From Perception to Cognition: Multisensory object recognition and navigation in the weakly electric fish *Gnathonemus petersii*

Dissertation

zur

Erlangung des Doktorgrades (Dr. rer. nat.)

der

Mathematisch-Naturwissenschaftlichen Fakultät

der

Rheinischen Friedrich-Wilhelms-Universität Bonn

vorgelegt von

Sarah Schumacher

aus Bad Neuenahr/Ahrweiler

Bonn 2017

Angefertigt mit Genehmigung der Mathematisch-Naturwissenschaftlichen Fakultät der Rheinischen Friedrich-Wilhelms-Universität Bonn.

1. Gutachter: Prof. Dr. Gerhard von der Emde, Bonn
2. Gutachter: Dr. Theresa Burt de Perera, Oxford

Tag der Promotion: 13.12.2017

Erscheinungsjahr: 2018

Teile dieser Dissertation sind veröffentlicht oder sind zur Veröffentlichung eingereicht:

1. **Schumacher, S.**, Burt de Perera, T., Thenert, J., von der Emde, G. (2016). Cross-modal object recognition and dynamic weighting of sensory inputs in a fish. Proceedings of the National Academy of Sciences: 201603120.

2. **Schumacher, S.**, Burt de Perera, T., & von der Emde, G. (2017). Electrosensory capture during multisensory discrimination of nearby objects in the weakly electric fish *Gnathonemus petersii*. Scientific reports, 7, 43665.

3. **Schumacher, S.**, von der Emde, G., Burt de Perera, T. (2017). " Sensory influence on navigation in the weakly electric fish *Gnathonemus petersii*." Animal Behaviour (Accepted)

Table of contents

Zusammenfassung

Innerhalb eines multisensorischen Systems können die einzelnen Sinne auf unterschiedliche, vorteilhafte Weise miteinander interagieren und so die Verlässlichkeit und Flexibilität der multisensorischen Wahrnehmung verbessern. Ein solches multisensorisches System findet man beim schwach elektrischen Fisch *Gnathonemus petersii*, der sowohl aktive Elektroortung als auch ein spezialisiertes visuelles System zur Wahrnehmung der Umwelt nutzt. Zusätzlich besitzen diese Fische ein mechanosensorisches Seitenliniensystem, das jedoch bisher kaum untersucht ist. Ziel dieser Arbeit war es, die Zusammenarbeit der einzelnen Sinne von *G. petersii* zu untersuchen und so neue Erkenntnisse über die Verarbeitung multisensorischer Informationen in diesen Fischen zu gewinnen.

Im ersten Teil meiner Arbeit habe ich die Methode der Zweifachwahldressur genutzt, um die multisensorische Objekterkennung bei *G. petersii* zu untersuchen. Zusätzlich habe ich anatomische Methoden verwendet, um einen Überblick über die morphologische Struktur des peripheren mechanosensorischen Seitenliniensystems zu erhalten. Die Ergebnisse dieser Versuche zeigen, dass *G. petersii* zur spontanen crossmodalen Objekterkennung befähigt ist, einer Fähigkeit, die bisher nur von wenigen Säugetieren bekannt war. Dabei können objektbezogene Informationen flexibel zwischen den Sinnen transferiert werden, um diese zur Objekterkennung zu nutzen. Die Ergebnisse zeigen weiter, dass diese Fische sensorische Informationen ähnlich verarbeiten wie es zuvor nur von Säugetieren bekannt war, indem die sensorischen Eindrücke dynamisch gegeneinander gewichtet werden. Diese dynamische Gewichtung führte zu einer Dominanz des elektrischen Sinns auf kurzer Distanz, die sich aufgrund der abnehmenden Verlässlichkeit der elektrischen Informationen mit zunehmender Objektentfernung verringerte. Während dieser Versuche zeigte sich kein Einfluss des mechanosensorischen Seitenliniensystems auf die Objekterkennung, was durch die Ergebnisse der anatomischen Studie erklärt werden kann, in der eine starke morphologische Degeneration gefunden wurde. Im zweiten Teil wurde in einem Navigationsexperiment der Einfluss unter-schiedlicher sensorischer Inputs auf die Navigation getestet. Die Ergebnisse zeigen, dass *G. petersii* eine egozentrische Strategie zur Navigation in bekannter Umgebung nutzt, die von visuellen Informationen unterstützt wird. Außerdem sind diese Fische in der Lage crossmodale Landmarkenerkennung zu nutzen um die Navigationsaufgabe zu erfüllen.

Zusammen zeigen die Ergebnisse meiner Arbeit, dass *G. petersii* die Vorteile seines multisensorischen Systems, in dem mehrere Sinne mit unterschiedlicher Reichweite ähnliche Informationen liefern, optimal nutzt. Dabei können die multisensorischen Informationen erstens synergetisch genutzt werden, indem sie die Wahrnehmung durch Integration verbessern. Sie können zweitens redundant genutzt werden, falls einer der Sinne ausfällt, und schließlich drittens komplementär, indem sie für unterschiedliche Aufgaben verwendet werden. Abschließend liefern meine Ergebnisse bemerkenswerte neue Erkenntnisse über die Grundlagen der multisensorischen Verarbeitung in *G. petersii* und verdeutlichen die außerordentlichen kognitiven Fähigkeiten dieser Fische.

Summary

Within a multisensory system, individual senses can interact in several beneficial ways increasing the reliability and flexibility of the multisensory percept. Such a multisensory system is found in the African weakly electric fish *Gnathonemus petersii*, which uses active electrolocation and a specialised visual system for the perception of its environment. Additionally, these fish possess a mechanosensory lateral line system, which, however, has been scarcely investigated. In this thesis I investigated how the sensory systems of *G. petersii* operate together and how multisensory information is processed.

In the first part of my thesis I used an object discrimination paradigm to investigate multisensory object recognition and I used anatomical methods to examine the structure of the mechanosensory lateral line system. The results show that *G. petersii* is capable of spontaneous cross-modal object recognition, a highly cognitive ability previously known only in a few mammalian species, during which object related information can be transferred between senses and used for object recognition in a flexible manner. Furthermore, I found that these fish process multisensory information similarly to mammals, by using dynamic weighting of sensory inputs. This dynamic weighting led to a dominance of the electric sense at close range, which gradually diminished with increasing object distance, due to a decreasing reliability of the electrosensory input. During these experiments, the mechanosensory lateral line system was not involved in object recognition, which might be explained by the results of my anatomical studies, showing a reduction of the peripheral lateral line system. In the second part of my thesis I used a navigational paradigm to test the influence of different sensory inputs on navigation. The results show that *G. petersii* uses an egocentric strategy aided by visual landmarks for navigation in a familiar environment and is able to use cross-modal landmark recognition to fulfil the task.

In conclusion, the results of my thesis show that the multisensory system of *G. petersii* optimally exploits the advantages of possessing multiple senses, which provide similar information on different spatial scales. Multisensory information can be used synergistically, improving multisensory performance through integration, redundantly, by providing backup if one sense is unavailable, and complementarily when tuned to slightly different tasks. Together, my findings provide new insights into the mechanisms underlying multisensory processing in *G. petersii*, which underline the extraordinary cognitive abilities of these fish.

