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Investigation of visual fields and visually-mediated behavior in the bonnethead shark (Sphyrna tiburo)

Amy L. Osmon
University of South Florida

Investigation of visual fields and visually-mediated behavior in the bonnethead shark (*Sphyrna tiburo*)

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Amy L. Osmon

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Department of Psychology
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Co-Major Professor: Toru Shimizu, Ph.D.
Co-Major Professor: David Mann, Ph.D.
Cynthia Cimino, Ph.D.
Michael Coovert, Ph.D.
Thomas Sanocki, Ph.D.

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Table of Contents

List of Tables

List of Figures

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ABSTRACT

The goal of this dissertation was to further examine the visual system and its importance to the bonnethead shark (*Sphyrna tiburo*). This species of hammerhead shark possesses the least amount of lateral cephalofoil expansion. Better understanding of their visual system and potential visually-mediated behaviors may increase understanding regarding adaptive benefits of their unique head shape. The dissertation revealed four factors regarding this species' visual system: 1) the extent of their optical visual fields span between 68-72 degrees laterally and cover their visual horizon, 2) they possess a fairly large (approximately 112 degree) blind spot directly in front of their cephalofoil, 3) they possess an average of 35 degrees of lateral head movement during sinusoidal swimming which likely increase the lateral extents of their optical visual fields, and 4) they can detect and show interest in small visual stimuli resembling their preferred prey species, the blue crab.

Overview

This project is a continuation of an earlier investigation into the visual system of the bonnethead shark, *Sphyrna tiburo* (Osmon, 2004). The previous study revealed heterogeneity of ganglion cells within the bonnethead retina. A slight increase in retinal ganglion cell density was found, in a fairly central location, running across a portion of the retinal meridian of this shark species. This pattern of increase in the number of retinal ganglion cells along the retinal meridian, termed a visual streak (Bozanno and Collin, 2000; Hueter, 1989) has been found in several other shark species, including the lemon, tiger, epaulette, small-spotted dogfish, blackmouth dogfish, and velvetbelly sharks. However, the increase in ganglion cell density was not sufficient to describe this area as a visual streak in the bonnethead shark, as the ratio of ganglion cells within the band to those outside the band was not as high as those found in other shark species. Within the retina of the lemon shark, the peak ganglion cell density within their visual streak was found to be 1,600 cells/mm^2 as opposed to a minimum of 500 cells/mm^2 outside the streak (Hueter, 1991). In comparison, the peak ganglion cell density within the "band" of higher ganglion cell density in the bonnethead shark was 1270 cells/mm^2 compared to a minimum of 218 cells/mm^2 (Osmon, 2004). Several bonnetheads also appeared to possess a small dorso-temporal area of increased ganglion cell density. As the bonnethead shark

appears to lack a strong visual streak and the dorso-temporal area of increased density was only found in several sharks, there is still much uncertainty regarding the functional significance of its visual system. It is also unknown how the laterally expanded cephalofoil of any hammerhead species, including the bonnethead, may affect vision.

The bonnethead shark is one of eight Sphyrnid species with an unusual hammer-shaped head. The smallest of the hammerheads, it also possesses the least amount of lateral cephalofoil expansion within Sphyrnids (Kajiura et al., 2003). The bonnethead shark cephalofoil shark comprises approximately 18-21% of its total body length as opposed to a maximum of 40-50% for *Eusphyra blochii*, the winghead shark (Kajiura et al., 2003).

An active predator, the diet of the bonnethead is predominantly comprised of blue crabs (Cortes, Manire, and Hueter, 1996; Hoese and Moore, 1958; Motta and Wilga, 2000). The bonnethead shark is also predated upon by larger fish and sharks. Bonnethead sharks are unique within the Sphyrnids as they are specialist feeders on crabs while other hammerheads feed on both fish and rays (Wilga and Motta, 2000). Though smaller than most Sphynrid species, bonnethead sharks are able to keep pace with and capture swift-moving portunids by opening their mouths and “engulfing” the crab (Wilga and Motta, 2000).

The ecology of this shallow water, benthic species has been extensively documented (Cortes et al., 1996; Cortes and Parsons, 1996; Hueter, 1996; Myrberg and Gruber, 1974). Various aspects of this species sensory systems

including olfactory and electrosensory abilities have also been investigated (Johnson and Teeter, 1985; Kajiura, 2003). Along with its small size and capacity to adapt well to captivity, the bonnethead shark is well-suited for an investigation into the relationship between its visual fields, visually-mediated behavior, and how vision, in general, may relate to its lifestyle.

Several hypotheses have been proposed regarding the functional significance of the hammerhead shark cephalofoil. These hypotheses include: increased hydrodynamic capabilities, directional sensitivity of the olfactory sense, expanded surface area for electroreception and olfaction, a broader visual field, as well as an area of binocular overlap behind the shark (Chapman and Gruber, 2002; Compagno, 1984; Johnson and Teeter, 1985; Kajiura et al., 2001; Kajiura et al., 2003; Martin, 1993; Nakaya, 1995, Strong, 1990; Tester, 1963).

The head shape has also been suggested to aid hammerhead sharks in prey handling, as they have been observed using their cephalofoil to pin down batoid prey in order to disable it (Chapman and Gruber, 2002; Strong, 1990). Though several observations of prey handling behavior utilizing the cephalofoil have been documented, this hypothesis has not been investigated under controlled conditions (Gruber and Chapman, 2002; Kajiura et al, 2005).

It appears less likely that the hammer-shaped head of Sphyrnids originally evolved to increase prey handling abilities, but that this behavior may simply be a secondary advantage of the Sphyrnid cephalofoil (Chapman and Gruber, 2002). Sphyrnids are not the only shark species who consume rays, and the diet of any of the hammerhead species is not exclusively composed of rays. Therefore, it is

more likely that the main function of the unique Sphyrnid cephalofoil is in offering some form of advantage in locating or detecting prey. Any advantage in handling prey such as rays is more likely a by-product of the cephalofoil shape.

Other hypotheses yet to be tested include whether or not hammerhead sharks utilize vision in stimulus detection or whether their head shape affects their lateral line sense. The extent of the bonnethead sharks' visual fields, including whether they possess any binocular overlap at the caudal extent of their bodies, and the size and location of the blind spot they likely possess in front of their head will be examined for this project. Information pertaining to this shark's visual fields and visually-mediated behavior may increase understanding of the function of their unique cephalofoil and how the cephalofoil may create a difference in sensory functioning between Sphyrnid and other Carchariniform sharks.

Until recently, sharks, as a group, were assumed to possess poor or nocturnally-oriented vision (Bozzano, Murgia, Vallerga, Hirano, and Archer, 2001; Hart, Lisney, Marshall, and Collin, 2004). However, many shark species possess large, well-developed eyes, which indicate vision may be important in their daily life (Bozzano et al., 2001; Fritsches, Marshall, and Warrant, 2003). Of the shark species investigated so far, most possess a duplex retina, another indication sharks' visual system may play a more prominent role in their survival than previously believed (Hart et al., 2004). Several studies have demonstrated that some shark species are able to discriminate between light and dark, as well as between various shapes, patterns, and colors (Aronson, Aronson, and Clark,

1967; Clark, 1963; Graeber and Ebbesson, 1972; Gruber, 1975; Tester and Kato, 1966; Wright and Jackson, 1964). This further suggests that vision may be important to the daily survival of some species and there is much left to learn regarding their visual capabilities and ecology.

Several shark species are believed to utilize their visual sense predominantly in prey detection, including great white, tiger, and pacific angel sharks. Strong (1990) investigated whether great white sharks would attack specific shapes over others. In 1963 Clark observed that tiger sharks appeared able to visually react to people standing above their tanks. Fouts and Nelson (1999) found that Pacific angel sharks will attack prey based on visual cues over other available sensory information. All three shark species are ambush predators. However, each type of shark consumes different prey species and utilizes a diverse range of prey capture techniques.

The great white utilizes several predatory attack modes, and often attacks from behind or underneath unsuspecting prey (Klimley, 1994; Strong, 1996; Tricas, 1985). Tiger sharks also utilize attack strategies where they ambush unsuspecting prey from below (Heithaus, Dill, Marshall, and Buhleier, 2002). Pacific angel sharks are lie-and-wait predators that hide motionless, just below the sandy substrate and attack prey that swim overhead (Fouts and Nelson, 1999).

Bonnethead sharks are not ambush predators and when patrolling for prey, most hammerhead species are known to swim just above the substrate (Kajiura, 2003). The bonnetheads main prey species is the swift-moving blue

crab. These crabs are found on or just below the substrate and can perform rapid changes of direction when above the substrate. According to Kajiura (2003) large hammerhead sharks appear to rely almost entirely on electroreception to detect prey hidden just below the substrate.

In sharks and electric fish, electroreception and the lateral line sense are believed to be important in several behaviors, including navigation, interactions with conspecifics and other species, as well as prey location and capture (Bodznick, Montgomery, and Tricas, 2004; Combs, New, and Nelson, 2002). The electroreceptive sense is limited, though, by distance, and may not always be able to provide specific information regarding location of stimuli from a distance. The electroreceptive sense of sharks may also be ineffective in definitively identifying a stimulus as prey, as studies have revealed that the behavioral reactions of many elasmobranches are the same to both natural and artificially produced electric fields (Bodznick et al., 2004). The lateral line is thought to be useful in prey detection and localization as this sense is able to identify vortex trails left by marine species as they move, but is also believed to be effective only for short distances (Hueter, Mann, Maruska, Sisneros, and Demski, 2004). If vision is limited or prey is cryptic, these sensory modalities are believed to increase in importance; however, if vision is not limited, then it may be important in detecting potential prey species and predators at a greater distance (Combs et al., 2002).

Therefore, it is feasible that bonnethead sharks may utilize their visual sense when conducting a general search for prey (i.e. prey that are moving along

the substrate) then switch to their electroreceptive or even lateral line senses to locate the exact position of the prey before capture. As the visual sense of any hammerhead shark has yet to be behaviorally tested, what role, if any, it may play in detection of prey or predators remains in question.

Literature review

Visual field organization

Visual fields can be defined as areas within the environment where an animal is able to detect light while their eye(s) are immobile or steady (Beugnon, Lambin, and Ugolini, 1987). Thus, visual fields define the specific regions of an individual animal's environment from which it can collect visual information (Martin and Katzir, 1994). Furthermore, the extent of an animal's visual field can place limitations on visually-mediated behavior by restricting areas of an animal's environment where it can detect visual targets (Martin, 1999; Martin and Katzir, 1994).

There are two types of interrelated, yet separate visual fields in animals: the functional and optical visual fields (Martin, 1999; Martin and Katzir, 1994). The optical visual field is the spatial area of an animal's environment where light can successfully enter an animal's eye (Martin, 1999). The functional (or retinal) visual field is the spatial area of an animal's environment where the animal's retinal receptors are able to detect a visual target and behaviorally respond to that target. The functional visual field is the integration of the visual fields from both eyes (Martin, 1999; Martin and Brooke, 1991).

The size, shape, breadth, and vertical extent of both types of visual fields vary between species (Martin and Katzir, 1999). Dependent on the type of animal, the visual field can be determined by several factors including: the size of their eyes, the mobility of their eyes, eye movements (i.e. saccades, etc.), the location of the eyes within the cranium of the animal (i.e. whether or not the eye is set deep within the eye socket or protrudes from the body), retinal specializations, and the amount of visual information necessary for an animal to locate and capture prey (Collin and Shand, 2003; Martin and Katzir, 1999; Martin, 1999).

Both the extent of as well as areas of the environment encompassed by an animal's visual field are important in maximizing a given species ability to detect potential prey, predators, and conspecifics (Collin and Shand, 2003). The size and shape of the visual field are also species specific, and often reflect areas within the environment that are biologically important to the species in question (Collin and Shand, 2003). The visual field located above an animal's head often differs from the part of the visual field that corresponds to areas below an animal's head (Collin and Shand, 2003). Without knowledge concerning the extent of an animal's visual field, it would be impossible to definitively assess the significance of their visual system, as the areas of their environment they could detect and react to would be incomplete.

The majority of visual field studies have focused on birds (Hayes and Brooke, 1990; Litvak, 1993; Martin, 1996; Martin, 1999; Martin, 2001; Martin and Katzir, 1994; Martin and Prince, 2001; Murphy, Howland, and Howland, 1995).

Studies of avian visual fields have revealed that they are often associated with the visual foraging styles utilized by birds (Hayes and Brooke, 1990; Martin and Katzir, 1994; Martin and Katzir, 1999; Martin and Prince, 2001). Ecological factors also likely to influence the topography of a given species visual fields (Martin, 1999; Martin and Katzir, 1994). According to Martin and Katzir (1999), there are three basic visual field designs corresponding to visual foraging techniques in birds. The first is a sizeable visual field associated with visually capturing prey in their bill (Martin and Katzir, 1999). The second is a visual field that is most expansive above the bird's head and likely used to detect predators above the bird (Martin and Katzir, 1999). The third is a horizontally broad, but vertically narrow visual field with a blind spot behind the bird's head (Martin and Kazir, 1999). This type of visual field is generally found in birds that visually capture prey using their feet (Martin and Katzir, 1999).

The first type of visual field in birds is extensive monocularly, especially dorsally and frontally, and is fairly narrow binocularly (Martin and Katzir, 1999). The bills of birds with this type of visual field are generally centered within their narrow binocular visual field (Martin and Katzir, 1999). Birds possessing this type of visual field topography need precise visual guidance to collect food items with their bills (Fernandez-Juricic, Erichsen, and Kacelnik, 2004; Martin and Katzir, 1999). They usually peck at either quick-moving or stationary objects, or capture quick-moving prey with their beak (Martin and Kazir, 1999). Birds possessing this type of visual field include the reef heron, night heron, rock

pigeon, some species of starling, and cattle egret (Fernandez-Juricic et al., 2004; Martin and Katzir, 1999).

Birds with the second type of visual field generally have an extensive view of the spatial areas above their heads and can either barely detect or cannot see their beak within their visual field (Fernandez-Juricic et al., 2004; Martin and Katzir, 1999). Birds with this type of visual field topography usually utilize touch or chemical information to locate and capture mostly stationary food items, either on the water's surface or just below it (Martin and Katzir, 1999). Since these birds do not need to utilize their visual sense to capture prey, and have extensive visual fields above their heads, the authors believe this type of visual field is dedicated to vigilance against aerial predators (Martin and Katzir, 1999). The European starling is an example of a bird with this type of visual field topography. This species feeds on invertebrates located upon or just below the substrate and is vulnerable to aerial predators when foraging (Martin, 1986). Other birds who possess this type of visual field include the Eurasian woodcock and the mallard (Fernandez-Juricic et al., 2004).

The third type of visual field consists of a horizontally broad, but vertically narrow binocular field of view and a large blind spot behind the head of the bird (Martin and Katzir, 1999). Only one bird has been found to possess this type of visual field, the Tawny Owl (Fernandez-Juricic et al., 2004; Martin and Katzir, 1999). There are three possible behaviors related to this type of visual field topography: detection of prey using acoustical senses, capture of prey with the

owl's feet, and the necessity of a silent approach to capture prey items (Fernandez-Juricic et al., 2004; Martin, 1990).

Few studies have documented or quantitatively measured the visual field of fishes (McComb and Kajiura, 2008). From these studies, it appears the visual fields of fish, like those of birds, are related to either prey or predator detection, as well as possibly related to schooling behaviors in some species. Roundtree and Sedberry (1998) found that visual fields of some teleost fish may be related to their shoaling/schooling behavior to detect and avoid predators. It appears that the broad lateral, and limited frontal and caudal visual fields likely possessed by many schooling fish species, are useful in large schools to detect potential predators (Roundtree and Sedberry, 1998). This idea is called the visual-field overlap hypothesis (Roundtree and Sedberry, 1998). Essentially, shoaling (grouping together in large numbers or a tightly-knit group) allows the visual fields of the group of fish to overlap, and increase the probability that one individual within the shoal will detect a potential predator (Rountree and Sedberry. 1998).

The visual field of a species can also change as it develops, following developmental changes within a species from prey (as a juvenile) to predator (as an adult)(Collin and Shand, 2003). Frogs provide an excellent example of this transformation between prey to predator and how it affects their visual fields. Immature frogs (tadpoles) are often predated upon by other species. During this stage in life, frogs (as tadpoles) possess monocular visual fields within each eye that can take in a large chunk of their aquatic environment (Collin and Shand,

2003; Sivak and Warburg, 1983). The visual field then alters to provide binocular overlap between the eyes when a tadpole becomes a frog (Sivak and Warburg, 1983). This increases their ability to locate and capture their prey (Sivak and Warburg, 1983), as an animal's depth perception increases in conjunction with the degree of binocular overlap (Collin and Shand, 2003).

It is thought that in general, species inhabiting open areas that are regularly predated upon by other animals likely possess a visual field that encompasses a wide swath of their environment (Collin and Shand, 2003). This type of visual field would aid them in scanning a large area of their visual environment for potential predators (Collin and Shand, 2003). The visual field of each eye in predators should generally overlap, as this would provide them with increased sensitivity, depth perception, and acuity to locate and capture prey (Collin and Shand, 2003).

Visual fields and sharks

All sharks have laterally placed eyes which oppose each other within the chrondocranium. This provides most species (depending on head shape) with a large visual field, but possibly little binocular overlap. There are few sharks whose visual fields have been quantitatively measured. However, in the few species where these data exist, the binocular overlap between the eyes appears to be fairly small, if it exists at all (Hueter et al, 2004). Sharks that constantly

swim or move throughout their environment may be able to extend their visual fields via sinusoidal swimming patterns (Hueter et al, 2004).

Hueter and Gruber (1982) revealed that juvenile lemon sharks have approximately eight degrees of binocular overlap in their frontal visual field. Unfortunately, scientific literature regarding the visual fields of Sphyrnidae shark species is lacking. The unusual head shape and eye placement at the extreme lateral ends of the Sphyrnids' head would appear to preclude them from obtaining any degree of anterior binocular overlap and may actually create an extensive blind spot. However, their visual fields, in combination with their sinusoidal swimming pattern, may allow for a small amount of binocular overlap behind their bodies. Though larger hammerhead species are not predated upon by other sharks or animals, smaller hammerhead species, such as the bonnethead shark may be able to use this potential binocular overlap in their posterior visual field for predator detection, as they are often predated upon by larger fish.

Measuring the extent of Sphyrnid sharks' visual fields appears especially important to better understand the organization of their visual system. If they do not possess any overlap between the visual fields of their eyes, this could provide some insight into the function of their visual system. For instance, if the visual fields of the bonnethead shark are broad and laterally expansive, and provide a great deal of information regarding their caudal visual environment, this could indicate vision is important in predator detection. If the visual fields of this shark species are broad and laterally expansive, but provide a wider field of view

to their sides and in front of the shark, vision may be important to prey detection as bonnethead sharks approach their prey while swimming with distinct side-to-side head movements (Parsons, 1990; Wilga, 1998; Wilga et al, 2000). Even if they possess an extensive blind spot within their frontal visual field they could feasibly utilize their visual sense to detect potential prey, at a distance, before striking due to their swimming motion. Use of vision in prey detection may also be indicated by a visual field that takes in more of the environment along the visual horizon and substrate just below the shark than above the shark's head.

The distinct swimming motion of the bonnethead shark may allow them to get the most out of the placement of their eyes within their unusual heads. For instance, they may be able to visually sweep across side of the visual environment in front of them while simultaneously scanning a large area of the visual environment behind them on the opposite side of their body. Thus, due to their continuous swimming motion, they may be able to continuously sample a large area of their frontal and caudal visual environment and detect potential prey species and predators at the same time.

Ram-feeders such as the bonnethead shark swiftly approach and scoop their prey into their mouth (Wilga and Motta, 2000). Therefore, electroreception is likely the most important perceptual system used to pinpoint prey items at close range for the bonnethead shark due to its feeding style and its preferred prey species (Kajiura, 2003; Wilga, 1998; Wilga and Motta, 2000). The electroreceptive sense of the bonnethead shark appears to only be effective within a short range, from around 10-22cm (Kajiura, 2003). Thus, vision could

potentially be utilized to locate prey roaming above the substrate at a distance, but not at close range, for example, in the moments just prior to capture, due to the location of the bonnetheads eyes within their laterally expanded cepahofoil.

Information regarding the visual field of this species and how this species behaviorally reacts to visual stimuli will increase understanding of their visual ecology. All three of these factors, shape and size of the visual field, recognition or reactions to visual stimuli, and estimates of visual acuity are imperative to understanding the significance of the visual system and visual activities of a given species (Watanuki, Kawamura, Kaneuchi, and Iwashita, 2000). Assessment of the possible role of vision in prey location or predator detection, the extent of the bonnethead shark's visual fields and their reaction to visual stimuli was evaluated.

Significance of visual fields and retinal topography

How photoreceptors and ganglion cells are distributed across the retina help set the limits on a species' visual sensitivity and resolution (Fritsches et al., 2003; Hueter et al, 2004). Visual pigments, rod to cone ratios, type of photoreceptors, and the topography of both photoreceptors and ganglion cells within the retina all provide clues as to the importance and role of a given species visual system (Bozzano et al., 2001). The spatial topography of photoreceptors and ganglion cells has been documented for several shark species (Bozzano and Collin, 2000; Hueter et al, 2004). Mapping retinal cell topography can help

delineate what areas of an animal's environment may be visually important to them (Collin and Shand, 2003; Pankhurst, 1989). For instance, tiger sharks possess an increase in retinal ganglion cells along their retina, just below the retinal meridian (Bozzano and Collin, 2000). This suits their predatory technique of attacking prey, such as seabirds from below (Bozzano and Collin, 2000). Though sharks do not possess an all-cone fovea, some possess adaptations within their retinal topography that likely increase their visual resolution within visually important areas of their environment. These adaptations include visual streaks and area centrales (Hueter et al, 2004).

The visual streak is an area of increased retinal cell density, usually located along the retinal meridian. This area subtends the visual horizon for the animal. Area centrales are small areas of increased retinal cell density that subtend areas of the animals visual environment where prey or predators are likely to be detected. Both types of retinal specialization are thought to increase visual resolution in areas where prey or predators are likely to be found within the animal's visual environment.

The visual streak is thought to be an adaptation for animals living in two-dimentional environments (Bozzano and Collin, 2000; Hueter et al, 2004). Examples of these types of environments would be aquatic animals living along the substrate, where their visual horizon would consist of the water/substrate boundary or at the surface of the water, where there would be an air/water boundary. Shark species that have been found to possess strong visual streaks include the tiger shark, lemon shark, and horn shark (Bozzono and Collin, 2000;

Hueter et al, 2004). The lemon shark and horn shark spend most of their time near the bottom and the tiger shark often hunts near the water's surface.

Concentric retinal areas (or area centrales) are thought to be used to increase the visual resolution with a limited area of an animal's visual environment (Bozzano and Collin, 2000; Hueter et al, 2004). Animals with concentric retinal areas are often found in three-dimentional environments such as reefs (Hueter et al, 2004). Whether the animal is a more sedentary ambush predator as opposed to an actively moving predator that chases swift-moving prey may also influence whether or not it possesses a visual streak or concentric retinal area (Hueter et al, 2004).

Factors that influence retinal cell topography include eye size, size of pupil, shape of pupil, where eyes are located within the head of a given species, mobility of eyes, how far they extend beyond the head, the amount of binocular overlap the species possesses, as well as the extent of the visual field of a species (Collin and Shand, 2003). Eye movements while scanning the environment do not change the extent of an animal's visual field (Collin and Shand, 2003). However, the binocular overlap possessed by an animal can change due to eye movements, as eye movements can slightly expand the visual field by taking in more of the environment (Collin and Shand, 2003).

Visually-mediated behavior

Species are often categorized into which sensory modality they are thought to predominantly rely on, such as being a visual, tactile, or electrosensory predator (Moller, 2002). Though all fish possess a lateral line, some species also possess an electrical sense. Both the lateral line and electrosensory systems of fish are thought to play similar roles in behavior, such as detection of prey, predators, and/or conspecifics as well as in social interactions (Bodznick et al., 2004; Moller, 2002). Depending on the species, olfaction is thought to be utilized in prey detection and location, as well as mating and social interactions, and vision in prey and predator detection, prey location and capture, and social interactions including schooling behaviors (Bozzano et al., 2001; Combs et al., 2002; Moller, 2002). However, in many marine species, such as sharks, where the conditions of their environment are subject to change, the ability to integrate information from a number of these sensory modalities would likely be valuable (Boznick, 1991). For instance, if a given animal relies heavily on one sensory modality, it may not provide information necessary for the animal to determine whether a stimulus is a prey item (Bodznick, 1991). However, integration of stimulus details from several sensory modalities may provide the necessary information for the animal to definitively identifying a stimulus as a prey item as well as locating and capturing it (Boznick, 1991).

Behaviorally, the visual sense of some shark species has been investigated utilizing both classical and operant conditioning as well as

manipulations of variables within a shark's natural environment (Clarke, 1967; Gruber, 1975; Fouts and Nelson, 1999; Hueter et al, 2004; Wright and Jackson, 1964; Rowland, 1999; Tester and Kato, 1965). Aspects of sharks' visual sense that have been tested using conditioning techniques include light/dark discrimination, adaptation to the dark, critical flicker fusion rate, and color sensitivity (Clarke, 1967; Gruber, 1975; Hueter et al, 2004). Results of these studies have shown that sharks learn quickly, are able to see in both bright and dim conditions, and can discriminate between colors and patterns (Hueter et al, 2004). For instance, lemon sharks are capable of discriminating between high contrast patterns, including horizontal, vertical, and oblique bars (Gruber, 1977).

Though observers in the field have anectodotally reported that sharks appear to use vision during prey capture (Hueter et al, 2004; Klimley, 1994; Strong, 1996), relatively few investigations have been conducted to confirm whether this is true (Fouts and Nelson, 1999; Hueter et al, 2004). The Pacific angel shark, an ambush predator, is the only shark known to definitively use vision to capture prey. Fouts and Nelson (1999) revealed this shark's use of vision by testing them in their natural environment while holding other sensory modalities constant. Great white sharks are also reported to use vision when approaching prey (Klimley, 1994; Strong, 1996). Field studies investigating the great white sharks' preference for different shapes, such as squares or oblong shapes (i.e. surfboards) are intriguing; however, whether the sharks also used olfaction, electroreception or their lateral line senses was not controlled for in these studies (Hueter at al, 2004).

In regards to the lateral line system of fishes, there are two types of sensory receptors: canal and superficial neuromasts (Montgomery, Macdonald, Baker, and Carton, 2002). Where superficial neuromasts appear to be involved in rheotaxis, the canal neuromasts seem to be useful in detecting the hydrodynamic trails cast off by movement of marine species (Montgomery et al., 2002). Depending on the fish, information from canal neuromasts within the lateral line appears to be the predominant sensory modality for prey detection and capture, or information from the canal neuromasts is integrated with information derived from the animal's other sensory modalities (Montgomery et al., 2002). In non-elecctric fish with poor vision or whose habitat is dim or turbid, the lateral line is likely to be heavily relied upon for prey detection and capture (Montgomery et al., 2002). In fish species with fair or good vision living in habitats with a fair amount of light, the lateral line system likely works in tandem with the visual system to provide detailed information that allows for prey detection and capture (Montgomery et al., 2002). Information obtained from the lateral line is likely only useful in providing an animal with information regarding the general location of a given stimulus at long range (Montegomery et al., 2002). Regardless of whether the visual system of a given species is more sensitive or possesses high resolution, is likely more useful in providing the location of a given stimulus at a longer range (Montgomery et al., 2002). Therefore, integration of information from both sensory modalities would confer an advantage on an animal in both detection and location of a stimulus (Montgomery et al., 2002).

An investigation comparing the visual system of reef fish with different predatory behaviors and periods of activity revealed that most predators, especially carnivores, possess larger eyes than non-carnivorous fishes (Pankhurst, 1989). Though visual acuity was estimated and not behaviorally tested within this study, acuity estimates appear to show that nocturnal species generally had vision with higher sensitivity and diurnal species possessed higher visual acuity (Pankhurst, 1989). Visual sensitivity and acuity was varied in species whose activity period was considered to be crepuscular, thus the visual systems of these fish were likely adapted to their feeding mode and preferred prey species or the activity period for these animals is incorrect (Pankhurst, 1989). Pankhurst (1989) believes that in general, the visual system of many reef fish appears to be primarily influenced by feeding behavior as opposed to period of activity.

Bozzano et al. (2001) revealed that use of vision to locate prey may not involve high visual acuity in some shark species, especially those feeding on large prey items or who consume swift-moving prey species (Bozzano et al., 2001). Instead, visual sensitivity (i.e. to movement) may be more important to prey location (Bozzano et al., 2001).

Vision may also be useful to some shark species for predator avoidance, if not for detection of prey. The ability to escape predators may depend on a variety of parameters, including distance-time variables (i.e. speed, acceleration, maneuverability, timing, and trajectory of escape) (Domenici et al, 2004). In this respect, vision may be important to smaller sharks, either as the primary means

of detecting potential predators, or in addition to information from other sensory modalities, to elicit a rapid escape response to a potential predator. Bonnethead sharks have been observed to dart away quickly from larger approaching stimuli (Myrberg and Gruber, 1974).

The fact that many sharks possess distinctive markings and coloration is indicative that vision may be important to them in recognizing conspecifics or other shark species, and therefore be important in social behavior (Myrberg, 1991). Sharks such as hammerheads and some carcharhinids appear to utilize postual displays, likely for some type of social communicative purpose (Myrberg, 1991). The distinctive markings possessed by some of these species may also serve to make their postural displays more salient (Myrberg, 1991).

According to Myrberg (1991) if these markings play a role in social interactions, it would have to be at close to mid-range distances. No studies of any shark's visual system have proven that their visual acuity would allow them to recognize these types of details at a distance. At extremely close distances, these markings may not be as useful in informing conspecifics of the shark's individual attributes as information the conspecifics receive from multiple sensory systems (Myrberg, 1991). However, distinctive markings may help to emphasize any postural displays performed by a given shark (Myrberg, 1991). These markings do not appear to be sexually dimorphic, therefore, they likely do not play a role in sex recognition (Myrberg, 1991). The markings could also be useful for species recognition (Myrberg, 1991). Regardless of size, there appear to be definite species-dependent dominance hierarchies among sharks (Gruber

and Myrberg, 1974; Myrberg, 1991). Therefore, possession of distinctive markings could aid sharks in quickly recognizing other species.

Johnson and Teeter (1985) investigated the orienting behavior of bonnethead sharks to olfactory stimuli. They found that bonnethead sharks were able to distinguish between differing odor intensity between their nares (Johnson and Teeter, 1985). Though they found that bonnethead sharks would readily react to (i.e. orient toward) an olfactory stimulus in a tank, from the shark's behavior, it appeared that other sensory modalities were also being utilized to hone in on the location of the olfactory stimulus (Johnson and Teeter, 1985). They believe that these sharks appear to readily orient toward an olfactory stimulus, however, in open water an olfactory stimulus likely dissipates before the shark is able to definitively locate the source (Johnson and Teeter, 1985). Therefore, other sensory modalities are likely useful, in combination with olfaction, to locate the source of an olfactory stimulus (Johnson and Teeter, 1985).

Like other shark species, bonnetheads have a mobile pupil, which may allow them to hunt in both bright and dim light (Hueter et al., 2004). As bonnetheads are active predators, they may not need vision with high acuity, but instead require high sensitivity to aid them in detecting prey. It is thought that more sedentary sharks, such as the nurse shark and angel shark, may possess vision with higher acuity than more active sharks as the need to adjust to constant motion within their environment is lacking (Hueter et al., 2004).

