairs) to detect air movements, and slit sensilla to detect cuticular strains and substrate-borne vibrations (Barth, 1985; Speck-Hergenröder and Barth, 1987; Baurecht and Barth, 1992; 1993; Barth *et al.*, 1993; Humphrey *et al.*, 1993; Barth *et al.*, 1995). During courtship the animals rely on substrate vibrations (for review see Barth, 1993). By means of these mechanosensory systems the animals detect either prey or predators, which both can produce substrate vibrations or air movements. Prey-like vibrations lead to hunting behaviour that is turning and approach, and predator-like signals lead to escape behaviour. When both receptor systems receive either a prey-like or a predator-like stimulus the effects add up. When the trichobothria receive a stimulus that is unlike prey, the approach reaction is inhibited (Hergenröder and Barth, 1983). Therefore, between both the signals from the trichobothria and from the slit sense organs a central neuronal interaction can be assumed. In the case of an ambiguous, and, hence, potentially dangerous signal, the use of an additional sensory input, such as vision, might help.

C. salei is virtually blind, if the light intensity falls below its threshold of sensitivity that is close to 0.01 lx (Barth *et al.*, 1993). This is the case at night in a natural rain forest (Barth and Baurecht, personal comunication). Without its visual system, the spider must rely on its mechanosensory systems, and if neither prey nor predator are moving, that is, if they produce neither air movements nor substrate vibrations, they cannot be detected.

In such situations, the worst case for *Cupiennius salei*, an additional sensory modality would be the only means of detection. The use of the olfactory system to detect prey or predators is not described so far for *C. salei.* Another modality, such as a tactile mechanism, seems to be possible. The very long (up to 7 cm) legs are covered with many tac-

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tile hairs, which might provide a usefull sensitive short range detection system. Therefore the animals could use their first pair of legs as an additional detection system and walk on only six legs.

Here it is shown for the first time that in complete darkness *C. salei* uses its first pair of legs as guide-sticks and switches its gait from an eight-legged to a six-legged animal.

Materials and Methods

Animals

Adult females of the species *Cupiennius salei* (Ctenidae) were used in all experiments. Two weeks prior to the experiments they were kept under a 12/12 LD rhythm at a room temperature of 22 °C and at 80% relative humidity. All animals were kept in glass jars separately and fed once per week with flies, cockroaches or house crickets. In an additional experiment two animals were used with the first pair of legs autotomized. This handicap does impair the animals only to a small extent, for they were observed to perform prey catching behavior and even complete copulations after placing a male in the cage.

Experimental setup

The experiments were carried out under three different light conditions: bright (200 lx), dim (0.1 lx), and "darkness" that is using infrared illumination at 950 nm ± 10 nm. The infrared light is invisible to these animals as their spectral sensitivity is zero beyond 700 nm (Barth *et al.,* 1993; Walla *et al.,* 1996). In order to monitor the position of the animals, a reflecting foil was glued onto the dorsal side of the prosoma (Scotchlite RP 7610, diameter 5 mm).

To elicit directed movements of the spiders, a black cardboard stripe (120 mm wide x 240 mm high) was presented as a target at a distance of 0.4m. This corresponds to an extension in the visual field of 17° x 34°. To determine gait and mode of locomotion of the spiders under different lighting conditions, the spiders were tested on a locomotion compensator after Kramer (1975) as described elsewere in great detail (Schmitz *et al.,* 1982; Wendler and Scharstein, 1986). The spiders were positioned on top of a black sphere with a diameter of 0.5 m (Fig. 1). The deviation of the animals (position of the reflecting foil) from the top of the sphere was measured by an infrared detector and used to drive two computer-controlled motors rotating the sphere. The movements of the unrestrained spiders were thereby compensated for in such a way that the spider was always walking on top of the sphere. The rotations of the sphere were measured and stored in a computer to calculate the direction and velocity of the animal's locomotion. The set-up and the programs for data acquisition and evaluation were kindly provided by Prof. Wendler (University of Cologne, Germany). The walking modes of the animals were filmed from above using an IR-sensitive CCD camera.