1. General Introduction

1. General Introduction

1.1. Sensory perception

All living organisms interact with their environment, therefore the ability to perceive information from the outside has high adaptive value. This drove the evolution of various structures (receptors) that are able to translate external physical or chemical stimuli into an internal signal, which can be used by the organism. While sensory receptors exist within most of the tree of life, and simple forms can even be found in unicellular bacteria or plants (Alonso & Stepanova, 2004; Braam, 2005; Falke & Hazelbauer, 2001; Gomelsky & Hoff, 2011; Martinac, Delcour, Buechner, Adler, & Kung, 1992; H. Smith, 2000), the zenith of diversity and complexity of receptor systems is found in animals. The rising pressure of food competition and predator prey interactions increased the need for environmental information and thus drove the evolution from single receptors to complex sensory systems and led to specific sensory adaptations within the animal kingdom. Such sensory systems often consist of hundreds or thousands of receptors, additional structures which improve the stimulus perception (e.g. the lens of the eye or the outer ear) and a neuronal pathway (e.g. the optic nerve and the visual cortex) (C. U. M. Smith, 2008).

Depending on the physical or chemical stimulus that transmits the information, and based on the underlying receptors, sensory systems can be grouped into certain categories. (1) Chemoreceptors perceive chemical cues and form the basis of the olfactory (smell) and gustatory (taste) system (Chandrashekar, Hoon, Ryba, & Zuker, 2006; Doty, 2015; Firestein, 2001). (2) Photoreceptors, like the ommatidia in insects and the rods and cones in vertebrates, translate photoenergy of electro-magnetic waves into neuronal signals. Arranged in complex visual systems they allow the perception of different components of light, such as the intensity, the wavelength (colour) or the polarisation (Kaas, 2004; Sanes & Zipursky, 2010). (3) Mechanoreceptors form the basis of several very different senses. Located in the skin and combined with structures like hairs and antennae mechanoreceptors can be used passively in the tactile sense or actively in the haptic sense. As proprio-receptors and stretch receptors they allow for the control of movement and within the vestibular system they contribute to the sense of balance (Paterson, 2007). The acoustic sense also relies on mechanoreceptors and allows the perception of the oscillatory pressure changes of sound waves (Stebbins, 1983). Similarly, the neuromasts (superficial or in canals) of the mechanosensory lateral line system in fish and amphibians detect water movement and currents (Coombs, Görner, & Münz, 2012). (4) Thermoreceptors detect temperature changes and are widely spread among animals but they are organised into complex sensory systems (pit organs) only in a few species like snakes or some beetles (Mainz, Schmitz, & Schmitz, 2004; Molenaar, 1992). In addition to these four most commonly known receptor types some animals additionally possess (5) magnetoreceptors or (6) electroreceptors. Magnetoreceptors mediate the perception of the earth magnetic field, which is mainly used for navigation (W. Wiltschko & Wiltschko, 2005). Electroreceptors are closely related to mechanoreceptors as they derive from lateral line neuromasts and detect self-generated or external electric fields (Bullock, Hopkins, & Fay, 2006; Szabo, 1965).

In order to obtain a comprehensive and robust percept of their surroundings, most animals possess not just one but several of the listed sensory systems and are able to use them together in different ways. Multisensory information can either be combined, increasing the informational input, or they can be integrated, increasing the reliability of an individual information. Multisensory systems provide many advantages. Information from multiple senses can be used redundantly, where one sense can be used as a backup if another sense is unavailable; they can be used synergistically, where the performance is improved due to multisensory integration; or they can be used complementarily, where different senses are tuned to specific tasks. Furthermore multisensory input might increase the flexibility of a system via information transfer between the individual senses. For example, some mammalian species are able to use object related information acquired with one sensory system to spontaneously recognise an object with another sense (Cowey & Weiskrantz, 1975; Davenport & Rogers, 1970; Gaydos, 1956; Herman, Pack, & Hoffmann-Kuhnt, 1998; Winters & Reid, 2010). This ability is called cross-modal object recognition.

In some mammalian species multisensory integration is achieved via dynamic weighting of the sensory inputs (Alais & Burr, 2004; Ernst & Banks, 2002; Fetsch, Turner, DeAngelis, & Angelaki, 2009; Sheppard, Raposo, & Churchland, 2013). The individual sensory inputs are weighted according to their reliability, which means that not all sensory inputs contribute to the overall perception to the same degree but the more reliable a sensory input is, the more it will contribute to the overall percept. This weighting often lead-s to the dominance of a specific sense and depends on the task and environmental condition and is additionally influenced by experience (Ernst & Bülthoff, 2004).

Like the organisation of the individual sensory system the sensory equipment is adapted to the ecological niche and the habitat of the animal. The main focus of this thesis is to investigate how the sensory systems of the weakly electric fish *Gnathonemus petersii* work together and how they operate during object recognition and navigation. The following chapters will introduce the three main sensory systems considered in this thesis (the active electric sense, vision and the lateral line system) and will also introduce the model animal, *Gnathonemus petersii,* including how its senses are adapted to the environment.

1.2. Cognition

The word cognition is not easily defined as it is interpreted slightly different in different sciences such as biology, psychology, neuroscience or philosophy. It derived from the Latin verb *cognoscere* or *cognosco* meaning "to recognise" (the verb recognise itself also deriving from this verbs). Cognition can be defined as the mechanism, by which environmental information is acquired, processed, stored and applied in behaviour (Shettleworth, 2010).

Usually when talking about cognition in a biological sense, functions like learning, memory and decision-making are considered. In context with human cognition and in psychology, it is more associated with intelligence and consciousness (something that is wilfully done in anticipation of a specific result). One can easily see how this leads to a very different debate about what intelligence and consciousness is and whether or not it is applicable to animals. In this thesis, the term cognition is based on the biological definition, which might be easiest explained by an example: When looking at a dice, sensory perception describes how the photoreceptors in the eye react to the object, perceiving and transmitting the information about the edges and the black and with contrast. Cognition on the other hand describes how the brain interprets this information, recognising a dice, counting the dots and making decisions based on this information. But of course there is no distinct point of separation and so perception might be interpreted as a part of cognition itself.

In this thesis I used two different behavioural paradigms, in which I manipulated the sensory input to the animal and observed the behavioural output to draw conclusions on the underlying cognitive mechanisms, thus using an approach arching from perception to cognition.

1.3. Electroreception

The ability to perceive electric fields from the environment, using electroreceptor organs, is known as electroreception or electrolocation and can be divided into passive and active sensing. While passive electroreception requires an external electric signal source, e.g. muscle contractions of other animals, active electrolocation is based on self-generated electric fields and requires a specialised electric organ to produce the electric signals. The perception of such electric fields, external or self-generated, is entirely unfamiliar to us humans. However, it shares some features with other sensory systems that are known to us. For example, comparable to vision or the haptic sense, electric fields can provide spatial information and thus inform about the shape or structure of objects within the environment. Like the acoustic sense, electrolocation provides timing and frequency information with the advantage of instant transmission through the medium (electric fields travel approximately with speed of light). Furthermore the perceived intensity of electrical signals depends on the distance to the source, which is comparable to the olfactory sense (Albert & Crampton, 2006).