Evidence indicates that vision may potentially be more important than previously believed in some shark species (Hart et al., 2004). This project tested the potential importance of vision in bonnethead sharks in prey detection at ranges over one meter (beyond their electroreceptive range). While information from studies of a given species morphology and physiology are often used to provide insight as to their behavior, any assumptions regarding behavior from these types of studies should be broad, and not specific in scope (Gruber and Myrberg, 1977). As so little in known regarding the behavior and ecology of sharks and elasmobranches in general, data from this study has pinpointed specific areas of future research that should provide a better understanding of the significance of the hammerhead cephalofoil as well as how the bonnethead shark interacts with its environment.

Methods

Determination of the visual field

Horizontal and vertical optical visual fields were assessed to uncover areas of the environment with biological importance to the bonnethead shark and determine the extent of the blind spot located directly in front of their cephalofoil.

Six sharks caught by line in shallow waters of Tampa Bay were immediately stored in ice. Morphometric measurements of each shark's head were recorded (to the nearest cm) including the width and length of the head (from from eye to eye and from the tip of the rostrum to the anterior edge of the cephalofoil), length and width of eye area at the extreme lateral extent of the cephalofoil, eye diameter, and total length of the sharks. This created reference landmarks for the visual field estimate.

A flat surface 180 degrees in diameter, separated via markings on the edges into sections from 0 to 90 degrees on either side was used to measure the extent of the shark's lateral visual fields. This apparatus was secured upon a level device, just below the ventral length of the shark's eyes. Zero degrees on the measurement surface was placed in tandem with the exact midpoint of the shark's eye, to ensure accurate readings of the extent of the shark's optical

visual field. Eyes were marked to represent the top and frontal leading edge. Once the measuring surface was leveled and positioned correctly, a thin rod held on a level device was used to measure the extent of the shark's lateral visual fields by placing the rod at the extreme edges of the pupil opening. Readings from the extreme edges of each pupil were recorded to determine the maximum extent of the shark's visual fields by marking the visual degree to which light would be able to enter the eyes horizontally and vertically. Thus, the number of degrees behind and in front of the shark that light is still able to reach into the eye and land on the retina was estimated.

Data analysis

Data from measurements of the visual fields were recorded for each shark and averaged together to provide an estimate of their visual field. This estimate was then utilized to create a graphic of this species' visual field. The extremes of the shark's visual fields were determined by observing the extent where the rod could enter the eye through the pupil.

Assessment of how lateral head movement influences the visual field

Lateral head motion during normal swimming behavior was assessed to ascertain how it affected the visual fields of bonnethead sharks.

Video of swimming patterns from six adult sharks (three male, three female) was analyzed frame-by-frame with MotionPro software to discern the degree of lateral head movement during swimming. This software normally measures the angle of a golfer's swing, but was used to measure the angle and degree of head movement during the bonnethead shark's normal swimming patterns for this project.

The sharks were recorded swimming normally in a 10 feet diameter tank from above. Video of the sharks was taped at Mote Marine Laboratory and Aquarium for this study. Only video showing the sharks swimming in a straight-forward trajectory was used for analysis. The length, width, and morphometric head measurements were recorded for each shark used in this analysis.

To ensure accuracy of the MotionPro software, video of three of the sharks were re-analyzed using clear plastic material centered at the top and sides of the computer screen. Frame-by-frame tracings of the sharks head were made on separate pieces of the transparent plastic material and then overlaid with each other for each shark and the angle of head movement was manually measured with a protractor.

Data Analysis

The degree of lateral head movement from center (when the shark is moving forward in a straight position) to both the left and right was

measured using MotionPro software and traced. The degree of lateral head movement for each shark was averaged to provide an estimate of the general degree of lateral head movement that occurs normally in the bonnethead shark while swimming.

The degree of head movement was mapped over a schematic drawing/picture of their estimated visual fields (from study #1); to assess the degree to which swimming patterns of this shark affects their visual fields. This also provided an estimate of how the visual field of this species is affected by their swimming patterns.

Visually-mediated behavior (prey detection and localization)

Reactions to a number of individual sensory stimuli (visual, electroreceptive, and olfactory) and combinations of these stimuli were assessed to reveal whether bonnethead sharks are capable of detecting small visual stimuli as well as to reveal whether vision may be useful in predatory behavior.

Behavioral control video

Sharks were videotaped swimming alone as well as when feeding on typical prey items (pieces of herring) placed into their tanks. Filming the sharks in several situations helped to discern typical swimming patterns from those associated with feeding behaviors. This video was

utilized to assess how behavioral reactions to test stimuli should be scored.

Scoring of behaviors included analysis of tail beat frequency, the amount of time spent within each quadrant of the tank (quadrant containing the stimulus, an empty stimulus box, or one of two empty quadrants); and whether or not the shark reacted to the stimulus. When a shark tightly circled and/or bumped the box containing the stimulus it was scored as a "reaction" to that stimulus.

Test subjects

Two groups of composed of three sharks each were tested in late August and late October. Sharks utilized for the study were caught in gillnets within Tampa Bay with the assistance of Mote Marine Laboratory and Aquarium. Sharks were then placed into small tanks on the boat and taken immediately to Mote Marine Laboratory and Aquarium where they were placed in a 10 foot diameter holding tank and allowed to acclimate to the tank for several weeks before behavioral testing began. Sharks were hand fed herring every other day post-testing. Sharks had been food deprived the day previous to testing to ensure motivation.

Tanks and equipment

Two tanks, both 10 feet in diameter were utilized for this study. Both tanks had filtering mechanisms that provided continuously flowing seawater. One tank was used as a holding tank, the other as the testing tank. Before testing, all sharks were kept in the holding tank where they could freely swim.

The testing tank had a 0.5 X 0.5m grid on the bottom (for reference regarding time spent in different areas of the tank during testing). The grid was created using brightly colored waterproof tape attached to the bottom of the tank. A video camera was placed over the center of the testing tank, providing a view of the entire tank. Data analysis was conducted using video of each testing session. Two plexiglass boxes, specially made for testing were dropped into the tank during trials. One of the boxes contained the stimulus and the other was empty. The plexiglass boxes were set in opposite (diagonal) sides of the tank, and which box contained the stimulus for a given trial was chosen at random to alleviate any potential place-specific confounds in the shark's behavior.

Several types of plexiglass boxes, made for each type of testing stimulus were utilized. For visual stimuli, testing boxes were transparent and able to be sealed to prevent any olfactory, electrosensory, or hydrodynamic cues during testing. For olfactory cues, the boxes had large holes drilled into them to allow the olfactory cue into the tank and

were blacked out with light colored tape that blended with the color of the tank, to alleviate any extraneous visual cues as to the stimulus. The olfactory stimulus was cut sections of raw herring, the fish species the sharks were fed. A third set of transparent plexiglass boxes with large holes drilled into the sides were used for different combinations of visual and olfactory stimuli. The stimulus boxes for trials using electrosensory stimuli were similar to those used for the visual stimulus condition, however these boxes had insulated cables attached to them containing a dipole used to emit the electrical stimulus. All stimulus boxes were weighted using lead sinkers so that they were not be able to be knocked over when a shark attempted to bite or bump them.

Stimuli

Visual

A latex replica of a blue crab, the predominant prey species of the bonnethead shark, was utilized for the visual stimulus. The latex crabs were weighted with lead sinkers to prevent them from floating to the top of the stimulus boxes.

Olfactory

The olfactory stimulus consisted of 5-7 pieces of raw herring, the fish species sharks were fed while in captivity. The herring was cut and prepared several minutes before testing and placed into the stimulus boxes and sealed before the boxes were placed into the tanks to prevent the herring pieces from being accessible to the sharks.

Electrosensory

Two cables connected to a nine-volt battery, based on the design used by Kajiura and Holland (2002) were utilized. This dipole formed a circuit that ran through the sea water contained in the tank and were grounded to assure that the voltage emitted from them was confined to the stimulus boxes and not distributed throughout the testing tank. Additional resistance was added after testing the first shark group, as reactions of this group suggested strength of the electrical output from the dipoles was too strong. Wires protruding from the dipole were 2cm in length, were located 1cm apart from each other, and utilized a resistance of 1 mega-ohm for the first group and 2 mega-ohms for the second group. The dipole was controlled by the experimenter and emitted pulsed electrical signals via touching wires controlling the diploes to the nine-volt battery. Temperature readings averaged 30°C for the first group of sharks tested

and 23°C for the second group. Salinity was recorded as 34.3psu and 32.9psu, respectively for the first and second shark groups tested.

Pre-Testing procedure

Each shark was placed into the testing tank and allowed to acclimate for five minutes for each pre-testing session. Then both testing boxes were lowered into the tank and left for 15 minutes. This helped to discern the time needed for the sharks to acclimate to the tank change as well as assess how long they would react to the stimuli during testing. During the acclimation period, the sharks were observed for signs of stress, such as high-speed swimming or bumping into the tank walls. On average, it took around three minutes before signs of stress disappeared. Once the sharks were acclimated to the tank, testing trials began. Videotaping commenced after sharks were placed within the test tank and the pump was turned off to aid in clarity of video images.

Testing procedure

Sharks were tested individually and were food-deprived for one day prior to testing to ensure motivation to capture prey (Johnson and Teeter, 1985). Just prior to each testing session, an individual shark was placed into the testing tank and allowed to acclimate for three to five minutes.

After the period of acclimation, a stimulus was placed into one of the stimulus boxes and both boxes were lowered into the tank via 30 pound fishing line using a PVC arm. The fishing line was threaded through the open center of the PVC pipe to allow the researcher to not be visible to the sharks during test trials.

For each trial, one of the stimulus boxes contained the sensory cue used for testing; which box the sensory cue was placed in before testing was randomly chosen. The stimulus boxes helped to prohibit the test subjects from detecting any other sensory cues besides the sensory cue(s) being tested. The shark was allowed to react to the stimulus or stimulus combination for 12 minutes. After the 12 minute time limit was over, the shark was placed back into the holding tank. A period of at least 15 minutes passed and the pump was turned back on before the next shark was placed into the testing tank to allow any traces of stimuli from the previous testing session to dissipate. The filtering mechanism was also turned on again after the sharks were removed from the test tank to allow traced from the previous testing session to dissipate.

Each type of sensory stimulus (visual, olfactory, and electroreceptive) was tested individually and in combination with each other. The stimulus or combination of stimuli that was utilized on a given day was randomized. Eight sensory conditions were tested: visual stimulus only, olfactory stimulus only, electrosensory stimulus only, visual plus olfactory stimulus, visual plus electrosensory stimulus, visual plus

olfactory and electrosensory stimulus, olfactory plus electrosensory stimulus, and one condition used a live blue crab. Pre-test trials using each experimental condition were conducted once for each shark in the first group of sharks tested to ensure the stimulus and test apparatus were sufficient to yield results.

The free-moving, live crab trials all took place on the last day of testing due to the difficulty in maintaining a live blue crab over a period of eight to ten hours within a small container.

Data analysis

The behavioral reaction of each shark to each stimulus during the 12 minute testing period was filmed. Video of each trial for individual sharks were analyzed frame by frame. Stimuli were lowered into the tank during testing sessions when the shark was in the exact center of the tank or on the opposite side of the tank from the stimulus or fake stimulus quadrants. After the stimulus boxes were placed into the tank the sharks were monitored via video to assess their reaction to the stimulus. The reactions were also re-analyzed and graded during frame-by-frame video analysis after completion of the trials. The behavioral reaction to each stimulus was assessed as positive if the shark spent a significant amount of time within the stimulus section of the grid compared to fake and other (empty) quadrants. The stimulus section of the grid was defined as the

square section of the grid that contained the stimulus box. The behavioral reaction was assessed as negative if the shark did not spend a significant amount of time within the stimulus section of the grid. Increases in turning behavior, (whether the shark tightly circled and attempted to bite or strike the stimulus), as well as how much time was spent investigating the stimulus (i.e. the amount of time spend in the stimulus grid section) were recorded.

Two groups of sharks were tested over a period of two weeks (each group of sharks was tested every other day for approximately one week). The first group contained two males and a female and were tested every other day from August 13th through August 18th. The second group of sharks contained two females and a male and was tested from November 27th until November 30th.

Results for each of the eight conditions for both groups were analyzed over the duration of each trial post-stimulus introduction and over trial durations, broken into thirds. The trials were broken down to assess whether the sharks were more reactive to the stimulus conditions within the first few minutes of each trial and less reactive over the duration of each trial. Results of the time spent in each quadrant were transformed into percent time spent in each quadrant for graphical purposes. Raw data regarding time spent within each quadrant was analyzed via SAS in a split plot factorial and the resulting data was then re-analyzed using two-tailed T-tests to assess significance.

Quadrants within the test tanks were defined as: “stimulus” quadrant (contained the trial condition stimulus), “fake” quadrant (contained the empty stimulus box), and “other” quadrants (empty quadrants). For analysis, the two empty quadrants (“other” quadrants) times were combined and averaged to assess the time spent away from the stimulus and fake quadrants.

Shark groups were analyzed separately to assess whether differences may have existed in behavioral response due to seasonal factors in addition to the collective data from both groups being analyzed as a combined group.

Results

Assessment of visual fields

Regardless of size and sex, sharks possessed a horizontal, lateral visual field extending between 34-38° frontally and caudally from the center of each eye equating to a total of approximately 68-72° laterally. Vertically, their visual fields extended between 30-32° dorsally and ventrally from the center of each eye resulting in a vertical visual field of 60-64°. No binocular overlap was found within these sharks frontal or caudal visual fields. The blind spot located directly in front of their head was estimated to be at least 112° in breadth. See Figures 1 and 2.

Figure 1: Horizontal optical visual field estimate

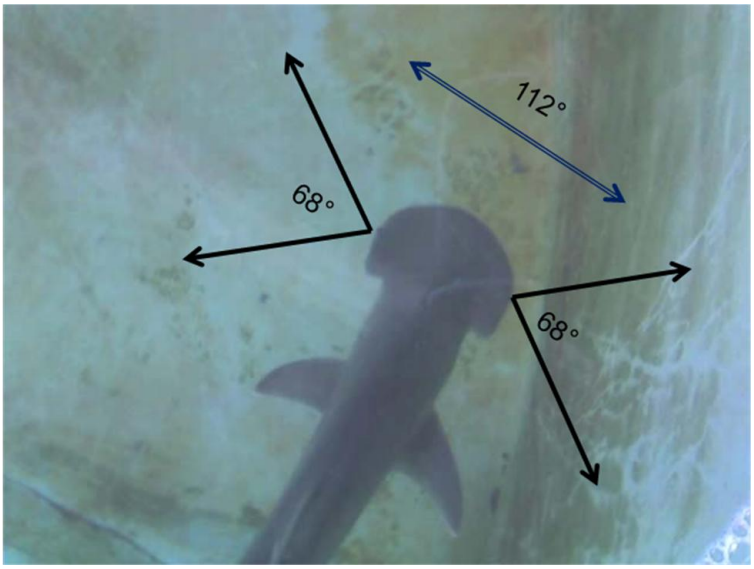
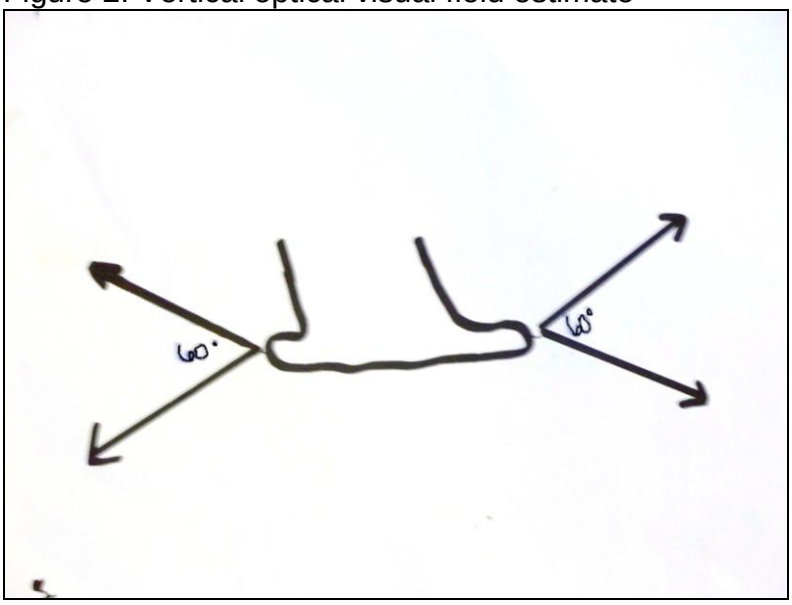


Figure 2: Vertical optical visual field estimate



Assessment of how lateral head movement influences the visual field

Results from tracings sharks swimming normally through a tank from video matched assessments obtained using MotionPro software. Measurements taken at the furthest extent of head motion during sinusoidal swimming behavior ranged between 32-37°, or an average of 35°, coming close to estimates of head motion given by Myrberg and Gruber (1974) of approximately 40°. See Figure 3. Composites of lateral optical visual field estimates were overlaid with head motion estimates to provide a rough approximation of how head motion during swimming behavior may affect this species visual fields. See Figure 4.

Figure 3: Extent of head motion during sinusoidal swimming behavior

Figure 4: Overlay of lateral visual field and head motion estimates

Use of vision in prey detection and localization: behavioral assessment

Data from each shark group tested (group one from August and group two from October) as well as the combined data from both groups were analyzed and quantified using a Split Plot Factorial ANOVA with SAS statistical software. These results were further analyzed using two-tailed t-tests to determine whether time spent in any quadrant differed significantly from others within conditions and between the two shark groups tested.

Results for each of the eight conditions for both groups were analyzed over the duration of each trial post-stimulus introduction and over trial durations, broken into thirds. The trials were broken down to

assess whether the sharks were more reactive to the stimulus conditions within the first few minutes of each trial and less reactive over the duration of each trial. Results of the time spent in each quadrant were transformed into percent time spent in each quadrant for graphical purposes. All graphs containing percentage time per quadrant data show the amount of time sharks spent within each quadrant post-stimulus introduction.

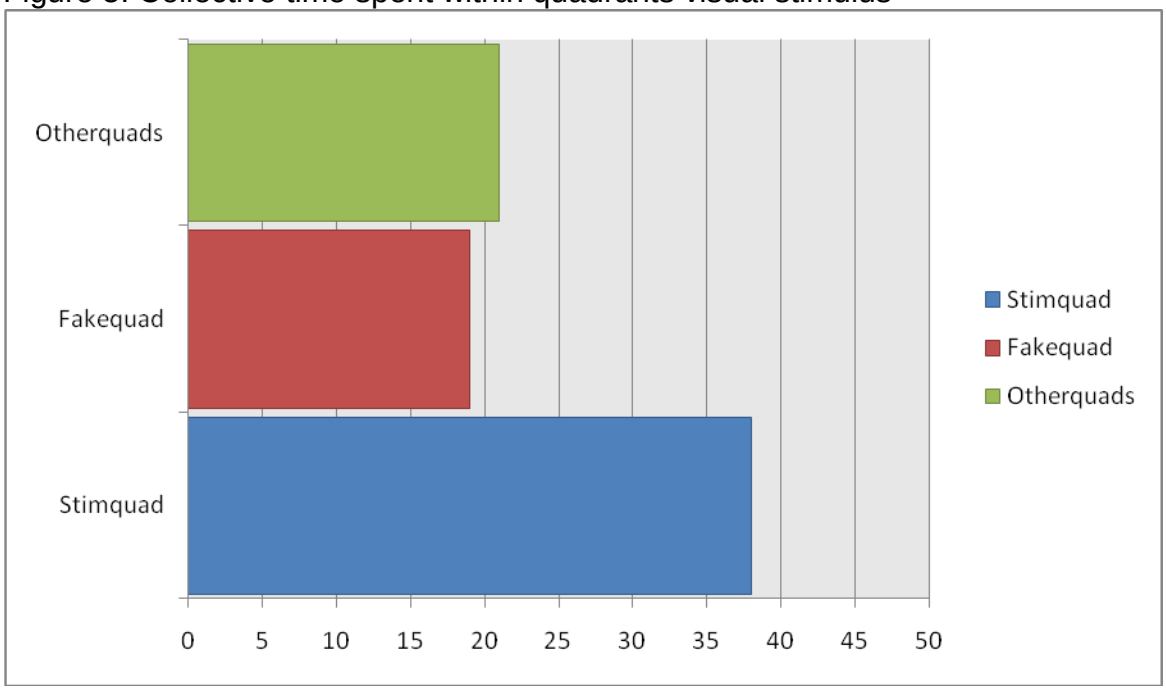
Tailbeat frequency was also analyzed to ascertain if there was any significant difference between tailbeat frequency pre and post stimulus introduction. Though tailbeat frequency increased just after the introduction of each stimulus, no significanct difference between the tailbeat frequency pre and post stimulus introduction was found.

Visual Stimulus Condition

Collective time spent within quadrants over trial durations

For trials containing the visual stimulus alone, the sharks collectively spent more time in the stimulus quadrant (38%) than in the quadrant containing the empty stimulus box (fake quadrant; 19%) and the empty quadrants combined (other quadrants; 21%; See Figure 5). Within this condition a significant difference was found between times spent in the stimulus versus the fake quadrants and stimulus versus both other quadrants (See Table 1).

Figure 5: Collective time spent within quadrants visual stimulus

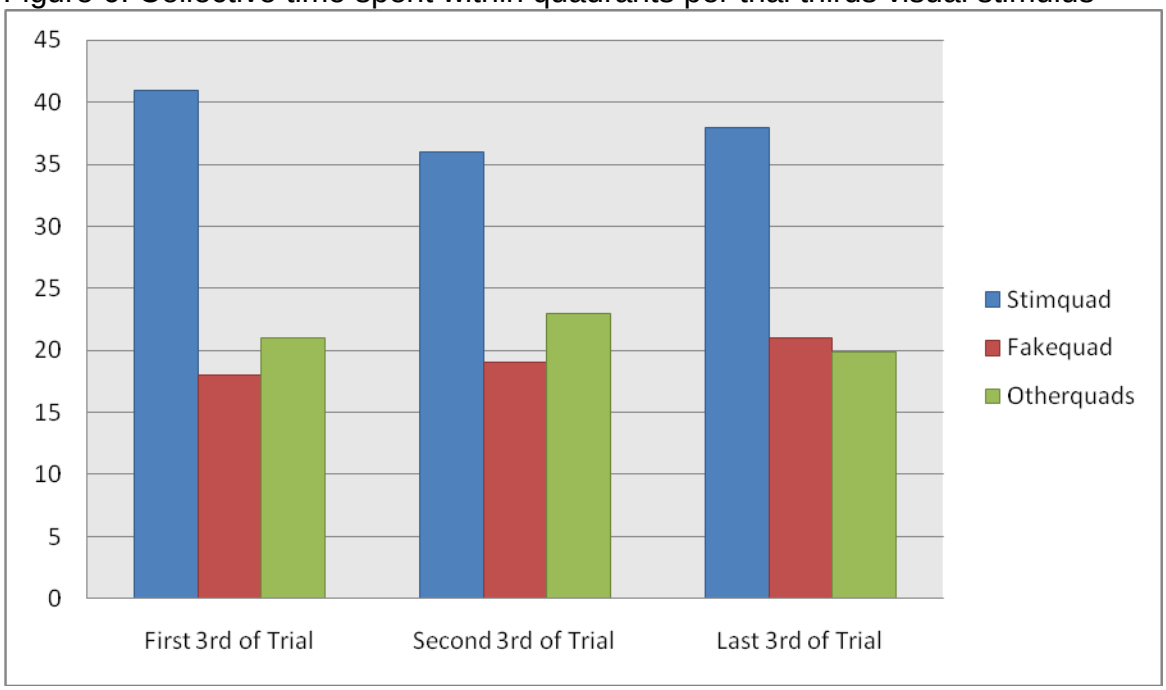


* Significant difference between stimulus, fake, first and second other quadrants

Collective time spent within quadrants per trial thirds

Sharks spent the most time within the stimulus quadrant during the first third of the trials (41%) than in the second or last trial thirds (36% and 38% respectively). Nearly the same amount of time was spent in the fake stimulus quadrant across each trial third (18% within the first third, 19% during second trial thirds and 21% within the last third). Time spent within the other quadrants was also nearly the same for each third of the trial: first third (21%), second third (23%), and last third (20%; See Figure 6). Significant differences were found between times spent within the stimulus and fake quadrants during the first and second trial thirds within this condition; see Table 2.

Figure 6: Collective time spent within quadrants per trial thirds visual stimulus

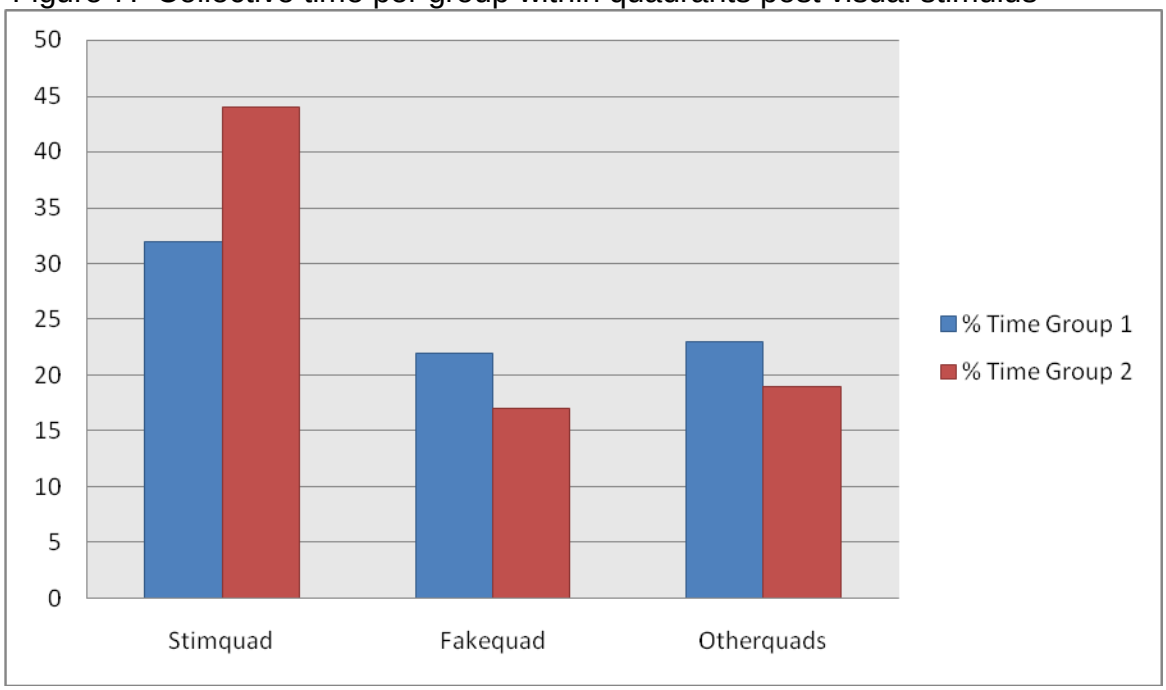


*Significance between stimulus and fake during first and second trial thirds

Time Spent in each Quadrant over duration per Group

Sharks from the first group tested spent 32% of their time within the stimulus quadrant, whereas sharks from the second group tested spent 44% of their time within this quadrant. Sharks from both groups spent around the same amount of time (22% group one and 17% group two) within the fake quadrant as well as within the other quadrants (23% group one and 19% group two). See Figure 7. A significant difference was found between time spent within the stimulus versus the fake quadrant in group one and between the stimulus and fake quadrants as well as between the stimulus and both other quadrants within group two (See Appendices A and B).

Figure 7: Collective time per group within quadrants post visual stimulus



* Significance between stimulus and fake group one; between stimulus, fake, and both other quadrants group two

Group Time per Quadrant per Trial Thirds

Within group one, sharks spent 39%, 32%, and 26% of their time, respectively, in the stimulus quadrant over trial thirds compared to 42, 41%, and 50% respectively in the second group. In the fake quadrant, group one spent 22% of their time here during the first trial third, 18% during the second third, and 25% during the last trial third. Group two spent 15% of their time in the fake quadrant during the first trial third, 19% during the second third and 18% during the last third. Sharks from the first group spent 20% of their time in the other quadrants during the first trial third, 25% during the second third, and 24% during the last trial third. Sharks from group two spent an average of 21% and 20%, respectively, of their time in the other quadrants during the first and second thirds

of the trials and 16% during the last trial thirds. See Figures 8 and 9. No significant differences were found between times groups spent within the same quadrants between trial thirds.

