様　式　Ｃ－１９、Ｆ－１９、Ｚ－１９　（共通）

科学研究費助成事業　　研究成果報告書

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研究課題名（和文）A closed-loop system to investigate visual flight behaviour

研究課題名（英文）A closed-loop system to investigate visual flight behaviour

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研究成果の概要（和文）：I have implemented a virtual reality stimulus display system, and used it to investigate the role of visual motion cues in butterfly foraging behaviour. This work is published, and is detailed in the attached document. Though less closely related to the original project aims, I have also...

研究成果の概要（英文）：I have implemented a virtual reality stimulus display system, and used it to investigate the role of visual motion cues in butterfly foraging behaviour. This work is published, and is detailed in the attached document. Though less closely related to the original project aims, I have also published another study showing that butterflies can detect motion using colour (rather than brightness) contrast, which has not previously been demonstrated in an insect.

More recently, I have built a novel pentachromatic projection system for the free-flight arena, and used this to investigate colour opponency in butterflies. These experiments are now complete and I am in the process of analyzing the results, with the intention to publish my findings in the near future. Additionally, I set up a collaboration with Cambridge University, which entailed me going there to built a similar closed-loop system to study aerial pursuit behaviour in flies. We plan to write a paper on this work very soon.

研究分野：Neuroethology

キーワード：butterfly　vision　virtual reality　colour　motion　parallax　opponency　flight

１．研究開始当初の背景

Virtually all animals possessing eyes are faced with the issue of how to reconstruct the three-dimensional layout of their surroundings from the two-dimensional images formed on their retinas. Insects' compound eyes generally do not allow stereopsis or accommodation to be used to estimate depth. Several examples of insects instead using visual motion to measure distance have been documented, from locusts peering to gauge the proximity of prey, to honeybees performing visual odometry en route between the hive and a flower patch. However, whether the use of parallax information is confined to specialised behaviours like these or represents a more general purpose sensory capability, is an open question.

２．研究の目的

The objective of the study is to investigate whether butterflies use motion cues in addition to colour and brightness information when foraging. We do this by manipulating the motion cues experienced by the animal as it flies to create the illusion that a target is situated at some position above or below the floor of the arena. Three particular questions we address are whether the apparent distance of targets affects (1) their attractiveness, (2) their likelihood of eliciting successful versus abortive approaches, and (3) the spatio-temporal structure of the descents the butterfly makes towards them.

３．研究の方法

Papilio butterflies were trained to feed from a blue circle displayed in the centre of a monitor placed on the floor of the experimental cage, before being tested on an unrewarded target. During testing, the animal's real-time 3D position was tracked at 60 Hz using two calibrated cameras (Fig. 1A). This information was used to modulate the appearance of the target in a closed-loop manner, with a latency of ~50 ms. Specifically, the size and/or position (corresponding to expansion and parallax cues, respectively) of the target was altered to give the impression that it was situated 4, 8, or 12 cm below the monitor surface, or 4 cm above it (Fig. 1B,C). As a control, we also played recordings of the stimuli generated by other individuals' closed-loop flight, to confirm that any effects identified could be attributed to visual motion *from the butterfly's perspective*. We analysed the recorded flight trajectories to ascertain what effects these manipulations of visual motion cues had on the structure and timing of the animals' approaches to the target.

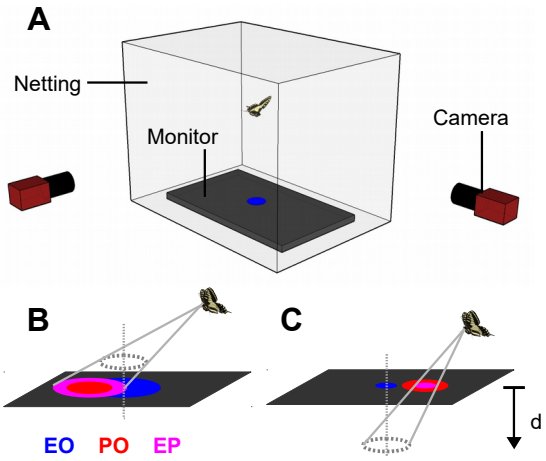

Fig. 1. Experimental set-up. (A) Schematic diagram of the experimental arena. (B,C) Illustration of the closed-loop stimuli generated for a virtual target above (i.e. negative apparent depth, *d*) (B) or below (C) the monitor. The expansion-plus-parallax (EP) stimulus is the projection of the virtual target to the monitor surface with respect to the butterfly's position; the expansion-only (EO) and parallax-only (PO) stimuli hold the position and size of the target on the monitor constant, respectively.