Since the transmission of electric signals requires a conductive medium, both types of electroreception are mainly restricted to aquatic or semi-aquatic animals (except for the echidna, which use electroreceptors on their snouts to search for food in moist soil (Albert & Crampton, 2006; Proske, Gregory, & Iggo, 1998)). Recently electroreception was also described in bees and bumblebees, however, this relies on a different mechanism that will be not discussed in this thesis (Clarke, 2015; Lihoreau & Raine, 2013).

Electroreception is an ancient feature of vertebrates, which was lost and re-evolved multiple times within the vertebrates (Baker, Modrell, & Gillis, 2013)(Figure 1 A). Thus the underlying electroreceptors can already be found in basal vertebrates like lamprey (Petromyzontiformes) and are present in several groups among the Chondrichthyes, Osteichthyes and Amphibia and were also found in a few mammalian species like Guiana dolphin (*Sotalia guianensis),* platypus (*Ornithorhynchus anatinus*) and echidna (*Tachyglossidae*) (Bullock, 1973; Bullock, Bodznick, & Northcutt, 1993; Czech-Damal et al., 2011; Jorgensen, 2005; Kalmijn, 1966; Murray, 1960; Scheich, Langner, Tidemann, Coles, & Guppy, 1986).

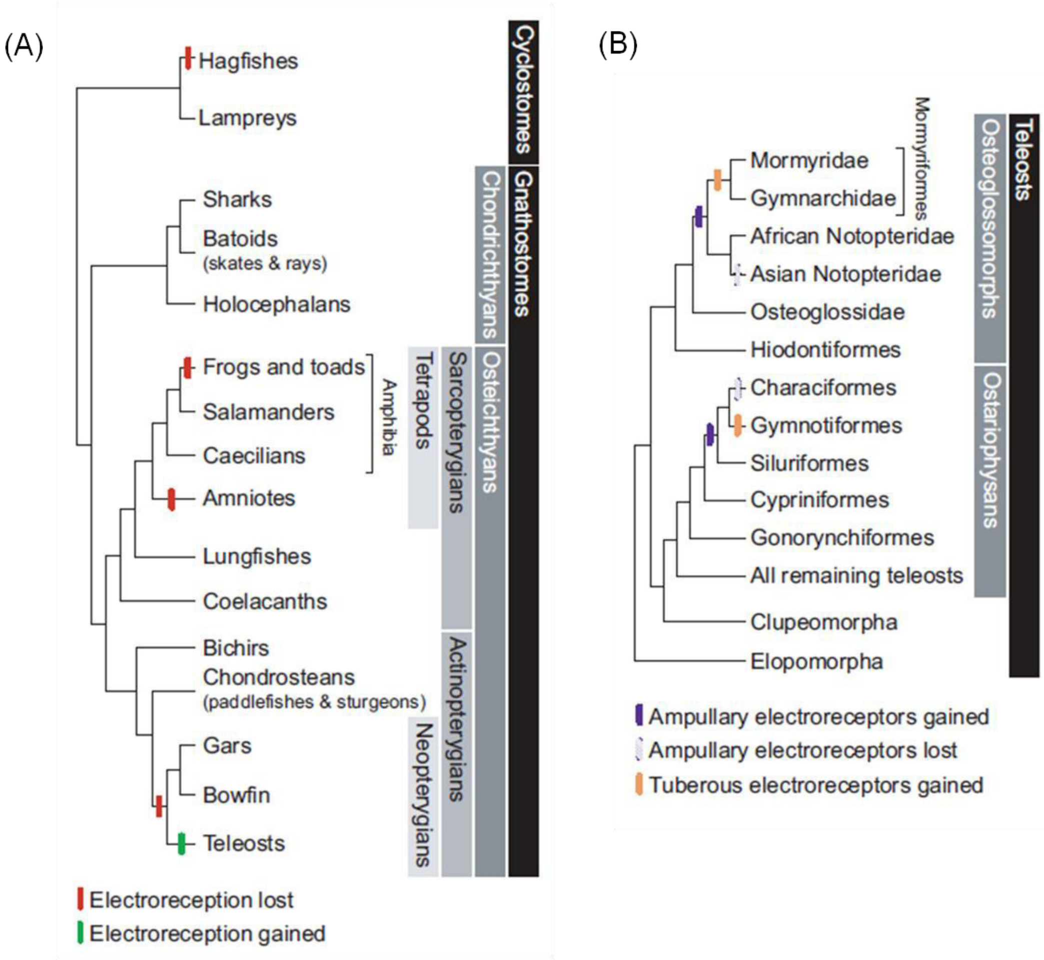

Figure 1: The phylogenetic distribution of electroreception within (A) the vertebrates and (B) the teleosts. Electroreception probably evolved early within the vertebrates and was lost in several lineages (A: red bars), including the lineage leading to the neopterygians, which include the teleosts. Within the teleosts electroreception was regained independently in two groups (A: green bar; B: blue bars) in the Osteoglossomorpha in the linage leading to the notopterids and the mormyriformes and in the Ostariophysi in the lineage leading to siluriforms, gymnotiforms and characiforms. In these two groups probably ampullary evolved and were lost again in the Asian notoperidae and in the characifromes (B: grey bars). Tuberous electroreceptors then evolved independently in the mormyriformes and the gymnotiformes. From (Baker et al., 2013).

1.3.1. Active electrolocation

While all the above groups are capable of passive electrolocation, the ability of active electrolocation has evolved convergently in only two groups: the African Mormyriformes and the South American Gymnotiformes (Lavoué et al., 2012). In contrast to passive electroreception, which only allows the location of an electrical signal source, active electrolocation provides detailed information about the environment. During active electrolocation the fish produce weakly electric signals with their electric organ (electric organ discharges or EODs) and perceive object evoked changes in the resulting self-generated electric field (Lissmann & Machin, 1958; Rasnow & Bower, 1997; Schlegel, 1975; von der Emde, 1990; von der Emde et al., 2010). These changes depend on the electrical properties of the object. For example objects with a higher conductivity than the surrounding medium focus the field lines and the fish perceives a local increase of the EOD amplitude, while objects with a lower conductivity than the surrounding medium spread the field lines which leads to a local decrease in the perceive EOD amplitude (Figure 2)(von der Emde & Schwarz, 2001). Objects project a specific electrical image on the surface of the fish´s skin, which informs about several object properties like its location, size, distance or shape (Rasnow, 1996; Schumacher, Burt de Perera, & von der Emde, 2016; von der Emde & Fetz, 2007; von der Emde & Schwarz, 2000; von der Emde, Schwarz, Gomez, Budelli, & Grant, 1998). However, additionally to these classical features, which can also be perceived by other senses like vision, active electrolocation also informs about the electrical properties of objects like their resistance or capacity and thus provides information about the material and whether the object is animated or not (von der Emde, 1992).

