Journal of Insect Physiology 57 (2011) 494–500

Contents lists available at ScienceDirect

Journal of Insect Physiology

journal homepage: www.elsevier.com/locate/jinsphys

Active sensing in a freely walking spider: Look where to go

A. Schmid *, C. Trischler

Department of Neurobiology, Faculty of Life Sciences, University of Vienna, Althanstrasse 14, 1090 Wien, Austria

ARTICLE INFO

Article history:
Received 26 November 2010
Received in revised form 21 January 2011
Accepted 24 January 2011
Available online 31 January 2011

Keywords:
Active sensing
Cupiennius salei
Dual-channel-telemetry
Eye muscles
Spider
Visual orientation

ABSTRACT

The Central American hunting spider *Cupiennius salei*, like most other spiders, has eight eyes, one pair of principal eyes and three pairs of secondary eyes. The principal eyes and one pair of the secondary eyes have almost completely overlapping visual fields, and presumably differ in function. The retinae of the principal eyes can be moved independently by two pairs of eye muscles each, whereas the secondary eyes do not have such eye muscles. The behavioural relevance of retinal movements of freely moving spiders was investigated by a novel dual-channel telemetric registration of the eye muscle activities. Walking spiders shifted the ipsilateral retina with respect to the walking direction before, during and after a turning movement. The change in the direction of vision in the ipsilateral anterior median eye was highly correlated with the walking direction, regardless of the actual light conditions. The contralateral retina remained in its resting position. This indicates that *Cupiennius salei* shifts it visual field in the walking direction not only during but sometimes previous to an intended turn, and therefore "peers" actively into the direction it wants to turn.

1. Introduction

The behavioural importance of the visual sense of arthropods has been outlined many times for different spider species. In different families of spiders (especially ctenids, salticids and lycosids) the behavioural role of the visual system has been the subject of several investigations. Most spiders have eight eyes, arranged in different patterns on the prosoma, representing two different types. Thus *Cupiennius salei* (Ctenidae, Araneae) has two principal eyes (anterior-median, AM) in which the photoreceptors are everse, and six secondary eyes (anterior-lateral, AL; posterior-median, PM; posterior-lateral, PL) in which the inverse photoreceptors point towards a reflecting tapetum at the back of the eye tube. The visual fields of the eight eyes cover most of the environment, whereas the visual fields of the AM and the PM eyes overlap almost completely (Land and Barth, 1992). Additionally, the anatomy of the principal and the three pairs of secondary eyes differs, and they have separate visual pathways (Strausfeld and Barth, 1993; Strausfeld et al., 1993).

Recent findings suggest that the spatial resolution of the PM eyes are in the range of 1° (Fenk and Schmid, 2010), which is impressive for a night active spider. *C. salei* shows attack behaviour solely because of visual stimulation (Fenk et al., 2010). These findings and the presence of different types of eyes suggest that this spider might rely on vision to a much greater extent than was previously assumed.

Salticids are diurnal hunters which detect their prey visually (Forster, 1985), and females select mates visually on the basis of initial movement (Clark and Uetz, 1992). The AM eyes in jumping spiders each have six different eye muscles and thus allow complex retinal movements like linear shifts and rotations (Land, 1969). In lycosids, the eyes were shown to have different roles and the visual system was also involved in conspecific interactions such as courtship behaviour (Rovner, 1993, 1996).

The visual system of *C. salei*, a Central American nocturnal hunter, has a remarkable sensitivity with a threshold below 0.01 lx (Land and Barth, 1992). The spectral range of the eyes lies between 340 and 680 nm (Land and Barth, 1992; Barth et al., 1993a,b; Walla et al., 1996). Each of the AM eyes has two separate eye muscles (dorsal and ventral) which can move the retina.

The physiological basis and the possible behavioural relevance of the retinal movements have previously been investigated (Kaps and Schmid, 1996). In this study the animals were tethered and completely immobilized in a conventional electrophysiological set-up, preventing any movements and thus did not permit conclusions regarding the use of eye-muscles under unrestricted moving conditions.

The development of extremely small electronic devices (SMD) has made it possible to construct miniature, lightweight telemetric transmitters which can be carried even by medium sized arthropods. The electrophysiological recordings of eye muscle activities and their wireless transmission from freely moving animals enable the investigation of the relevance of retinal movements under conditions that are very close to the natural ones.

* Corresponding author. Tel.: +43 1 4277 54475; fax: +43 1 4277 54507.
E-mail address: axel.schmid@univie.ac.at (A. Schmid).

0022-1910/$ – see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jinsphys.2011.01.014

The simultaneous measurement of the eye movements of both AM eyes was of particular interest since they can move independently (Kaps and Schmid, 1996). Therefore, a novel dual-channel telemetric transmitter device was used, which enables us to measure the activity of two different eye muscles during free walk. By simultaneously video recording the walking spiders‘, we were able to correlate their behavioural patterns with actual retinal movements inferred from the registrations of the eye muscle activities.

