ウェブサイト公開用

（様式 10）
（海外特別研究員事業）
令和　3 年　9 月　7 日

海 外 特 別 研 究 員 最 終 報 告 書

独立行政法人日本学術振興会 理事長　殿

採 用 年 度　令和 1 年度
受 付 番 号　201960238
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海外特別研究員としての派遣期間を終了しましたので、下記のとおり報告いたします。
なお、下記及び別紙記載の内容については相違ありません。

記

1. 用務地（派遣先国名）用務地：マーブルク　（国名：ドイツ　）

2. 研究課題名（和文）※研究課題名は申請時のものと違わないように記載すること。
移動方向のナビゲーションに関わる神経回路をシンプルな昆虫脳を利用して解明する

3. 派遣期間：平成・令和　1 年　7 月　15 日　～　令和　3 年　8 月　31 日（779 日間）

4. 受入機関名及び部局名
受入機関名：フィリップス大学マーブルク
部局名：生物科学科

5. 所期の目的の遂行状況及び成果…書式任意　**書式任意（A4 判相当 3 ページ以上、英語で記入も可）**

【記載事項】
- 研究・調査実施状況及びその成果の発表・関係学会への参加状況等
- 新型コロナウイルス感染症の影響にかかる特例措置のうち、国内採用開始・採用期間延長・翌年度渡航のいずれかの適用を受けた場合は、当該措置の適用による影響等

（注）「6. 研究発表」以降については様式 10－別紙 1～4 に記入の上、併せて提出すること。

「新型コロナウイルス感染症の影響にかかる特例措置の適用状況」

新型コロナウイルス感染症の感染拡大に伴い，受入研究機関では 1．2020 年 4 月 6 日から 5 月 14 日まで研究機関への立入りが制限され，2．2020 年 3 月 25 日以降，実験室あたりの入室人数が制限された。特に 2 の措置については 2021 年 8 月 31 日時点においても継続中である。本研究は特例措置のうち「採用期間延長」の適用を受けたことによって，上記制限によって滞った研究計画を採用期間内に終了し，研究成果を論文として国際誌に報告するまでの算段をつけることができた。

Introduction

Spatial orientation to visual surroundings is crucial for successful navigation, and mammalian brains possess ring attractor networks of neurons encoding an individual's head direction. Ring attractors are driven by internally generated self-motion cues but also use external visual cues for accuracy. However, mammalian brains consist of so many neurons that it is almost impossible to identify single neurons constituting visual input pathways to a ring attractor network.

Insect brains also possess head-direction coding systems and allow characterizing ring attractor elements in relatively simple neural circuits. Insect head direction is represented in the central complex (CX), a navigation center of the brain, to generate appropriate steering commands. The CX is a group of midline-spanning neuropils consisting of the protocerebral bridge, the upper and the lower divisions of the central body (CBU and CBL, also termed fan-shaped body and ellipsoid body), and the paired noduli. In several insect species, CX neurons are tuned to celestial cues, references to the solar position. Therefore, those CX neurons are suitable for head-direction coding relative to the sun.

Throughout the fellowship, I aimed to elucidate the anatomical and physiological properties of single neurons related to head-direction coding relative to the sun. I adopted two insect species for my study: (1) desert locusts (*Schistocerca gregaria*) and (2) Madeira cockroaches (*Rhyparobia maderae*). In those species, I intracellularly recorded neural activities of the CX neurons with sharp electrodes and visualized the recorded neurons by neuronal tracer injection.

(1) Results in desert locusts

As a long-range migratory insect, the desert locust has been a model animal for studying navigation systems. The locust ring attractor network contains a topographic, compass-like arrangement of neurons tuned to two celestial cues: direct sunlight direction and polarization pattern across the sky reflecting the position of the sun (Figure. 1) (Pegel et al., 2019; Zittrell et al., 2020). It is unclear whether congruent tuning to these two compass cues emerges within the network or is inherited from visual input elements to the ring attractor. To address this question, I recorded the input elements to the locust ring attractor (TL neurons, corresponding to R neurons in *Drosophila*) while applying visual stimuli simulating direct sunlight and polarization across the animal's dorsal visual field.

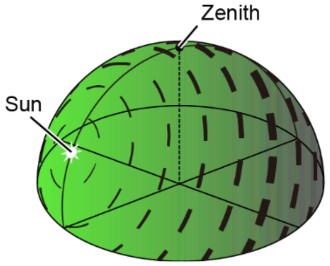

Figure 1. Schematic illustration of the polarization pattern across the sky. The angle of polarization (black bar orientation) is arranged tangentially along concentric circles around the sun. The degree of polarization (black bar thickness) reaches its maximum at a 90° distance from the sun.

I characterized receptive field properties to the visual stimuli in three TL neuron subtypes, TL2a, TL2b, and TL3 innervating layer 2, 3, and 5 of the CBL in the CX, respectively. These neurons have large receptive fields for skylight polarization (Figure 2A) and substantially contribute to coding polarization angles that match sky polarization patterns for particular sun positions (Figure 2B). They also possess spatially partitioned excitatory and inhibitory subfields for small light spots (Figure 2B), often located close to the solar position encoded by polarization tuning in individual TL neurons. These results suggest the congruent integration of celestial compass cues in those cells.

TL2 and TL3 subtypes differed in tuning properties. For example, the sensitivity to polarization angle was highly dependent on the stimulus position in TL2 neurons, corresponding to the highly varying degree of polarization in the sky. Therefore, signals from TL2 neurons might be advantageous under clear sky conditions. In contrast, most TL3 neurons showed uniform high sensitivity to polarization angle across large parts of the dorsal visual field. They should be suited to generate robust signals even under cloudy or hazy sky conditions. These TL2 and TL3 parallel input channels for integrated celestial cues likely allow robust yet dynamic head-direction coding in a ring attractor in the CX.

