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Is CPL Vision in the Peacock Mantis Shrimp an Adaptive Trait?

Peacock Mantis Shrimp (*Odontodactylus scyllarus*) belong to the order Stomatopoda which includes all species of Mantis Shrimp.[A, B] Like many other members of this order they possess a special trait, unheard of in other species to our knowledge, to detect Circularly Polarized Light (CPL). The unique nature of this trait poses questions about the evolutionary story of the Peacock Mantis Shrimp. Scientists studying these species have posed hypotheses as to why this trait might be adaptive and therefore a product of natural selection; some of these hypotheses have been put to the test through experiments. There is, however, always room for more knowledge, and so new experiments are welcomed in the study of this interesting species. Through these efforts we can begin to understand how this remarkable trait came to belong to the Peacock Mantis Shrimp and whether the trait is the result of an adaptive function.

The ability of *O. scyllarus* to detect CPL is an anatomical trait which first requires an understanding of both CPL and the eye anatomy of Mantis Shrimp before one can explore hypotheses as to its adaptive function. The type of light visible to humans is exclusively non-polarized, meaning that the waves oscillate randomly in many directions. Light wave polarization occurs when non-polarized light is reflected, for example on the surface of the water, and the waves oscillate in the same space.[10] This process produces Linearly Polarized Light (LPL) which orients itself either vertically or horizontally.[1] Many species including Mantis Shrimp are known to see and use LPL, but to humans this light appears only as a glare and we use polarized sunglasses and lenses to screen it out.[9] For CPL to occur underwater the LPL is bounced up to the water's surface and reflected back down.[10] Like its name suggests CPL waves oscillate in a circular orientation, traveling in the shape of a helix which rotates either clockwise or counter-clockwise. Scientists refer to clockwise rotating CPL as right handed (R-CPL) and counter-clockwise as left handed (L-CPL), and the distinction between the two can be important in designing experiments to test if Mantis Shrimp can use their trait effectively.[6]

In order to detect CPL Mantis Shrimp like *O. scyllarus* make use of highly advanced eye anatomy.[C] Like other arthropods they possess compound eyes made up of bands of photoreceptor, pigment and support cells known as ommatidia.[7] The areas of the ommatidia that allow some species to detect polarized light are the rhabdoms, each of which consists of seven photoreceptor cells that all have small openings where polarized light enters.[8] What is special to Mantis Shrimp however is a modified midband, the fifth and sixth rows of ommatidia, whose rhabdoms are a little different.[6,7] These modified rhabdoms have a special eighth cell that sits on top of the normal cluster of seven.[2] The eighth cell's opening for polarized light is angled at forty five degrees to the seven below it; it rotates the plane in which light oscillates and converts CPL into LPL for the Mantis Shrimp to be able to see.[8, 9] This special eighth cell (R8) is known as a quarter-wave plate and has a man-made counterpart in CD and DVD players, but remarkably the Mantis Shrimp's biological version outclasses our technological one since it works well even when the wavelength changes.[8] It is also worth mentioning that *O. scyllarus* and some other species of Mantis Shrimp have additional anatomical traits pertaining to CPL. Using imaging polarimeters and polaroid filters to detect CPL patterns scientists have been able to find areas on the telson and antennal scales of *O. scyllarus* that strongly reflect CPL. These areas are known to be used in communicative displays within the species.[2]