In contrast to the visual system there is no focusing mechanism like a lens within the active electric system, therefore electrical images are always blurred. The degree of blurriness strongly depends on the object size, distance and material, which has implications on the spatial resolution of active electrolocation. For example the electrical image of an object that is close by might be relatively sharp allowing easy object recognition. On the other hand, if the same object is far away it will project a blurry electrical image on almost the whole body surface, preventing object recognition. Therefore during object recognition, the perceptual range of the electric sense is restricted to only a few centimetres (Fechler, 2016; Fechler et al., 2012; Schwarz, 2000; von der Emde & Schwarz, 2002). Despite these constraints, many studies have shown that active electrolocation enables weakly electric fish to detect and recognise objects successfully even in the absence of light.

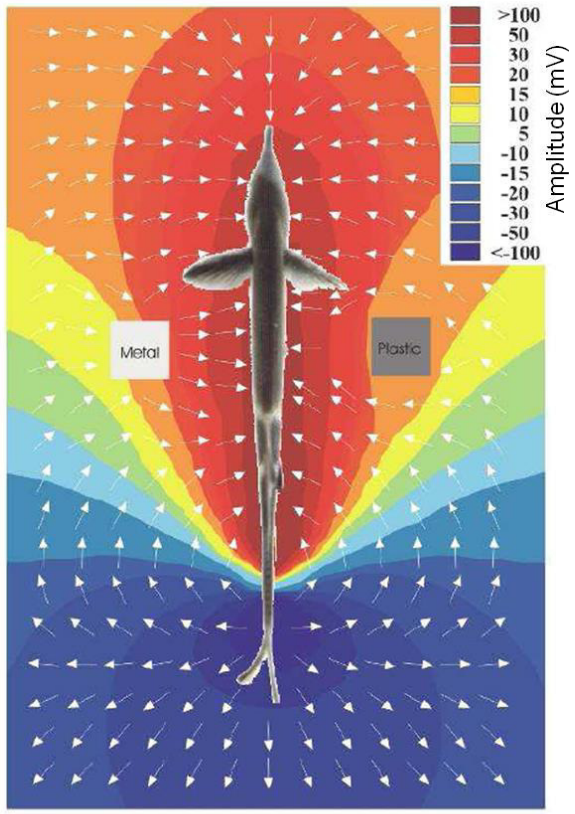

Figure 2: Influence of objects with different resistances on the electric field of *Gnathonemus petersii* during active electrolocation. A good conductor like metal focuses the field lines, indicated by the white arrows, leading to an increase of the amplitude (colour-coded). An isolator like plastic, on the other hand, spreads the field lines leading to a slight decrease of the amplitude. Changed after (von der Emde & Schwarz, 2001).

1.3.2. Electroreceptor organs

Electroreceptor organs can be broadly categorised into two groups: the ampullary electroreceptors (including the basal end bud electroreceptor organs of lampreys), which are used for passive electroreception of low frequency external electric fields, and the tuberous electroreceptors sensitive to high frequency signals, which are used for active electrolocation and electrocommunication.

Ampullary electroreceptors derive from mechanosensitive lateral line neuromasts and probably evolved in basal vertebrates. As illustrated in Figure 1 A) these original ampullary receptors were lost several times within the vertebrates and convergent forms were regained at least twice within the teleosts (Figure 1 B). The non-teleost ampullary organs react to cathodal stimuli, while the teleost ampullary organs are sensitive to anodal stimuli, supporting the hypothesis of a convergent evolution.

Ampullary receptor organs are characterised by a canal filled with a conductive fluid (mucous), which is connected to the external medium by a pore within the epidermis of the skin and that leads to a lumen containing the receptor cells (Figure 3 A and B) (Baker et al., 2013; Jorgensen, 2005).

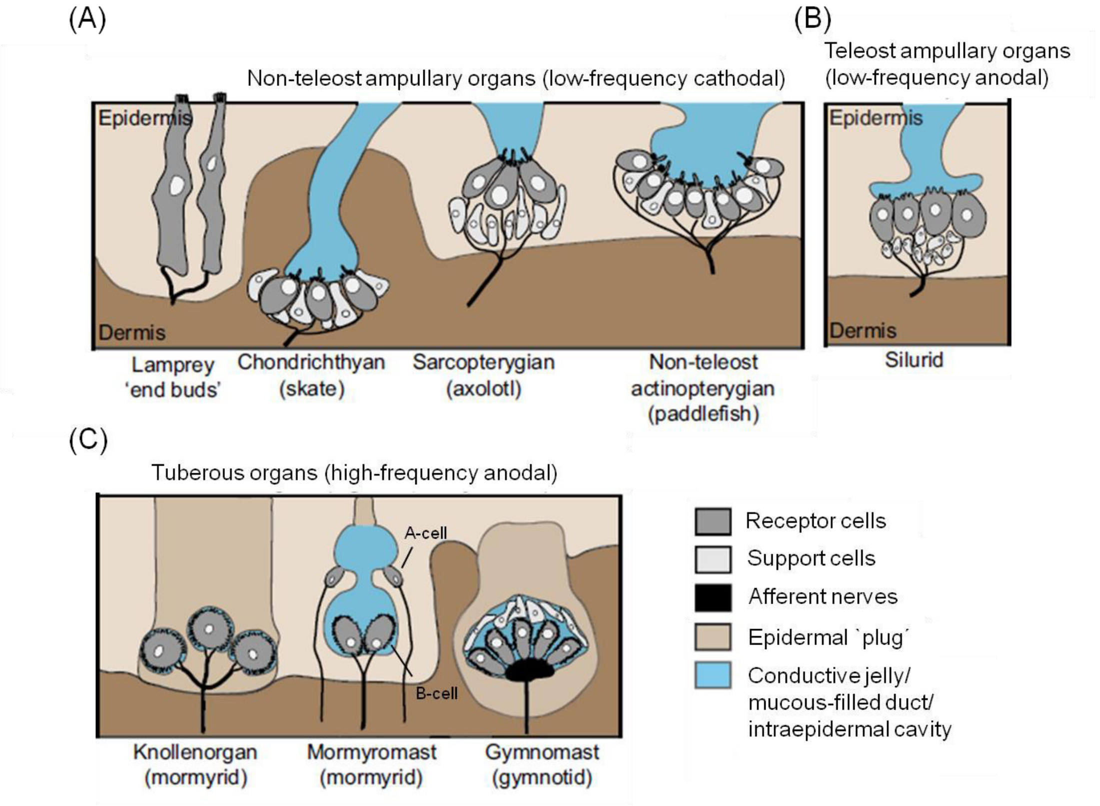

Figure 3: Schematic drawing of the different types of electroreceptor organs. Ampullary electroreceptor organs (A+B) respond to low frequency stimuli and mediate passive electroreception. They usually consist of several receptor cells (dark grey) with short microvilli, which are located at the base of a mucous-filled duct (blue) that opens to the surrounding medium (an exception are the end buds of lamprey). The receptor cells are interspersed by support cells (light grey). Ampullary organs are found in several non-teleost groups (A), where they respond to cathodal stimuli and in teleosts (B), where they respond to anodal stimuli. In two groups of teleost fish additionally tuberous electroreceptor organs (C) can be found, which are sensitive to high-frequency anodal stimuli and thus mediate active electrolocation. In these tuberous organs the receptor cells are located in a intraepidermal cavity, which is connected to the surrounding medium via plugs of loosely arranged epidermal cells. The mormyriformes possess two different types of tuberous organ (knollenorgans and the mormyromasts), while gymnotiformes possess only one type (gymnomasts). Changed after (Baker et al., 2013).

