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Author(s)	Ogawa, Sho; Yoshida, Shigeki; Yamawaki, Yoshifumi
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Role of co-contraction of antagonist muscles during predatory strike in the mantis

Sho Ogawa, Shigeki Yoshida, and Yoshifumi Yamawaki*
Department of Biology, Faculty of Science, Kyushu University, Japan
*y.yamawaki@kyudai.jp

1 Introduction

Animal behaviors are performed by coordinated activities of many muscles that are controlled by the nervous system. The praying mantis visually detects and catches prey with rapid foreleg movements called strike [1]. The foreleg trajectory in strike varies according to prey distance and direction [2]. The mantis foreleg attaching the prothorax consist of five segments: coxa, trochanter, femur, tibia, and tarsus (Figure 1). The trochanter is almost fused with the femur, and the tarsus is not used during strike. Therefore, the foreleg movement during strike can be described by three joint angles: the prothorax–coxa (P–C), coxa–trochanter (C–T), and femur–tibia (F–T). In other words, foreleg movements are mainly performed by coordinated activities of coxal promotor and remotor, trochanteral extensor and flexor, and tibial extensor and flexor.

We have investigated the activities of trochanteral extensor and flexor during strike in the mantis and suggested that the duration of extensor activity mainly determine the amplitude of rapid extension in C–T joint [3]. Unexpectedly, we observed substantial activity of flexor during rapid C–T extension, which leads to co-contraction of extensor and flexor. Co-contraction of the trochanteral flexor and extensor probably increases the stiffness and stability of the C–T joint. This might be helpful to reduce the disturbance by prey movements and/or to increase motor control accuracy during strike. If this is the case, the co-contraction of antagonists should also be observed in other muscles involved with foreleg movements during strike.

In this study, we combined motion analysis of foreleg movements during strike with electromyogram (EMG) recordings from coxal promotor and remotor, trochanteral extensor and flexor, and tibial extensor and flexor to examine how muscle activities affect the foreleg trajectory.

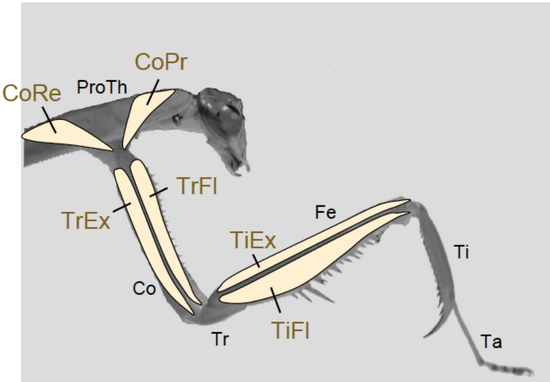

Figure 1: The mantis foreleg and schematic drawings of muscles involved with strike behavior. ProTh, prothorax; Co, coxa; Tr, trochanter; Fe, femur; Ti, tibia; Ta, tarsus; CoPr and CoRe, coxal promoter and remotor; TrFl and TrEx, trochanteral flexor and extensor; TiFl and TiEx, tibial flexor and extensor.

2 Materials and Methods

2.1 Animals and Preparation

We used adult females of the Chinese praying mantis *Tenodera sinensis.* The mantises were reared from eggs collected in the suburbs of Fukuoka, Japan [4] . They were fed fruit flies (*Drosophila melanogaster*) or cricket nymphs (*Achetus domesticus*) based on body size.

During experiments, the mantises were tethered via the dorsal pronotum and settled on a Styrofoam ball that floated on an air current produced by a fan. The longitudinal axis of the mantis's body was inclined at an angle of approximately 30° relative to the horizontal plane.

2.2 Motion analysis

The mantis strike was elicited by a living cricket or visual stimuli generated on the computer display [3]. The strike behaviours were recorded at 200 frames/s with a high-speed camera (HAS-220R, Ditect, Japan) positioned on the right side of the mantis. We measured the P–C, C–T, and F–T joint angles of the right foreleg frame-by-frame in video recordings. The joint angles were smoothed by convolving with a Gaussian window (time resolution = 5 ms, width σ = 5 ms).

2.3 Electromyogram recordings

We recorded the EMGs of the muscles, coxal promotor and remotor, trochanteral extensor and flexor, and tibial extensor and flexor. For EMG recordings, we inserted a pair of wire electrodes into the cuticle of prothorax, coxa, or femur through two holes that were made with an insect pin. Electrical signals were amplified with an AC amplifier (MEG-6108, Nihon Kohden, Japan) and filtered at 3 kHz and 150 Hz through a high/low pass filter. Signals were digitised and recorded at a sampling rate of 25 kHz using an analogue–digital converter (CED 1401, Cambridge Electronic Design, UK). The EMG data were analysed using Spike2 v5 (Cambridge Electronic Design, UK).