It is strange to think that the existence of one little R8 cell is the cause of this unique trait to see CPL, but it helps scientists understand how the evolutionary story of the Peacock Mantis Shrimp may have played out. Nicholas Roberts of the University of Bristol suggests that this advanced eye anatomy was the result of only slight alterations to the existing anatomy and therefore relatively "easy" to evolve.[8] And when we consider the fact that the R8 cell seems to be the only significant difference between CPL sensitivity and CPL blindness in species that can already detect polarization, his suggestion makes a lot of sense. Unfortunately, the nature of this trait does not lend itself to study through the fossil record. The morphological details of extinct Stomatopod species are incompletely known, with little to no surviving eye specimens that could give scientists enough detail to determine CPL sensitivity. However, it is possible in the near future the fossil record could provide clues through different means. Joachim T. Haug led a team studying Mesozoic fossil specimens of Mantis Shrimp that found the telsons closely resembled those of extant species.[5] Informed by what we know about the CPL reflecting scales of *O. scyllarus* we might predict that the trait to detect CPL corresponds on the phylogenetic tree to the trait that produces the CPL reflecting telson. A team led by Megan L. Porter has also begun sequencing the DNA of the opsin coding genes in some Stomatopod species with the hope of tracing the evolution of their complex visual system. Their early results show that these genes are quite distinct from other arthropods, and fairly diverse within Stomatopods. They also suggest that more complex visual systems evolved in species that lived in shallow waters where a broader light spectrum was present.[3] Although they were not searching for the gene, or genes, that produce the R8 cell, the diversity within Stomatopods they discovered is still helpful and could provide more precise information in the future. Because the trait to detect CPL is unique to Stomatopods, but not present in all Stomatopods, the most feasible point of its evolution is located after Mantis Shrimp split from other crustaceans and before the branching off of family Odontodactylidae.

There are two main hypotheses within the scientific community that studies Mantis Shrimp to suggest an adaptive function to this trait.[D] The first hypothesis (Hypothesis A) proposes that the trait to detect CPL aids in intra-species communication. This communication serves sexual selection; therefore an individual with CPL vision will have an increased overall fitness.[1] According to this hypothesis the male Peacock Mantis Shrimp uses it's CPL reflecting scales in the courtship displays for females and aggressive displays for other males that have been observed.[7] If this is true the use of CPL imaging by scientists would show the presence of CPL in these displays.[1] The hypothesis also claims that the need for a CPL line of communication developed because other forms of polarized light can be detected by some of the Mantis Shrimp's predators like cuttlefish, squid and octopi.[9] The CPL line of communication however would be secret. This informs a prediction that Mantis Shrimp would continue to communicate via CPL in the presence of predators. Both males and females would experience an increase in relative fitness for possessing the trait to detect CPL because they are both receiving communicative signals from males, so the trait for CPL detection should be present in both sexes. However, females would not increase their fitness by being able to use CPL reflecting displays themselves, so we might predict an absence of CPL reflection in areas like the telson of females.[1] Of course, Hypothesis A's most important prediction would be that Mantis Shrimp with their ability to detect CPL intact would reproduce more effectively than those with their ability impaired. This expands to include the prediction that if you were to render male Mantis Shrimp's CPL reflecting areas inept those individuals would experience a drop in fitness.

Experiments have been conducted to test the predictions of Hypothesis A. A team led by Tsyr-Huei Chiou studying CPL vision in *O. scyllarus* ran tests using CPL imaging technology by photographing the telson area through both a right and left-handed polarizing filter to determine whether the area was reflecting CPL.[E] They found that males were reflecting CPL in that area for communicative displays. The results also showed that the CPL reflecting areas found on males were indeed absent on females. The same team initially examined the Mantis Shrimp's ability to detect CPL and did not report a difference between the sexes as predicted. [1]

The other predictions have not yet been tested but it's reasonable to assume that experiments can be designed to test them. The prediction that Mantis Shrimp will continue to use their CPL displays in the presence of a predator species could be tested by similar means as the previously described experiment. Male Mantis Shrimp could be prompted to use their CPL displays by being shown another Mantis Shrimp, male or female could provoke a display, and with CPL imaging technology we could record it. Then we could introduce a predator's presence, making sure the Mantis Shrimp isn't in any real danger by placing the predator in a cage that allowed the Mantis Shrimp to see and smell it, and see if the Mantis Shrimp continue to communicate with CPL.