Figure 8: Time per Thirds within Visual Condition Group One

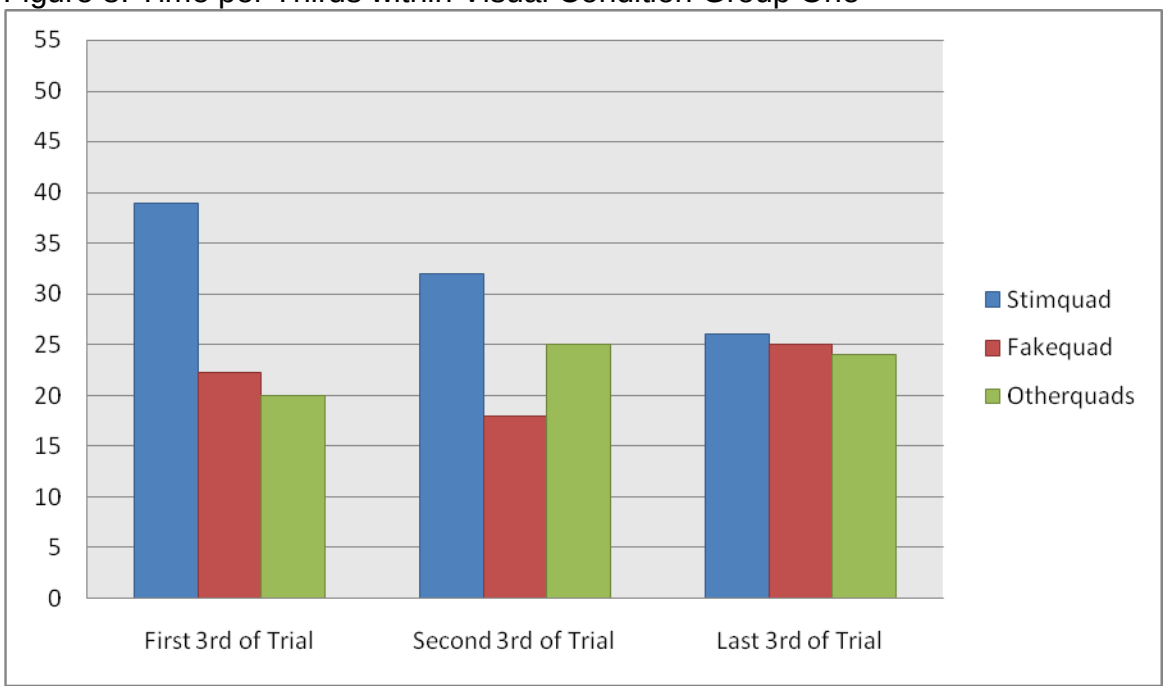
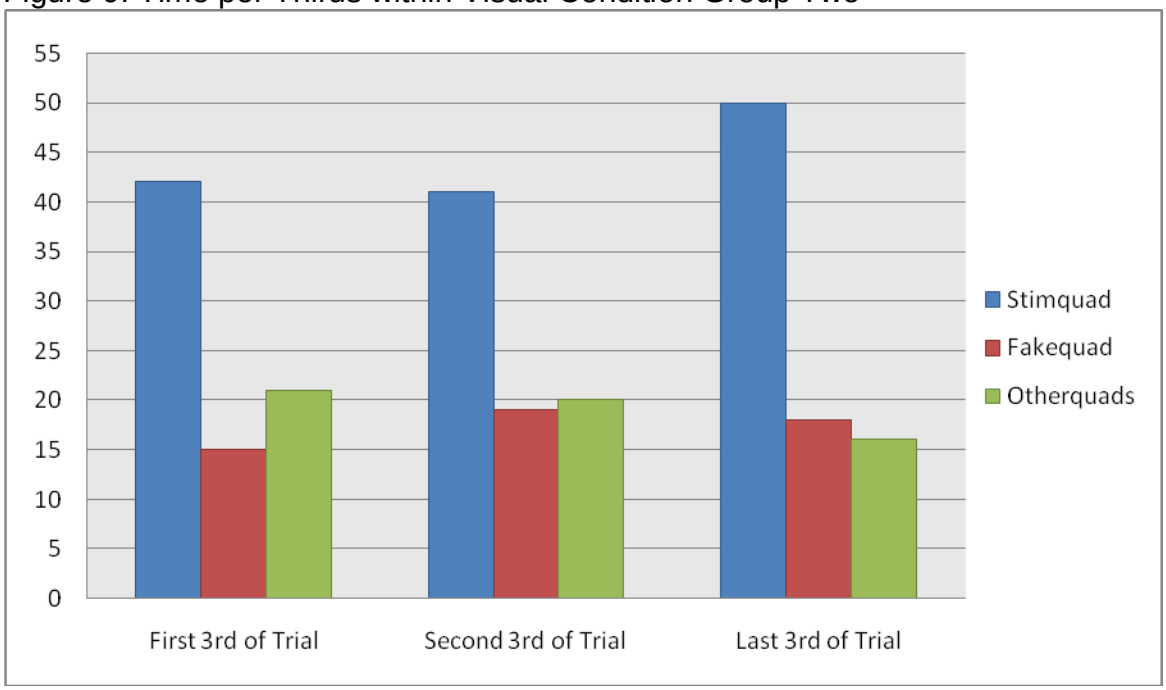


Figure 9: Time per Thirds within Visual Condition Group Two

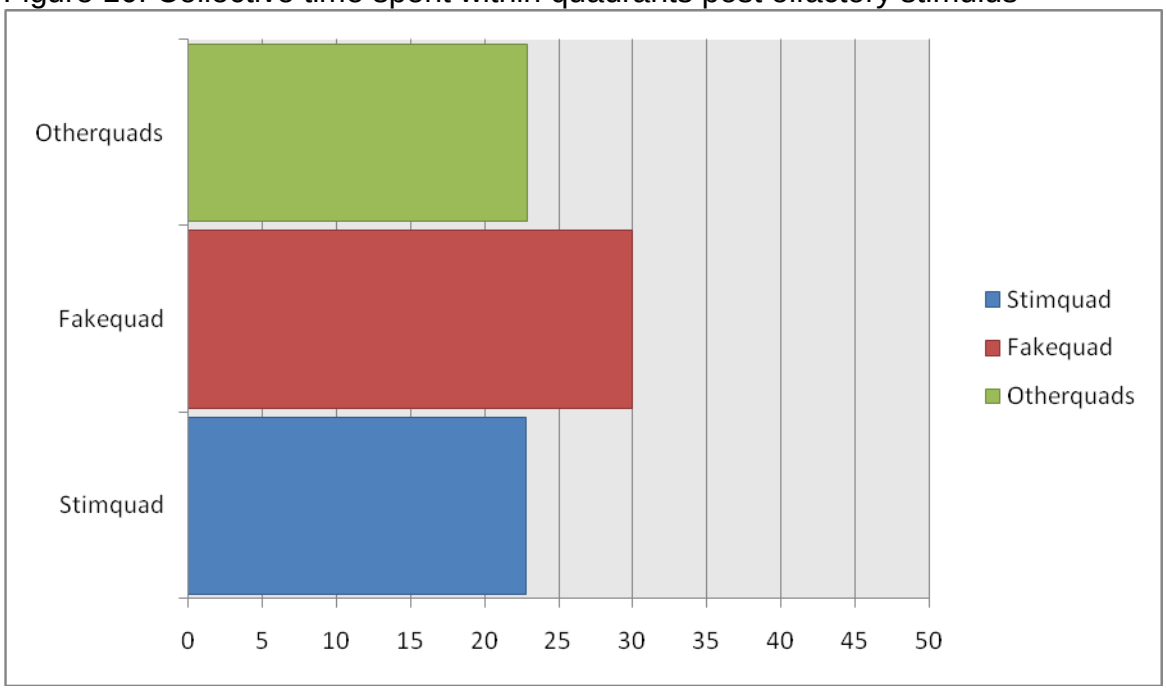


Olfactory Stimulus Condition

Collective time spent within quadrants over trial durations

Within the olfactory condition trials, sharks spent the most time in the quadrant containing the 'dummy' stimulus ('fake stimulus'), 30% and the same amount of time in the stimulus and empty (other) quadrants, 23%; See Figure 10). No significant difference was found between times spent within any quadrant in this condition.

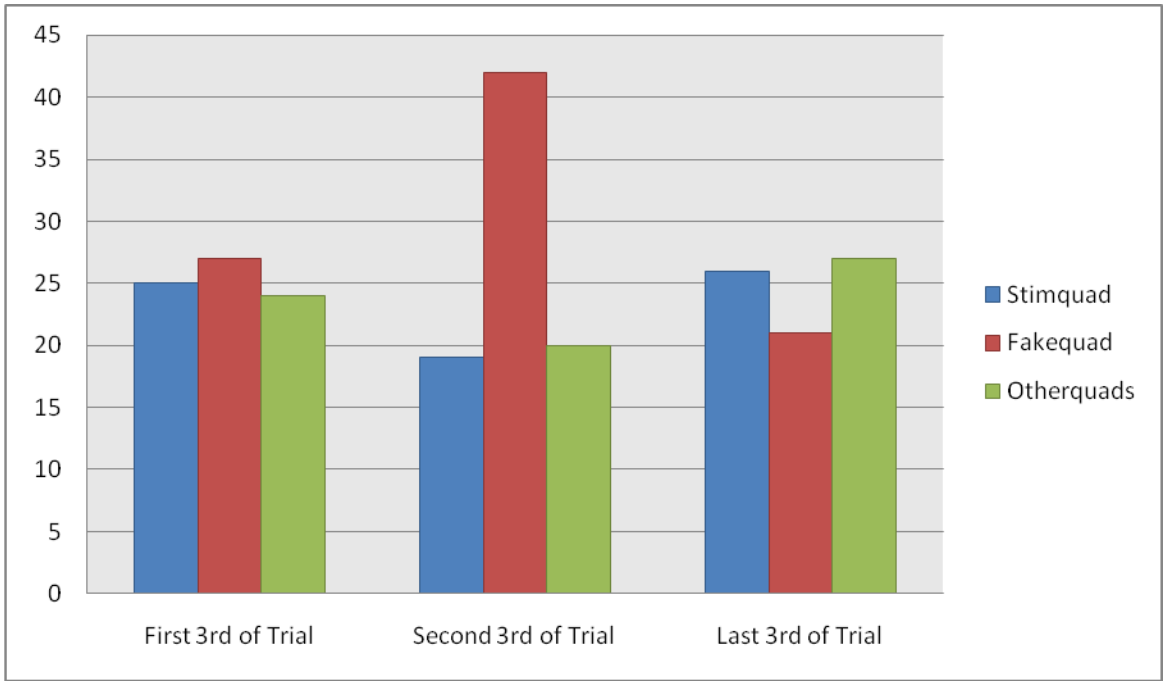
Figure 10: Collective time spent within quadrants post olfactory stimulus



Collective time spent within quadrants per trial thirds

Sharks spent 25% of their time within stimulus quadrant during the first third of the olfactory stimulus trial, 19% during the second third, and 26% during the last trial third. Within the fake stimulus quadrant, sharks spent 27% of their time within this quadrant during the first trial third, 42% during the second third, followed by 21% during the last third. The average time spent within the other quadrants during the first third of the trials was 24%, within the second third 20% of time was spent between the other quadrants, and 27% of time during the last third of trials. See Figure 11. No significant difference was found between times spent within quadrants in any trial third.

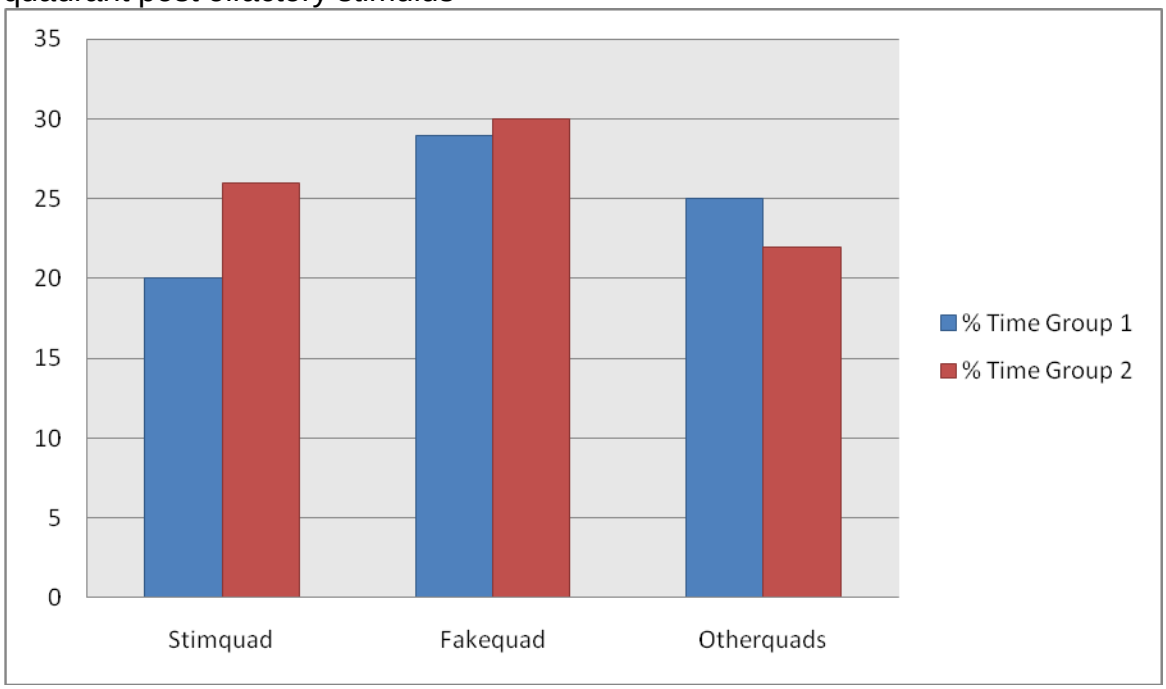
Figure 11: Collective time spent within quadrants per trial thirds post olfactory stimulus



Time Spent in each Quadrant over duration per Group

Groups one and two spent fairly similar amounts of time within the stimulus quadrant (20% and 26% respectively) during this condition. Within the fake quadrants, both groups were again similar in time spent over the duration of trials, as group one spent 29% of their time here and group two spent 30% of their time within this quadrant. Within the other quadrants, group one spent 25% of their time there and group two 22% percent, which were once again nearly the same. See Figure 12. No significant difference was found between either of the shark groups in time spent within any quadrant in this condition.

Figure 12: Percent time each group and groups combined spent in each quadrant post olfactory stimulus



Group Time per Quadrant per Trial Thirds

Sharks within the first group spent 15% of their time within the stimulus quadrant during the first trial third, 17% during the second third, and 29% during the last third. Within group two, sharks spent 35% of their time within the stimulus condition during the first third of trials, 21% during the second trial thirds, and 23% during the last third of the trials. Within the fake quadrant, group one spent 33% of their time here during the first third of trials, 39% during the second third, and 16% during the last third. Group two spent 22% of their time within the fake quadrant during the first third of trials, 44% during the second third, and 25% during the last third. For group one, 26% of their time was spent within the other quadrants during the first third of trials, 22% during the second third, and 28%

during the last third. Group two spent 22% of their time within the other quadrants during the first trial third, 17% during the second third of trials, and 26% of time here during the last trial thirds. See Figures 13 and 14. No significant differences were found within this condition.

Figure 13: Group one Time per Quadrant per Trial Third

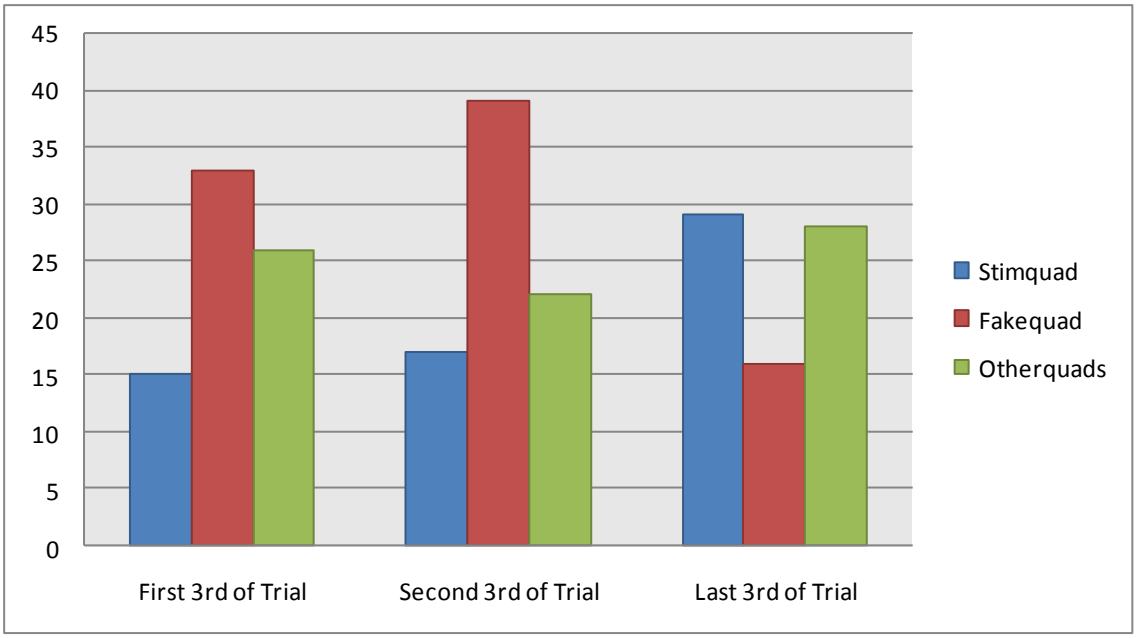
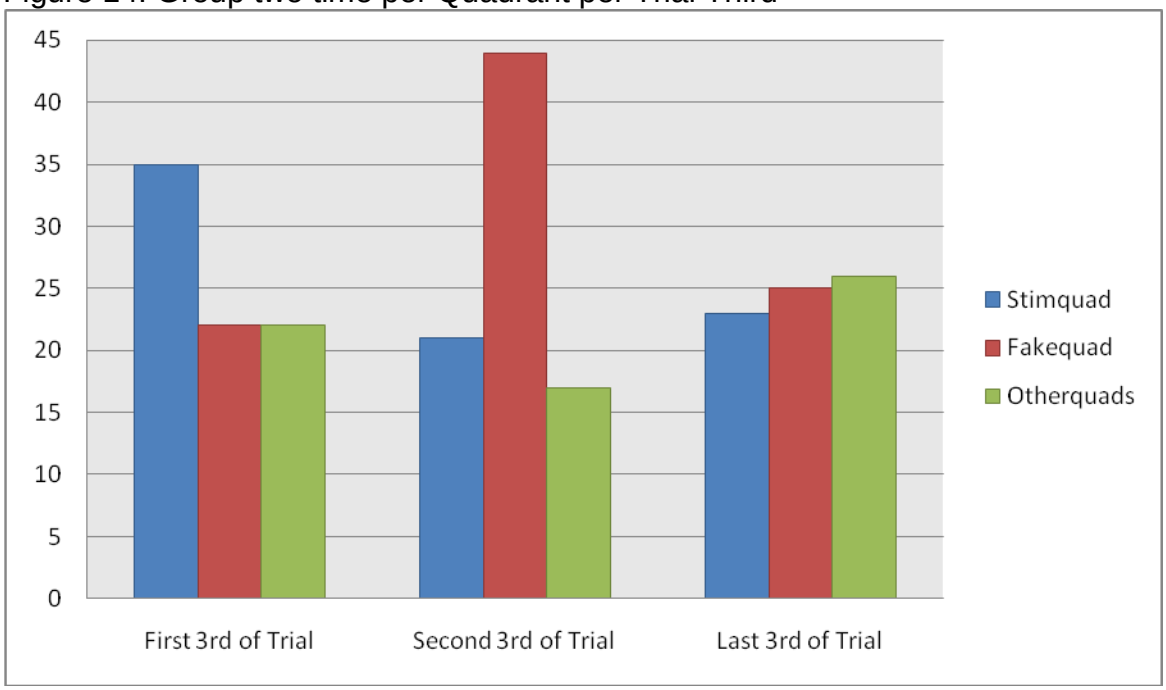


Figure 14: Group two time per Quadrant per Trial Third

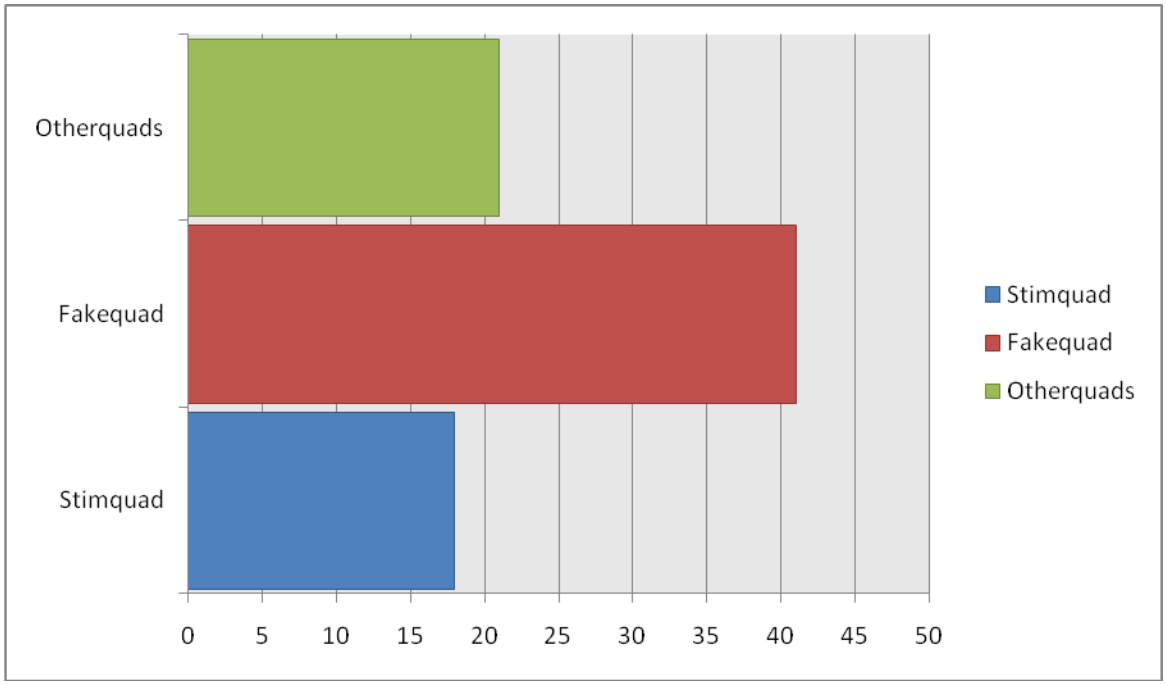


Electroreceptive Stimulus Condition

Collective time spent within quadrants over trial durations

Sharks spent more time in the fake stimulus quadrant (41%) and similar amounts of time in the stimulus (18%) and other quadrants (21%) within the electroreception stimulus condition (see Figure 15). Significant differences were found between time spent within the stimulus and fake quadrants as well as between time spent within the fake quadrant and the first other quadrant in this condition (See Table1).

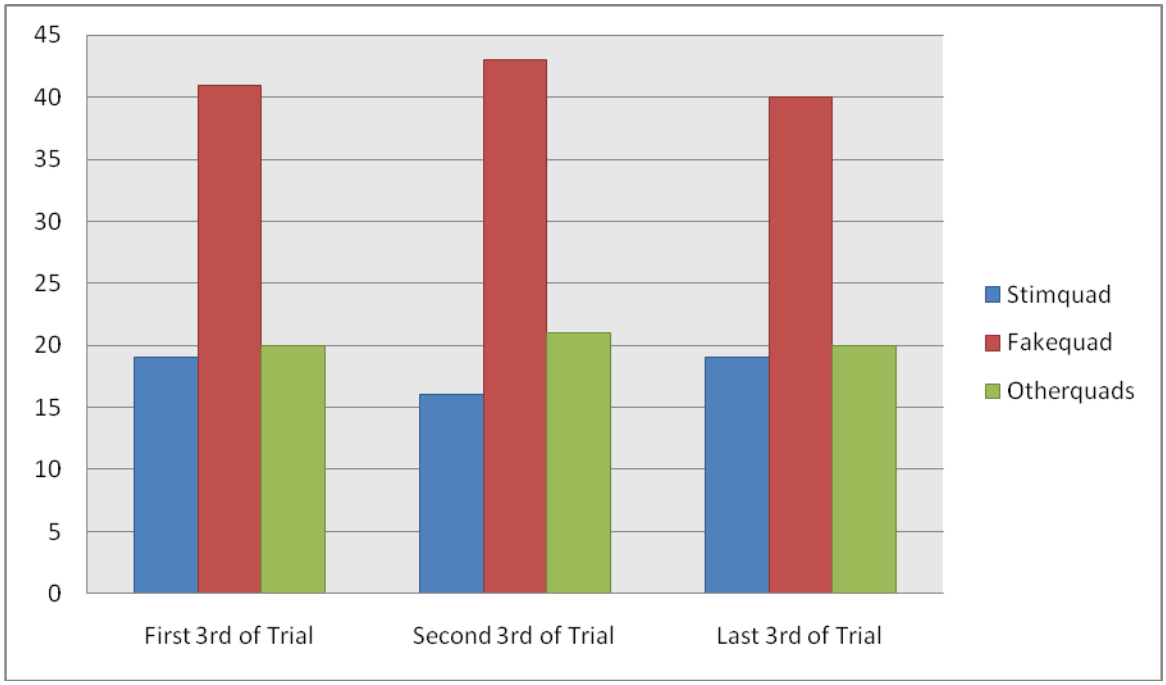
Figure 15: Percent time spent in each quadrant post electroreceptive stimulus introduction



Collective time spent within quadrants per trial thirds

Sharks spent the most time in the fake stimulus quadrant over all three thirds of each trial (41% for the first third and 43% for the second third, and 40% over the last thirds). They spent nearly the same amount of time within the stimulus quadrant over the duration of each trial third (19%, 16%, and 19% respectively) than in the other quadrants (20%, 21%, and 20% respectively; see Figure 16). A significant difference in the time spent between the stimulus and fake quadrant was found during the second trial third in this condition; see Table 2.

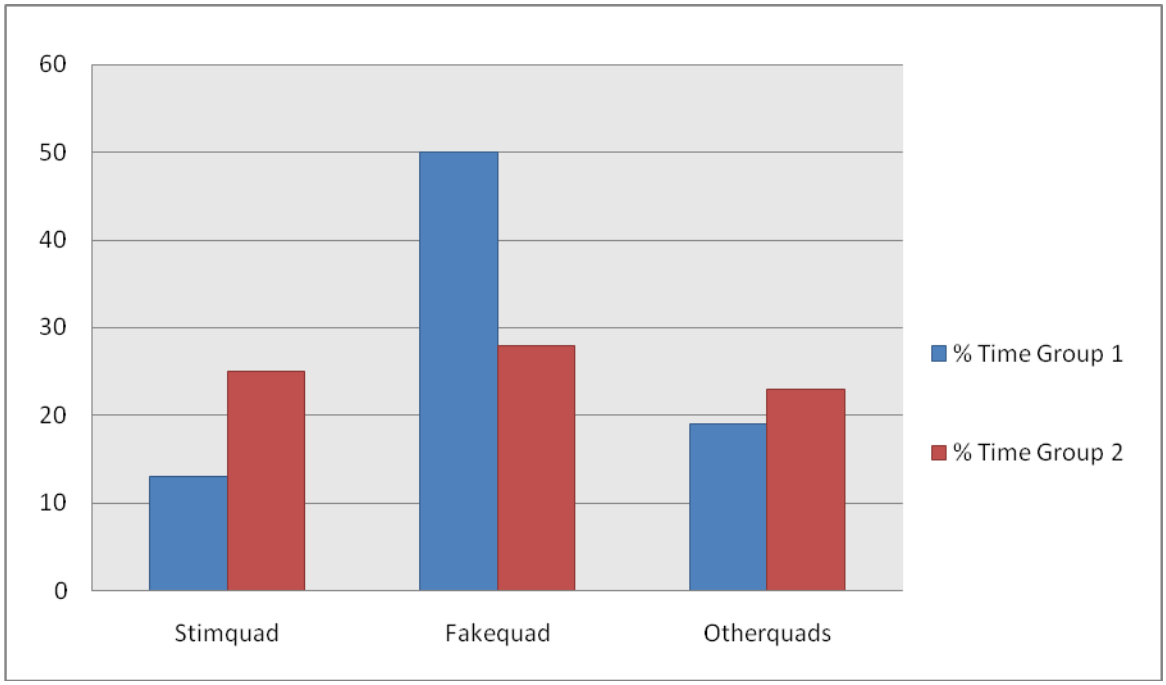
Figure 16: Time spent in each quadrant per trial thirds post electroreceptive stimulus introduction



Time Spent in each Quadrant over Duration per Group

Group one spent 13% of their time within the stimulus quadrants and group two spent 25% in this quadrant. Both groups spent the most time within the fake quadrant, however, group one spent more time (50%) within this quadrant than group two (28%), though this difference was not significant. Both groups spent nearly the same amount of time within the other quadrants (19% group one and 23% group two) within the electroreceptive stimulus condition. See Figure 17. No significant differences were found between groups over trial durations in this condition.

Figure 17: Percent time per quadrant over duration post electroreceptive stimulus



Group Time per Quadrant per Trial Thirds

Sharks from group one spent 11% of their time within the stimulus quadrant during the first trial third, 10% during the second third and 18% during the last third compared to 30% during the first third, 25% during the second third, and 21% during the last third for the second shark group. Within the fake quadrant, group one spent 54% of their time here during the first third of trials, 49% during the second third and 46% during the last third of the trials. Group two spent 21% of their time within the fake quadrant during the first third of trials and 33% during the second third and 30% during the last trial thirds. Sharks from group one spent 17% of their time within the other quadrants during the first third of trials, 21% and 18% within these quadrants during the second and last

trial thirds, respectively. Within the other quadrants for the second group, 25% of their time was spent here during the first trial thirds and 21% and 24% during the second and last trial thirds, respectively. See Figures 18 and 19.

Figure 18: Group one time per quadrant per trial thirds

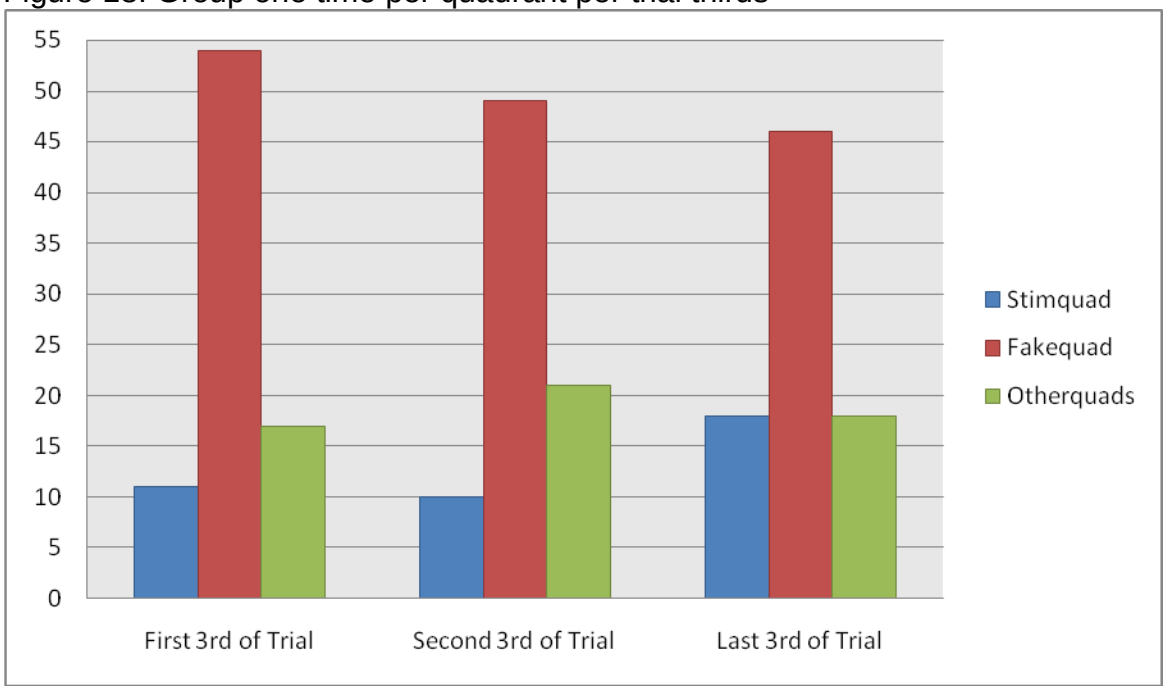
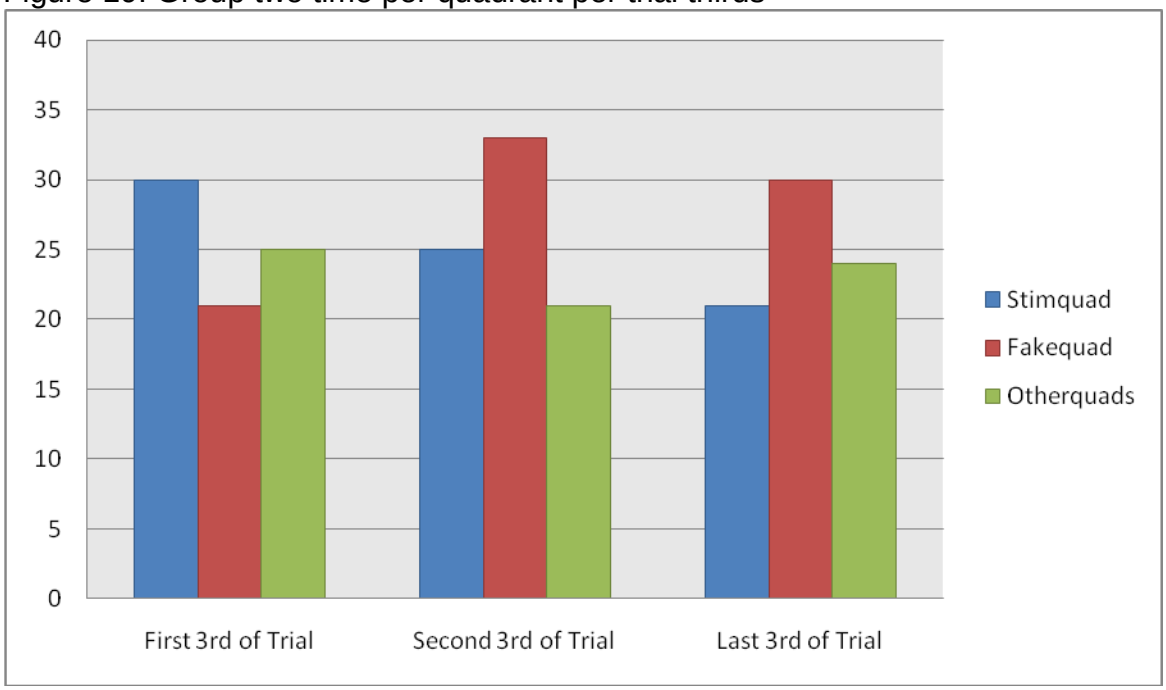


Figure 19: Group two time per quadrant per trial thirds

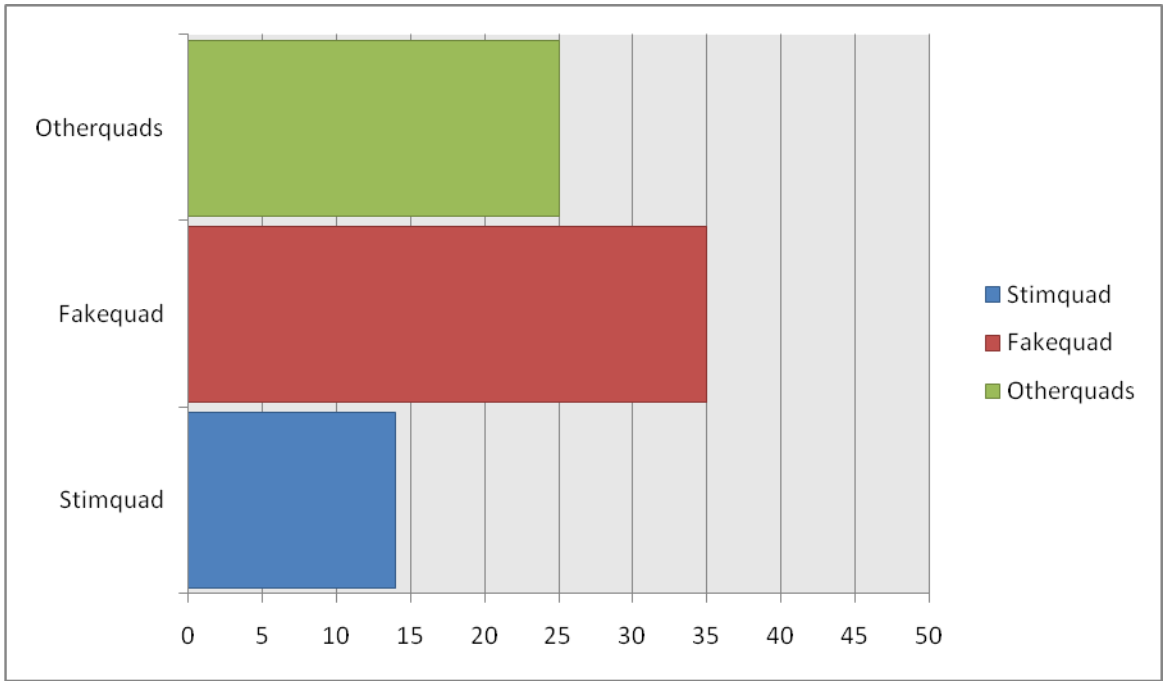


Visual and Electroreceptive Stimulus Combination Condition

Collective time spent within quadrants over trial durations

Within this condition, the sharks spent more time in the fake stimulus quadrant (35%) than the other quadrants (25%), and the least amount of time in the stimulus quadrant (14%; see Figure 20). A significant difference was found between time spent within the stimulus and fake quadrants in this condition; see Table 1.

