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Research Article

What Would it Mean if White Sharks, *Carcharodon Carcharias*, Possessed Disconjugate Optokinetic Stimulation?

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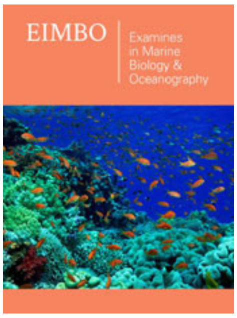

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Abstract

Disconjugate eye movements are a feature of some animal species, but it is unknown whether white sharks, *Carcharodon carcharias*, possess independent eye moments, as well. Here, the question of what it could mean if they exhibited this ability is discussed. Video evidence shows the possibility of independent eye movements with a white shark looking at two distinct targets aimed at them consecutively. Different interpretations of the videos core frames are discussed with disconjugate optokinetic stimulation as the most highly advanced possible explanation of this observation. Such an ability would enable a white shark to scan its entire visual field and confer an advantage in terms of being able to observe two prospective food sources on either side of its head, allowing it to decide which target represents the more likely success. Such a mechanism could help to explain the high success rate of white sharks when hunting down very agile pinnipeds.

Keywords: Behavior; Disconjugate optokinesis; Eye movement; Hunting; White shark

Introduction

The white shark, *Carcharodon carcharias*, a typical apex predator, relies on a keen sense of vision to hunt down agile prey, in particular pinnipeds such as seals and sea lions [1-3]. It follows that a considerable proportion of the white shark's brain would be dedicated to processing visual stimuli to enable efficient hunting [4]. As with other shark species, the eyes of white sharks are positioned laterally, meaning that only one eye at a time can observe an object positioned alongside their bodies, and only when the object is between the overlapping fields of vision could both eyes focus on the same object. So, what potential advantages could white sharks acquire if they were able to move both eyes independently, and so observe two objects on both sides of their heads simultaneously?

Disconjugate optokinesis, the ability to move both eyes independently, is a feature that is known to occur in some aquatic animals. While most bony fishes have yoked or conjugate vision [5-7], some species have the ability to move both eyes independently [5,8,9]. Since sharks' eyes are positioned similarly to those of bony fishes (except for a few species, e.g., the bigeye thresher shark, *Alopias superciliosus*), it is reasonable to assume that their vision is also characterized by conjugate optokinesis. However, optokinesis has not yet been studied in sharks, so it is not known whether their eyes indeed function in a yoked manner.

The concept that white sharks may utilize a mechanism that could employ more independent eye movements stems from video-evidence. In the video, a white shark seems to use both visual axes to observe objects on opposite sides of its body simultaneously, leading to the possibility of disconjugate optokinesis. This potential ability would confer a considerable advantage when hunting, allowing a shark to scan the areas on both sides while, for instance, closely surveying pinniped haul-outs [10-13]. Disconjugate optokinesis would likewise be useful in efforts to prevent kleptoparasitism; the stealing of already immobilized or killed prey by other white sharks [14]. Such advantages would no doubt largely contribute to the effectiveness of a white shark's foraging strategy. It is understood that no firm conclusion can be drawn from this single video, but it offers an intriguing perspective into the potential use and selective advantage of disconjugate eye movement among white sharks.

Methods and Result

The video was captured on November 21, 2017, off the coast of Guadalupe Island, Mexico. An approximately 4m long male white shark can be seen circling a cage positioned at the surface. Bait was also placed on the surface about 5m distant directly opposite from the videographer in the cage. The video was shot with 1080i and 120fps. Where necessary, sequences were analyzed frame-by-frame, using Final Cut Pro X (version 10.4.8) by Apple® and sequential pictures examined at intervals of 1/60 second. The shark's left eye motions were interpreted primarily based on changes in the positions of its lens relative to the outer rim of its eye socket.

Chronology of the encounter

The shark made several passes by the side of the cage facing the videographer, during which it maintained an average relative speed of approximately 0.3 tailbeats/second. During one of these passes that started in a slight ascent, the shark approached, based on its longitudinal axis, in the general direction of the videographer and so seemed to look directly at him. As the shark drew closer, its eye contact with the videographer became confined to the shark's left visual field. Once the shark was closest to the videographer, its left eye was slightly above the videographer's head but stayed fixed on him. As the shark's head started to turn away from the videographer, the left eye, which could not see the surface-positioned bait on the other side of the head, kept focusing on the videographer. The left eye stayed in this fixed position until the field of vision of the left eye could also catch sight of the bait; at that point, that eye moved in a slightly temporo-nasal direction to enable a stereoscopic view of the bait. Since the turn of the head was swift, with only 0.70 seconds elapsing until the shark aligned the entire frontal portion of its body with the bait, the left eye remained on the diver no longer than 0.40 seconds after it began to turn its head. The presented observation can be gathered from the supplementary video.