Testing whether Mantis Shrimp with their ability to detect CPL intact reproduce more successfully than those with the trait impaired might require a longer, cross-generational study. Such a study would include comparing groups of CPL detecting individuals with CPL blind individuals of both sexes in their reproductive fitness.[F] Phase one of this experiment would involve four separate populations of *O. scyllarus* in tanks. Tank 1 would be a control group containing females and males that remain CPL sensitive, Tank 2 would contain CPL sensitive females and CPL blind males, Tank 3 would contain CPL blind females and CPL sensitive males, and Tank 4 would contain females and males that are both CPL blind. The reproductive fitness of each tank will be recorded by measuring the number of matings that result in offspring. We might predict that the tanks where communication via CPL is hindered will produce less offspring. Phase two would involve two separate populations; Tank 1 containing a female population that is 100% CPL sensitive and a male population that is 50% CPL sensitive and 50% CPL blind, Tank 2 containing a female population that is 50% CPL sensitive and 50% blind with a male population that is 100% CPL sensitive. This phase serves to measure how sexual competition is affected by CPL communication. In Tank 1 we would record which group of males has more offspring and in Tank 2 which group of females has more, Hypotheses A suggests that CPL sensitive groups of both sexes will have more reproductive fitness.

The other prevailing hypothesis (Hypothesis B) suggests that the adaptive function of the trait for CPL vision is to aid Mantis Shrimp in navigating their environment. CPL is prevalent in the underwater environment which *O. scyllarus* inhabits today as well as in the evolutionary past of the species.[9] Hypothesis B indicates that Mantis Shrimp include CPL vision in their arsenal of advanced eyesight because it helps them see with higher contrast in turbid water where light is being scattered and converted into CPL, making it easier for them to visually separate object and background by distinguishing between R-CPL and L-CPL.[1] This heightened sense of sight corresponds to more precision and a faster response time which increases the fitness of the animal.[10] This Hypothesis predicts that Mantis Shrimp can not only distinguish between R-CPL and L-CPL in their environment, but can also be shown to use this ability to reach favorable outcomes that increase fitness. It also predicts that Mantis Shrimp using CPL vision in murky water, where other aspects of their advanced eyesight are less effective, would exhibit faster response times and more precision in hitting targets.[1]

Two attempts were made at testing the prediction that Mantis Shrimp would distinguish between R-CPL and L-CPL and use the information to their advantage. In 2008 the team led by Tsyr-Huei Chiou conducted an experiment using operant conditioning and food as a reward to see if Mantis Shrimp would learn to associate a particular handedness of CPL with a reward.[G] Cylinders with an end that reflected either R-CPL or L-CPL were used to deliver food. One set of Mantis Shrimp was trained to associate R-CPL with a food reward and the other set learned to associate L-CPL with the reward. Then, when the food reward was no longer present the Mantis Shrimp still chose the cylinders with the CPL handedness they had been conditioned to at a rate significantly above chance.[1] This experiment confirms the prediction, but an earlier attempt did not. In 2006 Justin Marshal, along with others who would also go on to participate in the 2008 study, described a very similar experiment using operant conditioning and the same cylindrical containers. However, the results between individuals varied and did not provide enough evidence for the prediction.[4]

To test the other prediction of Hypotheses B an experiment must be designed.[H] The response time and precision of Peacock Mantis Shrimp hitting targets in turbid water could be recorded by filming their attacks on bait in a tank. This experiment would compare individuals with their CPL vision intact with individuals that have been made CPL blind as they try to grab targets that reflect CPL. It should also include control groups where the same Mantis Shrimp are instead trying to grab a target that isn't reflecting CPL. If the results of such an experiment showed that the individuals with CPL vision outperformed those without, the prediction would be confirmed.

While these two hypotheses are not mutually exclusive, there seems to be more evidence at the moment to suggest the driving force of the trait's evolution was to aid sexual selection as a means of communication as described by Hypothesis A. If only one hypothesis is correct the incorrect one would most likely be Hypothesis B. If both hypotheses are true however we would need to question whether one adaptive function initiated the trait's evolution first or if both adaptive functions worked in tandem. Perhaps if more evidence in support of Hypothesis B arises then more hypotheses need to be proposed that include these options.