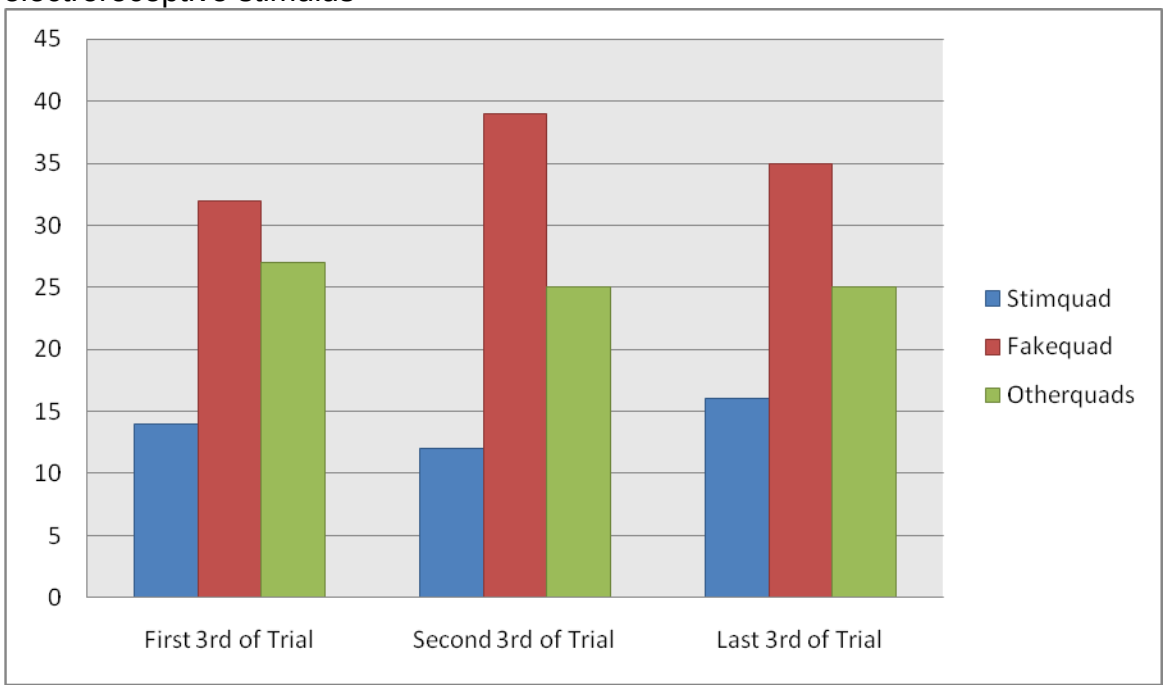
Figure 20: Collective time per quadrant post visual and electroreceptive stimulus combination



Collective time spent within quadrants per trial thirds

Sharks spent nearly the same amount of time in the stimulus quadrant over each third of each trial (14%, 12%, and 16% respectively). Sharks spent the majority of time within the fake quadrant in this condition (32%, 39%, and 35% respectively). Sharks spent nearly the same amount of time within the other quadrants over each trial third, spending 27% of time here during the first third, 25% of time during the second and last trial thirds. See Figure 21. Significant differences were found between time spent within the stimulus and fake quadrants over each trial third in this condition, see Table 2.

Figure 21: Collective time spent within quadrants per trial thirds post visual and electroreceptive stimulus

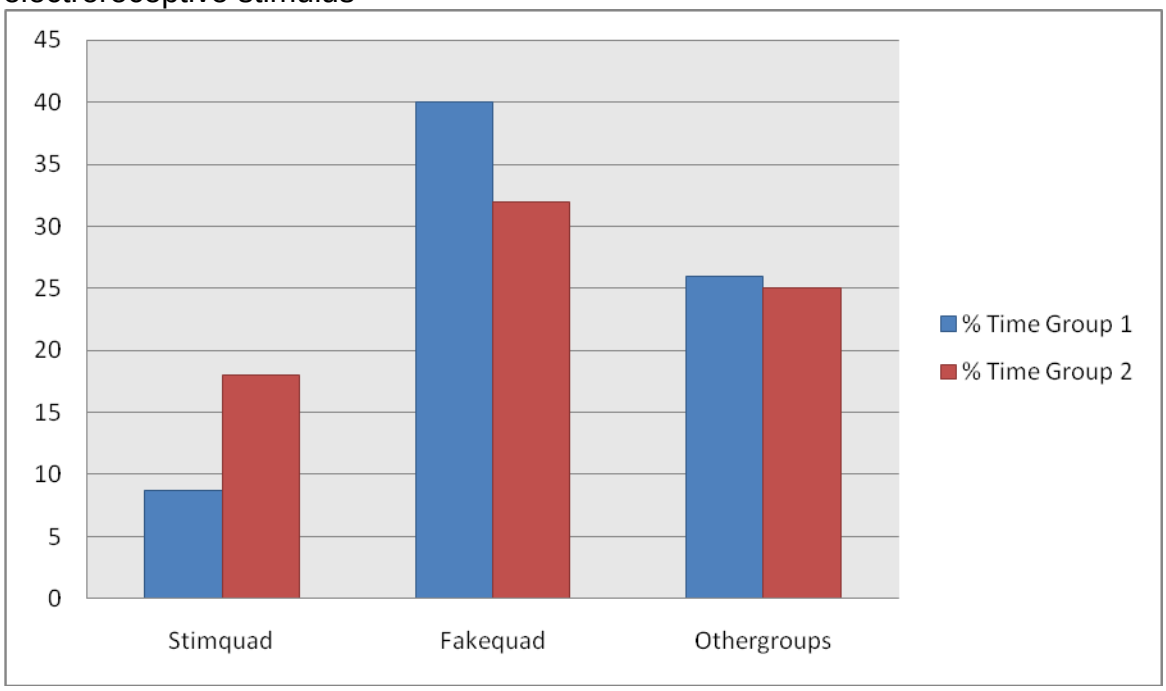


Time Spent in each Quadrant over Duration per Group

Within this stimulus condition group one spent 9% of their time within the stimulus quadrant and group two spent 18% of their time within this quadrant. Group one spent 40% of their time within the fake stimulus quadrant whereas group two spent 32% of their time within this quadrant. In the other quadrants, both groups spent nearly the same amount of time (26% group one and 25% group two) within this quadrant. See Figure 25. A significant difference was found between group one and group two in time spent within the fake quadrant in this condition (see Appendix C). Within the first group, a significant difference was found in time spent between the stimulus and fake quadrants, stimulus and

first other quadrant, and between the fake and second other quadrant (see Appendix A).

Figure 22: Percent time per quadrant over duration per group post visual and electroreceptive stimulus



Group Time per Quadrant per Trial Thirds

Group one spent 9% of their time within the stimulus quadrant in each trial third. Within the fake quadrant, group one spent 39% of their time here during the first third of trials, 48% during the second third, and 32% during the last trial thirds. Group one spent 26% of their time within the other quadrant during the first third of trials, 21% during the second third, and 30% during the last trial third. See Figure 23.

Group two spent 17% of their time within the stimulus quadrant during the first third of trials, 15% during the second third and 21% during the last third. Within the fake quadrant over trial thirds, group two spent 28%, 32% and 37% of their time here respectively. Within the other quadrants, group two spent 28% of their time here during the first third of trials, 27% during the second third, and 21% during the last trial thirds. See Figure 24. Overall, no significant differences were found between group one and group two over trial thirds in this condition. However, within the first group a significant difference was found in the time they spent between the stimulus and fake quadrants during the first third of trials (see Appendix C).

Figure 23: Percent Time per Quadrant per Trial Third Group One

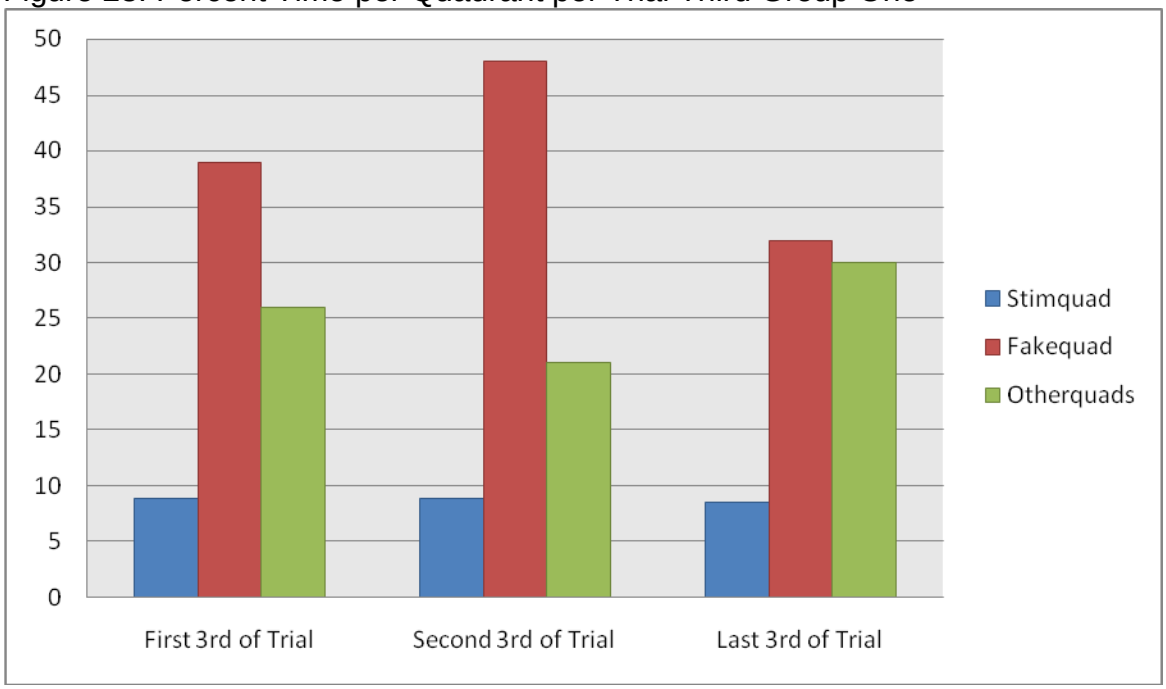
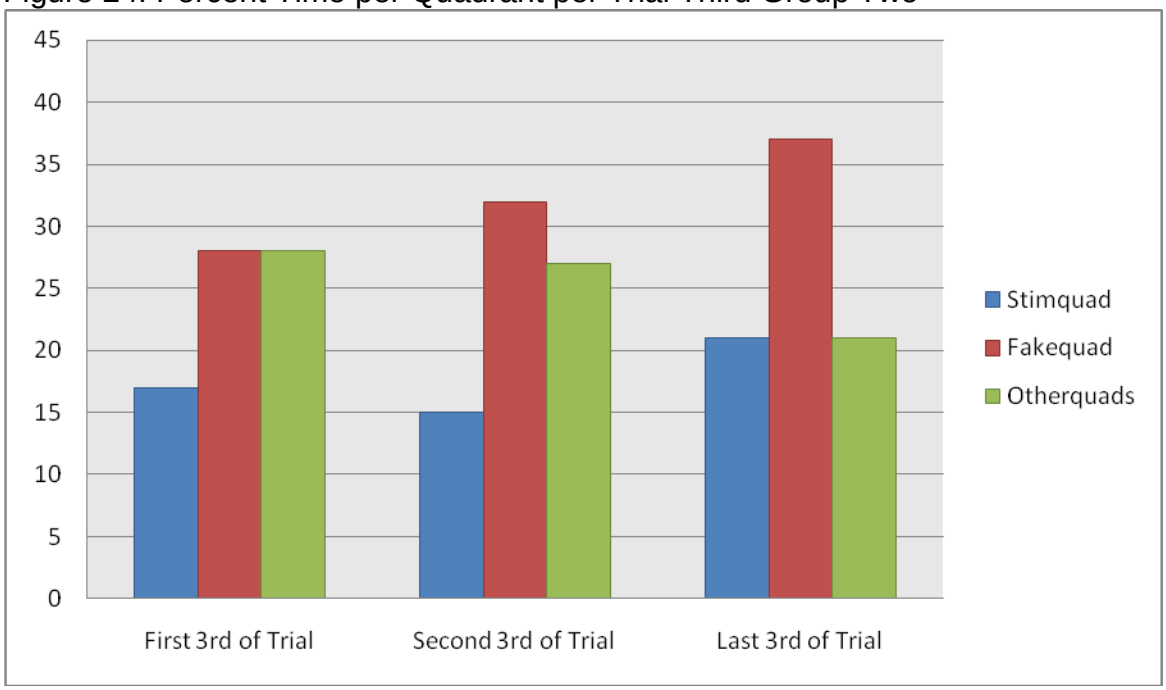


Figure 24: Percent Time per Quadrant per Trial Third Group Two

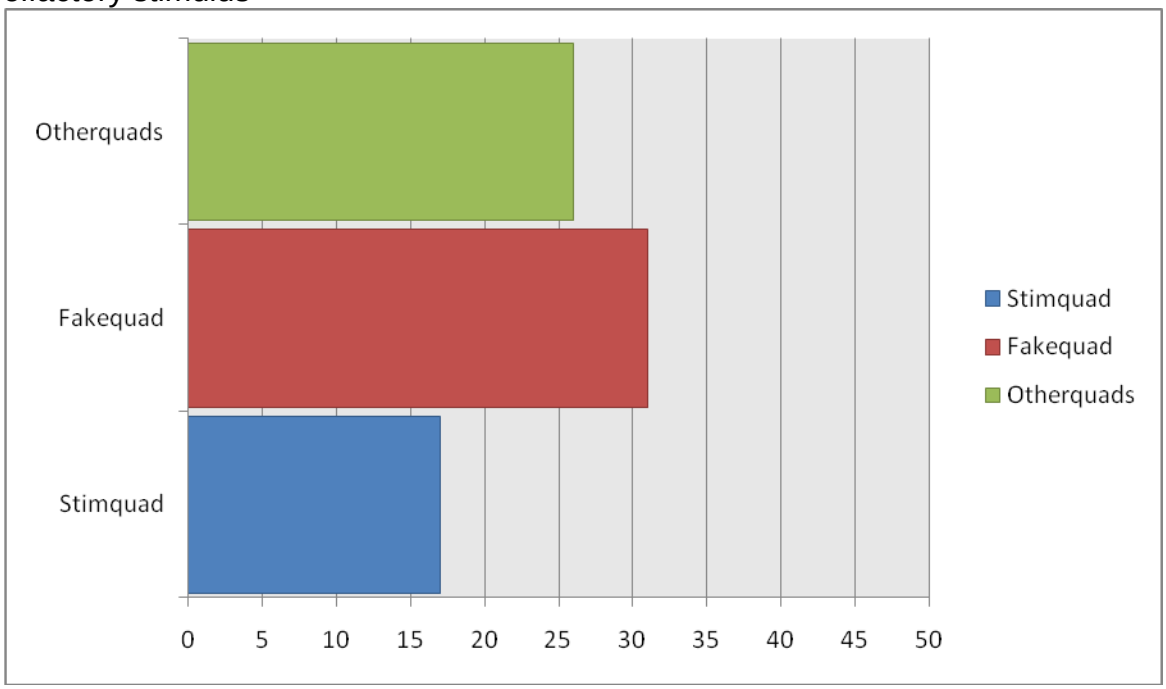


Electroreceptive and Olfactory Stimulus Combination Condition

Collective time spent within quadrants over trial durations

There was a difference in the percentage of time the sharks spent between the stimulus quadrant (17%), fake quadrant (31%), and other quadrants (26%; see Figure 25). A significant difference was found in time spent within the stimulus and fake quadrants and the stimulus quadrant and first other quadrant in this condition; a significant difference was also found between times spent within the first and second other quadrants (See Table 1).

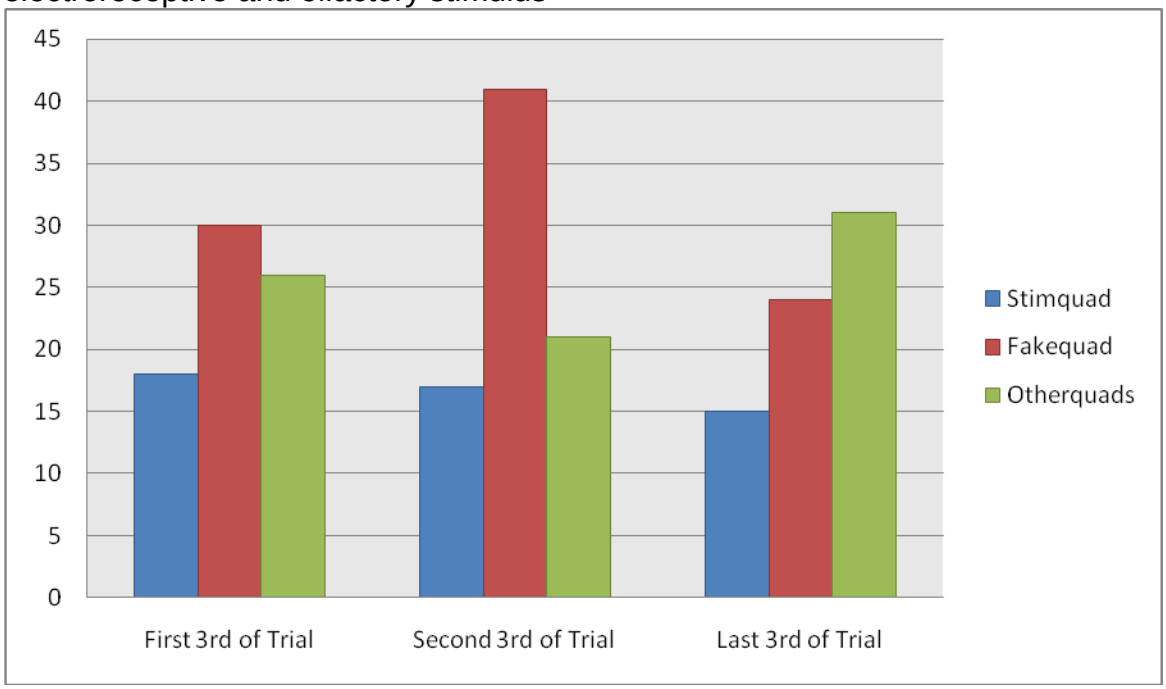
Figure 25: Collective time spent within quadrants post electroreceptive and olfactory stimulus



Collective time spent within quadrants per trial thirds

Sharks spent the majority of their time in the fake stimulus quadrant over all trial thirds (30%, 41%, and 24% respectively). Less time was spent within the stimulus quadrant than any other quadrant over trial thirds (18%, 17%, and 15% respectively). Within the other quadrants sharks spent 26% of time here during the first trial third, 21% during the second third, and 31% during the last trial third; see Figure 26). No significant differences were found in this condition over trial thirds.

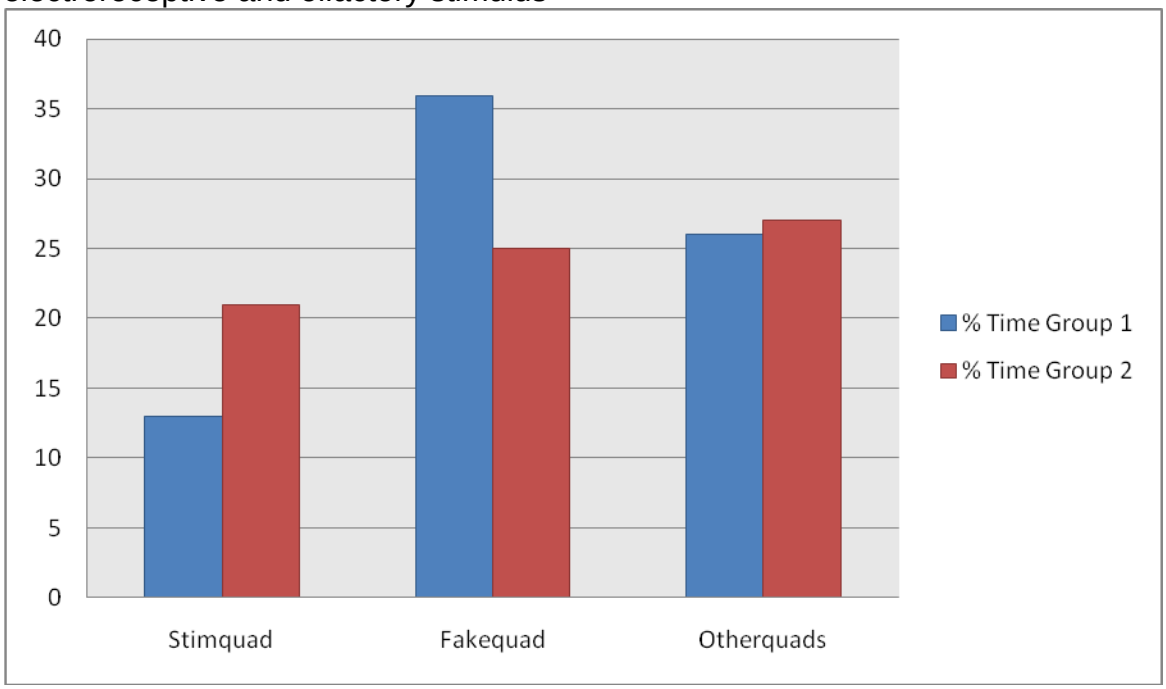
Figure 26: Collective Time spent within quadrants per trial thirds post electroreceptive and olfactory stimulus



Time Spent in each Quadrant over Duration per Group

Group one spent (13%) of their time within the stimulus quadrant and group two (21%) in this stimulus condition. Within the fake quadrant, group one spent 36% of their time here and group two spent 25% in this quadrant. Both groups spent nearly the same amount of time within the other quadrants (26% and 27% respectively). See Figure 27. A significant difference was found within the first group in the time they spent within the stimulus and fake quadrants, between the fake and second other quadrant, and between both other quadrants (other one and other two) within this condition (see Appendix A). However, no significant difference was found between the groups in the time they spent between quadrants in this condition.

Figure 27: Percent time per group per quadrant over duration post electroreceptive and olfactory stimulus



Group Time per Quadrant per Trial Thirds

Group one spent 15% of their time within the stimulus quadrant during the first trial third, 11% during the second third, and 12% during the last trial third. Group two spent 20% within the stimulus quadrant during the first third of the trials, 25% during the second third and 20% during the last third. Within the fake quadrant, group one spent 32% of their time here during the first third of the trials, 54% during the second third, and 22% during the last third. Group two spent 28% of time within the fake quadrant during the first third of trials, 21% during the second third, and 26% during the last third. Twenty-seven percent of time was spent within the other quadrant during the first third of trials, 17% during the second third, and 33% during the last third of trials within the first group. The

second group spent 26% of time within the other quadrant during the first trial third, and 27% during the second and last trial thirds. See figures 28 and 29.

Figure 28: Percent Time per Quadrant per Trial Third Group One

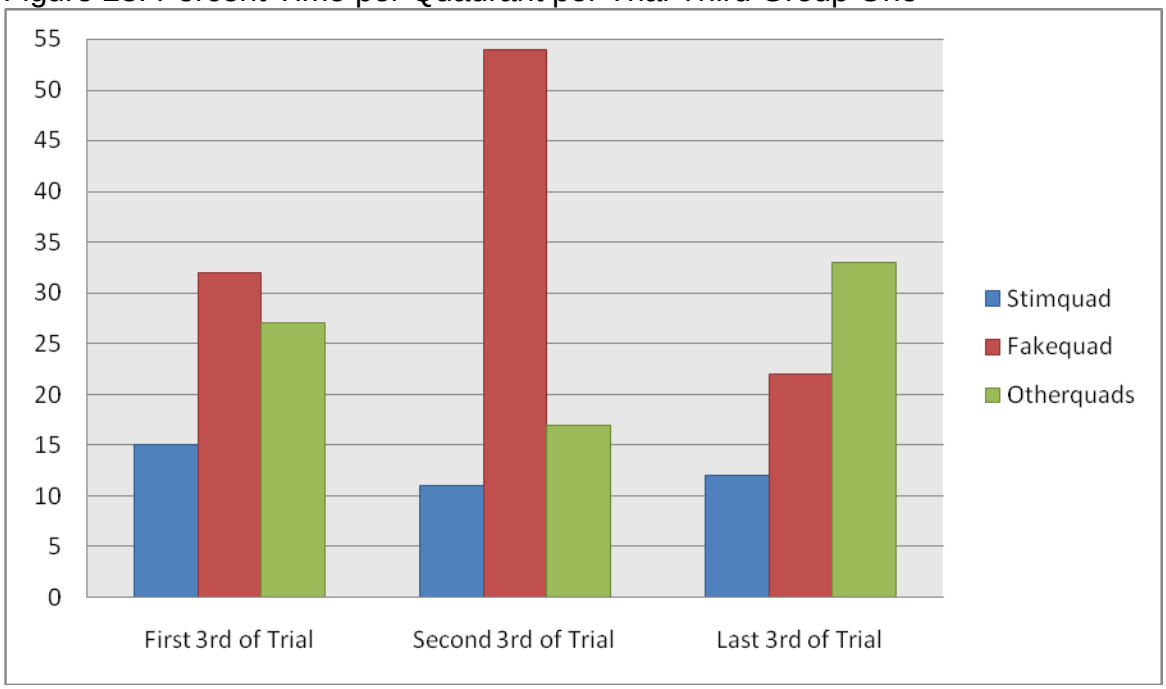
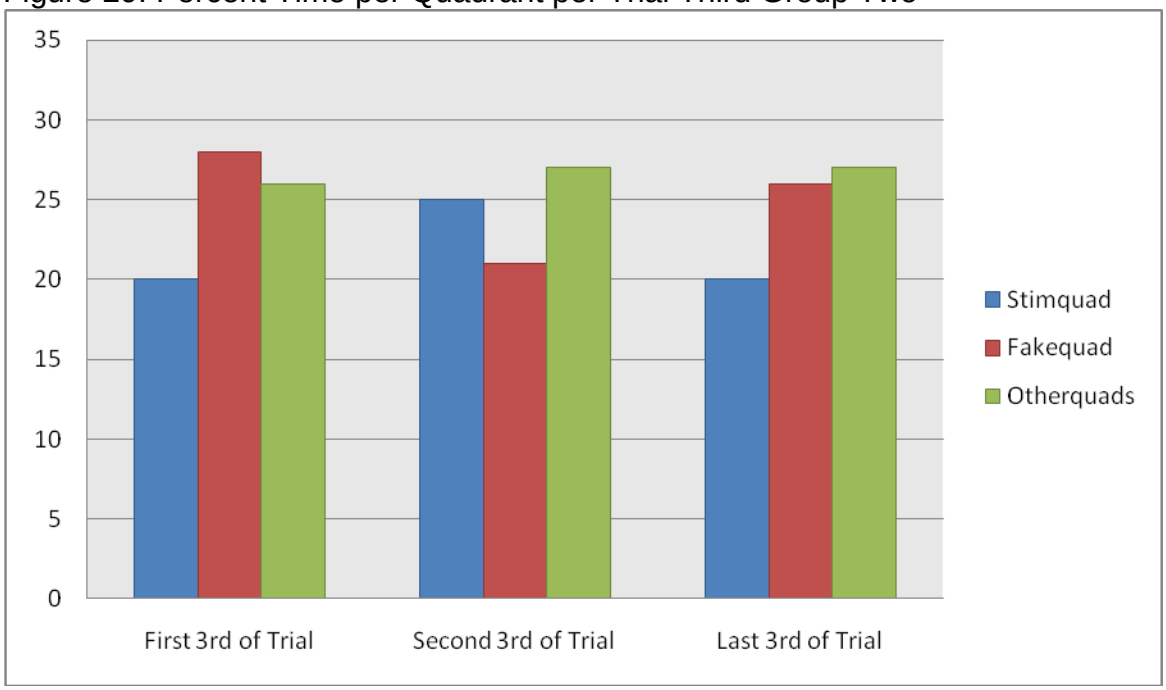


Figure 29: Percent Time per Quadrant per Trial Third Group Two

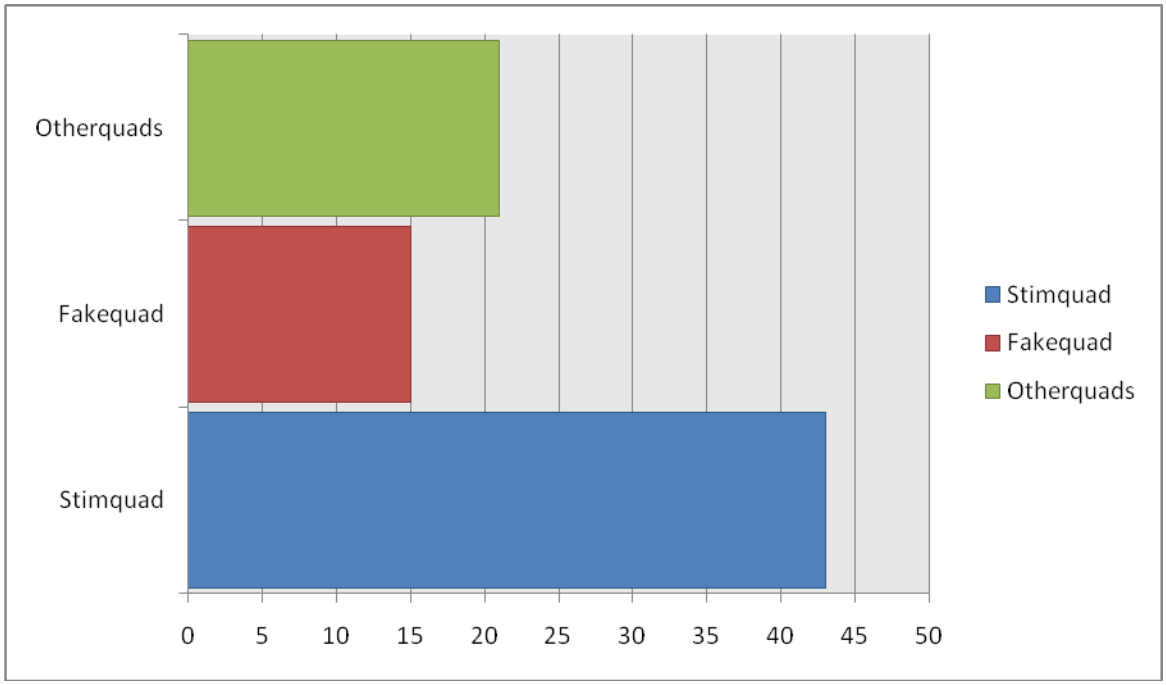


Visual and Olfactory Stimulus Combination Condition

Collective time spent within quadrants over trial durations

The sharks spent more time in the quadrant containing the stimulus (43%) than in the quadrant containing the fake stimulus (15%) and the other quadrants (21%). See Figure 30. A significant difference was found between time spent within the stimulus and fake quadrants as well as between the stimulus and second other quadrant within this condition (see Table 1).