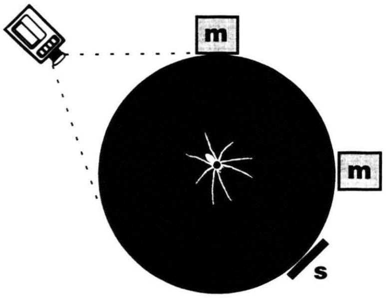

Fig. 1. Top view of a walking compensator with the spider (note the reflecting foil) on top of the sphere. The spider orients itself towards a black cardboard stripe (**s**). The sphere is driven by two motors (**m**) and the animal is filmed by an infrared-sensitive CCD camera.

Results and Discussion

The spiders did walk on the sphere, only startle-responses are too fast to be compensated for by the motor devices. On such incidents the animals jumped from the sphere. On several occasions the animals walked continuously for more than 1 h. In *Cupiennius salei*, both gait and speed are very variable and also differ during fast and slow voluntary walks (Seyfarth and Bohnenberger, 1980). Longlasting, directed walks can be obtained by presenting a visual target that makes the animals walk into a distinct direction. During such constant and directed walks gait, speed, and stop/go-ratio are more reproducible than during walks elicited by mechanical stimulation (Seyfarth, 1985).

The fact that the distance from the spider to the target remained constant did not appear to deter the animal from performing constantly directed, long-lasting walks. Six different experiments were carried out with six animals possessing all eight legs, and two animals with six legs, the first pair being autotomized. All experiments were carried out under three different illuminations.

Walking mode at high and low light intensities

The sequence of the legs is very variable, because the timing of each leg within a complete step cycle can change from step to step. Moreover, the permanently changing velocity and walking direction adds to the complexity. In the experiments the stepping order varied from 4–3–2–1 to 4–2–3–1 which is the alternating tetrapod gait (Seyfarth, 1985; Wilson, 1966). At higher velocities these gaits can be changed to 1–3–2–4. At both light intensities (200 lx and 0.1 lx), the animals walked in similar ways and there was no difference in average walking velocity or in the orientation towards the target. The range of the walking velocity was 2.2–4.9 cm/s with an average of 3.2 cm/s (SD = 0.91). The go/stop – ratio varied between 0.26 and 0.66 with an average of 0.44 (SD = 0.12; N = 6, n = 18) The animals always used eight legs and very rarely, during short pauses, took tentative steps, that is when the up and down movements of the front legs have a bigger amplitude and are moved slower than during a walking step. An example of the walking velocity, direction, and the stop-and-go mode for one spider is shown in Figure 2. Discontinuous walking was also be observed in a lycosid spider (Baatrup and Bayley, 1993).

Walking mode in complete darkness

The walking mode changed immediately when the light was switched from bright to infrared illumination. The spider then stopped for 2–4 s, raised its first pair of legs and then continued walking in a completely different style. The sequence of the steps was changed to 4–3–2 (+ 1st leg moving up) and 4–3–2 (+ 1st leg moving down). The animals walked on only six legs, the first pair was stretched out and constantly moved up and down. There was no longer any orientation towards the target. This confirmed that the wavelength of the light, used in this experiment, was

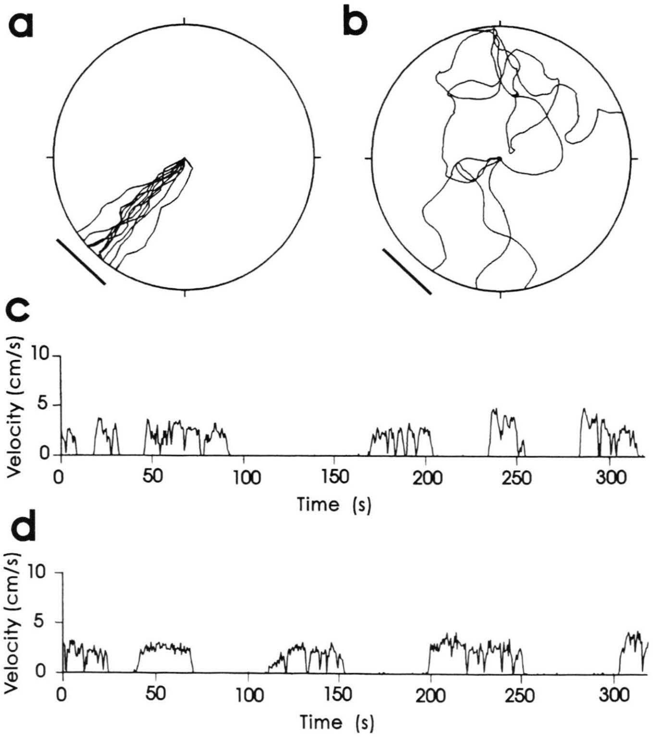

Fig. 2. Locomotion of a spider towards a black target **a** and the velocity distribution during a walk of more than 300s **c.** Disorientation of a spider in complete darkness **b** and the velocity distribution during a walk of more than 300 s **d**.