Tuberous receptor organs on the other hand, are only found in two groups of teleosts, the mormyriformes and the gymnotiformes, and probably evolved convergently. While the gymnotiformes possess only one type of tuberous receptor organ (gymnomasts), the mormyriformes possess two different types called mormyromasts and knollenorgans, which are used for different aspects of electroreception (Figure 3 C).

The mormyromasts respond to changes in the self-generated EOD and thus are used for active electrolocation. They consist of two chambers, containing two different types of receptor cells, which are tuned to different tasks. The so called A-cells are connected to the outer chamber and are sensitive to changes in the EOD amplitude, caused by pure resistive differences between objects and the surrounding medium. The B-cells are connected to the inner chamber of the tuberous organ and react to changes in the EOD waveform as well as to amplitude changes. Such changes are evoked by animate objects with complex impedance (resistive and capacitive differences) like plants or animals.

The knollenorgans are sensitive to EODs of conspecifics and thus are used during electrocommunication. Morphologically tuberous receptor organs are characterised by receptor cells surrounded by a intraepidermal cavity, which is conductively connected to the outside medium via plugs of loosely packed epidermal cells (Baker et al., 2013; Jorgensen, 2005).

All electrosensory receptor cells are secondary receptors, which means they do not transmit the signal directly via axons but are synaptically innervated by afferent nerve fibres. Depending on their position on the body all electroreceptor cells are innervated either by the anterior or the posterior lateral line nerve. In teleosts the electrosensitive fibres of both lateral line nerves project to the electrosensory lateral line lobe (ELL) and in non-neopterygian fish they project to the dorsal octavolateral nucleus (DON) (Bell & Maler, 2005).

The ELL is the first central processing stage for all electrosensory input in teleosts. In mormyrids it can be differentiated in four functional areas, which are secondary innervated by the different types of receptor cells. The afferent fibres innervating the receptor cells of the ampullary organs terminate within the ventrolateral zone of the ELL, the afferent fibres of the mormyromast A-cells terminate in the medial zone of the ELL, the afferent fibres of the mormyromast B-cells terminate in the dorsolateral zone of the ELL, and the afferent fibres of the knollenorgans terminate in the nucleus of the ELL. This morphological separation shows that different modalities of electrolocation are processed in parallel in the ELL. From the ELL projections go to several other brain regions including several multisensory regions like the torus semicircularis, the optic tectum, the valvula cerebelli, the thalamus and the pallium (Bell & Maler, 2005; Heiligenberg, 1987; Prechtl et al., 1998).

1.3.3. Electric organs

The ability of some fish to produce strong electric shocks has been know for centuries, however their origin was unknown for quite a long time. Extensive research, which was started already by the ancient Greeks, finally led to the discovery of special electric organs, which generate the strong electric discharges. However similar organs were also found in fish, which did not produce noticeable electric shocks and up until the middle of the last century the function of those organs was unclear. Only in the 1950s Hans Werner Lissmann discovered that these electric organs produce weak electric signals, which are used for orientation and communication (Lissmann, 1951, 1958; Lissmann & Machin, 1958).

Electric organs are only found in fish and have evolved at least six times independently (Figure 4) (Gallant et al., 2014). Despite quite large anatomical differences between the electric organs of the different groups, there are strong similarities in their function, which makes the electric organ a very interesting modal for studying convergent evolution. The size and location of the electric organ is quite different in the individual groups. For example in many Gymnotiformes the electric organ spreads nearly through the whole length of the fish, while in the Mormyriformes the location of the electric organ is restricted to the caudal peduncle (Figure 5) (Bruns, 1971).

All electric organs consist of electrocytes, which are connected in series with each other. Those converted muscle cells lost the ability to contract and instead change their membrane potential when being excited by the corresponding electromotorneuron (EMN). Innervation is achieved via stalks, which are either penetrating the electrocyte or are non-penetrating. The resulting voltage of the single electrocytes is summed which leads to the generation of the specific EOD. While this fundamental organisation is identical in all electric organs the morphology of the electrocytes varies widely in the different groups (Gallant et al., 2014).

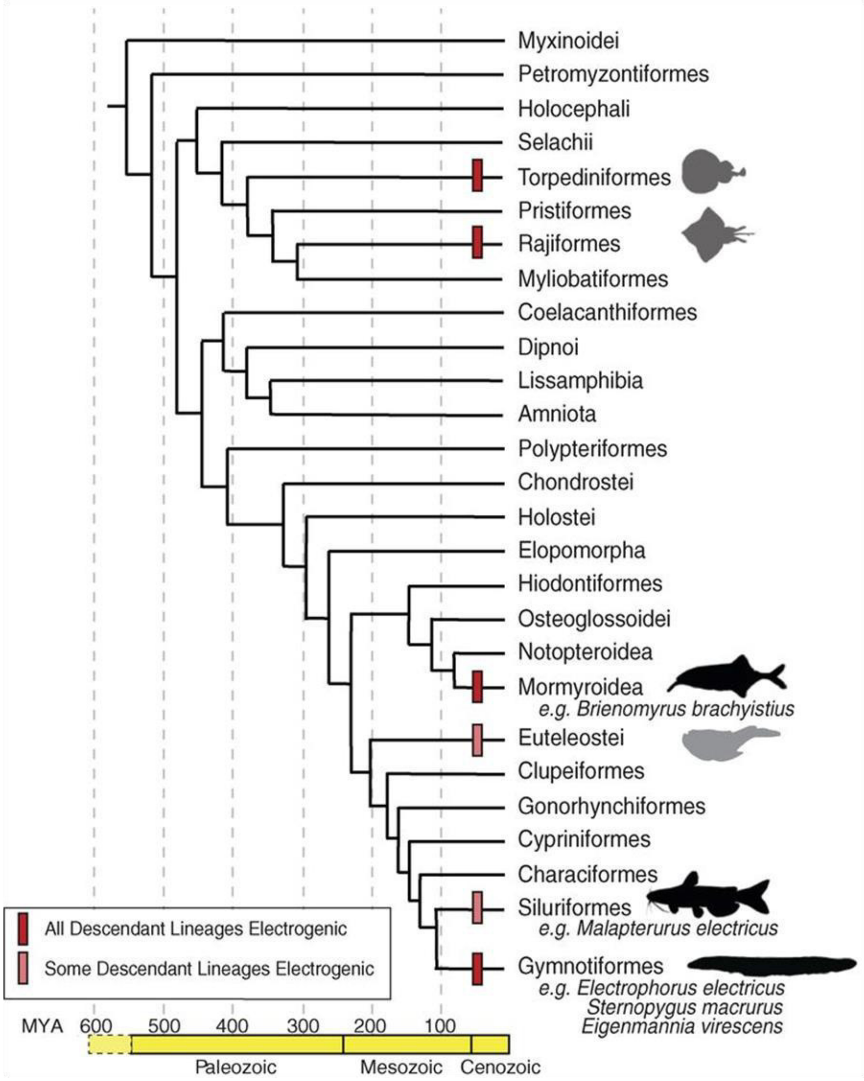

Figure 4: Phylogenetic distribution of electric organs. Within the vertebrates, electric organs and thus the ability to produce electric signals (weak or strong) has evolved several times independently (indicated by the red bars) in very different groups. While most of these groups produce strong electric shocks used for prey capture and self-defence, the electric organs of the mormyriformes and gymnotiformes produce weakly electric signals used for orientation and communication. From (Gallant et al., 2014).