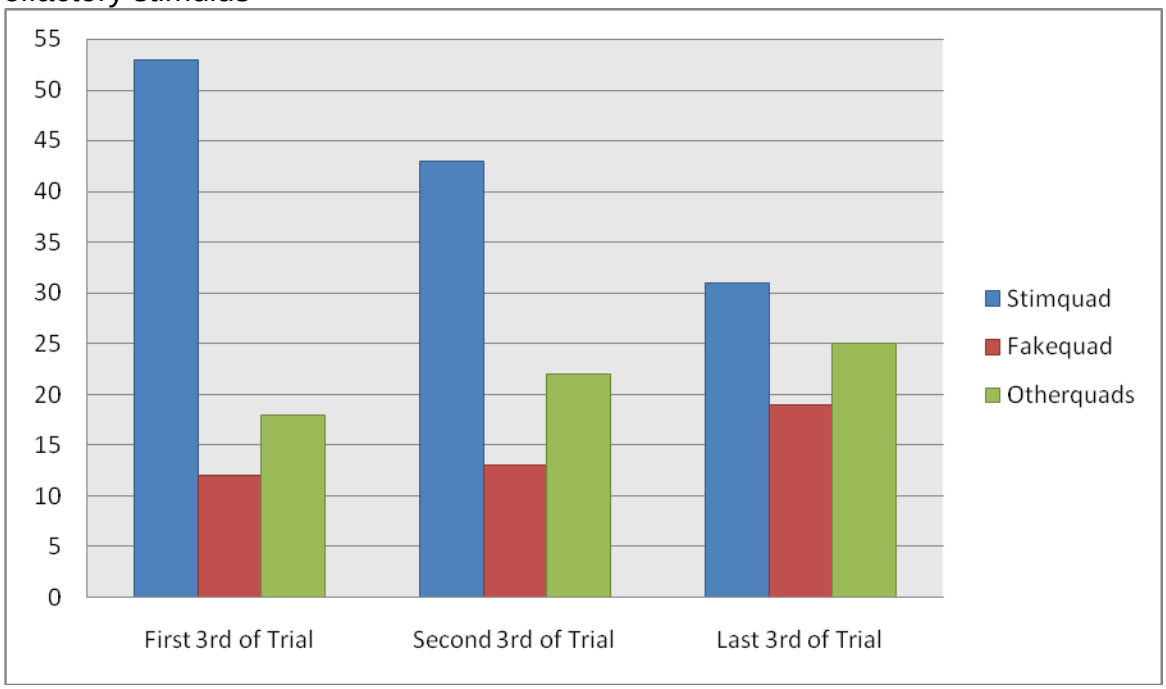
Figure 30: Collective time spent within quadrants post visual and olfactory stimulus



Collective time spent within quadrants per trial thirds

Sharks spent the most time overall within the stimulus quadrant with 53% of their time spent in this quadrant during the first third of the trial, 43% during the second third, and 31% during the last third. Within the fake stimulus quadrant, sharks spent 12% of their time here during the first trial third, 13% during the second third, and 19% during the last third of the trial. Eighteen percent of time was spent in the other quadrant during the first trial third, 22% during the second third of each trial and 25% during the first third of each trial; see Figure 31. Significant differences were found between time spent within the stimulus and fake quadrants during the first and second trial thirds within this condition, see Table 2.

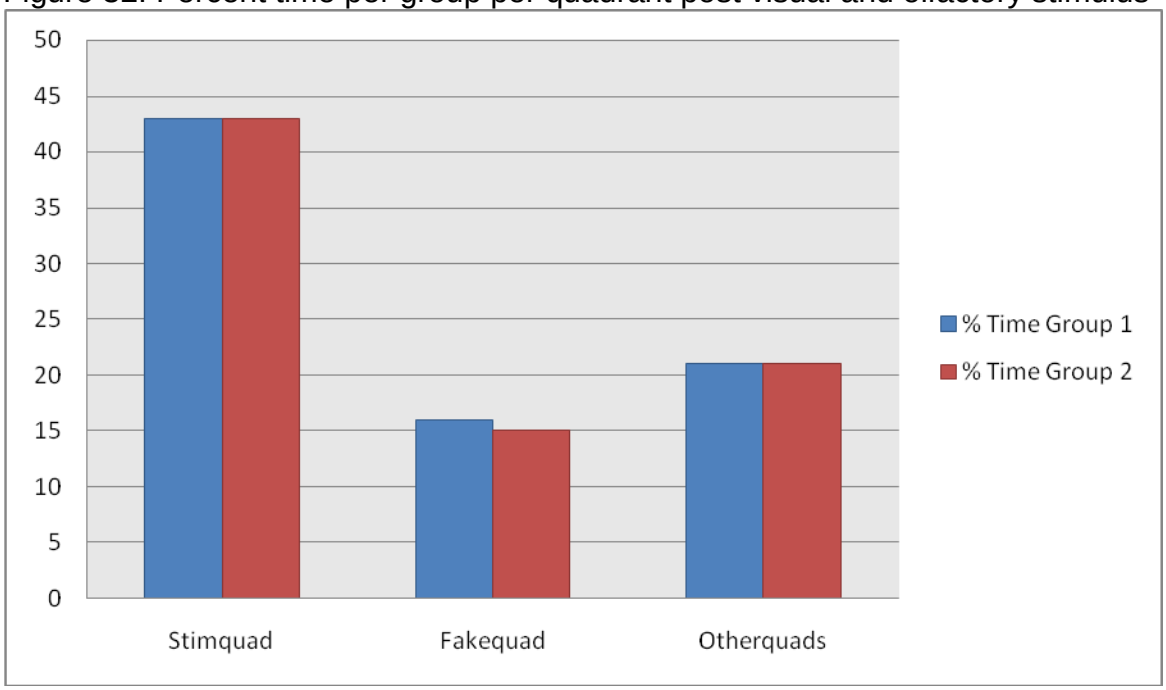
Figure 31: Collective time spent within quadrants per trial thirds post Visual and olfactory stimulus



Time Spent in each Quadrant over Duration per Group

Both groups spent the majority of their time within the stimulus quadrant during this condition (43% for both groups). Within the fake stimulus condition, group one spent 13% of their time here and group two spent 16% of their time within this condition. Both groups also spent nearly the same amount of time within the other quadrants during this condition, with group one spending 22% of their time within this quadrant and group two spending 21% of their time within this quadrant; see Figure 32. No significant differences were found between groups and times spent within any quadrant in this condition over trial duration.

Figure 32: Percent time per group per quadrant post visual and olfactory stimulus



Group Time per Quadrant per Trial Thirds

Group one spent 50% of their time within the stimulus quadrant over the first trial third, 41% over the second third, and 38% during the last third. Within the fake quadrant, the first group spent 12% of their time during the first and second trial thirds, and 15% within this quadrant over the last trial third. Group one spent 19% of their time within the other quadrant over the first third of the trials, 23% during the second third, and 24% over the last third.

Group two spent 57%, 46%, and 25% of their time within the stimulus quadrant over all trial thirds, respectively. Within the fake quadrant, group two spent 11% of their time here during the first third of trials, 15% during the second third, and 23% over the last trial third. Sixteen percent of time was spent within the other quadrants over the first third of trials within group two, 20% over the

second third, and 26% over the last trial third. See Figures 33 and 34. A significant difference was found between time spent within the stimulus quadrant between the first and last trial thirds within the second group (see Appendix C). No significant differences were found between each group in time they spent within quadrants over trial thirds.

Figure 33: Percent Time per Quadrant Group One

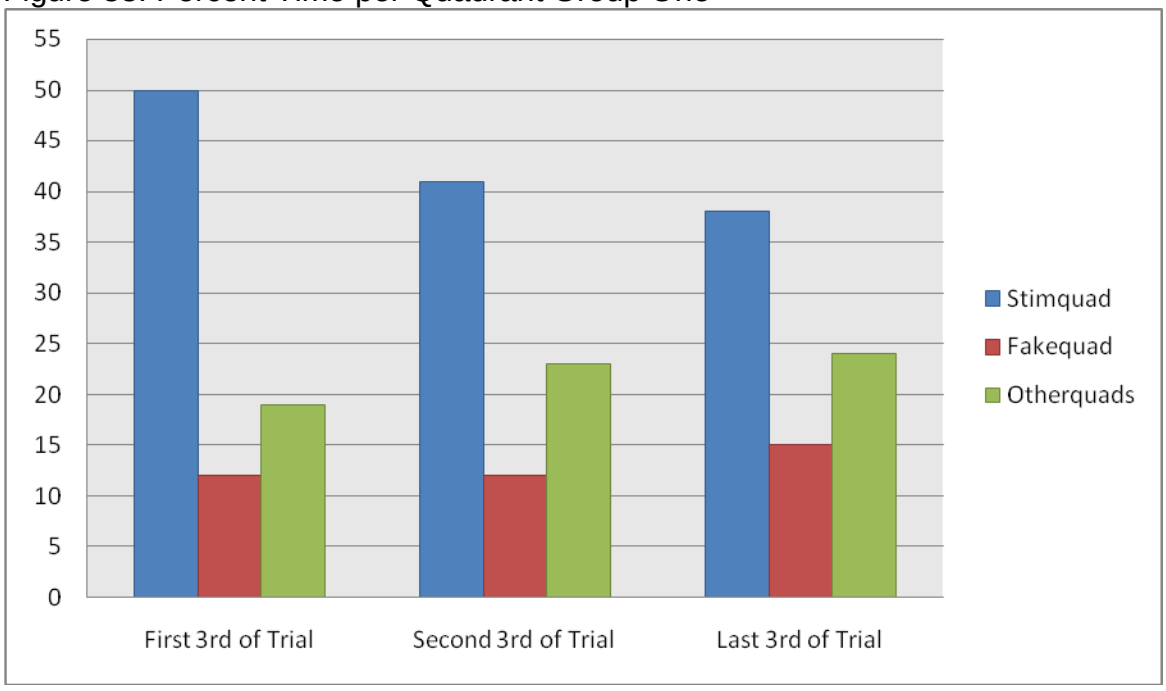
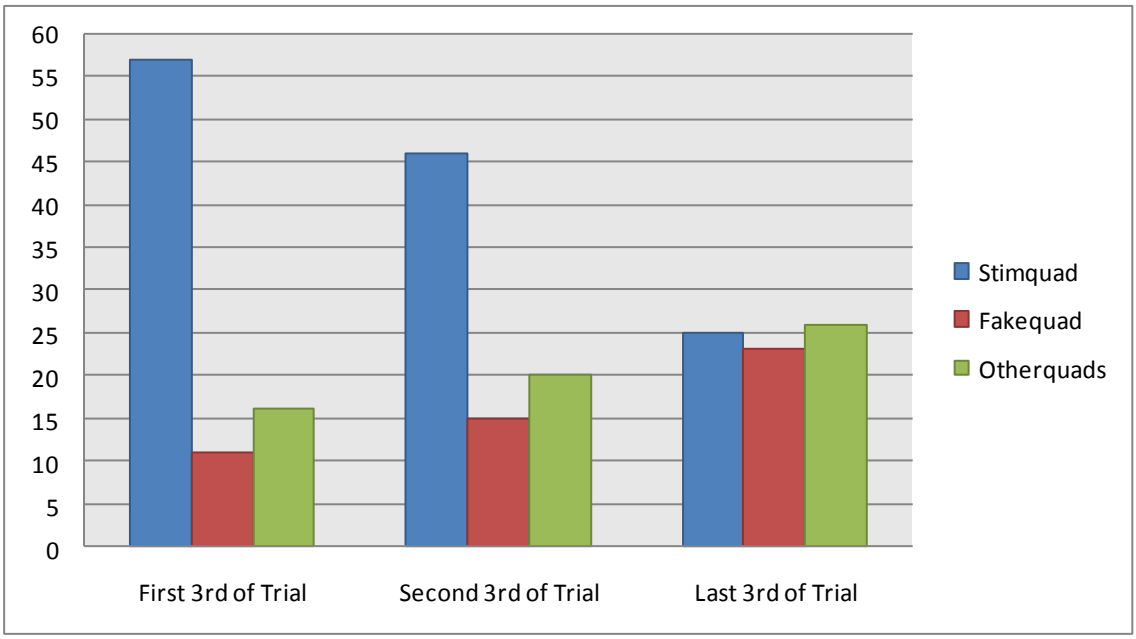


Figure 34: Percent Time per Quadrant Group Two

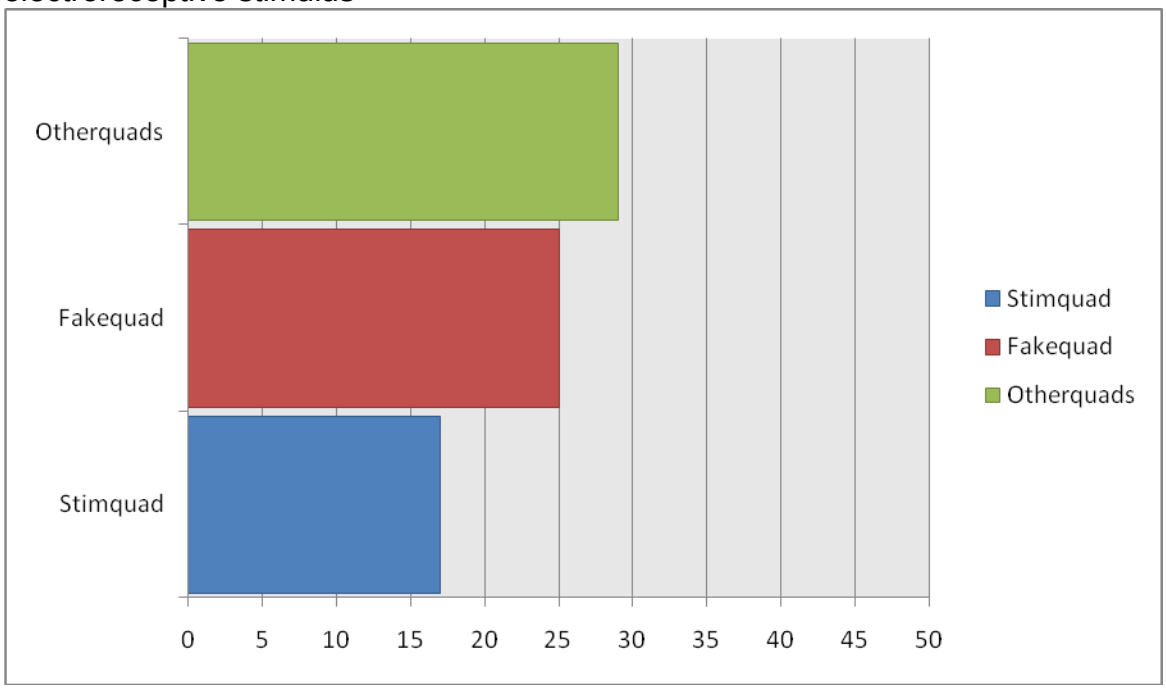


Visual, Electroreceptive and Olfactory Stimulus Combination Condition

Collective time spent within quadrants over trial durations

Within the visual, electroreceptive, and olfactory stimulus combination condition the sharks spent nearly the same percentage of time in all quadrants, spending 25% in the stimulus and fake quadrants and (29%) in the other quadrants; see Figure 35). No significant differences were found between collective times spent in any quadrant over trial durations in this condition.

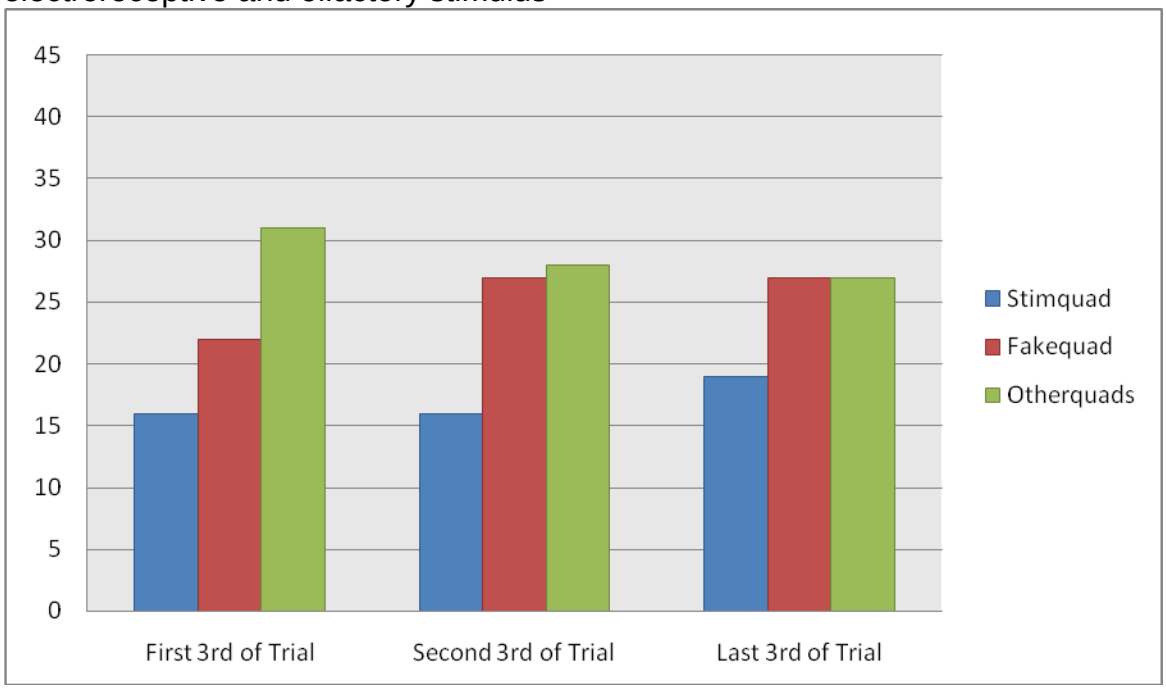
Figure 35: Collective time spent within quadrants post visual, olfactory, and electroreceptive stimulus



Collective time spent within quadrants per trial thirds

Sharks spent nearly the same amount of time within the stimulus quadrant over all trial thirds, with 16% of time during in the first and second trial thirds, and 19% during the last third of each trial. Within the fake stimulus quadrant, sharks spent 22% of their time here during the first trial third, and the same amount of time during the second and last thirds (27%). More time was spent in the other quadrants during the first third of each trial (31%), followed by 28% during the second third of each trial and 27% during the last third of each trial; see Figure 36. A significant difference was found between times spent within the stimulus and fake quadrants over all trial thirds within this condition (see Table 2).

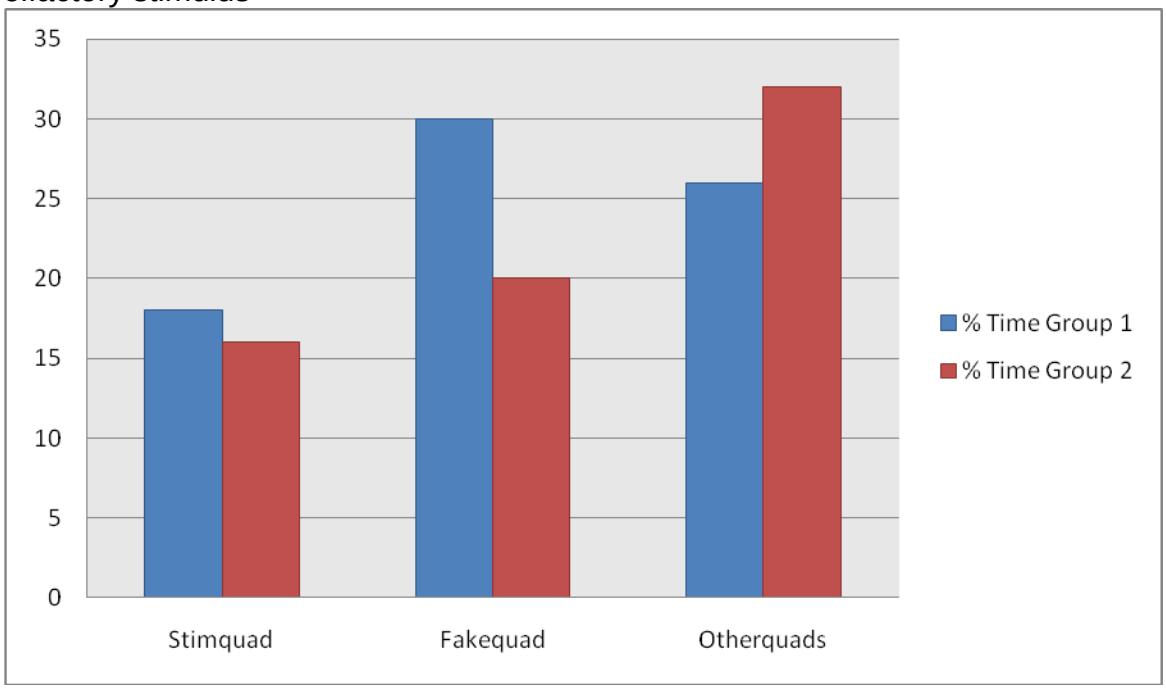
Figure 36: Collective Time spent within quadrants per trial thirds post visual, electroreceptive and olfactory stimulus



Time Spent in each Quadrant over Duration per Group

The first shark group spent 18% of their time within the stimulus quadrant whereas group two spent 16% of their time within this quadrant. Within the fake quadrant, group one spent 30% of their time within the fake stimulus quadrant and group two spent 20% of their time here. Within the other quadrants, group one spent 26% of their time here whereas group two spent 32% of their time within this quadrant. See Figure 37.

Figure 37: Time per quadrant per group post visual, electroreceptive, and olfactory stimulus



Group Time per Quadrant per Trial Thirds

Group one spent 16% of time within the stimulus quadrant over the first trial third, 12% over the second trial third, and 25% during the last third of trials. Within the fake quadrant, group one spent 27% of their time here during the first trial third, and nearly the same amount of time during the second and last trial thirds, 32% and 31% respectively. Twenty-eight percent of their time was spent within the other quadrant over the first two trial thirds and 22% during the last third.

Group two spent 16% of time within the stimulus quadrant over the first third of trials, 20% over the second third, and 13% time within this quadrant during the last third of trials. Sixteen percent of time was spent within the fake

quadrant over the first third of trials within group two, 21% during the second third, and 24% over the last third of trials. Within the other quadrant, 34% of time was spent here during the first third of trials, 30% during the second third, and 32% over the last trial third. See Figures 38 and 39. No significant differences were found between groups in times spent within each quadrant over trial thirds. However, there was a significant difference within the first group between time spent within the stimulus and fake quadrants during the first third of the trial (see Appendix C).

Figure 38: Percent Time per Quadrant over Trial thirds Group One

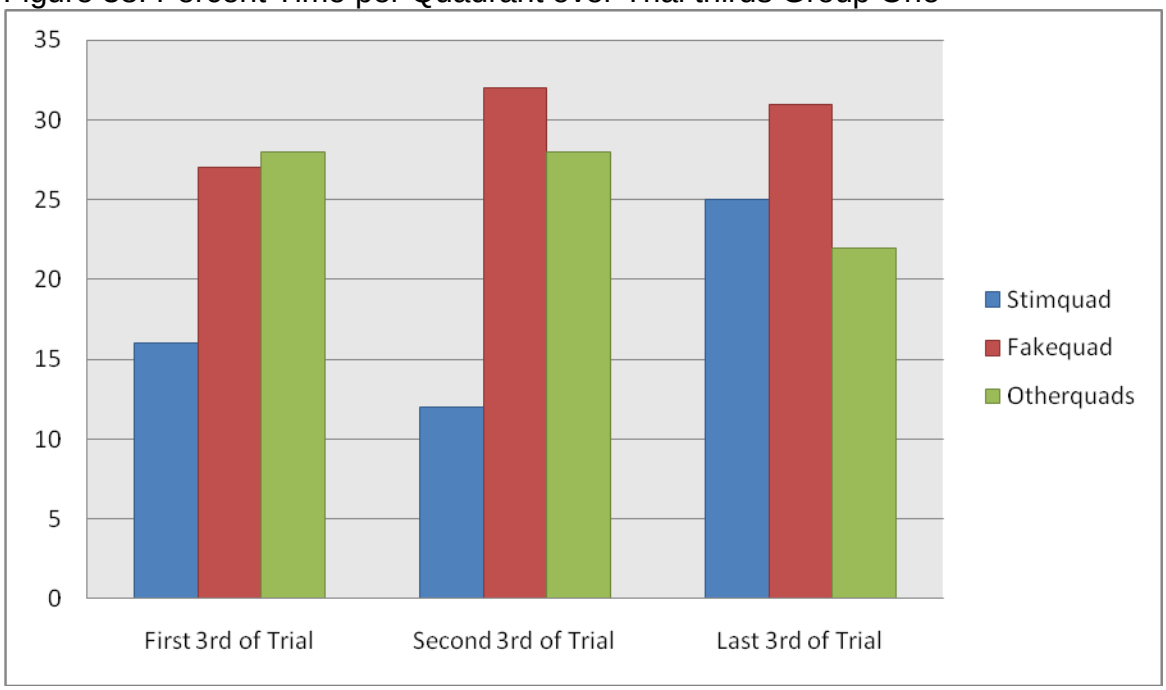
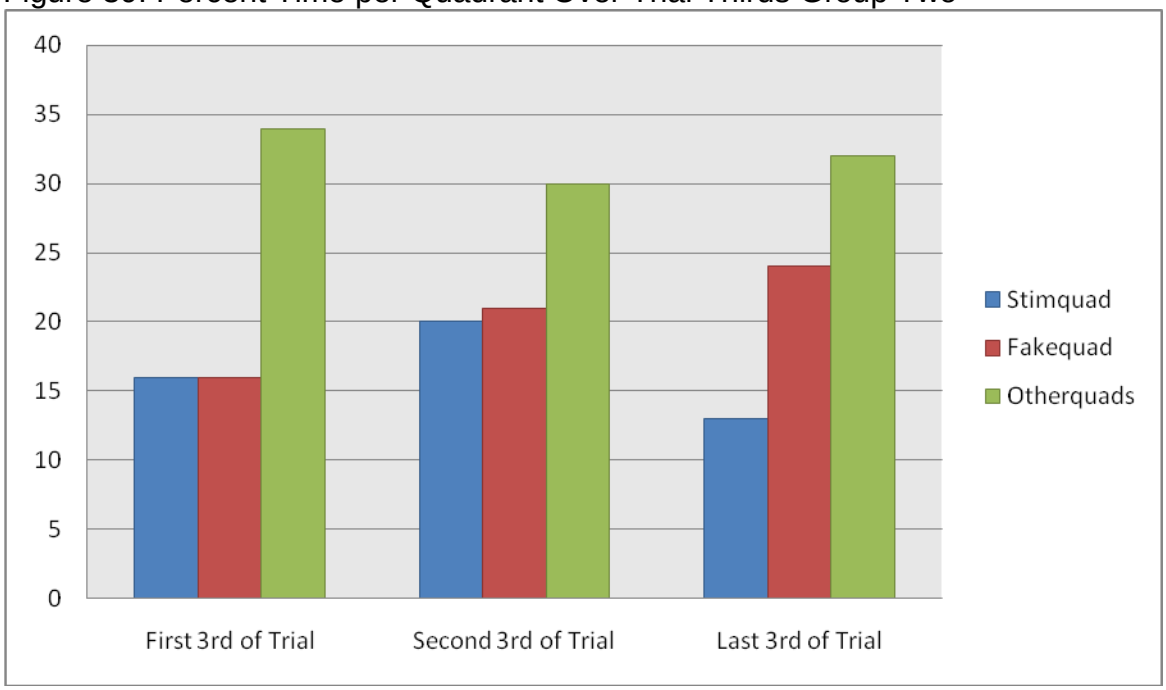


Figure 39: Percent Time per Quadrant Over Trial Thirds Group Two

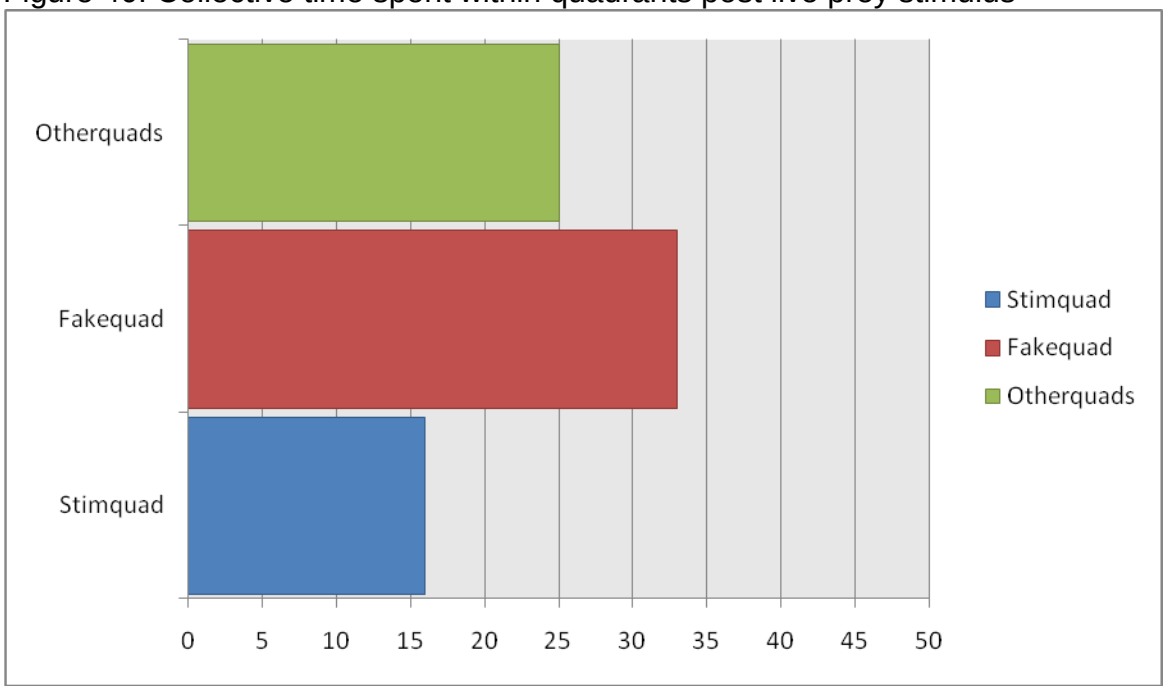


Live Prey (blue crab) Stimulus Condition

Collective time spent within quadrants over trial durations

When using live blue crabs as a stimulus, the sharks spent the more time in the fake quadrant (33%) than in the stimulus quadrant (16%) or other quadrants (25 %; See Figure 40). Significant differences in time were found between the stimulus and fake quadrants, stimulus and first other quadrant, fake and second other quadrant, and between both other quadrants in this condition (see Table 1).