The study of this species, and this particular trait, is still relatively young. Luckily for the Stomatopod enthusiasts, CPL technology has practical applications for human life which should keep scientific interest in this trait alive and provide more insights about how it arrived in the Peacock Mantis Shrimp.[10] The hypotheses described thus far all suggest that the trait is the result of natural selection as opposed to other evolutionary mechanisms like drift. With further study we can determine more definitively what evolutionary story is the most feasible and if the trait is indeed adaptive.

Appendix

A.)

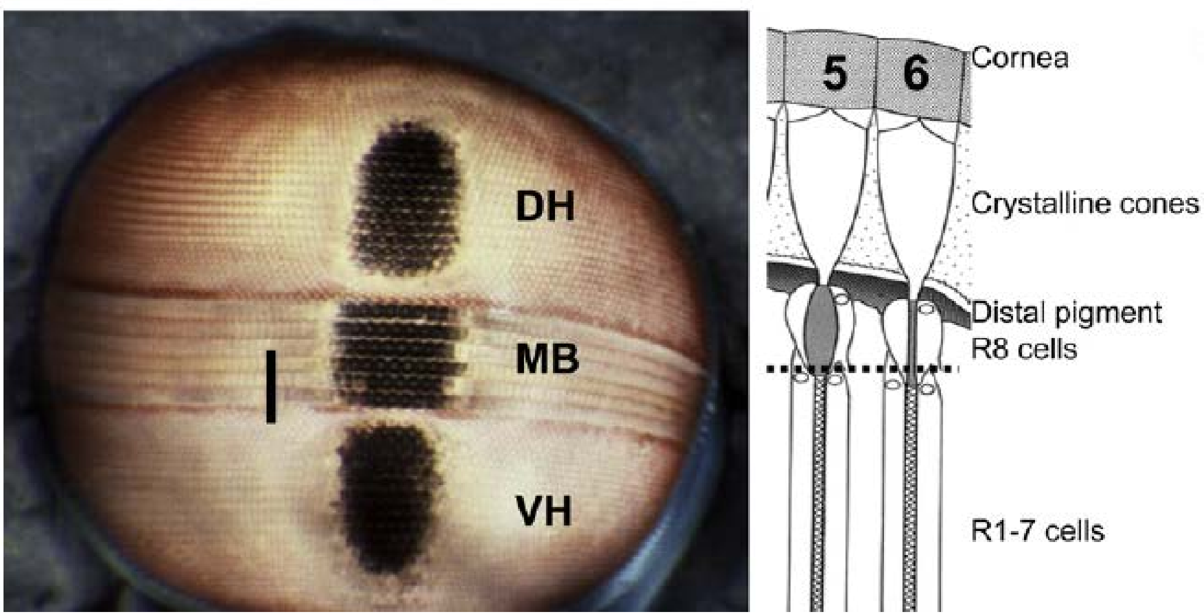
George Grall. 2014. Peacock Mantis Shrimp. National Aquarium. http://www.aqua.org/explore/animals/mantis-shrimp. (Accessed December 14, 2014)

B.)

Classification of *O.scyllarus*

Kingdom, Animalia
Phylum, Arthropoda
Subphylum, Crustacea
Class, Molacostraca
Order, Stomatopoda
Family, Odontodactylidae
Genus, Odontodactylus
Species, Scyllarus

C.) Compound Eyes of the Mantis Shrimp and diagram of rhabdoms.