To generate an EOD a command signal from the medulla is transmitted to the electrocytes, leading to a synchronous excitation of all cells. An individual electrocyte generates a potential of ca. 100 mV. The typical waveform of the resulting EOD (Figure 5) depends on the structure of the stalk and the surface area of the cell membrane as well as the number of electrocytes arranged in series (determines the voltage) and in parallel (determines the current) (Zupanc & Bullock, 2005). Broadly EODs are categorised into wave-type EODs and pulse-type EODs. Wave-type EODs are continuous sinusoidal signals, which are more or less constant in frequency within an individual but differ in frequency between species and also between individuals. Most species of the South American Gymnotiformes and one genus of the African Mormyriformes (Gymnarchus) produce wave-type EODs. Pulse-type EODs are short bi- or tri-phasic signals, which are emitted with very variable frequencies. Most of the mormyrid fish, including *G. petersii*, produce such pulse-type EODs.

The individual adaptations of the active electric system in *G. petersii* will be explained in more detail in a later chapter.

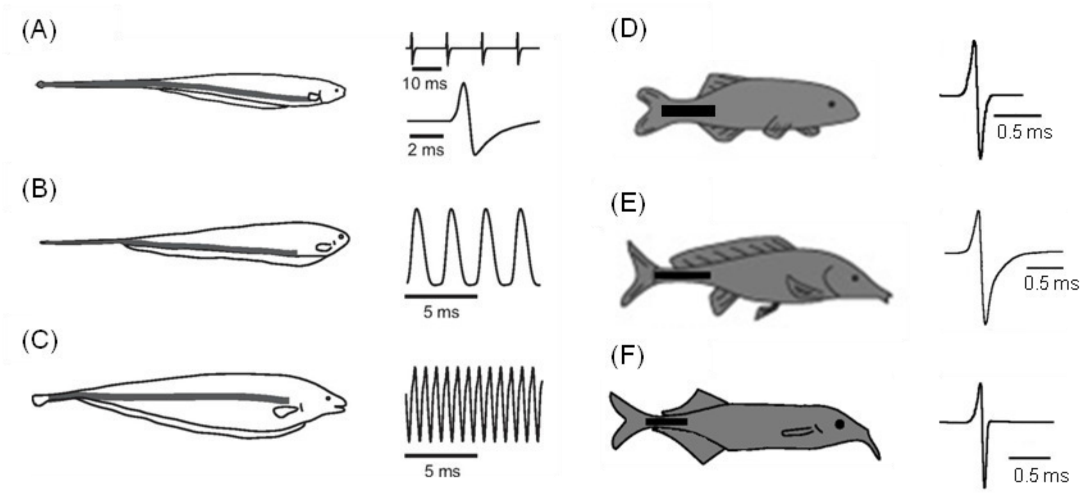

Figure 5: Location of the electric organs and EODs of gymnotiform (A-C) and mormyrid (D-F) fish. The location of the electric organ is indicated in grey (A-C) or black (D-F). *Brachyhypopomus gauderio (A) is a gymnotiform pulse-type fish, Eigenmannia* sp. (B) and *Apteronotus albifrons* (C) are gymnotiform wave-type fish and *Marcusenius altisambesi* (D), *Mormyrus rume* (E) and *Gnathonemus petersii* (F) are mormyrid pulse-type fish. (A-C) changed after (Salazar, Krahe, & Lewis, 2013), (D and E) changed after (Gebhardt, Böhme, & von der Emde, 2012), (F) changed after (von der Emde et al., 1998).

1.4. Vision

For us humans, vision is the most important sense during orientation as it provides detailed information about our close surroundings and also allows us to obtain a broad overview of the distant environment. Within the long evolution of vision, a wide range of different visual systems, from simple photoreceptors to the complex lensed eye, have evolved; each are specialised for different aspects of light reception. The underlying physical stimulus for all visual systems are electromagnetic waves of a specific wavelength originating from the sun (or artificial light sources), which are reflected by objects in the environment. The spectrum of visible light depends on the visual pigment of the photoreceptors and varies between species. In humans it lies between 380 nm and 780 nm.

During the day, light is an extremely reliable and constant information source, which is available nearly on the whole planet (except of the deep sea and some caves). Even during night sunlight reflected by the moon and starlight allows specialised eyes to perceive the environment. The immense importance of light as an information and energy source is reflected by the fact that the activity of most animals is determined by the presence or, as a contra strategy, the absence of light via circadian clocks.

1.4.1. Evolution, development and anatomy of the vertebrate eye

"*To suppose that the eye, with all its inimitable contrivances... could have been formed by natural selection, seems, I freely confess, absurd in the highest possible degree... Yet reason tells me, that if numerous gradations from a perfect and complex eye to one very imperfect and simple, each grade being useful to its possessor, can be shown to exist... and if any variation or modification in the organ be ever useful to an animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, can hardly be considered real.*" Charles Darwin (1809–1882)(Darwin, 1859)

The evolution of the eye was, and in some ways still is, controversially discussed since the publication of Darwin´s "Origin of species". Critics even saw the eye as evidence against the theory of evolution and argued that such a complex structure could not have evolved through natural selection, because there was no functional intermediate form of an eye. However, since then extensive research has led to the discovery of several types of eyes with different degrees of complexity (especially in mollusks), which show that intermediate forms exist (Figure 6) (Arendt, 2003; Fernald, 1997, 2000; Land & Fernald, 1992).

The evolution of eyes started more than 600 million years ago with the appearance of the first photoreceptors and the first visual systems emerged around 540 million years ago during the so called Cambrian explosion. The immense diversity among eyes of different groups of animals led to the discussion whether eyes evolved independently several times in different groups or whether there was a single common ancestor to all types of eyes. While for quite a long time most scientists supported the hypothesis of convergent evolution, the investigation of the Pax-6 gene and some other genes, which are involved in eye construction, that were found in all bilaterian animals, might promote a monophyletic origin of all bilaterian eyes (Arendt, 2003; Arendt & Wittbrodt, 2001; Fernald, 2000; Gehring, 2004; Gehring & Ikeo, 1999; Lamb, Collin, & Pugh, 2007). The vertebrate eye probably evolved in a common ancestor of jawless and jawed vertebrates (possibly even earlier), as is supported by the very similar structure of the eyes, the retina and the opsins of lampreys and jawed vertebrates (Lamb et al., 2007).