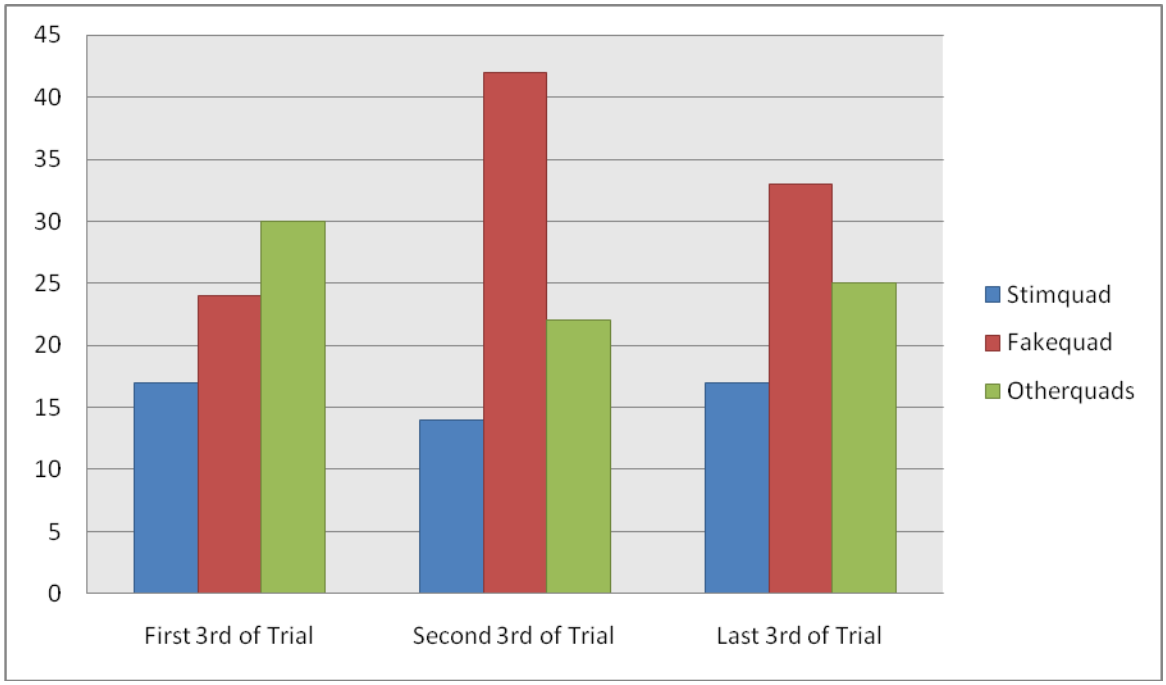
Figure 40: Collective time spent within quadrants post live prey stimulus



Collective time spent within quadrants per trial thirds

Within the stimulus quadrant, sharks spent nearly the same amount of time in this quadrant during each third of each trial (17%, 14%, and 17% first, second, and last thirds respectively). More time was spent in the fake stimulus quadrant during the second third of each trial (42%), followed by 24% during the first third of each trial and 33% during the last third of each trial. Within the other quadrants, sharks spent 30% of time here during the first third of each trial, followed by 22% during the second third of each trial and 25% during the last third of each trial; see Figure 41. A significant difference was found between time spent within stimulus and fake quadrants during the second trial third in this condition, see Table 2.

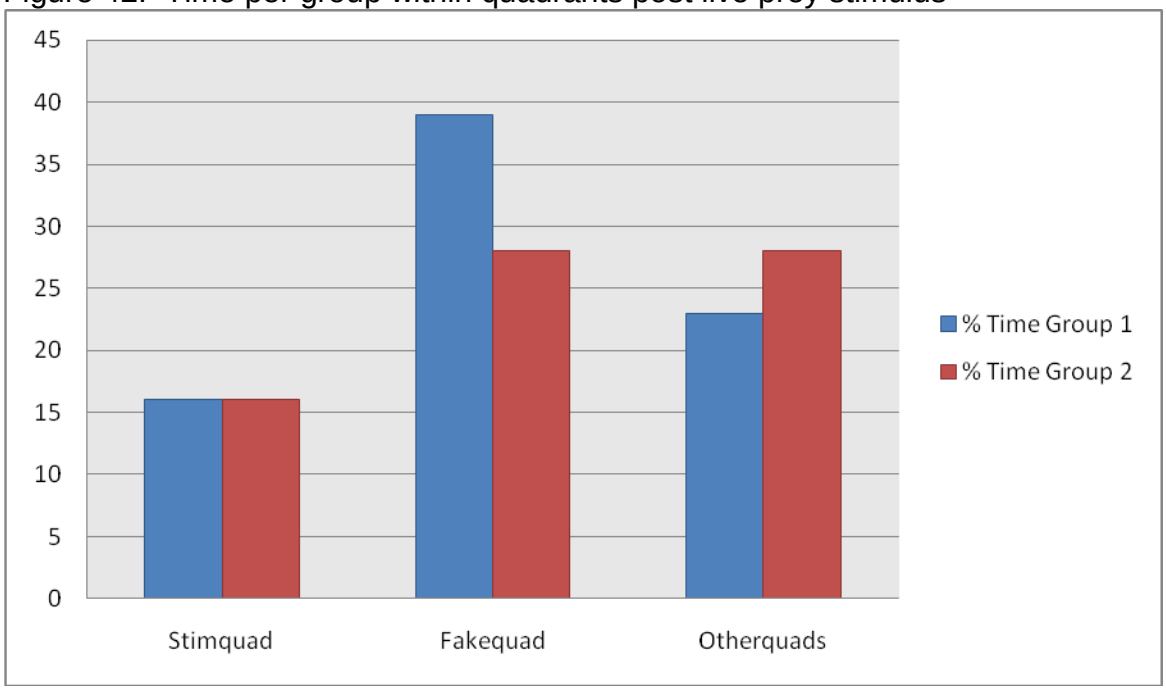
Figure 41: Collective Time spent within quadrants per trial thirds post live prey stimulus



Time Spent in each Quadrant over Duration per Group

Groups one and two spent the same amount of time (16%) within the stimulus quadrant in this condition. Within the fake stimulus quadrant, group one spent 39% of their time compared to 28% for group two. Within the other quadrants, group one spent 28% of their time within these quadrants and group two 25% of their time here. See Figure 42. No significant differences were found within the first shark group in this condition, however a significant difference was found within group two between times spent between the two other quadrants; see Appendix B. No significant differences were found between time spent within any quadrant between group one and group two in this condition.

Figure 42: Time per group within quadrants post live prey stimulus



Group Time per Quadrant per Trial Thirds

Groups one and two spent approximately the same amount of time within the stimulus quadrant, with group one spending 17% of their time in the quadrant during the first third, and 15% of time within this quadrant during the second and last trial thirds. Group two spent 17% of their time within the stimulus quadrant during the first third of the trials, 13% during the second third, and 19% during the last trial third. Within the fake stimulus quadrant, both groups again spent the same amount of time within this quadrant during the first trial third (24% group one and 25% group two). During the second trial thirds, group one spent 52% of their time within the fake quadrant and group two spent 33% of time here. During the last trial thirds within the fake quadrant group one spent 42% of time here and group two spent 25% of time in this quadrant. Within the other quadrants,

group one spent 30%, 16%, and 21%, respectively, within this quadrant over trial thirds and group two spent 30%, 22%, and 25% of their time in this quadrant over the respective trial thirds. See Figure 43 and 44. No significant differences were found between group times over trial thirds in this condition.

Figure 43: Percent Time per Quadrant per Trial Third Group One

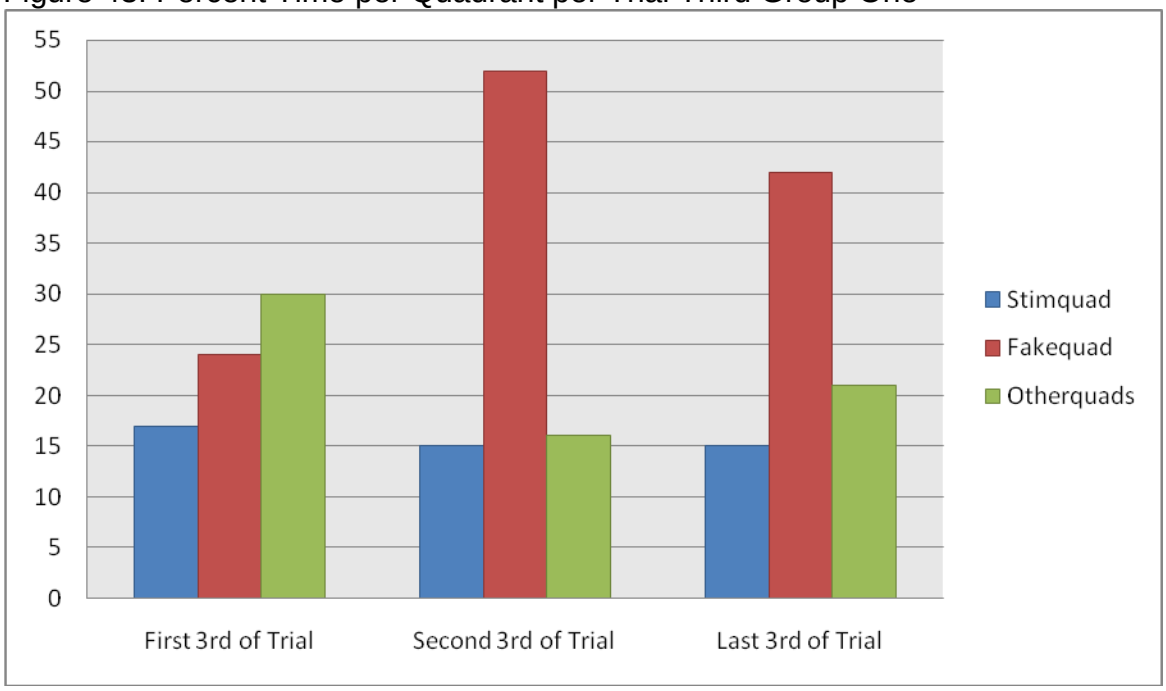


Figure 44: Percent Time per Quadrant per Trial Third Group Two

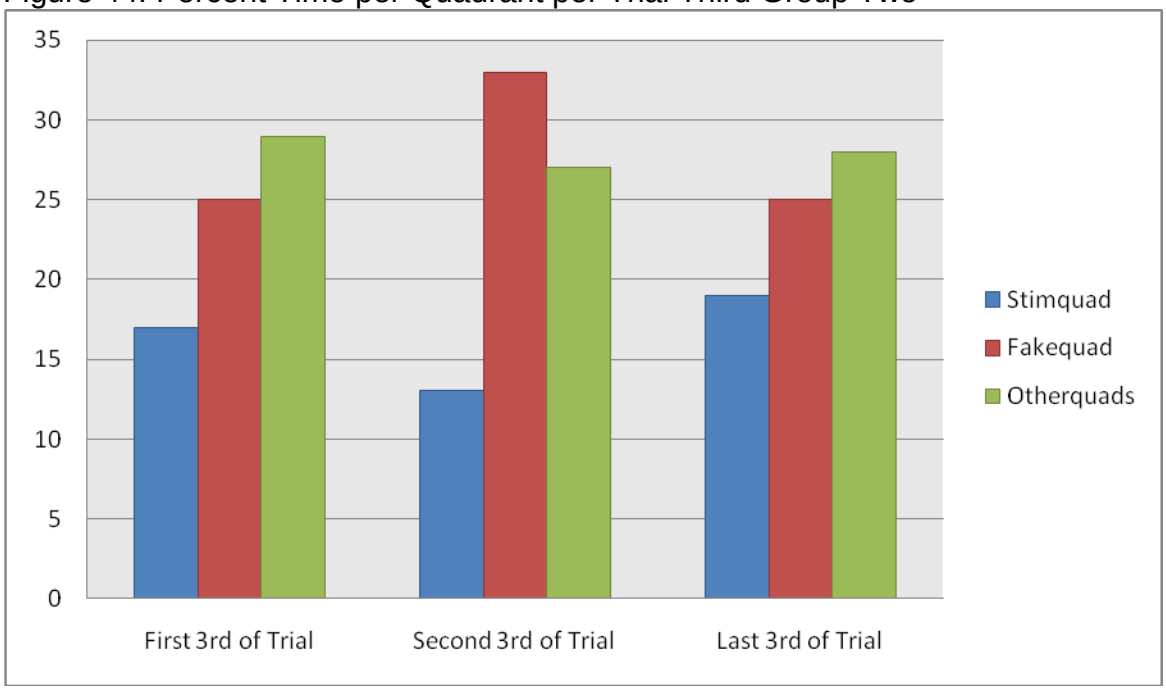


Table 1: Statistical Analyses: Split Plot Factorial Design ANOVA
Combined Groups Duration (Significant Results)

Condition	Quadrants	T Score	SD	P value
Vision				
	Stimulus v Fake	4.4651	13.3	0.0012
	Stimulus v Other1	3.6505	13.3	0.0045
	Stimulus v Other2	3.9994	15.4	0.0025
Electroreception				
	Stimulus v Fake	2.4693	33.9	0.0356
	Fake v Other1	2.3482	35.8	0.0434
Vision & Electroreception				
	Stimulus v Fake	3.8794	19.1	0.0037
Electroreception & Olfaction				
	Stimulus v Fake	2.6776	19.9	0.0253
	Stimulus v Other1	2.8577	20.4	0.0189
	Other1 v Other2	2.3419	20.2	0.0439

Table 1Continued

Condition	Quadrants	T Score	SD	P value
Vision & Olfaction				
	Stimulus v Fake	3.7394	38.6	0.0039
	Stimulus v Other2	3.6332	27.4	0.0046
Live Crab				
	Stimulus v Fake	2.5109	27.8	0.0309
	Stimulus v Other1	2.3408	26.9	0.0413
	Fake v Other2	2.6026	25.1	0.0264
	Other1 v Other2	2.4274	24.1	0.0356

Table 2: Combined Groups Thirds (Significant Results)

Condition	Third	Quadrants	T Score	SD	P value
Vision					
	First	Stimulus v Fake	4.1545	6.4	0.0020
	Second	Stimulus v Fake	4.5716	4.7	0.0010
Electroreception					
	Second	Stimulus v Fake	3.8047	8.5	0.0042
Vision & Electroreception					
	First	Stimulus v Fake	2.8548	7.7	0.0189
	Second	Stimulus v Fake	3.1482	10	0.0118
	Third	Stimulus v Fake	2.3323	9.1	0.0446
Vision & Olfaction					
	First	Stimulus v Fake	3.9191	12.9	0.0029
	Second	Stimulus v Fake	3.1239	11.6	0.0108

Table 2 Continued

Condition	Third	Quadrant	T score	SD	P value
Live Crab					
	Second	Stimulus v Fake	2.3184	14.6	0.0429

Discussion

Analyses Overview

Results from the three studies revealed bonnethead sharks possess an extensive blind spot directly in front of their cephalofoil. However, they appear to be capable of scanning a sizeable area of their visual environment (especially along the visual horizon) due to fairly broad lateral visual fields and lateral head motion that occurs during sinusoidal swimming. Vision may also play a role in this species predatory behavior, as they can detect, and appear interested in small visual stimuli that resemble their preferred prey species, the blue crab. Interest in small visual stimuli was enhanced when the visual stimulus was combined with an olfactory stimulus.

Estimates of the optical visual field suggest the bonnethead shark possesses monocular vision; however the lateral visual field appears relatively broad, especially when combined with data regarding degree of head movement during normal sinusoidal swimming. Their frontal visual field was found to be extremely limited due to their elongated head shape and eye placement at the extreme ends of their cephalofoil. As expected, no binocular overlap was found within their caudal visual field from the estimated optical visual field measurements. An expansive blind spot (of up to 112-113°) is located directly in front of their cephalofoil, which would greatly restrict visual information regarding the

environment immediately in front of them. However, the degree of lateral head movement that occurs within their normal sinusoidal swimming patterns may alleviate some of the blind spot by extending their lateral and caudal visual fields on opposite sides of their body.

A behavioral study including visual, electroreceptive, and olfactory stimuli attempted to ascertain whether these sharks can visually detect small stimuli, and other sensory modalities were tested in addition to vision to ascertain what the role of vision may be in this species predatory behavior.

Bonnethead sharks were found to be able to visually detect small objects in good water clarity conditions at close range (within 3 meters). This matches other observations of bonnethead behavior (Myrberg and Gruber, 1974; personal observation). However, this study was not able to illustrate exactly how these sharks use their visual system and was not meant to uncover exactly how vision was used, but whether it was possible these sharks visually detect small objects and to provide clues as to whether they may use vision in predatory behavior. As these sharks are social, are predated upon by larger fish, and feed on small, swiftly moving prey, vision could be useful in their daily survival. If these sharks are found to be diurnal or feed often over the span of 24 hours, vision would be helpful for detection of predators, prey, and conspecifics as the bonnetheads would need to be able to deal with varied and constantly changing environmental conditions (i.e. water quality and different lighting conditions).

This study also revealed the electroreceptive stimuli for bonnetheads (to detect prey) likely differs from that of larger hammerheads and even though

hammerhead sharks are be attracted to weak electroreceptive stimuli, they also appear to avoid strong electroreceptive stimuli, and may be indifferent (don't react) to some electroreceptive stimuli that may not resemble prey or predators.

These sharks likely require more than use of olfaction and electroreception to detect prey and appear to learn or habituate to stimuli quickly. This study also uncovered that the retinal ganglion cell topography of these sharks likely coincides with the visual horizon, given their broad, lateral visual field. Further study of neural physiology and behavior in this shark species may reveal if sensory integration, learning (plasticity) and/or both are responsible for the large telencephalon this shark possesses.

Visual Field Analysis

This study estimated the optical visual fields, area of an animal's environment where light can enter the eye (Martin, 1999). An animal's visual field contains important information regarding visual targets, whether they be prey, predators, or conspecifics (Martin, 1999). The horizontal physical visual field of the bonnethead was estimated to laterally extend between 34-38 ° (mean=35.3; SD=1.51) and the vertical physical visual field was estimated to extend between 30-32° (mean=31; SD=0.82). Bonnetheads appear to possess a fairly broad, lateral visual field and a potentially large blind spot (possibly as large as 112°) located directly in front of their cephalofoil. The optical visual field estimates indicate these sharks possess monocular vision with no binocular overlap within their frontal or caudal visual fields. Behaviorally, it is possible this

shark could utilize their visual sense to detect prey, predators and social body language cues of other bonnethead sharks. Though cephalofoil shape is sexually dimorphic in bonnethead sharks, no differences in the optical visual fields were found in this study. However, future research is needed to investigate whether differences in cephalofoil shape due to sexual dimorphism may affect the functional visual field of this species.

Visual fields comprise areas within the environment where a species can detect visual information (Beugnon, Lambin, and Ugolini, 1987; Martin and Katzir, 1994). Thus, visual fields can limit an animal's behavior by restricting the areas of its environment where visual targets can be sensed (Martin, 1999; Martin and Katzir, 1994).

The size, shape, breadth, and vertical extent of visual fields vary between species (Martin and Katzir, 1999). Determination of these aspects of visual fields are important to better understanding a species ability to detect potential prey, predators, and conspecifics. In addition they implicate environmental areas biologically important to a species (Collin and Shand, 2003). Thus, knowledge concerning the shape and size of an animal's visual field is essential for assessing the significance of their visual system.

Few studies have documented the visual field of fish, especially those of sharks (Hueter et al, 2004; McComb and Kajiura, 2008). Findings from these studies suggest visual fields of fish may be related to prey, predator, or conspecific detection, as well as schooling behavior (Hueter et al, 2004; McComb and Kajiura, 2008). Currently, only three studies of the visual fields in sharks or

batoids have been published Harris's study of the spiny dogfish (1965), Hueter and Gruber's study of the lemon shark (1982), and an exploration of batoid visual fields from McComb and Kajiura (2008).

Considering the unique shape of their cephalofoil, measuring the extent of Sphyrnid sharks' visual fields appears especially important in understanding the organization of their visual system. The unusual head shape and eye placement of hammerhead sharks appears to prevent them from obtaining any binocular overlap within their frontal visual fields, and instead creates an extensive blind spot directly in front of them. However, their sinusoidal swimming pattern should allow them to increase the area of their visual environment they are able to scan within their frontal and caudal visual fields.

As it appears bonnetheads possess a broad laterally expansive visual field, this would provide them with a wide lateral field of view; suggesting vision could be important to prey and predator detection. Especially as their visual field covers the environment along the visual horizon and area of ocean substrate just below the shark where their preferred prey species, blue crabs, are often found. Visual fields that provide a wide, lateral field of view suggest vision may be important to prey detection (Collin and Shand, 2003), even though many predatory species often possess eyes with some degree of binocular overlap (McComb and Kajiura, 2008). As bonnethead sharks approach their prey while swimming with distinct side-to-side head movements (Parsons, 1990; Wilga, 1998; Wilga et al., 2000), even with an extensive blind spot within their frontal visual field, bonnetheads could feasibly use their visual sense to detect potential

prey and predators at a distance due to the 35 degrees of lateral head motion that occurs within their normal swimming behavior. If all hammerhead sharks are found to possess no overlap between the visual fields of their eyes, it should provide more insight into possible functions of their visual and other sensory systems.

This species distinct lateral swimming motion could allow them to maximize their unusual eye placement at the furthest extents of their laterally expanded cephalofoil. This would allow them to visually sweep a large swath of the environment in front of them as well as scan large areas of the caudal visual environment on the opposite side of their body. If able to process information from both monocular visual fields simultaneously, they could continuously sample a large area of their frontal and caudal visual environment on opposite sides of their body to detect prey and predators at the same time. Whether or not they are able to process information from the visual fields of both eyes congruently is unknown, however, and should be investigated in future research, especially given the large size of their telencephalon. Even if they are found to be unable to simultaneously process visual information from both eyes; taking turns processing information from their lateral-frontal, then lateral-caudal visual fields should still allow them to simultaneously scan for predators and prey while swimming.

Species that are often predated upon and live within open areas, may benefit from a wide visual field encompassing a wide portion of their environment or even a visual field containing monocular visual fields that encompass a large

portion of their environment (Collin and Shand, 2003; McComb and Kajiura, 2008). Possessing a broad visual field should allow an animal to take in a large portion of their visual environment (Collin and Shand, 2003). This may also be true of bonnethead sharks, as they are predated upon by other shark species as well as larger fish and are generally found within shallow bays where water conditions can be fairly clear for parts of the year.

Visual detection of predators may be more important to bonnethead sharks than previously known, however it appears electroreception may be most important in localizing prey items once bonnetheads are within close proximity. The electroreceptive sense of the bonnethead shark appears to be effective within a short range, from around 10-22cm (Kajiura, 2003). Therefore, electroreception is likely the most important perceptual system for establishing the exact area prey items when they are located at close range for the bonnethead shark due to its feeding style and preferred prey species (Kajiura, 2003; Wilga, 1998; Wilga and Motta, 2000). The broad lateral visual fields of bonnetheads would be useful to detect prey at distances beyond the reach of their electroreceptive sense, regardless of whether they possess any degree of binocular overlap. Binocular overlap provides increased depth perception, but as bonnethead sharks feed on swiftly moving species who can quickly bury under the substrate, increased depth perception provided by binocular vision may not be as important as detecting motion or contrast, which would not require a high degree of depth perception.

Behaviorally, bonnetheads appeared most interested in the visual stimulus and the combination of the visual and olfactory stimulus within this study. Thus, olfactory stimuli could elicit search behavior, then vision could be used to locate prey roaming above the substrate at a distance and allow them to draw closer to the area in which prey are located so the shark could use their electroreceptive sense to pinpoint the exact location of prey items.

Maps of this sharks' retinal ganglion cell topography (Osmon, 2004) match the visual horizon, given the shape and lateral scope of their visual field. Thus, their retinal appears well suited to detecting visual information along the area of their visual horizon lateral to the shark's body. The increase in retinal ganglion cell density found within the dorsal-temporal area of their retina (a possible area centralis), if confirmed to exist, may be useful to detect visual stimuli along the leading areas of their visual environment that are scanned during sinusoidal swimming patters. This could allow the bonnethead sharks to react more quickly to visual stimuli, whether they are prey, predators, or conspecifics.

Analysis of lateral head movement and influence on visual field

Measurements using frame-by-frame tracings of swimming bonnetheads on video and MotionPro software indicate bonnethead sharks possess a moderate degree of lateral head movement, between 32-37° (mean=33.8; SD=1.94) during normal swimming behavior. This degree of lateral head movement appears sufficient to increase the area of visual environment they are

able to scan and decrease the size of the blind spot within their frontal visual field.

These findings match estimates from Myrberg and Gruber (1974) in their ethogram of bonnethead shark behavior. Myrberg and Gruber (1974) estimated bonnethead sharks possess around 40 degrees of lateral head movement during normal sinusoidal swimming behavior. As these sharks appear to possess an average of 35 degrees of lateral head movement, it would allow them to scan a considerable portion of their lateral-frontal and lateral-caudal visual fields while moving through the water.

Thus, it is feasible these sharks may utilize their visual sense to detect prey, predators, or conspecifics within their lateral-frontal and lateral-caudal visual fields. It is also plausible that these sharks may be able to alleviate some of the broad blind spot directly in front of their cephalofoil via lateral head movement associated with patrolling behavior. This would allow bonnethead sharks to visually detect prey from a distance when in focal search mode, until other sensory modalities took over for actual prey capture and manipulation. These sharks would also be able to visually detect larger predators, likely at a greater distance than detection of prey. If the head movement estimates are later re-confirmed, future research aimed at delineating their functional visual fields, along with behavioral testing would allow more precise assessment of how they use vision in prey and predator detection.

Visual stimulus detection and possible role in predatory behavior

Results from the behavioral study indicate bonnetheads found the visual stimulus and combination of the visual and olfactory stimuli most attractive, as they spent the majority of trial durations within close proximity to the stimuli (i.e. within the stimulus quadrant of the tank; See Figure 45). Sharks appeared most avoidant of the electroreceptive stimulus, visual and electroreceptive stimulus combination and live blue crab stimulus. Within the visual and electroreceptive stimulus combination condition sharks spent a significant amount of time in tank areas (quadrants) other than the quadrant containing the stimulus during these trials. As all conditions where significant results occurred contained a visual stimulus, including the live crab condition as this condition contained a biological organism emitting olfactory, visual, and electroreceptive information; it is likely that vision plays a role in their daily survival.

In the visual and olfactory stimulus combination condition & olfactory stimulus condition, all sharks except one male, exhibited a brief response to the stimuli immediately after introduction into the testing tanks. However, interest, as assessed by the amount of time sharks spent within the stimulus quadrant during trials, was not apparent in the olfactory condition though it was readily apparent in the visual and olfactory stimulus combination condition.

The brief reactions to the visual and olfactory stimulus combination and olfactory stimulus included increased swimming speed and tight circling behavior around the box containing the stimulus immediately after stimulus introduction.

This reaction ceased within 10-15 seconds and behavior after the reaction suggested sharks quickly lost interest in the olfactory stimulus when presented alone. When presented with the combination of visual and olfactory stimuli, sharks interest faded more gradually over trial durations. As the testing tank was small, the olfactory stimulus could have quickly and evenly distributed throughout the testing tank, thus making their reactions to it brief and making it impossible for the sharks to localize the source of the odor during olfactory stimulus trials.

It was hypothesized sharks would react most strongly to conditions containing an electroreceptive stimulus and localization of a stimulus source would be most accurate (indicated by sharks circling and attempting to bite the stimulus) and occur most quickly in the condition where all three sensory cues (visual, electrosensory, and olfactory) were combined. Previous research has shown hammerhead sharks readily react to weak electroreceptive stimuli when in close proximity to the stimulus (Kajiura, 2003; Kajiura and Holland, 2002). However, in this study sharks consistently avoided the stimulus quadrant or were indifferent to it in all conditions containing an electroreceptive stimulus except the visual and electroreceptive stimulus combination. A potential reason for this may be the strength of the electroreceptive stimulus used in this study. Though the dipole device was based on the design of Kajiura (2003) and Kajiura and Holland (2002), it may not have included enough resistance to sufficiently decrease stimulus strength or smaller

bonnethead sharks may react more negatively to electroreceptive signals that larger hammerheads find attractive.

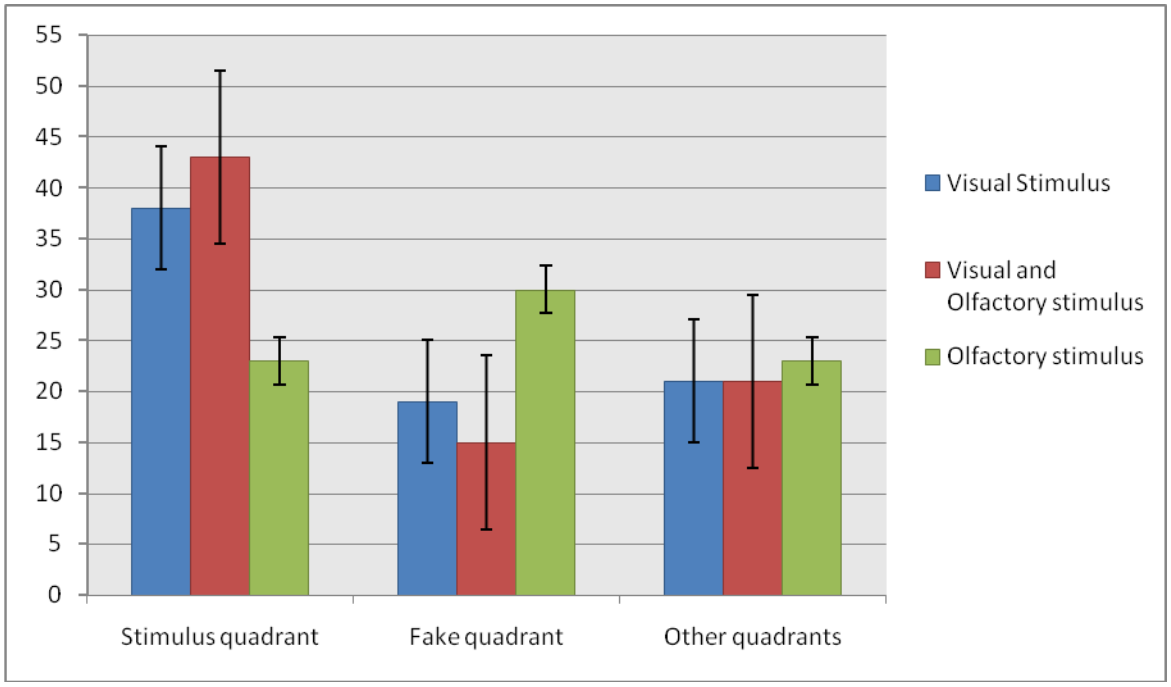
Sharks also did not react positively to a live blue crab, their preferred prey species (Cortes, Manire, and Hueter, 1996; Cortes, and Parsons, 1996; Hoese and Moore, 1958; Motta and Wilga, 2000; Myrberg and Gruber, 1974). Possible reasons for these negative responses will be discussed in detail within the next section.