Discussion

The main driver of an animal's visual system seems to be its foraging ecology [15]. Given the high speed and agility of the animals on which white sharks feed, in particular, pinnipeds [14,16,17], their visual system needs to be highly evolved. Among the strategies that white sharks have developed for attacking such swift prey [14,17,18], their primary preference seems to be to ambush from behind and below [12,16-18]. When a shark is approaching a loose group of pinnipeds, various potential targets may present themselves at the same time on either side of the shark. Thus, in such situations, the shark must decide which member of the group to attack. It could be invaluable to the shark to have the ability to observe potential targets with each eye working independently at the same time, essentially doubling the area that it can survey. First, we discuss the very moment of the video that offers potential evidence that could indeed indicate some form of independent eye movement and debate this possibility from different perspectives. We then look at this potential ability from the viewpoint of how it could enhance a white shark's hunting behavior.

Disconjugate eye movements

The precise moment on the video that indicates the potential existence of independent eye movements is when the shark's head turned away from the diver before the left eye-which was still fixed on the videographer- and was able to see the bait. This very moment indicates that the shark must have been aware of the exact position of the bait, while still looking at the diver with its left eye. The ability to compare two objects in opposite fields of view has been demonstrated in such teleosts as sandlances, *Limnichthyes fasciatus*, and pipefish, *Corythoichthyes intestinalis* [5,6,9]. These species can perform the operation described above, fixing one eye on a stationary object. In contrast, the opposite eye proceeds to follow another stimulus or, in the case of such species as pipefish and goldfish, *Carassius auratus*, moving their eyes independently when surveying their surroundings but in a coordinated fashion when tracking a target [6,19]. Butterflyfishes, *Chaetodon rainfordi*, and red-eared sliders, *Pseudemys script*a, on the other hand, display a more yoked form of optokinesis but can operate their eyes independently during specific responses [6,20].

The observation of a white shark, as seen in the video footage, could be similar to any of the above visual configurations. Another possibility could be that the shark could have shifted its focus alternately between its two eyes. Kirmse [21] suggests during such a shift that the visual input from the less attended eye would gather continuous information until a more conspicuous target within the entire visual field is selected, at which point the animal would adopt binocular vision. However, it is unlikely that visual information from the less attended eye remains unprocessed owing to the blocking or suppression of the fovea, the minute depression in the retina where vision is most acute, as has been observed in other animals, including some bird species [22-24].

Additionally, there is the possibility of cognitive mapping [25-27]. Could the white shark have memorized the exact position of the bait relative to the cage from a distance where both objects were still in its binocular vision, during its first few passes, and then just acted on it? The cognitive mapping may indeed play a role in the chronology of this event, but it would not indicate what the right eye was doing during the encounter with the videographer. At this point, the possibility cannot be excluded that at least some degree of independence between the two shark's eyes could exist, allowing the ability to keep track of two visual targets, one within each of its visual fields simultaneously. The fact that the white shark changed its head direction before the bait entered its left field of vision suggests that its right eye had indeed kept the bait in view, at least peripherally within its functional or retinal visual field [28,29], but possibly on a lower level of processing, until the shark's primary focus shifted [30].

If white sharks did possess disconjugate eyesight, then each eye would also focus independently of the other. This capacity would be especially crucial for tracking objects that are at unequal distances from the two eyes. Focusing on multiple objects in this way would likely be challenging, with the oscillating head movements of the white shark while swimming necessitating gaze stabilization and fixation [31]. However, such a mechanism has already been documented in tadpoles, which compensate for the retinal shifting caused by their form of locomotion through compensatory movements of the eyes and head [32]. Since previous research suggests that sharks prefer to keep their eyes as stable as possible to limit optic flow [7,33], they would thereby obtain the highest resolution possible with the least amount of blur.

Could light intensity also play a factor?

In some regions, white sharks prefer to attack pinnipeds in low light conditions [14,34,35], and several studies have shown that sharks maintain a delicate balance between detectability and visibility when chasing their prey [11,16,36]. Thus, the fovea, where visual acuity is highest, of white sharks consists primarily of the rod photoreceptors that are used in low-light situations [37], likely as a result of this species' adaptation to hunting in such conditions [10,14,35]. Although the reaction time of rods is slower than that of cone photoreceptors, which are used for color vision [38-40], the latter is likely unimportant for this species owing to this hunting preference of dark-colored pinnipeds. Through the use of eyes, and thus fovea, with independent movement, a shark could determine which prey to follow based on improved contrast.