During embryonic development the vertebrate eyes emerge through evagination of the diencephalon, first forming optic grooves, which finally close-over and form so called optic vesicles. These optic vesicles invaginate and build the optic cup, leading to the typical structure of the retina, where the photoreceptors are arranged furthest away from the incoming light. The lens is then build through differentiation of the surface ectoderm (Lamb et al., 2007).

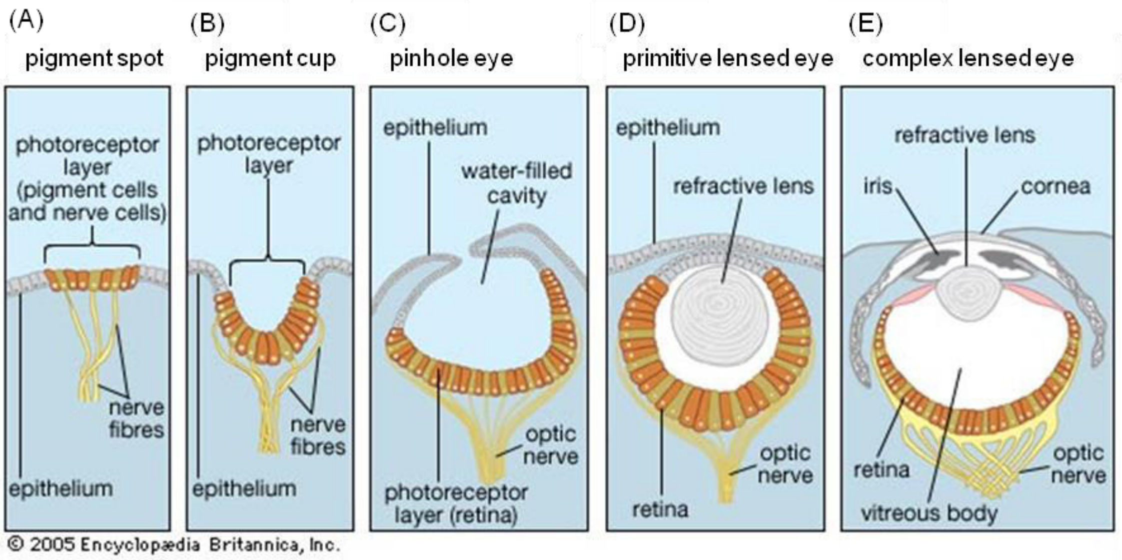

Figure 6: Different eye types of molluscs with different degrees of complexity. The simplest eye, a pigment spot (A), allows the perception of light gradients and is found for example in the limpet *Patella*. Slightly more advanced is the pigment cup (B) found in slit-shell molluscs Pleurotomaria, it reduces the angle of incoming light and thus allows the perception of light direction. The next step of complexity is represented by the pinhole eye (C) found e.g. in *Nautilus.* It allows the dim perception of shapes. In the primitive lensed eye (D), as it is e.g. found in the marine snail Murex, the incoming light is focused on the retina, which allows a sharper perception of shapes and the necessary light intensity. The more complex lensed eye of octopuses and squids (E) (very similar to the lense eye of vertebrates) allows sharp sight at different distances thanks to the adjustable form of the lense and additionally the amount of incoming light can be regulated via the iris. Changed after (Ayala, 2007), original from Encyclopaedia Britannica.

Figure 7 shows a schematic of the anatomy of a lens eye as exemplified by the human eye. The eponymous lens of the vertebrate eye consists of a capsule, an epithelium and fibres. The lens fibres are transparent thin cells, which contain no organelles. The lens is biconvex and together with the cornea focus the incoming light on the retina. Zonule fibres attached to the cilliary muscles suspend the lens in place and through contraction of the cilliary muscles change the curvature of the lens. Via this accommodation of the lens the focal point of the eye can be adjusted, which allows sharp sight of objects at different distances (Forrester, Dick, McMenamin, Roberts, & Pearlman, 2015; Kolb, 2007a).

The eye consists of three layers: 1) The sclera, also known as the white of the eye, is the outermost layer of the eye. It consists of collagen tissue, which has protective functions and is responsible for maintaining the form of the eye against internal and external forces. The white sclera is intermitted by the transparent cornea at the front of the eye. The cornea is responsible for about 70% of the refractive power of the eye, allowing sharp sight (Cassin, Solomon, & Rubin, 1984). 2) The choroid is the vascular layer of the eye and as such responsible for the blood supply. Furthermore, melanin pigments in this middle layer absorb remaining light, which was not absorbed by the retina, regulating unwanted reflection. At the front of the eye the choroid is connected to the cilliary body, which includes the cillary muscles, controlling the form of the lens, and the iris, which controls the size of the pupil and thus the amount of incoming light. 3) The innermost layer of the eye is the retina. The retina contains the photoreceptors and retinal neurons and is therefore responsible for the photoreception and is also the first processing stage of visual input (Forrester et al., 2015; Kolb, 2007a). The structure and the function of the retina will be described in more detail in the next chapter.

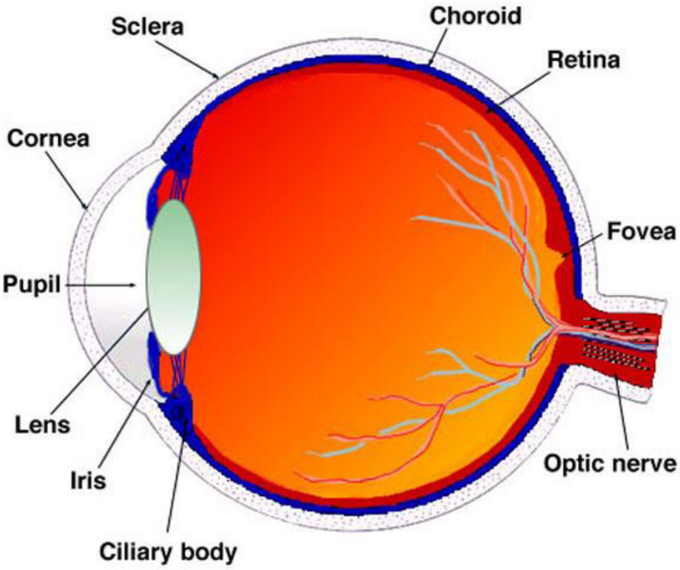

Figure 7: Schematic sagittal section through the human eye. The eye consists of three major layers, the sclera a protective layer, the choroid a vascular layer and the retina containing the photoreceptors. Light enters the eye via the pupil, the size of which is adjusted by the iris, and is focused on the retina by the cornea and the lens through refraction. Thereby the light from the frontal direction is focused on the fovea, the point of the retina with the highest density of cone photoreceptors. The cilliary muscles of the cilliary body keep the lens in place and adjust its form during accommodation to allow sharp sight at different distances. Information from the retina is transmitted to the brain via the optic nerve. From (Kolb, 2007a).