The dorsal eye muscle consists of 15–18 striated fibres and is 600 μm long. The ventral eye muscle is longer (650 μm) and consists of 20–22 striated fibres. The dorsal eye muscle arises dorso-lateraly on the AM eye tube and attaches to the dorso-median carapace between the PM eyes. The ventral muscle is attached to the ventro-lateral surface of the eye tube and inserts at the carapace on the ventral internal surface of the clypei. Retinal movements are brought about by two forces, contractions of the dorsal and ventral eye muscle, and in addition, the passive elastic restoring forces of the eye tube and eye muscles. The change in the direction of gaze caused by the eye muscles depends on the contraction states of the two eye muscles. The direction of gaze can vary from dorso-lateral to lateral to ventrolateral depending on the

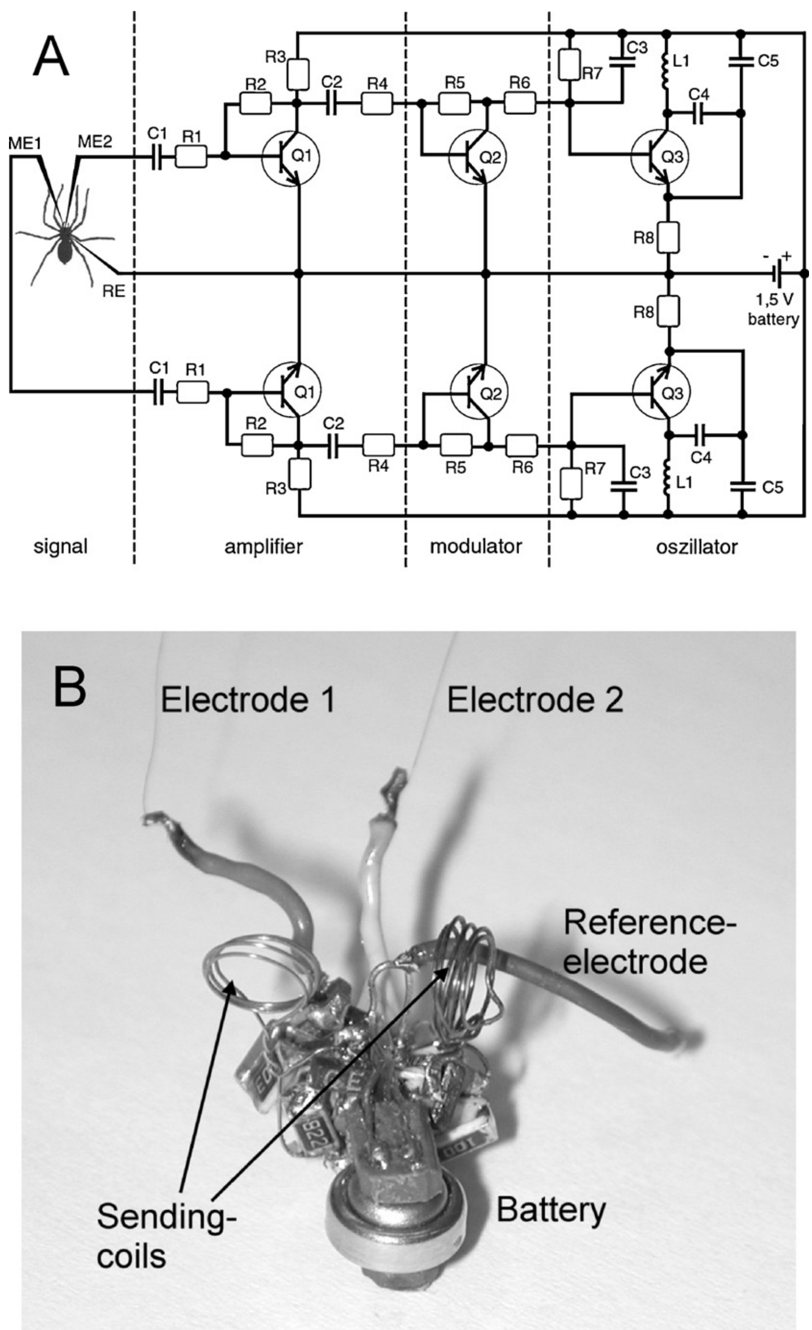

Fig. 1. (A) Circuit diagram of the novel double-channel telemetric device, with all electronic units, as it is connected to the spiderś eye muscles. The two L1 units are the sending coils. The entire device is fixed with beeswax on the prosoma of the spider. ME 1 and 2 are the recording electrodes, and RE the common reference electrode. The SMD parts used to build the device are: resistors R, transistors Q, capacitors C, coils L and a battery. (B) Photo of the dual channel transmitter device, with electrodes and sending coils, the diameter of the battery is 5.8 mm.