４．研究成果

(1) We measured how long butterflies took from the onset of the stimulus to performing their first descent towards the target, which we took as a metric of (negative) attractiveness. They were quicker to approach targets that appeared closer, with parallax cues apparently playing a greater role than expansion (Fig. 2A). This provides clear evidence that butterflies perceive motion cues and use them to guide their foraging behaviour.

(2) Motion cues affected the "ease" with which butterflies could land on targets, measured in terms of the frequency of failed approaches prior to the first successful one. Interestingly, expansion and parallax cues had effects of opposing polarity (Fig. 2B). Indeed, highly accurate approach behaviour could be elicited by physically impossible virtual objects that gave conflicting expansion and parallax cues.

(3) We found no clear evidence that apparent distance affected the speed, deceleration, or steepness of approaches. Considering all these observations together, we conclude that

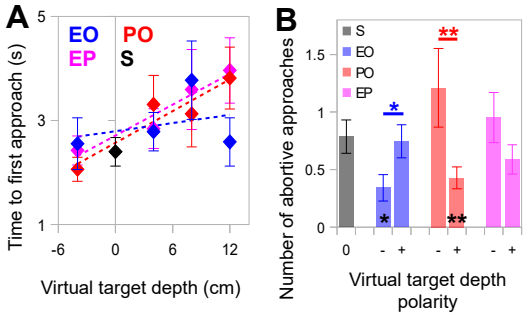

Fig. 2. Motion cue effects. (A) When parallax cues are present (i.e. the PO and EP conditions), the butterflies are slower to approach targets the further away they appear to be. S denotes the static (control) condition, where the target size and position is fixed. (B) Expansion and parallax manipulation can each individually reduce the frequency of abortive approaches, but these effects are of opposing polarity and appear to cancel out in the more realistic case (EP) where both cues are present.

while parallax cues increase the attractiveness of a target object, *Papilio* do not perform true three-dimensional navigation. Rather, they appear to employ a simple edge-tracking scheme in two-dimensional retinal space.

(4) From a methodological perspective, this study represents a successful demonstration of a sophisticated and novel virtual reality stimulus presentation system for flying insects. This technique is a valuable tool not just for our lab, but for the wider behavioural community. I have already embarked upon a collaboration with University of Cambridge, implementing a similar system to study aerial pursuit in killer flies, and I have plans for another collaboration with the University of Exeter to study bumblebee flight.

５．主な発表論文等
（研究代表者、研究分担者及び連携研究者には下線）

〔雑誌論文〕（計　2　件）

1. Stewart FJ, Kinoshita M & Arikawa K (2015). The roles of visual parallax and edge attraction in the foraging behaviour of the butterfly *Papilio xuthus*. *J Exp Biol* **218**, 1725–1732.

2. Stewart FJ, Kinoshita M & Arikawa K (2015). The butterfly *Papilio xuthus* detects visual motion using chromatic contrast. *Biology Letters* **11**, 20150687.

〔学会発表〕（計　7　件）

1. Stewart FJ, Kinoshita M & Arikawa K: Opposing effects of expansion and parallax cues in foraging butterflies The 11th International Congress of Neuroethology; Jul 2014, Sapporo.

2. Stewart FJ, Kinoshita M & Arikawa K: Visual course control of flower visiting behavior in *Papilio*: *Koto* in behavioral biology. Zoological Society of Japan; Sep 2014, Sendai.

3. Stewart FJ, Kinoshita M & Arikawa K: Chromatic motion vision in the butterfly *Papilio xuthus*. Gordon Research Conference: Neuroethology; Jun 2015, Lucca, Italy.

4. Stewart FJ, Kinoshita M & Arikawa K: The butterfly *Papilio xuthus* detects visual motion using chromatic contrast. Special invited seminar, University of Cambridge, UK, Sep 2015.

5. Stewart FJ, Kinoshita M & Arikawa K: Chromatic motion vision in the butterfly *Papilio xuthus*. Japanese Society for Comparative Physiology and Biochemistry; Dec 2015, Hiroshima.

6. Nagaya H, Stewart FJ, Arikawa K & Kinoshita M: Leaf selection in ovipositing *Papilio* butterfly. Japanese Society for Comparative Physiology and Biochemistry; Dec 2015, Hiroshima.

7. Stewart FJ, Kinoshita M & Arikawa K: Colour opponency in a tetrachromatic butterfly. The 11th International Congress of Neuroethology; Mar 2016, Montevideo, Uruguay.

〔図書〕（計　0　件）

〔産業財産権〕
○出願状況（計　0　件）

○取得状況（計　0　件）

〔その他〕
ホームページ等
http://www.esb.soken.ac.jp/research/index.html#finlay_stewart

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