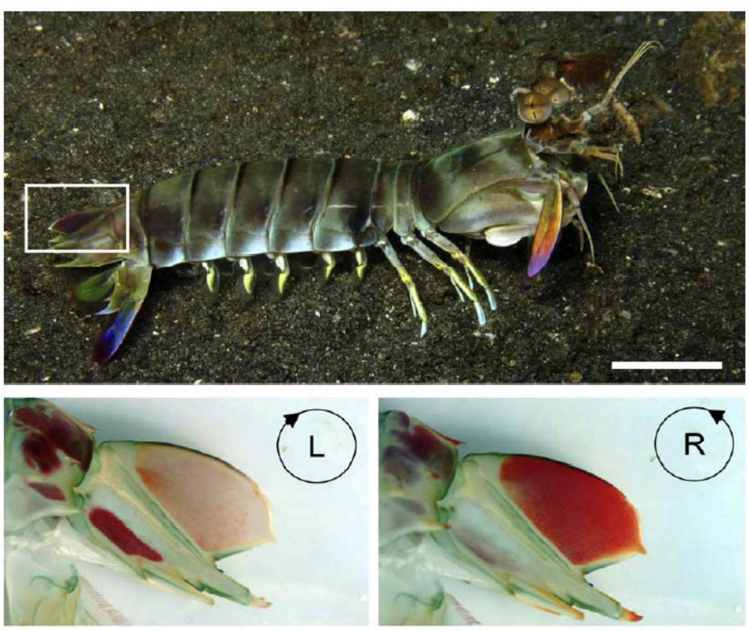
Tsyr-Huei Chiou. 2008. Circular Polarization Vision in a Stomatopod Crustacean. *Current Biology* 18: 429-434.

D.) Table of predictions for each hypothesis

Hypothesis A:	Predictions	
	Tested	Untested
The addaptive function of the trait to detect CPL is to aid in intra-species communication which serves sexual selection.	- Use of CPL reflecting display areas by males in courtship and agressive displays. Confirmed by test. - Trait to detect CPL is present in both sexes. Confirmed by test. - Absence of CPL refelcting display areas in females. Confirmed by test.	- Use of CPL communication displays in the presence of a predator species. Experiment proposed. - Individuals with CPL sensitivity will reproduce more than the CPL blind. Experiment proposed. - Males with CPL reflecting areas blocked would reproduce less.