The results are under review for publication (as of September 2021). In addition, I am a co-author of a paper analyzing the anatomical relationship between the CX and adjacent brain areas in desert locusts (Hensgen et al., 2021).

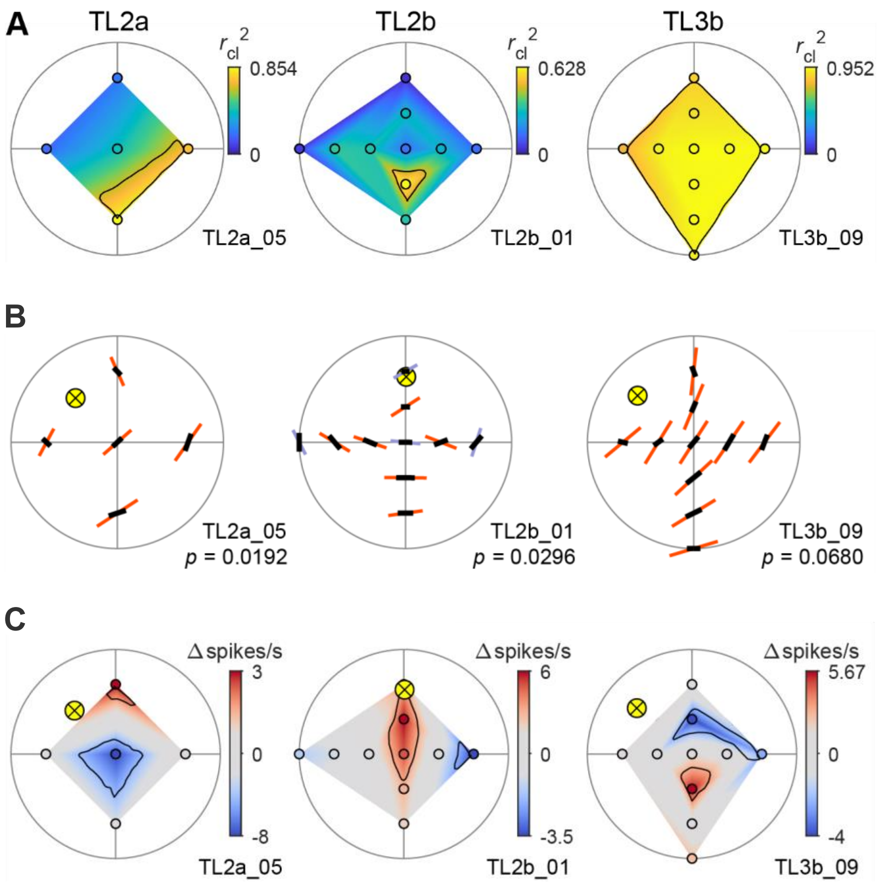

Figure 2. Example tuning patterns of three individual neurons to the angle of polarization (A) and unpolarized light spot (B) across the dorsal visual field. For data visualization, the spherical dorsal visual field is represented on a two-dimensional polar-coordinate grid, where the radius (ρ) is defined as 1 – elevation/90° ($0 \leq \rho \leq 1$) and the angle (θ) equals the spherical azimuth ($0° \leq \theta < 360°$). The elevation and azimuth are indicated relative to the animal's head, and thus, the pole corresponds to the zenith above the animal.
A, Polarization sensitivity maps. The sensitivity to polarization ($0 \leq r_{cl}^2 \leq 1$, statistical value of circular-linear correlation) is color-coded at each tested position (circles) and linearly interpolated in between. Black lines surround receptive fields.
B, Polarization response patterns. The preferred angle of polarization is shown by red (statistically significant r_{cl}^2 value) or gray (nonsignificant) bar orientation at each tested position. The best-matching sky polarization patterns (black bars) are superimposed on the responses. The red (gray) and black bar lengths scale with neural sensitivity and degree of polarization, respectively. A crossed yellow circle indicates the solar position used to generate the polarization pattern. *p* values are matching results between neural response and sky polarization patterns; $p < 0.05$ is significant.
C, Light-spot response maps. Spike rate modulation (Δspikes/s value) caused by light spot is color-coded at each tested position (circles) and linearly interpolated in between. Black lines surround excitatory (red) and inhibitory (blue) receptive fields. The preferred solar positions encoded by polarization tuning are also shown (crossed yellow circles).

(2) Results in Madeira cockroaches

The Madeira cockroach has been used for circadian clock studies. As a nocturnal insect, the cockroach strongly relies on antennal information for spatial orientation, but celestial-cue sensitive neurons were identified in the optic lobe, the primary center of the insect visual system (Loesel and Homberg, 2001). In addition, a physiological signature of head direction coding relative to a bright visual cue was extracellularly recorded in the CX (Varga and Ritzmann, 2016). Those activities also encoded the history of head rotation direction in manners strikingly similar to those reported in mammals (Varga and Ritzmann, 2016). In the experiment, however, the head direction cells were not identified morphologically.

For the first step to elucidate the celestial-cue-dependent head-direction coding in the cockroach, I intracellularly recorded CX neuron responses to polarization stimulus from the zenith. I identified the CX neuron subtypes sensitive to the angle of polarization for the first time in the cockroach. Based on their morphology, those neurons were classified into input elements (TL neurons) and compass elements of ring attractors in the insect head direction systems. Ph.D. students in the laboratory take over further experiments and analyses, and one of the Ph.D. students presented the results at the 113th Annual Meeting of the German Zoological Society (August-September 2021, online) together with her achievements.

References
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