Disconjugate eye movement and white sharks

The success rate of a white shark when attacking fast-swimming prey such as seals is close to 60% during its preferred low-light conditions [35]. This is quite astonishing, considering the agility of pinnipeds. Therefore, it cannot be rejected that this high success rate could be due to the ability to observe more than one potential target and to scan the entire visual field with two eyes functioning independently. In light of the potential existence of disconjugate eye movement in sharks, research should investigate the fitness benefits of this conceivable characteristic, for example, by performing a choice experiment in which two food sources of different caloric values are offered simultaneously to an approaching shark.

Fitness benefits are a constant mechanism in the evolution of animals, so if this phenotype exists, it also must have been a force throughout the evolution of *Carcharodon*. The first species of this lineage likely appeared in the Thanetian period approximately 55 million years ago [41]. Although there is not much known regarding how these early sharks hunted, they already possessed serrated, sawblade teeth, enabling them to feed on early marine mammals, and then seals in the present evolutionary period [42-44]. Considering that the agility of pinnipeds likely improved over time, optimizing eye use in *Carcharodon* to the extent discussed here, could have helped to turn white sharks into the most overpowering super predators among today's shark species.

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References

1. Boustany AM, Davis SF, Pyle P, Anderson SD, Boeuf BJ, et al. (2002) Expanded niche for white sharks. Nature 415 (6867): 35-36.
2. Fallows C, Gallagher AJ, Hammer N (2013) White sharks (*Carcharodon carcharias*) scavenging on whales and its potential role in further shaping the ecology of an apex predator. Plos One 8(4): e60797.
3. Hussey NE, Cann HM, Cliff G, Dudley SFJ, Wintner SP, et al. (2012) Size-based analysis of diet and trophic position of the white shark (*Carcharodon carcharias*) in South African waters. In: Domeier ML (Ed.), Global perspectives on the biology and life history of the white shark. USA.
4. Lisney TJ, Bennett MB, Collin SP (2007) Volumetric analysis of sensory brain areas indicate ontogenetic shifts in the relative importance of sensory systems in elasmobranchs. Raffles B Zool Suppl 14: 7-15.
5. Fritsches KA, Marshall NJ (1999) A new category of eye movements in a small fish. Curr Biol 9(8): 272-273.
6. Fritsches KA, Marshall NJ (2002) Independent and conjugate eye movements during optokinesis in teleost fish. J Exp Biol 205(Pt 9): 1241-1252.
7. Land MF (2015) Eye movements of vertebrates and their relation to eye form and function. J Comp Physiol A 201(2): 195-214.
8. Land MF (1999) Visual optics: The sandlace eye breaks all the rules. Curr Biol 9(8): 286-288.
9. Pettigrew JD, Collin SP, Ott M (1999) Convergence of specialized behaviour, eye movements and visual optics in the sandlance (*Teleostei*) and the chameleon (*Reptilia*). Curr Biol 9(8): 421-424.
10. Hammerschlag NR, Martin RA, Fallows C (2006) Effects of environmental conditions on predator-prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus*) at Seal Island, South Africa. Environ Biol Fish 76(2-4): 341-350.
11. Laroche RK, Kock AA, Dill LM, Oosthuizen WH (2008) Running the gauntlet: A predator-prey game between sharks and two age classes of seals. Anim Behav 76(6): 1901-1917.
12. Skomal GB, Hoyos PEM, Kukulya A, Stokey R (2015) Subsurface observations of white shark *Carcharodon carcharias* predatory behaviour using an autonomous underwater vehicle. J Fish Biol 87(6): 1293-1312.
13. Towner AV, Leos BV, Langrock R, Schick RS, Smale MJ, et al. (2016) Sex-specific and individual preferences for hunting strategies in white sharks. Funct Ecol 30(8): 1397-1407.
14. Martin RA, Rossmo DK, Hammerschlag N (2009) Hunting patterns and geographic profiling of white shark predation. J Zool 279(2): 111-118.
15. Martin GR (2014) The subtlety of simple eyes: The tuning of visual fields to perceptual challenges in birds. Phil Trans Roy Soc Lond B 369(1636).
16. Huveneers C, Holman D, Robbins R, Fox A, Endler JA, et al. (2015) White sharks exploit the sun during predatory approaches. Am Nat 185(4): 562-570.
17. Klimley AP, Boeuf BJ, Cantara KM, Richert JE, Davis SF, et al. (2001) The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. Mar Biol 138(3): 617-636.
18. Fallows C, Fallows M, Hammerschlag N (2016) Effects of lunar phase on predator-prey interactions between white shark (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*). Environ Biol Fish 99(11): 805-812.