outside the spectral sensitivity range of *C. salei*. The walking velocity did not change and varied between 1.9 and 4.7 cm/s with an average of 3.3 cm/s (SD = 1.06). The stop-and-go mode persisted with prolonged pauses between two active phases leading to go/stop – ratios varying from 0.16 to 0.28 with an average of 0.21 (SD = 0.05; N = 6, n = 12) which is significantly lower than under illumination ($p < 0.05$, chi^2). Figure 3 shows the direction and walking mode in complete darkness. The prolonged pauses may indicate a cautious way of walking. During these pauses the front legs not only moved slowly up and down but also sideways sometimes in a circular way. The spiders seem to scan as much as possible of the area in front. The animal, therefore, would be able to detect either prey or predators within the range of its forelegs.

The pauses, which also occur during normal walking, might also be due in part to the discontinuous oxygen supply to the prosoma and subsequently to the leg muscles. The high haemolymph pressure in the prosoma during walking – necessary for the hydraulic extension mechanism of some of the joints of the spider leg (Parry and Brown, 1959; Blickhan and Barth, 1985) – is not transmitted to the opisthosoma. This indicates that during walking a valve-like structure in the petiolus is closed (Paul and Bihlmayer, 1995). Therefore the oxygen deficit that is built up during walking must be cut down during the pauses (Angersbach, 1975). An additional reason for this discontinuous type of walking may be the use of mechanosensory systems, that is trichobothria or slit sensilla, during the pauses to collect further information from the environment.

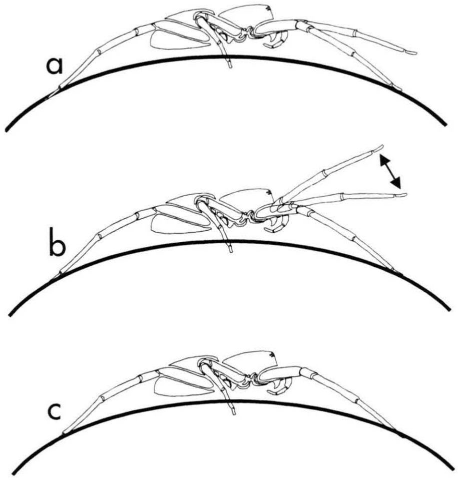

Fig. 3. Leg postures of *Cupiennius salei* on the sphere. **a** normal walking spider with eight legs. **b** up-and-down movements of the first pair of legs in complete darkness. **c** leg positions of a spider without its front legs. The guide-stick-like function of the first pair of legs is not replaced by the second pair of legs.

This experiment shows not only a change in the go/stop – ratio and a switch in the walking mode of *C. salei* but also a new component in the use of a walking leg as an antenna. The underlying neuronal network allows both functions of the first pair of legs and the visual system provides the input to switch between the two modes of movements.

Walking mode with the first pair of legs autotomized

To find out whether all legs can be used as antennae or whether this function is peculiar to the first pair of legs only, the same experiments were done for the first time with animals which had their first pair of legs autotomized. At high and low light intensities the animals walked quite "normal" using the remaining six legs, but the sequence was changed to 4–3–2 . They walked directed towards the target and the go/stop – ratio was not different from that of the intact animals. Therefore it is not possible to state alone from the pattern of motion, whether a six-legged or an eight-legged spider is walking. In complete darkness no change in function of any of the legs could be observed, and the animals continued walking on six legs. The short pause after switching the light from bright to infrared remained. In Figure 3 lateral views of an eight-legged spider in bright light and in the dark, and also of a six-legged spider are shown. The twofold function of the legs – as guide-sticks or as walking legs – is restricted to the first pair of legs. The differences in the underlying neuronal network are unknown, but one might suppose that the visual input to the neuropils of the first legs is more prominent than that to the other legs. This result indicates that a visual input causes a change in behaviour which can not be explained by a rigid locomotion pattern or a preprogrammed central information processing, but by adaptive changes caused by visual inputs. This further indicates multimodal interaction of the visual- and the mechanosensory system in controlling locomotion in the spider *Cupiennius salei.*

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