3 Results and Discussion

The tethered mantises showed foreleg movements similar to those reported in previous studies [2], [5]. The mantis strike consists of two phases: approach and sweep [2] (Figure 2). In the approach phase, the P–C and F–T angles increase. The sweep phase can be further divided into two steps: thrust and capture [6]. During the thrust, the C–T angle rapidly increases; then, the F–T angle rapidly decreases during the capture.

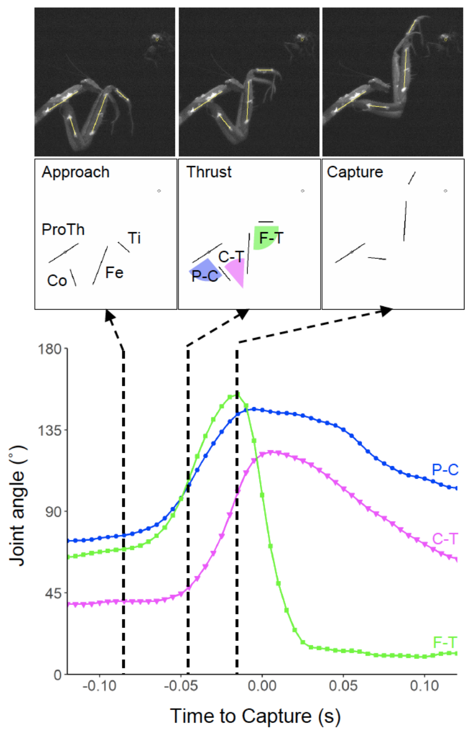

Figure 2: A sample recording of foreleg movements during strike. The prothorax–coxa (P–C, blue circles), coxa–trochanter (C–T, magenta inverted triangles), and femur–tibia (F–T, green squares) angles are plotted as a function of time relative to the capture midpoint. Line drawings above the plot represent prothorax (ProTh), coxa (Co), femur (Fe), and tibia (Ti) at the initiation time of approach, thrust, and capture.

In all of P–C, C–T, and F–T joints, co-activation of antagonist muscles during strike was observed (Figure 3). During slow promoting of P–C joint in the approach phase, a long burst of large spikes was observed in EMG recordings from coxal promotor. The duration of the promotor burst tended to be correlated with the angular increment of P–C joint. The promotor burst was accompanied with a long burst of small spikes of coxal remotor. The remotor burst tended to start earlier compared to the promotor burst when the angular increment of P–C joint is small.

During slow extension of F–T joint in the approach phase, long bursts of both tibial extensor and flexor were observed. In contrast, during rapid extension of C–T joint in the thrust and rapid flexion of F–T joint in the capture, bursts of both extensor and flexor were relatively short.

These results suggested that co-contraction of antagonist muscles is required for the control of P–C, C–T, and F–T joint movements during strike. In a pointing task performed by humans, increasing co-contraction activity presumably improves endpoint accuracy [7]. Thus, co-contraction of antagonists may be one of general solutions when an animal needs to precisely control leg movements.

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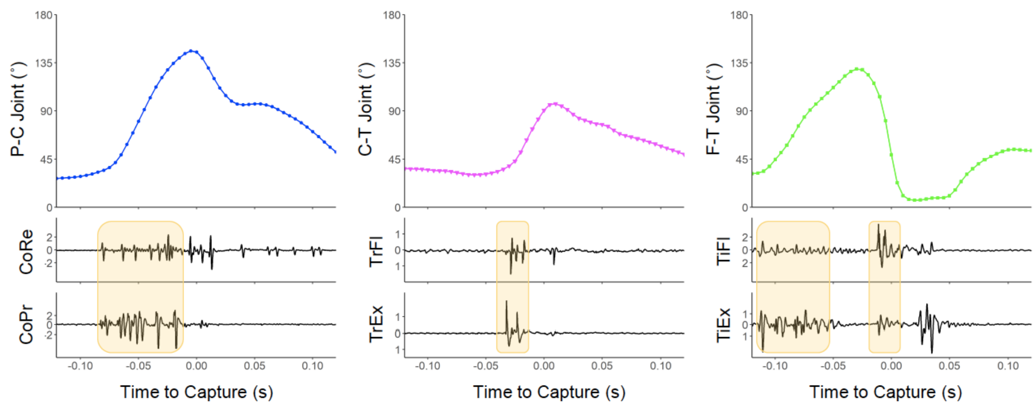

Figure 3: Sample electromyogram (EMG) recordings during strike. The top is a plot of prothorax–coxa (P–C, left), coxa–trochanter (C–T, center), or femur–tibia (F–T, right) joint angle during strike as a function of time relative to capture midpoint. Middle and bottom traces are EMG recordings of the coxal remotor and promotor (CoRe and CoPr, left), trochanteral flexor and extensor (TrFl and TrEx, center), or tibial flexor and extensor (TiFl and TiEx, right), respectively. Co-activation of antagonist muscles (orange areas) was observed for each recording.