Data collected from the behavioral study was broken down and analyzed in several manners to assure any subtle variations in behavior would be detected. First, data regarding time spent within each quadrant (stimulus, fake, and others) from all sharks were recorded over the duration of trials for each condition. Second, data from each condition was divided into thirds. Data was broken into thirds over trial duration, as sharks have often been noted to quickly lose interest in behavioral stimuli (Kajiura and Holland, 2002, Johnson and Teeter, 1984). By breaking data into thirds, any early behavioral reactions to stimuli would be better able to be observed and quantified. Third, data from within each of the two shark groups tested were compared over trial durations and trial thirds to assess any significant differences between reactions of sharks in each group tested due to possible seasonal alterations in behavior, as groups were tested approximately two and a half months apart.

Results of this study suggest vision does play a role in locating objects of interest. However, further behavioral testing is needed to reveal

the exact role of vision in predatory behavior within this species natural environment.

Figure 45: Comparison of Visual, Visual and Olfactory, and Olfactory Stimulus condition results; (time per quadrant over trial durations) with standard error



Analysis of Visual Stimulus Condition

Species are often categorized into which sensory modality they are thought to predominantly rely on to detect prey, predators, and conspecifics, such as being primarily visual, auditory, tactile, olfactory, or electrosensory (Bodznick, Montgomery, and Tricas, 2004; Bonazzo and Collin, 2000; Bozzano, Murgia, Vallerga, Hirano and Archer, 2001; Fernandez-Juricic, Erichsen and Kacelnik , 2004; Graeber, 1978; Gruber, 1977; Hayes and Brooke, 1990;

Johnsen and Teeter, 1985; Kajiura, Forni, and Summers, 2005; Moller, 2002; Montgomery, Macdonald, Baker, and Carton, 2002; New, Fewkes and Khan, 2000; Pankhurst, 1989; Strong, 1996; Watanuki, Kawamura, Kaneuchi and Iwashita, 2000). Sharks are popularly believed to rely heavily on their olfactory and electrosensory senses. Sharks, including hammerhead sharks such as the bonnethead shark, have been shown to possess an acute sense of electroreception (Kajiura, 2003; Kajiura and Holland, 2002). According to Kalmijn (1982) sharks appear able to detect voltage gradients of 1-2nV/cm and hammerhead sharks react to voltage gradients of 0.025μ V cm^{-1} (Kajiura and Holland, 2002). However, little is known regarding the visual capabilities and role of vision in hammerhead shark behavior. The results of this study suggest sharks detected, and in certain visual stimulus conditions, were interested in the visual stimulus.

Within the visual stimulus condition, sharks collectively spent a significant amount of time over trial durations within the stimulus quadrant compared to the fake and both other quadrants. Though they spent a significant amount of time within close proximity to the stimulus in this condition, their interest in the visual stimulus was not overt, as no definitive reactions (circling behavior, biting or bumping the stimulus box) were recorded during visual condition trials.

Between the two shark groups tested, the first group did not appear to show as much interest in the visual stimulus as the second group, as they spent (32%) of their time in the stimulus quadrant over trial durations compared to (44%) for the second group. Within the first group tested,

only time spent within the stimulus versus the fake quadrant was significant, whereas time spent between the stimulus quadrant and all other quadrants was significant in the second group. However, times spent in any quadrant over trial durations between the two shark groups were not found to be significant.

The discrepancy between times spent within the stimulus quadrant compared to all other quadrants between the two groups supports that the second group appeared most interested in the visual stimulus. This result was also reflected in times spent within the stimulus quadrant between the groups when trials were broken into thirds.

When trial durations were broken into thirds, sharks from the first group spent the most time in the stimulus quadrant during the first third of trials (39%) and nearly the same amount of time here during the second and last trial thirds (32% and 26% respectively). In the second group of sharks tested, nearly the same amount of time was spent within the stimulus quadrant (42%, 41%, and 50% respectively) over all trial thirds. Though the first group spent less time in the stimulus quadrant overall than the second group tested, there was no significant difference between the groups in time spent within the stimulus quadrant over the duration of trials within this condition. As all sharks displayed interest in the visual stimulus condition, in regards to the time they spent within the stimulus quadrant within this condition, it suggests they may utilize vision to detect and hone in on potential prey items that are within close proximity (within

three meters) in conditions with good water clarity, as the visual stimulus simulated a small blue crab.

One possible reason for the difference between the groups could be pre-testing of the visual stimulus in first shark group. Pre-exposure to the visual stimulus occurred at least once prior to actual testing to sharks within the first group tested. These sharks were pre-exposed before testing to ensure the visual stimulus utilized was viable for test trials and whether the testing apparatus would provide sufficiently accurate results. Thus, pre-exposure to the visual stimulus prior to testing may have allowed sharks within the first group to habituate to the visual stimulus, decreasing any reaction they may have had to it during actual test trials. Sharks have been noted to learn quickly and are easily conditioned using visual stimuli (Clark, 1967; Gruber, 1975; Hueter et al., 2004; Wright and Jackson, 1964; Tester and Kato, 1965). Habituation may also be important to teleost fish in learning what types of stimuli to avoid in regards to predator avoidance (Kelley and Magurran, 2003; Laland, Brown, and Krause, 2003).

Thus, without rewards or consequences being associated with the stimuli, sharks may have become somewhat indifferent to the stimulus after repeated presentations. As interest in the visual stimulus decreased over trial thirds, indicated by a decrease in the amount of time spent within the stimulus quadrant over trial thirds, habituation to the stimulus may have occurred, especially within the first shark group. Thus, by the last

third of the trials these sharks may have been exhibiting normal swimming patterns within the tank.

Therefore, results from the second shark group tested likely provide a more accurate representation of bonnethead sharks' response to visual stimuli resembling their preferred prey species. Though sharks have been noted to quickly lose interest in behavioral stimuli, especially electroreceptive and olfactory stimuli (Kajiura, 2003; Johnson and Teeter, 1985), and teleost fish are known to decrease reaction to stimuli over successive exposures (Laland et al., 2003), future research is necessary to definitively confirm habituation occurs with visual stimuli, especially as sharks in the second group tested (no pre-exposure to visual stimulus prior to testing) did not seem to lose interest in the visual stimulus over trial duration.

In their ethogram of bonnethead shark behavior, Myrberg and Gruber (1974) found patrolling behavior increased over the course of the day, reaching its highest level during the late afternoon. This would suggest bonnetheads have a diurnal activity pattern. However, the retinal ganglion cell topography of these sharks would suggest they either possess a more nocturnal activity pattern (Osmon, 2004), or that vision for contrast detection is more important than acuity. As these sharks feed frequently and possess a high metabolism (Parsons, 1990); they may actively feed during both day and night.

According to Montgomery et al. (2002) a species visual system does not appear to need to be geared toward acute vision to aid a species in detecting

visual stimuli such as prey and predators at a distance. In fact, according to Montgomery et al (2002) and Bozzano et al., (2002) being sensitive to motion or contrast detection may be more useful in localizing stimuli at a distance than other sensory systems (such as electroreception). This may be especially true if the species feeds on large or quickly-moving prey (Bozzano et al., 2001).

As ram feeders, bonnetheads scoop prey from the substrate into their mouths (Wilga and Motta, 2000) and likely use electroreception to pinpoint prey items within close proximity in the moments just prior to capture (Kaijura, 2003). However, as the electroreceptive sense of bonnetheads is only effective within 10-22cm (Kajiura, 2003) vision may be useful to locate prey wandering above the substrate at a distance greater than their electroreceptive sense is effective, thus allowing them to get close enough to their prey to use their electoreceptive sense to capture it.

As bonnetheads, like many other shark species, are able to adjust their pupil depending on the amount of light present within the environment, this may allow bonnetheads to hunt in various lighting conditions (Hueter et al, 2004). Thus possession of a visual system geared toward high sensitivity to contrast or movement may be more adaptive, especially as bonnetheads require constant motion to breathe and this would negate the need of their visual system to adapt to an environment in constant motion, which would require more acute vision (Hueter et al, 2004). Thus, bonnetheads may gain an advantage in detecting visual stimuli at a distance greater than their electroreceptive sense by possessing a retina designed for contrast/motion detection. If this is so, utilizing

all sensory modalities would be most advantageous, as this would allow them to detect and capture prey in many different environmental conditions (i.e. clear or turbid water and in light or dark conditions).

Anecdotal evidence exists that some shark species may rely on vision during prey capture (Hueter et al, 2004; Klimley, 1994; Strong, 1996); however, not enough research has been completed to confirm this in most species (Fouts and Nelson, 1999; Hueter et al, 2004). Fouts and Nelson (1999) conducted one of the only studies investigating vision in sharks while holding other sensory variables constant. Their study focused on the Pacific angel shark, the only shark currently known to rely predominantly on vision to capture prey (Fouts and Nelson, 1999). Another shark believed to use vision to detect and pinpoint the location of prey is the Great white shark (Klimley, 1994). Support for this comes from a behavioral study regarding predatory behavior upon various shaped stimuli, as they appear to only attack specific shapes (Strong, 1996).

However, both species possess different feeding modalities and consume prey species that differ from the feeding modality and diet of the bonnethead shark. Bonnetheads are ram-feeders predating primarily on blue crabs (Cortes et al, 1996; Cortes and Parsons, 1996; Hoese and Moore, 1958). These crabs are able to rapidly change direction and are often found just above the substrate (Kajiura, 2003). Shark species predating on swift-moving prey items, such as bonnethead sharks, may gain an advantage by utilizing their visual system as well as possessing a visual system that is sensitive to movement (Bozzano et al., 2001). The great white and angel shark are both ambush predators. The great

white often ambushes marine mammals from below and the angel shark hides just under the substrate and ambushes small fish that swim over the sharks' location (Fouts and Nelson, 1999; Klimley, 1994). More recently, Greenland sharks within the St. Lawrence River, not known for their visual abilities, were found to be able to potentially use vision to locate prey items (Harvey-Clark, Gallant, and Batt, 2005).

Thus, it is possible vision is one of several sensory modalities the bonnethead shark uses to help localize prey found above the substrate once it is detected via olfactory cues or with the lateral line system. It is known that larger hammerhead sharks may rely heavily on electroreception to detect cryptic prey when within close proximity (Kajiura, 2003). However, use of vision in prey localization could allow a hammerhead shark to get close enough to electroreceptively pinpoint the exact location of prey items if above the substrate or if the crab quickly buries itself under the substrate when predators approach.

In addition to detection of prey items, vision may also be useful to smaller sharks such as bonnetheads for predator avoidance. Use of vision to detect the close proximity of large objects can produce a rapid escape response in smaller shark species (Domenici et al, 2004).

Bonnethead sharks have been noted to quickly dart away from large stimuli (Myrberg and Gruber, 1974). In their study, Myrberg and Gruber (1974) noted that bonnetheads would occasionally react to divers with an aggressive posture. However, the only times this occurred was when a diver was located to either side of the sharks (laterally) and the shark was within at least six feet of the

diver (Myrberg and Gruber, 1974). This suggests bonnetheads utilize vision and can see large visual stimuli within at least two meters (around 6 feet). Though the current study focused on predatory behavior, these sharks may also utilize their visual sense to detect larger predatory fish.

Further evidence for use of vision in bonnethead sharks may be found in their social behavior. Hammerhead sharks, including bonnetheads, are often found in loose groups and have been noted to use postural displays, possibly denoting a loose social organization (Klimley, 1996; Myrberg and Gruber, 1974). At least 18 different postures and swimming patterns have been documented in the bonnethead shark (Myrberg and Gruber, 1974). Many of these postures and swimming patterns were believed to be social in nature, and possibly represent a loose social structure within the bonnethead shark (Myrberg and Gruber, 1974). Thus, vision may be important to prey detection and localization, in predator detection and avoidance, as well as for communication with conspecifics (Myrberg, 1991; Myrberg and Gruber, 1974).

Though vision may play a role in detecting prey, the extent to which it is utilized in prey detection cannot be definitively assessed within this study. Water clarity within testing tanks was likely better than average conditions that are present within Tampa Bay where the sharks were caught. In addition, the tank was relatively small, thus the sharks may have been able to detect the visual stimuli more easily than they would when normally patrolling for prey in the wild where their attention to stimuli

may be divided dependent on their current situation, as species must deal with multiple stimuli simultaneously within the natural environment.

Analysis of Visual and Olfaction Stimulus Condition

The combination of visual and olfactory stimuli appeared to be the most interesting condition to the sharks, as there was a significant difference found between the time spent in the stimulus quadrant versus the fake and one of the empty (other) quadrants from data of all sharks combined. Within this condition sharks collectively spent 43% of their time within the stimulus quadrant compared to 13% within the fake quadrant and 22% within the other quadrants combined.

Sharks were also consistent in spending the most time within stimulus quadrant over trial thirds. As both groups showed a positive reaction to this stimulus condition, from the amount of time spent within the stimulus quadrant compared to quadrants without a stimulus and time spent within the stimulus quadrant was higher in this condition over the visual stimulus condition, the olfactory stimulus may have heightened sharks interest in this stimulus combination, at least initially.

As olfactory stimuli are known to elicit predatory search behavior in sharks (Kajiura and Holland, 2002; Johnson and Teeter, 1984; Myrberg and Gruber, 1974), sharks may have been more interested in this condition over the visual stimulus alone. Other research (Kajiura and Holland, 2002; Johnson and Teeter, 1984) as well as the author's

personal observations from feeding sharks used in this study suggests olfactory stimuli elicit food search behavior in sharks.

During feeding sessions an increase in tight, sharp circling behavior throughout the tank and swimming speed (due to an increase in tail beat frequency) was noted once sharks detected the odor of herring cubes dropped into the tank. If herring cubes were dropped into the water as a shark swam by, sharks would often pass by the olfactory stimulus. Once the olfactory stimulus was detected, sharks reacted by swimming in tight circles within the tank, sometimes missing the herring cubes at the bottom of the tank several times, before they finally located the exact source of the stimulus.

According to Kleerekoper et al (1975) nurse sharks have little difficulty localizing the source of an olfactory stimulus in water containing a current, however, in non-moving (calm) water conditions, nurse sharks took longer to pinpoint the exact location of an olfactory stimulus and would search, instead, within the general vicinity of the stimulus until it was located (Kleerekoper et al, 1975). Further support for the possible difficulty in using olfactory stimuli alone to pinpoint the location of an olfactory stimulus source comes from Johnson and Teeter (1984). They found olfactory stimuli appeared to travel within a “blob” in a current and thus moving water may slow dissipation of olfactory stimuli (Johnson and Teeter, 1984).

Though both groups showed a decrease in time spent within the quadrant containing the stimulus compared to all other quadrants in this condition, this

difference was not significant in the first group, but was found to be significant within the second shark groups. Overall, sharks may have lost some interest in the stimulus over time, especially as the olfactory stimulus may have dispersed throughout the testing tank and/or fallen below sensory thresholds over trial durations. However, it appears that the initial interest in the stimulus quadrant within the second group quickly and significantly faded over trial duration. Unlike the results from the visual condition, within the visual-olfactory condition the amount of time spent within the stimulus quadrant decreased slightly over the duration of trial thirds in both shark groups. Time the first shark group spent within the stimulus quadrant fell from 50% during the first trial third to 38% during the last third and from 57% in the first trial third to 25% during the last third for the second shark group.

Within this study, most sharks were noted to have a brief, but short-lived reaction to the olfactory stimulus immediately after its presentation within the visual-olfactory stimulus condition. As the tank pump was off and no current existed within the tank during test trials, the olfactory stimulus may have dispersed quickly and evenly throughout the small testing tank. This may explain why the visual and olfactory combination condition was the only condition within the study where interest was high within the first third of the trial and gradually decreased over trial duration and explain the significant decrease in time spent within the stimulus quadrant found within the second group. This decrease in interest over trial thirds within the first group may not have been as significant due to pre-exposure to the visual stimulus prior to testing within this

group. Thus, their level of interest was likely not as acute as that of sharks within the second group tested. After dissipation of the olfactory stimulus, interest in the stimulus quadrant may have waned within the second group, as the visual stimulus was not as attractive to them without the addition of the olfactory stimulus. The collective decrease in interest in the stimulus over trial thirds may also be sign that sharks became less interested in the stimuli over time (habituation), regardless of whether the olfactory stimulus dissipated within the tank.

Though interest in the stimulus appeared nearly the same in the second shark group between the visual stimulus condition (44% of time in stimulus quadrant) and visual-olfactory stimulus combination conditions (43% of time in stimulus quadrant), there was an increase in time spent within the stimulus quadrant between the visual stimulus condition (32%) and visual and olfactory stimulus combination condition (43%) within the first shark group. Thus, if previous exposure to the visual stimulus was the reason for the subtle response in the visual stimulus condition within the first group of sharks tested, the addition of the olfactory stimulus may have also negated some habituation to the visual stimulus in this condition, at least initially.

An additional possibility for the sharks' interest in this condition may be the small visual stimulus (resembling their preferred prey species). As more investigation occurred within the correct area within this condition (localization of stimulus to the stimulus quadrant), combining a small

visual stimulus with an olfactory stimulus may have caused the sharks to investigate whether or not the stimulus within this condition was a potential prey item.

Analysis of Olfaction Stimulus Condition

Though all sharks briefly reacted to the stimulus via tight circling within the tank or bumping into the stimulus box immediately after initial stimulus presentation, except the male in the second group tested, no significant difference in time spent within the stimulus quadrant as compared to time spent within all other quadrants combined was found. In fact, sharks spent roughly the same about of time in the stimulus quadrant (23%) as in the fake quadrant (30%) and combined other quadrants (23%) over trial durations.

When data was parsed into thirds for each trial, no definitive trend was found in the times each group spent within each quadrant as well. Both shark groups spent relatively the same amount of time within the all quadrants over trial thirds and no significant differences were noted between shark groups in time spent in any quadrant over trial durations in this condition.

In their study of bonnethead olfaction, Johnson and Teeter (1985) found bonnetheads could easily differentiate varied odor intensities between their nares. Thus, it is quite possible that bonnethead sharks are not only able to detect, but also to discern the direction in which an

olfactory stimulus is located. While this is quite plausible, Johnson and Teeter (1984) employed methods where olfactory stimuli were introduced to the sharks via tubes located directly in front of the shark's nares. This could have allowed the sharks to more easily differentiate the intensity of the olfactory stimuli within their study, as in the natural environment, olfactory molecules would likely not be as concentrated when reaching a shark's olfactory receptors. In addition, Johnson and Teeter (1984) noted bonnetheads behavior toward olfactory stimuli also suggested the involvement of other sensory modalities to localize the exact source of an odor. Within the marine environment a current containing an olfactory stimulus could dissipate before a shark had a chance to hone in on the exact location of an olfactory cue, or the odor could flow in a direction away from the actual source of the stimulus. Thus, other sensory modalities, in addition to olfaction, may be required to definitively locate the source of an olfactory stimulus in the open water (Johnson and Teeter, 1985). Therefore, though bonnetheads have been shown to readily orient toward an olfactory stimulus, other sensory modalities may be necessary to establish the exact location of an olfactory stimulus (Johnson and Teeter, 1985).

In still tank water, an olfactory stimulus appears to quickly and evenly disperse throughout the tank (Johnson and Teeter, 1985). This may help explain the shark's lack of reaction within this study, except for the brief increase in tail beat frequency and tight circling behavior noted immediately after presentation of

the olfactory stimulus. If the odor stimulus evenly dispersed within the tank, it was likely difficult for the sharks to pinpoint the exact location of the odor source. In addition, dispersion of the olfactory stimulus throughout the tank could have caused the stimulus to fall below threshold levels which would allow the sharks to maintain a behavioral reaction to the odor.

Olfaction is utilized by many species to detect and locate prey items (Bozzano et al., 2001; Combs et al., 2002; Moller, 2002). It may also be useful in mating and social interactions (Bozzano et al., 2001; Combs et al., 2002; Moller, 2002). Bonnetheads are no different than other sharks in possessing a keen sense olfactory sense (Johnson and Teeter, 1985), something sharks are popularly known to possess. Olfaction appears to be an important stimulus in regards to alerting sharks of the nearby presence of food, especially as sharks often initiate food searching behavior when exposed to an olfactory stimulus (Kajiura and Holland, 2002; Johnson and Teeter, 1984). In fact, Johnson and Teeter (1985) believe food searching behavior stimulated by olfactory stimuli is likely used to help a shark stay within close proximity to the source of an olfactory stimulus. Turing behaviors associated with the food search behavior elicited by olfactory stimuli were also believed to aid a shark in keeping track of an olfactory stimulus, especially in water where current or other factors could disturb the path of the left by the odor as it travels along the current (Johnson and Teeter, 1985). This suggests olfaction

may often be more useful to sharks in detecting the presence of prey than it is to pinpointing the exact location of prey items.

Requiring information from other sensory systems to pinpoint the location of an olfactory stimulus source matches observations of the sharks' behavior when fed after testing sessions. Sharks would often pass the herring cubes when initially placed into the tanks. Once sharks detected the odor of the herring, they would increase their swimming speed and begin to perform tight circles within the tank. The circling behavior would eventually bring them close to the herring, though they would often pass the exact location of the herring on the bottom of the tank several times before consuming the fish. Thus, odor may be easily detected, but more difficult to pinpoint the exact location of without input from other sensory modalities.

Vision may also not have played a large role in their behavior when being fed. In videos of feeding sessions, it was difficult to visually ascertain the location of the herring cubes, as the cubes were no larger than one cubic inch in diameter and blended well with the background color of the tanks. At times, it was difficult for the experimenter to visually locate the herring cubes from above the tank. As human vision is more acute than bonnetheads, visually locating the herring cubes would have been extremely difficult for the sharks.

As conditions within the marine environment of sharks are subject to change, the ability to integrate information from a number of sensory modalities,

such as utilizing olfaction to detect prey along with vision to localize and capture prey, should be valuable (Boznick, 1991). Excessive reliance on one sensory modality would likely limit the amount of information available to an animal and make it difficult to determine whether a detected stimulus is a prey item, con-specific, or predator (Bodznick, 1991). However, if details of a stimulus from several sensory modalities are integrated, it could provide enough information to allow an animal to recognize a stimulus as a predator or prey item, in addition to aiding the animal in locating and capturing prey or evading predators (Boznick, 1991).

Thus, within the olfactory condition, the possibility exists that sharks were initially interested in the quadrants containing the stimulus boxes; however, as they lacked visual, electroreceptive, and possibly even olfactory cues (if the odor had evenly dispersed within the tank fairly quickly) it would have made pinpointing the exact location of the olfactory stimulus difficult and if the stimulus decreased to below sensory thresholds, the sharks could have lost interest in the stimulus quickly and resumed normal swimming behavior throughout the tank. Though bonnetheads appear to notice olfactory stimuli fairly quickly, within moving water, the stimulus may dissipate before the shark can pinpoint the location of the stimulus source, thus other sensory modalities are likely required to definitively localize the source of an olfactory stimulus (Johnson and Teeter, 1985).

The fact that no significant differences were found in time spent within any quadrant over trials suggests the sharks may have had difficulty

in definitively locating the odor source using olfaction alone, or that the stimulus fell below sensory thresholds quickly. Thus bonnethead sharks likely need input from other senses to pinpoint the location of an odor source.

Analysis of Electroreceptive Stimulus Condition

Collectively among sharks, significant differences were found between time spent in the stimulus and fake quadrants during the second trial third within this condition. Differences between groups in time spent within quadrants between were not significant. Though differences between times spent within the stimulus versus the fake quadrant came close to significance within the first group, no significant differences were found within either group in this condition. As times spent within the fake quadrant, as compared to the stimulus quadrant were close to significance within the first group, but not within the second shark group tested, this suggests sharks within the first group were possibly more avoidant of the electroreceptive stimulus and sharks within the second group were more indifferent to this stimulus.

Within the electroreceptive condition, sharks collectively spent less time in the stimulus quadrant than in quadrants not containing a stimulus. Sharks spent the most time in the fake quadrant (41%) over the stimulus and other quadrants (18% and 21% respectively), emphasizing some possible avoidance to the electroreceptive stimulus.

As these results do not match those from other investigations of hammerhead sharks reactions to electrical stimuli (Kajiura, 2003; Kajiura and Holland, 2002), it appears the electroreceptive stimulus used in this study may have been too strong or unidentifiable as a prey item. Kajiura and Holland (2002) noted that an electrical signal from a dipole would decrease in intensity the further away an organism is from the dipole. Thus, at a distance, the ability to detect a weak electrical stimulus should fall below sensory thresholds (Kajiura and Holland, 2002). As sharks within the first group tested in this study appeared avoidant of the stimulus quadrant during electroreceptive stimulus trials, it is likely the stimulus was strong enough to be detected by the sharks over 30cm away, and thus the electrical stimulus likely did not represent a prey item, but possibly a predator or a very strong electrical stimulus that could not be identified as prey or predator by the sharks without information from other sensory modalities.

Results from the first shark group suggest they may have been avoiding the stimulus quadrant. During trials containing an electroreceptive stimulus, the large male shark from the first group was noted to have darted quickly away from the stimulus when it neared its location. The larger male from the first group tested within this study appeared to react most negatively to electroreceptive stimuli, as this shark spent no time within the stimulus quadrant over electroreceptive stimulus trial duration and spent little to no time within the stimulus quadrant in all conditions that contained an electroreceptive stimulus.

Data from analysis of trial thirds between the shark groups, supports observations that sharks in the first group may have been more wary of the electroreceptive stimulus. Sharks within the first group spent an average of 11%, 10%, and 18% of their time within the stimulus quadrant over each trial third, respectively and 54%, 49%, and 46% of their time within the fake stimulus quadrant over each successive trial third. However, sharks within the second group appeared fairly indifferent to the electroreceptive stimulus in this condition. The amount of time they spent within the stimulus, fake, and both other quadrants over trial durations and thirds was fairly similar (25% in the stimulus quadrant, 28% in the fake quadrant, and 23% between both other quadrants over trial duration). Over trial thirds, sharks within the second group did show a slight increase in the time they spent within the fake quadrants over trial thirds (from 21% during the first third to 33% and 30% during the last two thirds of trials). This could be an artifact or the sharks trended away from the stimulus quadrant over time.

During electroreceptive testing with the first group, two cables were used for the dipole (i.e. strong stimulus) and three cables were used to create the dipole in second group (i.e. to decrease stimulus strength). As the large male within the first group tested completely avoided any contact with the stimulus quadrant within the electroreceptive condition and the negative reactions to the electroreceptive stimulus of other sharks within the first group, an extra cable was added to reduce the strength of the

electroreceptive stimulus before testing with the second shark group. However, the electroreceptive stimulus still appeared to be too strong for the sharks in the second group to recognize and react to it as a potential prey item. This may explain the difference in time spent within the stimulus quadrant between the two groups in this condition, as the first group was more avoidant of the stimulus quadrant and the second group appeared more indifferent to the stimulus within this condition.

The nearly significant difference in time spent within the stimulus and fake quadrants within the first group was likely caused by extreme avoidance of the stimulus quadrant by the male shark in this group. Especially as results between groups in time spent in the stimulus, fake and both other quadrants were not significant. However, the pattern of time sharks spent within the quadrants indicates the electroreceptive stimulus was strong enough to be slightly aversive (to the first group) or biologically unidentifiable (second group) to the sharks. The stimulus may have represented a potential predator to sharks within the first group tested, or it may not have represented any previously encountered biological entity to all sharks used in the study, but the increased strength of the electroreceptive stimulus during testing of the first group was likely aversive to them.

The dark black cables composing the dipoles could have also created an extraneous visual stimulus that upset or made the sharks wary. However, if this was so, both shark groups should have reacted similarly

to the stimulus quadrant and also avoided the quadrant containing the extra stimulus box (fake quadrant) as the empty stimulus box also had cables attached to it to appear identical to the stimulus box containing the active dipoles. It would also be likely that if the dipole cables were an aversive extraneous visual stimulus, results from this electroreceptive condition would be similar to those of all other conditions containing an electroreceptive stimulus, which did not occur, as all sharks appeared to dislike the visual and electroreceptive stimulus condition and sharks from the first group appeared more wary of the electroreceptive and olfactory stimulus condition.

Differences recorded in times spent within the stimulus condition between the two shark groups (13% for group one and 25% for group two) could also have been influenced by differences in composition of tank water between August and November when testing of the two separate groups took place. As differences between groups in time spent within any quadrant were within this condition were not significantly different, any differences in the strength of the electroreceptive stimulus due to water chemistry may not have been enough to significantly alter the reactions of the sharks to the electroreceptive stimulus. Therefore differences between groups in reaction to the electroreceptive stimulus were more likely caused by the strength of the electroreceptive stimulus between the groups and not due to water quality in the testing tank between August and November.

Though information on the function of vision in sharks is scant, the behavioral reactions of sharks to electrical stimuli are better understood (Kalmijn, 1971, 1982; Kajuira, 2003; Kajuira and Holland, 2002; Tricas, 1982; Tricas et al., 1995; Sisneros et al., 1998). These studies have found many shark species electroreceptive systems can detect small electrical stimuli within a short range (Kajiura, 2003; Kajiura and Holland, 2002). Bonnethead sharks do not possess as many electroreceptive pores as scalloped hammerheads and other carcharhinidaes species (Kajiura and Holland, 2002). Aas bonnetheads possess the smallest cephalofoil of all Sphyrnids, they may not benefit from an increased electroreceptive search area as larger hammerheads and therefore need to rely on other sensory modalities to localize prey (Kajiura and Holland, 2002).

As the electroreceptive sense is limited by distance, it may not provide enough information regarding stimulus identity or location from a distance (Boznick et al, 2004; Combs et al., 2002). The idea that the electroreceptive sense of sharks may not be effective to definitively identify the nature of a stimulus is supported by studies noting sharks behavioral reactions are the same to natural and artificial electrical fields (Boznick et al., 2004). As the electroreceptive stimulus appeared to be too strong to be associated with prey in this study, it may be the best explanation of sharks' reactions (avoidance and/or indifference) to this and other conditions containing an electrorepcetive stimulus within this study.

Analysis of Vision and Electroreception Stimulus Condition

Within this condition, sharks spent significantly more time in quadrants other than the stimulus quadrant. Sharks spent 35% of their time in the fake quadrant followed by 25% between both other quadrants, and 14% within the stimulus quadrant in this condition. When time spent within the quadrants for each group during this stimulus condition were compared, the first group spent less time here (8%) than the second group (18%), which may have partially been caused by the difference in electroreceptive stimulus strength between groups, as the electroreceptive stimulus strength was reduced for the second group tested.