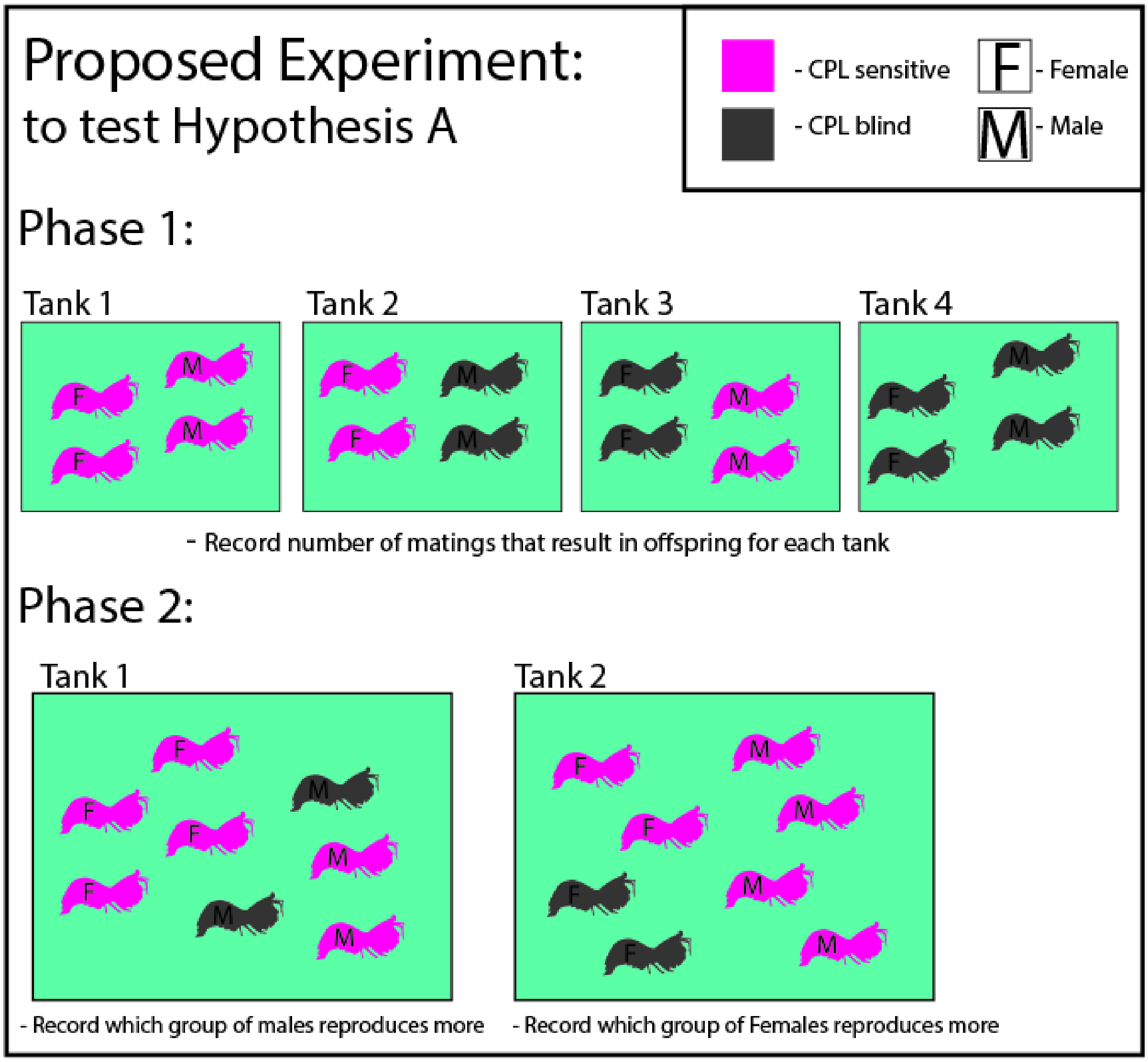
Hypothesis B:	Predictions	
	Tested	Untested
The addaptive function of the trait to detect CPL is to aid in navigating their environment.	- Individuals will be able to distin-guish between R-CPL and L-CPL and can be trained to use this ability to reach outcomes that increase their relative fitness. Confirmed by test.	- Use of CPL vision will correspond to faster response times and more precision in hitting targets. Experi-ment proposed.

E.) Telson area photographed through L-CPL and R-CPL polarizing filters.

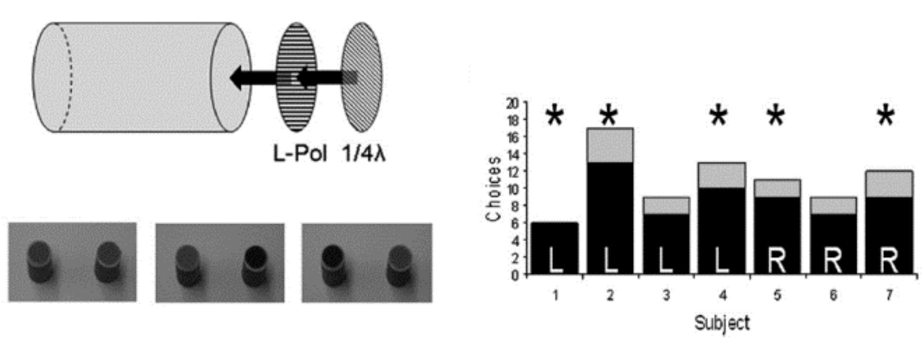


Tsyr-Huei Chiou. 2008. Circular Polarization Vision in a Stomatopod Crustacean. *Current Biology* 18: 429-434.

F.)