19. Easter SS (1972) Pursuit eye movements in goldfish (*Carassius auratus*). Vision Res 12(4): 673-688.
20. Ariel M (1990) Independent eye movements of the turtle. Vis Neurosci 5(1): 29-41.
21. Kirmse W (1990) Kritische übersicht zur selektiven sensomotorik des blickens und multifovealen spähens bei vögeln. Zool Jb Physiol 94(2): 217-228.
22. Engelage J, Bischof HJ (1988) Enucleation enhances ipsilateral flash evoked responses in the ectostriatum of the zebra finch (Taeniopygia guttata castanotis Gould). Exp Brain Res 70(1): 79-89.
23. Hellmann B, Güntürkün O (2001) Structural organization of parallel information processing within the tectofugal visual system of the pigeon. J Comp Neurol 429(1): 94-112.
24. Voss J, Bischof HJ (2003) Regulation of ipsilateral visual information within the tectofugal visual system in zebra finches. J Comp Physiol A 189(7): 545-553.
25. Cain P, Malwal S (2002) Landmark use and development of navigation behaviour in the weakly electric fish *Gnathonemus petersii* (Mormyridae; Teleostei). J Exp Biol 205(24): 3915-3923.
26. Haight JL, Schroeder JA (2011) Spatial cognition in zebrafish. In: Kalueff AV, Michael S (Eds.), Zebrafish Models in Neurobehavioral Research. USA, pp. 235-248.
27. Lee SA, Ferrari A, Vallortigara G, Sovrano VA (2015) Boundary primacy in spatial mapping: Evidence from zebrafish (Danio rerio). Behav Process 119: 116-122.
28. Martin GR, Prince PA (2001) Visual fields and foraging in procellariiform seabirds: Sensory aspects of dietary segregation. Brain Behav Evol 57(1): 33-38.
29. Martin GR, Katzir G (1994) Visual fields and eye movements in herons (*Ardeidae*). Brain Behav Evol 44(2): 74-85.
30. Voss J, Bischof HJ (2009) Eye movements of laterally eyed birds are not independent. J Exp Biol 212(10): 1568-1575.
31. Masseck OA, Hoffmann KP (2009) Comparative neurobiology of the optokinetic reflex. Ann NY Acad Sci 1164(1): 430-439.
32. Combes D, Ray D, Lambert FM, Simmens J, Straka H (2008) An intrinsic feed-forward mechanism for vertebrate gaze stabilization. Curr Biol 18(6): 214-243.
33. Land MF (1999) Motion and vision: Why animals move their eyes. J Comp Physiol A 185(4): 341-352.
34. Fallows C, Martin RA, Hammerschlag N (2012) Comparison between white shark-pinniped interactions at seal Island (South Africa) with other sites in California. In: Domeier ML (Ed.), Global Perspectives on the Biology and Life History of the White Shark. USA, pp. 105-117.
35. Martin RA, Hammerschlag N (2011) Marine predator-prey contests: ambush and speed versus vigilance and agility. Mar Biol Res 8(1): 90-94.
36. Goldman KJ, Anderson SD (1999) Space utilization and swimming depth of white sharks, *Carcharodon carcharias*, at the South Farallon Islands, Central California. Environ Biol Fish 56(4): 351-364.
37. Gruber SH, Cohen JL (1985) Visual system of the white shark, *Carcharodon carcharias*, with emphasis on retinal structure. Mem Calif Acad Sci 9: 61-72.
38. Cao D, Zele AJ, Pokorny J (2007) Linking impulse response functions to reaction time: Rod and cone reaction time data and a computational model. Vision Res 47(8): 1060-1074.
39. Land MF, Nilsson DE (2012) Animal eyes. Oxford University Press, USA.
40. Miloševic M, Višnjic JŽ, Damjanovic I, Nikčevic M, Andjus P et al. (2009) Temporal analysis of electroretinographic responses in fish with rod-dominated and mixed rod-cone retina. Gen Physiol Biophys 28(3): 276-282.
41. Jambura PL, Kindlimann R, López RF, Marramà G, Kriwet J, et al. (2019) Micro-computed tomography imaging reveals the development of a unique tooth mineralization pattern in mackerel sharks (Chondrichthyes; *Lamniformes*) in deep time. Sci Rep 9(1): 1-13.
42. Diedrich C (2011) The world's oldest fossil seal record. Nat Sci 3(11): 914-920.
43. Diedrich CG (2013) Evolution of white and megatooth sharks, and evidence for early predation on seals, sirenians, and whales. Nat Sci 5(11): 1203-1218.
44. Koretsky IA, Barnes LG (2006) Pinniped evolutionary history and paleobiogeography. Mesozoic and Cenozoic vertebrates and paleoenvironments: Tributes to the career of Prof. Dan Grigorescu. pp. 143-153.