Results over each trial third suggest each shark group was slightly avoidant of the stimulus quadrant. The consistency between both groups in spending more time in quadrants other than the stimulus quadrant, especially the large amount of time spent within the fake quadrant (located furthest from the stimulus quadrant within the tank) within this condition suggests sharks may have been more wary of the stimuli within this condition than in any other condition containing an electroreceptive stimulus. The significant difference found between time spent within the stimulus and fake quadrants for all sharks support this. Between shark groups, the first group spent significantly more time in the fake quadrant than the second group. Though the second group did not show a significant difference between time spent between the stimulus and fake quadrants or fake and first other quadrant as the first group did, they did

spent more time within the fake quadrant in this condition than they did within any other condition tested containing an electroreceptive stimulus.

Potential reasons why the sharks spent less time in the stimulus quadrant in the visual and electroreceptive combination condition than during the electroreceptive condition may due to their perception of the stimulus combination used in this condition. The addition of a visual stimulus to the strong electroreceptive stimulus may have increased the sharks' wariness of items within the stimulus quadrant, especially as they do appear to notice visual stimuli. Though the visual stimulus was not large and resembled a small blue crab, if noticed, it may have been confusing to the sharks due to the strength of the electroreceptive stimulus especially if the electroreceptive stimulus was able to be associated with the signals emitted by prey or predators. As bonnetheads are predated upon by other sharks and larger fish, the combination of a visual stimulus along with an unknown electroreceptive stimulus may have increased their wariness of the stimulus.

Overall, the results from this condition suggest the sharks collectively avoided the stimuli within this condition, and their avoidance was more pronounced than it was within other conditions containing an electroreceptive stimulus. Thus, combining a visual stimulus with a strong electroreceptive stimulus may increase wariness as the electroreceptive stimulus was likely too strong for recognition as prey, but possibly not

strong enough to be considered the signature of a predator or was not biologically recognizable to the sharks.

Analysis of Electroception and Olfaction Stimulus Condition

Overall, sharks collectively spent more time in the fake quadrant (31%) than in any other quadrants, including the stimulus quadrant (17% % and 26% respectively). Time spent in the quadrants over trials thirds reflected the results of time spent in quadrants over trial durations.

As results were fairly uniform overall between the two shark groups in spending more time within the fake quadrant (though sharks in group one spent slightly more time in the fake quadrant than group two in this condition) it suggests possible indifference to the electroreceptive and olfactory stimulus condition within sharks in the second group.

Sharks within the first group appeared to be more wary of the stimulus quadrant in this condition, as significant differences were found between the time they spent within the stimulus quadrant and all other quadrants (fake and both other quadrants) as well as between the times they spent within the fake quadrant as compared to the second other quadrant. This further suggests the electroreceptive stimulus may have been too strong in this group.

Sharks within the first group were more avoidant of the stimulus within this condition than they were in the electroreceptive stimulus condition. A possible explanation for the increase in group one's wariness

of this stimulus compared to that of the electroreceptive and visual and electroreceptive stimulus combination condition may be that olfaction may not be as important to these sharks when combined with an unknown or biologically unidentifiable electroreceptive stimulus. Hence, as the electroreceptive stimulus was stronger for the first group tested, they showed slightly more avoidance than sharks in group two, possibly due to the increased strength of the electroreceptive stimulus. Overall sharks appeared to show more indifference to the electroreceptive and olfactory stimulus combination. In this explanation, the electroreceptive stimulus may have superseded interest in the olfactory stimulus, even though olfactory stimuli generally elicit predatory or searching behavior in these sharks (Kajiura and Holland, 2002; Johnson and Teeter, 1984).

Another possibility is that pre-exposure to trials containing a visual, electroreceptive, olfactory, or other combination of stimuli before exposure to the electroreceptive and olfactory stimulus combination may also explain sharks indifference to this stimulus combination. This is especially true if sharks are able to learn or habituate quickly to stimuli. As these sharks possess one of the largest brains of all shark species, and have been observed to lose interest in some stimuli (Kajuira and Holland, 2002), this is plausible.

A last possible explanation for the reactions of sharks within this stimulus condition could be habituation and previous exposure to the visual, electroreceptive, and olfactory stimulus before testing the

electroreceptive and olfactory stimulus combination. As seen in Appendix D, most sharks had prior exposure to the three main stimuli and various combinations of these stimuli before testing of the electroreceptive and olfactory stimulus combination. As many of the test trials using this condition were conducted later in the study (days 2, 3, or 4 of testing) the increase in number of trials per shark prior to testing this condition combined with their ability to learn and known decrease in reaction to repeated presentations of stimuli (Kajiura and Holland, 2002) may have also contributed to their reactions to the stimuli within this condition.

Analysis of Visual, Electroreception and Olfaction Stimulus Condition

Collectively, sharks spent the most time in quadrants other than the stimulus quadrant within this condition (17% in the stimulus quadrant compared to 25% in the fake quadrant and 29 % in the other quadrants combined) suggesting disinterest in the visual, electroreceptive, and olfactory stimulus combination. Time spent within the stimulus quadrant and away from the stimulus quadrant was fairly similar to the results from the electroreceptive and olfactory stimulus combination condition. Thus, the combination of the three main stimuli within this study (visual, electroreceptive, and olfactory) appeared to be one of the least interesting stimulus combinations to the sharks within the study. No significant difference was found in time spent within the stimulus quadrant between the two groups or within any of the groups over trial durations. However a

significant difference was found between group one and group two in the times they spent within the fake quadrant, further emphasizing the increased avoidance, regardless of whether it was caused by wariness or disinterest, of the stimulus quadrant of sharks within the first group tested.

Sharks were fairly consistent in the time they spent in quadrants other than the fake quadrant over the duration of trial thirds. As the visual-electroreceptive-olfactory condition trials occurred on the last day of testing for the first shark group, being pre-exposed to stimuli prior to testing and the increase in the number of trials sharks were exposed to makes it plausible that sharks within this group may have stopped responding naturally to stimuli by the end of testing sessions and any wariness of the electroreceptive aspect of the stimulus combination was negated or they avoided the area where a stimulus was located due to disinterest.

Pre-exposure to the visual, electroreceptive, visual and electroreceptive combination before the visual, electroreceptive, and olfactory stimulus combination could have habituated sharks to those stimuli and created indifference to the visual, olfactory, and electroreceptive stimulus condition in these trials. Thus as sharks within both groups were exposed to most stimulus used within this study prior to testing of the visual, electroreceptive, and olfactory stimulus combination and had already been tested using the behavioral procedure for at least two to three days previous to testing this condition, it may have cause

habituation or indifference to the stimulus by both shark groups. Thus, sharks collective avoidance of the stimulus quadrant could have been caused by avoidance of the area where they detected a stimulus and not due to the properties of the stimulus.

Another possibility for the sharks' reaction in this condition was if the olfactory stimulus within this condition dispersed quickly, it would likely not have much effect on the sharks' behavior. Thus, the sharks may have been reacting to the visual and electroreceptive stimulus combination within this condition but been less avoidant of the stimulus quadrant due to pre-exposure to the visual, electroreceptive, and visual and electroreceptive stimulus combinations prior to testing of all three stimuli (visual, electroreceptive, and olfactory) together.

Analysis of Live Prey Stimulus Condition

Sharks did not appear to be interested in the live crab within this condition as they collectively spent only 16% of their time within the stimulus quadrant compared to 33% of their time in the fake quadrant and 25% in the other quadrants combined. The majority of sharks' time was spent within the fake quadrant followed by the other quadrants, and lastly the stimulus quadrant within this condition. Overall, none of the sharks appeared overtly interested in the crab as there were no recorded definitive reactions to it and the majority of their collective time was spent away from the stimulus quadrant within this condition. Collectively, there

was a significant difference between time spent within the stimulus and fake quadrants, stimulus and first other quadrant, and fake and second other quadrant within this condition. However, no significant differences in time spent between any quadrants were found within the first group, though significant differences between the stimulus and first other quadrant were found within the second group.

The time spent among each of the quadrants within this condition over trial thirds as well as over the duration of trials between the two shark groups was nearly identical, especially time spent within the stimulus quadrant. Thus, the response of sharks to the live crab suggests indifference to or even possible avoidance of the live crab as a stimulus. As this condition was randomly tested during the last day of testing in both groups, it suggests the sharks may have been learning they would be unable to attain any stimulus presented to them or possibly becoming used to being hand fed and thus avoided the stimulus quadrant as they would not be able to attain the crab or were indifferent to this stimulus.

Several studies have revealed that sharks learn quickly (Clark, 1963; Aronson, Aronson and Clark, 1967; Graeber and Ebbesson, 1972; Tester and Kato, 1966; Wright, and Jackson, 1964), this could be especially true of hammerhead sharks, which possess some of the most sophisticated brains and largest telencephalons of currently known species (Yopak, Lisney, Collin, and Montgomery, 2007). The telencephalon of the bonnethead shark appears to represent around 50-

52% of their entire brain weight (personal observation) which matches estimates of the proportion of telencephalon found in other Sphyrnid species, such as the scalloped hammerhead (54%) and great hammerhead (67%) sharks (Yopak et al., 2007). Though the increase encephalization within the bonnethead telencephalon may also relate to how they integrate sensory information. Demski (1996) found information from the visual and electrosensory systems are likely integrated within the pallium of the telencephalon. Thus, learning, sensory integration and/or other behaviors may explain the large brains possessed by bonnethead sharks.

Though the blue crab is this species preferred prey item (Cortes and Parsons, 1996; Cortes et al, 1996; Hoese and Moore, 1958), as this condition was randomly tested with other conditions on the last day of testing for each shark group; if the sharks were learning, may explain their lack of reaction to their preferred prey species. A second possible explanation is that as the sharks were kept in captivity for several weeks to a month before testing could begin and were being fed herring on a regular schedule. If the sharks expected to receive food after testing, they may have not been as interested in the crab within the stimulus box and preferred to wait and be fed on their normal schedule. A third possibility is that the sharks may not have been food deprived long enough to be highly motivated to hunt for prey. Though these sharks have a high metabolism and feed often compared to other shark species

(Parsons, 1990), depriving them of food for only a day to a day and a half before testing may not have been enough to allow them to be motivated to react to the stimulus.

Summary

Enough evidence exists to suggest vision could be more important than previously believed to sharks as well as be used for several purposes (Hart et al., 2004; Myrberg, 1991; Myrberg and Gruber, 1974). However, little of this evidence comes from studies of behavior but from studies of sensory morphology and physiology. Understanding of the structure and physiological functioning of sensory systems can provide insight regarding a given sensory systems role in behavior. However, assumptions regarding behavior, supported solely by physiological data are limited to broad generalizations (Gruber and Myrberg, 1977). The specific role of any sensory modality in behavior or how sensory modalities are integrated within specific behaviors cannot be definitively established without behavioral data (Gruber and Myrberg, 1977). The results from this study were meant to integrate known physiological and ecological data concerning bonnethead sharks with testing of several sensory stimuli and be a first step in uncovering whether vision plays a role in predatory behavior of bonnethead sharks.

Findings from this study further indicate the main function of the unique Sphyrnid cephalofoil may be to offer these sharks an advantage in detecting and further localizing prey and/or predators (Kajiura, 2003; Kajiura and Holland, 2002). As

sharks within both groups tested showed interest in the visual stimulus condition and the visual-olfactory combined stimulus condition, it is feasible that bonnethead sharks may utilize their visual sense when conducting a general search for prey (i.e. prey that are moving above the substrate) to get within close proximity to prey, then switch to their electroreceptive sense to locate the exact position of prey before capture. Due to avoidance of the visual stimuli when combined with the strong electroreceptive stimulus, these sharks may use visual information to help identify electroreceptive information as well.

The combination of a fairly strong electroreceptive stimulus with a visual stimulus may have caused avoidance of the stimulus quadrant in this condition. Adaptive behavior would dictate visual or olfactory cues (or any cues associated with prey items) would not be as important to pursue if a predator or possible threat (unidentifiable object) was near. Even though the visual stimulus was small, it could have been enough to have made the sharks more wary of the stimulus quadrant and its contents in the visual and electroreceptive stimulus combination condition than in the electroreceptive stimulus condition. This is especially true given the reactions to the visual and olfactory stimulus combination condition and the visual stimulus condition.

As this is one of a handful of studies that has behaviorally tested the visual sense of any hammerhead shark, the exact role their visual sense plays in detection of prey or predators remains in question and must be further studied.

References

Archer, S.N., Djamgoz, M.B.A., Loew, E.R., Partridge, J.C., and S. Vallerga, eds. (1999) Adaptive mechanisms in the ecology of vision. Kluwer Academic Publishers. Dordrecht.

Aronson, L.R., F.R. Aronson & E. Clark. 1967. Instrumental conditioning and light-dark discrimination in young nurse sharks. Bull. Mar. Sci. 17: 249-256.

Beugnon, G., Lambin, M., and A. Ugolini (1987) Visual and binocular field size in Talitrus saltator Montagu (*Crustacea Amphipoda Talitridae*). Monitore Zoologico Italiano. 21(2): 151-155.

Bodznick, D. (1991) Elasmobranch vision: multimodal integration in the brain. Journal of Experimental Zoology, Supplement 5:108-116.

Bodznick, D., Montgomery, J., and T. Tricas (2004) Electroreception: extracting behaviorally important signals from noise. p. 389-403. In: Sensory processing in aquatic environments. Eds: Collin, S., and J. Marshall. Springer publishers. Ny,Ny.

Bonazzo, and Collin, S.P. (2000) Retinal ganglion cell topography in seven species of elasmobranch. Brain Behavior Evolution 55: 191-208.

Bozzano, A., Murgia, R., Vallerga, S., Hirano, J., and S. Archer (2001) The photoreceptor system in the retinae of two dogfishes, Scyliorhinus canicula and Galeus melastomus: possible relationship with depth distribution and predatory lifestyle. Journal of Fish Biology 59: 1258-1278.

Chapman, D., and S. Gruber (2002) A further observation of the prey-handling behavior of the great hammerhead shark, *Sphyrna mokarran*: predation on the spotted eagle ray, *Aetobatus narinari*. Bulletin of Marine Science 70(3): 947-952.

Collin, S., and J. Shand (2003) Retinal sampling and the visual field in fishes. In: Sensory processing in aquatic environments. P. 139-170. Eds: Collin, S., and J. Marshall. Springer publishers. Ny,Ny.

Combs, S., New, J.G., and M. Nelson (2002) Information-processing demands in electrosensory and mechanosensory lateral line systems. Journal of Physiology-Paris 96(5-6): 341-354.

Compango, L.V. J. (1988) Sharks of the world. Carcharhiniformes. FAO Fish Synops. Volume 4, Part2.

Cortes, E. and G.R. Parsons (1996) Comparative demography of two populations of the bonnethead shark (*Sphyrna tiburo*) in southwest florida. Canadian Journal of Fisheries and Aquatic Science 53: 709-718.

Cortes, E., Manire, C.A., and R.E. Hueter, (1996) Diet, feeding habits, and diel feeding chronology of the bonnethead shark, *Sphyrna tiburo*, in southwest florida. Bulletin of Marine Science 58: 353-367.

Demski, L.S. and R.G. Northcutt (1996) The brain and cranial nerves of the white shark: an evolutionary perspective. In: Great white sharks: the biology of carcharodon carcharias. Klimly, A.P. and D.G. Ainley, eds. P. 112-121.

Domenici, P., Standen, E.M., and R.P. Levine (2004) Escape manoeuvers in the spiny dogfish (*Squalus acanthias*). Journal of Experimental Biology 207:2339-2349.

Fernandez-Juricic, E., Erichsen, J.T., and A. Kacelnik (2004) Visual perception and social foraging in birds. Trends in Ecology and Evolution 19(1): 25-31.

Fritsches, K.A., Marshall, N.J., and E.J. Warrant (2003) Retinal specializations in the blue marlin: eyes designed for sensitivity to low light levels. Marine and Freshwater Research 54: 333-341.

Graeber, R.C. (1978) Behavioral studies correlated with central nervous system integration of vision in sharks. Sensory Biology of Sharks, Skates, and Rays. E.S. Hodgson and R.F. Mathewson, eds. Office of Naval Research, Arlington, Va. Pg. 11-105.

Graeber, R.C., and S.O.C. Ebbesson (1972) Visual discrimination learning in normal and tectal-ablated nurse sharks (*Ginglymostoma cirratum*). Comparative Biochemistry and Physiology 42A: 131-139.

Gruber, S.H. (1977) The visual system in sharks: adaptations and capability. American Zoologist. 17: 453-470.
Gruber and Chapman (2002)

Gruber, S.H., Gulley, R.L., and J. Brandon (1975) Duplex retina in seven elasmobranch species. Bulletin of Marine Science. 25: 353-358.

Guo, J, and A. Guo (2005) Crossmodal interactions between olfactory and visual learning in drosophila. Science 309:307-310.

Hart, N.S., Lisney, T.J., Marshall, N.J., and S.P. Collin (2004) Multiple cone visual pigments and the potential for trichromatic colour vision in two species of elasmobranches. Journal of Experimental Biology 207: 4587-4594.

Harvey. C.J., Gallant, J.J., and J. H. Batt (2005) Vision and its relationship to novel behavior in St. Lawrence River Greenland sharks, *Somniosus microcephalus*. Canadian Field-Naturalist 119(3): 355-359.

Hayes, B.P. and M.D. Brooke (1990) Retinal ganglion cell distribution and behavior in procellariiform seabirds. Vision Research 30(9): 1277-89.

Heithaus, M.R., Dill, L.M., Marshall, G.J., and B. Buhleier (2002) Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass habitat. Marine Biology 140: 237-248.

Hoese, H.D. and R.B. Moore (1958) Notes on the life history of the bonnetnose shark, *Sphyrna tiburo*. The Texas Journal of Science 10: 69-71.

Hueter, R.E. (1988) Retinal Topography and the retinotectal projection pattern in the juvenile lemon shark (*Negaprion brevirostris)*. Society of Neuroscience Abstracts. 14:1119.

Hueter, R.E. (1989) The organization of spatial vision in the juvenile lemon shark (*Negaprion brevirostris*): retinotectal projections, retinal topography, and implications for the visual ecology of sharks. Dissertation Abstracts International Part B: The Sciences and Engineering . 50: 138.

Hueter, R.E. (1991) Adaptations for spatial vision in sharks. The Journal of Experimental Zoology Suppliment 5: 130-141.

Hueter, R.E. and S.H. Gruber (1982) Recent Advances in studies of the visual system of the juvenile lemon shark (*Negaprion brevirostris*). Florida Scientist 45: 11-28.

Hueter, R.E., Mann, D.A., Maruska, K.P., Sisneros, J.A. and L.S. Demski (2004) Sensory biology of elasmobranches. In: Biology of sharks and their relatives. Ed.: Carrier, JC, Musick, J.A. and M.R. Heithaus P. 325-368.

Johnsen, P.B. and J.H. Teeter (1985) Behavioral responses of the bonnethead (*Sphyrna tiburo*) to controlled olfactory stimulation. Marine Behavior and Physiology 11:283-291.

Kajiura, S.M. (2003) Electroreception in neonatal bonnethead sharks, *Sphyrna tiburo*. Marine Biology 143: 603-611.

Kajiura, S. (2001) Head morphology and electrosensory pore distribution of carcharhinid and sphyrnid sharks. Environmental Biology of Fishes 61: 125-133.

Kajiura, S., Forni, J.B., and A.P. Summers (2003) Maneuvering in juvenile carcharhinid and sphyrnid sharks: the role of the hammerhead shark cephalofoil. Zoology 106:19-28.

Kajiura, S., Forni, J.B., and A.P. Summers (2005) Olfactory morphology of carcharhinid and sphyrnid sharks: does the cephalofoil confer a sensory advantage? Journal of Morphology 264: 253-263.

Kajiura, S.M. and K.N. Holland (2002) Electroreception in juvenile scalloped hammerhead and sandbar sharks. Journal of Experimental Biology 205: 3609-3624.

Kajiura, S., Tyminski, J.P., Forni, J.B., and A.P. Summers (2005) The sexually dimorphic cephalofoil of bonnethead sharks, *Sphyrna tiburo*. Biological Bulletin 209:1-5.

Kalmjin, A.J. (1971) The electric sense of sharks and rays. Journal of Experimental Biology 55:371-383.

Kalmjin, A.J. (1982) Electric and magnetic field detection in elasmobranch fishes. Science 218(4575): 916-918.

Kelley, J.L. and A.E. Magurran (2003) Learned predator recognition and antipredator responses in fishes. Fish and Fisheries 4: 216-226.

Kim, D. (2007) Prey detection mechanisms of elasmobranchs. BioSystems 87: 322-331.

Klimley, P. (1994) Predatory behavior of the white shark. American Scientist 82(2): 122-133.

Laland, K.N., Brown, C. and J. Krause (2003) Learning in Fishes: from three-second memory to culture. Fish and Fisheries 4: 199-202.

Litvak, M.K. (1993) Response of shoaling fish to the threat of aerial predation. Experimental Biology of Fishes. 36: 183-192.

Maladonado, P. E., Maturana, H., and F. J. Varela (1998) Frontal and lateral visual systems in birds: frontal and lateral gaze. Brain, Behavior, Evolution. 32(1): 57-62.

Martin, A. (1993) Hammerhead shark origins. Nature 364: 494.

Martin, G.R. (1996) The eye of a passeriform bird, the European starling (Sturnus vulgaris): eye movement amplitude, visual fields and schematic optics. Journal of Comparative Physiology A. 159: 545-557.

Martin, G. R. (2001) Visual fields and foraging in procellariiform seabirds: sensory ascpects of dietary segregation. Brain, Behavior, Evolution. 57(1): 33-38.

Martin, G.R. and M.D. Brooke (1991) The eye of a procellariiform seabird, the manx shearwater, *Puffinus puffinus*: visual fields and optical structure. Brain, Behavior, and Evolution. 37(2): 65-78.

Martin, G.R. and G. Katzir (1994) Visual fields and eye movements in herons (Ardeidae). Brain, Behavior, and Evolution. 44: 74-85.

Martin, G.R. and G. Katzir (1999) Visual fields in short-toed eagles, *Ciraetus gallicus* (Accipitridae), and the function of binocularity in birds. Bran, Behavior, and Evolution. 53: 55-66.

Martin, G.R. and P.A. Prince (2001) Visual fields and foraging in procellariiform seabirds: sensory aspects of dietary segregation. Brain, Behavior, and Evolution. 57(1): 33-38.

McComb, D.M. and S. M. Kajiura (2008) Visual Fields of Four Batoid Fishses: a Comparative study. The Journal of Experimental Biology. 211: 482-490.

Moller, P. (2002) Multimodal sensory integration in weakly electric fish: a behavioral account. Journal of Physiology, Paris. 96: 547-556.

Montgomery, J.C., Macdonald, F., Baker, C.F., and A.G. Carton (2002) Hydrodynamic contributions to multimodal guidance of prey capture behavior in fish. Brain, Behavior, and Evolution 59: 190-198.

Murphy, C.J., Howland, M., and H.C. Howland (1995) Raptors lack lower-field myopia. Vision Research 35(9): 1153-1155.

Myrberg, A. (1991) Distinctive markings of sharks: ethological considerations of visual function. Journal of Zoology, Suppliment 5: 156-166.

Myrberg, A. and S. Gruber (1974) The behavior of the bonnethead shark. Copeia. 2: 358-374.

Nakaya, K. (1995) Hydrodynamic function of the head in the hammerhead sharks (Elasmobranchii: Sphyrnidae). Copeia 1995: 330-336.

New, J., Fewkes, L.A., and A.N. Khan (2000) Strike feeding behavior in the muskellunge, *Esox masquinongy*: contributions of the lateral line and visual sensory systems. Journal of Experimental Biology 204:1207-1221.

Osmon, A.L. (2004) The organization of the visual system in the bonnethead shark (*Sphyrna tiburo*). Masters Thesis, University of South Florida.

Peterson, E.H., and M.H. Rowe (1980) Different regional specializations of neurons in the ganglion cell layer and inner plexiform layer of the California horned shark, *Heterodontus francisci*. Brain Research. 201: 195-201.

Pankhurst, N.W. (1989) The relationship of ocular morphology to deefing modes and activity periods in shallow marine teleosts from New Zealand. Environmental Biology of Fishes 26: 201-211.

Parsons, G.R. (1990) Metabolism and swimming efficiency of the bonnethead shark, *Sphyrna tiburo*. Marine Biology 104: 363-367.

Rowland, W.J. (1999) Studying visual cues in fish behavior: a review of ethological techniques. Environmental Biology of Fishes 56: 285-305.

Rountree, R.A. and G.R. Sedberry. (1998) A preliminary model of shoaling behavior based on visual field overlap patterns. Fish Feeding Ecology and Digestion: Gutshop '98. International Congress on the Biology of Fish, Towson University, Baltimore MD, July 27-30, 1998. Physiology Section, American Fisheries Society. MacKinlay, D.D., and D. Houlihan. (eds.). Vancouver BC, Canada. Pg. 57-60.

Sivak, J.G. and M.R. Warburg (1983) Changes in the optical properties of the eye during metamorphosis of an anuran, *Pleobates syriacus*. Journal of Comparative Physiology 150: 329-332.

Stone, J. and E. Johnston (1981) The topography of primate retina: a study of the human, bushbaby, and new and old world monkeys. Journal of Comparative Neurology. 196(2): 205-223.

Strong, W.R., Gruber, S.H., and F.F. Snelson (1990) Hammerhead shark predation on stingrays: an observation of prey handling by Sphyrna mokkarran. Copeia. 1990: 386-340.

Strong, W.R. (1996) Shape discrimination and visual predatory tactics in white sharks. In: Great White Sharks: The Biology of Carcharodon carcharias. Klimley, A.P. and D.G. Ainley, eds. p. 229-240.

Tester, A.L. (1963) Olfaction, gustation, and the common chemical sense in sharks. p. 255-285. In: Sharks and Survival. Gilbert, P.W., ed. D.C. Heath and Company, Boston.

Tester, A.L., and S. Kato (1966) Visual target discrimination in blacktip sharks (*Carcharrhinus melanopterus*) and grey sharks (*C. menisorrah*). Pacific Science 20: 461-471.

Tricas, T.C. (1985) Feeding ethology of the white shark, Carcharodon carcharhinus. Southern California Academy of Sciences Memoirs 9: 81-91.

Walls, G.L. (1942) The vertebrate eye and its adaptive radiation. Bloomfield Hills, MI. Cranbrook Institute of Science.

Watanuki, N., Kawamura, G., Kaneuchi, S., and T. Iwashita (2000) Role of vision in behavior, visual field, and vidual acuity of cuttlefish, *Sepia esculenta*. Fisheries Science 66: 417-423.

Wilga, C.A. (1998) Evolution of feeding mechanisms in elasmobranches: a functional and morphological approach. Diss. Abst. Int. Part B: The Sciences and Engineering 58(11): 5840.

Wilga, C.A. and P.J. Motta (2000) Durophagy in sharks: feeding mechanics of the hammerhead *Sphyrna tiburo*. The J. Exp. Bio. 203: 2781-2796.

Wright, T. and R. Jackson (1964) Instrumental conditioning of young sharks. Copeia. 1964: 409-412.

Yopak, K.E., Lisney, T.J., Collin, S.P., and J.C. Montgomery (2007) Variation in Brain Organization and cerebellar foliation in chondrichthyans: sharks and holocephalans. Brain, Behavior, and Evolution 69: 280-300.

Appendices

Appendix A: Group One Duration (Significant Results)

Condition	Quadrants	T Score	SD	P value
Vision				
	Stimulus v Fake	3.9634	9.6	0.0166
Vision & Electroreception				
	Stimulus v Fake	5.9243	19.2	0.0041
	Stimulus v Other1	3.6953	23.4	0.0209
	Fake v Other2	6.6166	11.3	0.0027
Electroreception & Olfaction				
	Stimulus v Fake	2.8938	28.7	0.0444
	Fake v Other2	3.0402	25.2	0.0384
	Other1 v Other2	2.7812	28.3	0.0498

Appendix B: Group Two Duration (Significant Results)

Condition	Quadrants	T Score	SD	P value
Vision				
	Stimulus v Fake	3.58338	22.7	0.0241
	Stimulus v Other1	3.1941	19.9	0.0331
	Stimulus v Other2	4.1496	20.9	0.0143
Live Crab				
	Other1 v Other2	3.0789	30.8	0.0370

Appendix C: Other Significant Results

Group 1 versus Group 2 Duration (Significant Results)

Condition	Quadrants	T Score	SD	P value
Vision & Electroreception				
	Fake	4.9432	5.2	0.0001

Group 1 Thirds (Significant Results)

Condition	Third	Quadrants	T Score	SD	P value
Visual, Electroreception and Olfaction					
	First	Stimulus v Fake	22.5167	0.58	0.0020

Group 2 Thirds (Significant results)

Condition	Thirds	Quadrants	T Score	SD	P value
Visual and Olfaction					
	First v third	Stimulus	4.6675	8.14	0.0430

Appendix D: Order of Testing

Shark	Order of Testing							
Male 1	V	VO	O	E	EO	VEO	VE	Live
Female 1	E	O	V	VO	EO	VEO	VE/NA	Live
Small Male 1	V	VO	O	E	VEO	EO	VE	Live
Male 2	V	VO	O	EO	E	VEO	Live	VE
Large Female 2	V	O	EO	E	VO	VE	Live	VEO
Small Female 2	O	VO	V	VE	E/NA	Live	VEO	EO

Appendix E: Reactions to Stimuli

Stimulus Condition	Shark	Reaction
Olfactory		
	Male 1	Brief circling
	Small male 1	Brief circling
	Female 1	Brief circling
	Large female 2	Brief circling
	Small female 2	Brief circling
Visual and Olfactory		
	Male 1	Circling
	Small male 1	Circling
	Female 1	Circling
	Large female 2	Circling
	Small female 2	Circling

Appendix E: Reactions to Stimuli

Stimulus Condition	Shark	Reaction
Visual and Electroreceptive		
	Male 1	Avoidance
Electroreceptive		
	Male 1	Avoidance

Appendix F: Percent time within quadrants pre and post stimulus introduction

Stimulus Condition		Stimulus Quadrant	Fake Quadrant	Other Quadrants
Visual		**%**	**%**	**%**
	Pre	28	22	25
	Post	38	19	22
Olfactory				
	Pre	21	29	25
	Post	22	27	24
Electroreceptive				
	Pre	16	48	18
	Post	17	42	21
Visual and Electroreceptive				
	Pre	19	4	39
	Post	13	35	21

Appendix F: Percent time within quadrants pre and post stimulus introduction

Stimulus Condition		Stimulus Quadrant	Fake Quadrant	Other Quadrants
Electroreceptive and Olfactory				
	Pre	30	24	23
	Post	21	43	29
Visual and Olfactory				
	Pre	19	28	26
	Post	48	12	19
Visual, Electroreceptive and Olfactory				
	Pre	29	25	23
	Post	15	24	30
Live Prey				
	Pre	23	28	25
	Post	15	31	27

About the Author

Amy Osmon received a Bachelor's Degree in Psychology from The Ohio State University in 1995. She began a Master's Degree in Anthropology at Florida State University in 1996, and worked as an archaeologist for the National Park service. She began the Ph.D. program in Psychology at the University of South Florida in 1999. Miss Osmon is currently an Associate Professor of Psychology at Daytona State College where she is co-advisor of the Psychology Club, involved in the CWIS (Center for Interdisciplinary Writing and Research), and is a mentor to International Students within Daytona State's Global Education and Affairs program.