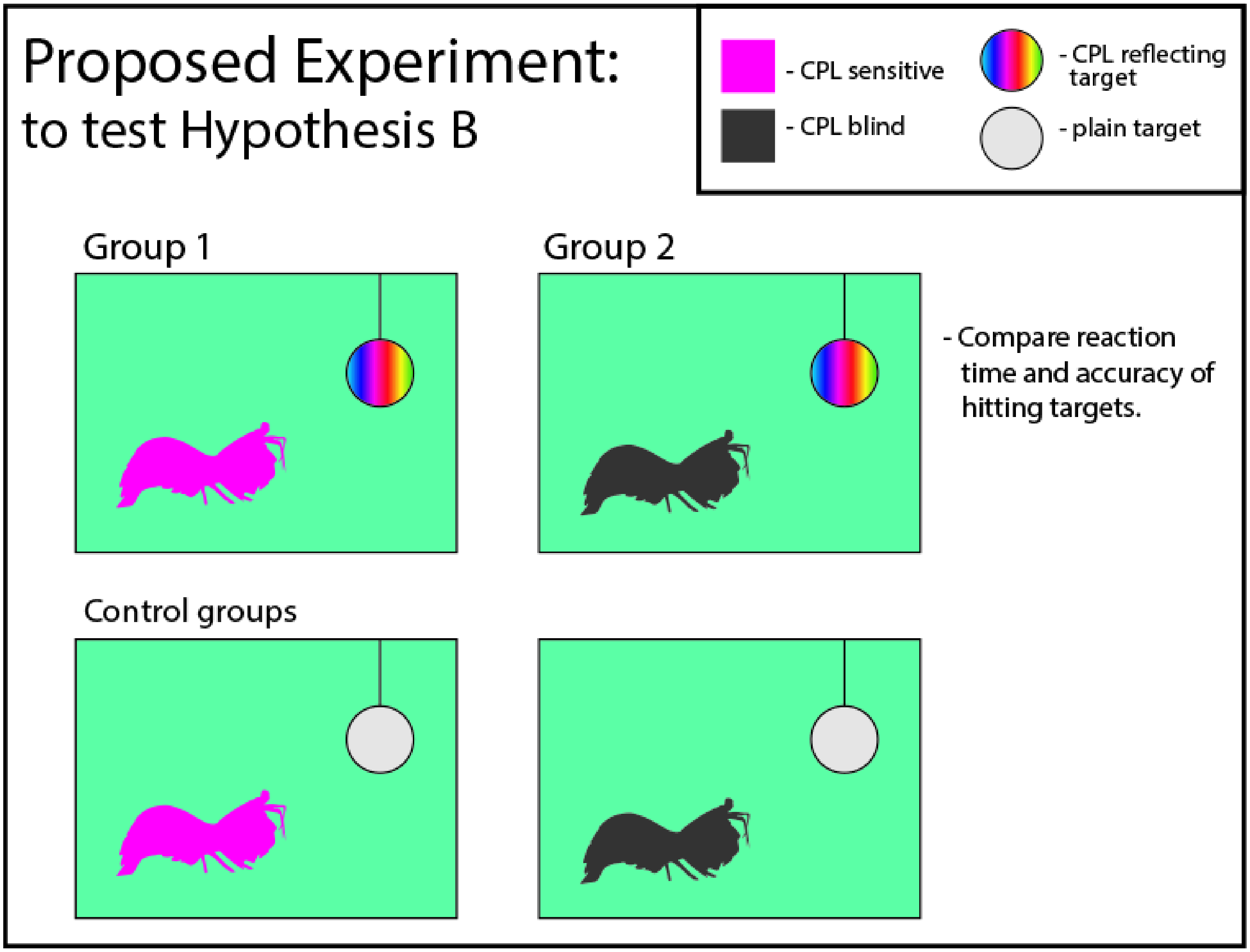


G.) Feeding cylinders shown to the left, results to the right (black bars represent correct choices).



Tsyr-Huei Chiou. 2008. Circular Polarization Vision in a Stomatopod Crustacean. *Current Biology* 18: 429-434.

H.)


Proposed Experiment:
to test Hypothesis B
- CPL sensitive
- CPL blind
- CPL reflecting target
- plain target
Group 1
Group 2
- Compare reaction time and accuracy of hitting targets.
Control groups

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