1.4.2. The vertebrate retina

The vertebrate retina consists of three cell layers: the outer nuclear layer with the cell bodies of the photoreceptors, the inner nuclear layer with the cell bodies of the bipolar, horizontal, interplexiform and amacrine cells and the ganglion cell layers (Figure 8). These cell layers are connected via two synaptic layers: the outer plexiform layer with synapses between the photoreceptors and the bipolar cells and the inner plexiform layer with synapses between the bipolar cells and the ganglion cells and in between the bipolar, the horizontal and the amacrine cells (Bear, Connors, & Paradiso, 2007; Cohen, 1963; Dowling, 1987; Dowling & Boycott, 1966). The internal (or inner) limiting membrane divides the retina from the vitreous body (internal space of the eye) and is built by the plasma membranes of the Müller cells (predominant glia cells in the retina) and other retinal glia cells (Heegaard, Jensen, & Prause, 1986). A second boundary layer also built by Müller cells, the external (or outer) limiting membrane, is found between the photoreceptor outer segments and the outer nuclear layer (Fine & Zimmerman, 1962).

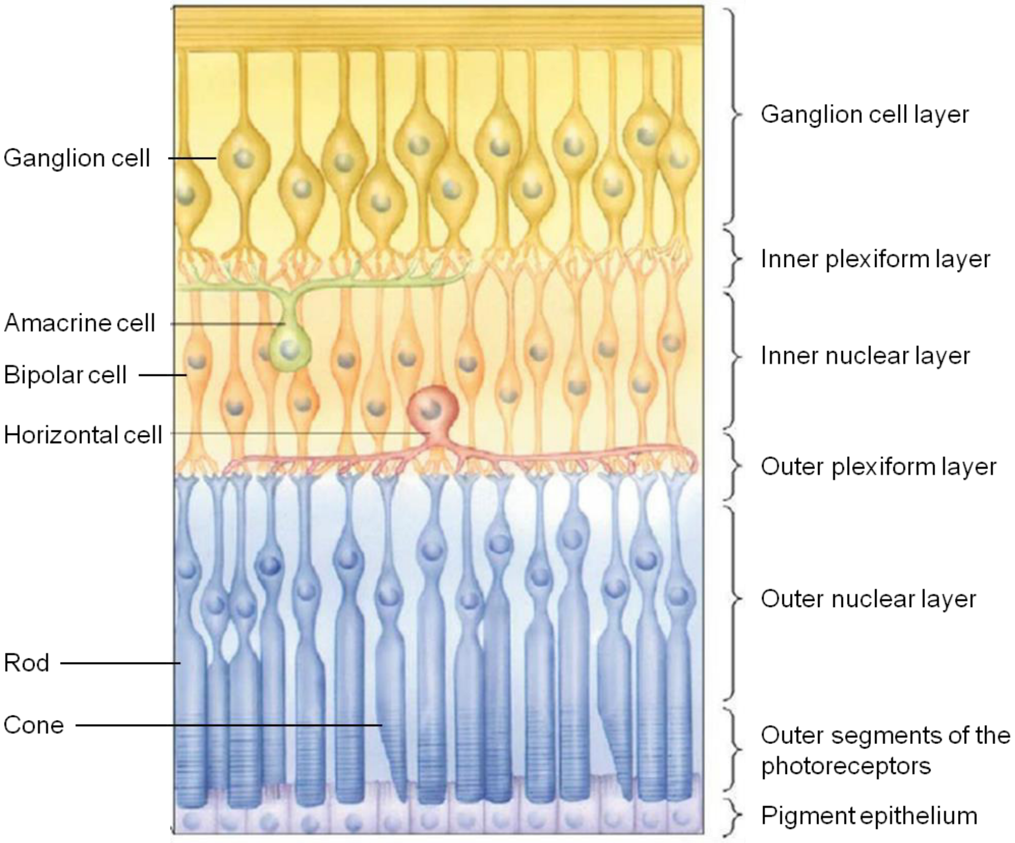

Figure 8: Structure of the vertebrate retina. The vertebrate retina consists of three cell layers: the outer nuclear layer containing the cell bodies of the two different types of photoreceptors (rods responsible for dim-light vision and cones responsible for bright-light vision), the inner nuclear layer containing the cell bodies of the horizontal, bipolar, amacrine and interplexiform cells (latter not shown in this figure) and the ganglion cell layer containing the cell bodies of the ganglion cells. These cell layers are connected via two plexiform layers, the outer plexiform layer with the synapses between the photoreceptors, the bipolar and the horizontal cells and the inner plexiform layer with the synapses between bipolar, amacrine and ganglion cells. The outer segments of the photoreceptors contain the visual pigment, which is provided by the pigment epithelium, and are responsible for the phototransduction process. Changed after (Bear et al., 2007).

1.4.2.1. Photoreceptors and phototransduction

Within the vertebrate retina there are two types of photoreceptors, rods and cones. In principle both types of photoreceptors consist of an outer segment, an inner segment, the cell body and an axon with the synapse. The outer segments contain the discs with the visual pigments, which are responsible for the light absorption and transduction. They are located in the subretinal gap at the most distal position from the incoming light. This organisation prevents that the outer segments receiving too much light, which would lead to a bleaching of the visual pigments, and allows the connection to the pigment epithelium, which is responsible for the regeneration of the visual pigment. The inner segments contain the mitochondria and thus provide the energy necessary for phototransduction. The axon and the synapse connect the photoreceptors with the retinal neurons.

While this main structure is identical in both photoreceptor types, there are morphological and functional differences between rods and cones (Figure 9). Rods mediate dim-light vision and can even detect single photons (Hecht, Shlaer, & Pirenne, 1942). Their outer segments are longer but also slimmer than those of the cones. The synaptic terminals of the rods are typically smaller and more spherical. Cones are used in bright light and their outer segments are cone-like shaped. The discs of the cones are foldings of the cell membrane, while in rods the double membrane discs build stacks, which are disconnected from the cell membrane and free floating inside the outer segment membrane (Burns & Lamb, 2003; Cohen, 1963; Dowling, 1987; Kolb, 2011).

The transduction of photo energy to neuronal signals is mediated by the visual pigments contained in the outer segments. The visual pigment consists of a protein called opsin bound to a light absorbing chromophore, which either derives from vitamin A_1 (retinal) or vitamin A_2 (retinal$_2$), and is embedded within the disc membrane. The visual pigments built from opsin and retinal are called rhodopsins and are mainly found in terrestrial and marine vertebrates. Opsin and retinal$_2$ build the visual pigments called porphyropsins, which are found in most fresh water vertebrates (Wald, 1958).

Within these two broad categories different subtypes of visual pigments with individual absorption spectra exist, which are activated by the absorption of light with a specific wavelength. There is usually one subtype of visual pigment in rods and one to four different subtypes within the cones. Usually a given cone possesses only one subtype of visual pigment, which results in formation of cone subtypes with a specific spectral sensitivity. The perception of colour depends on the processing of input of photoreceptors with at least two different absorption maxima. Since in most animals rods and cones are not active at the same time(cones during day and bright light and rods during dim light at night), colour vision is mediated by differential activation of the different cone subtypes (Dowling, 1987; Kalloniatis & Luu, 2015; Kolb, 2011).

In vertebrate photoreceptors the phototransduction process is achieved via a hyperpolarisation of the receptor cell: In darkness there is a constant dark current mediated by open sodium channels, which leads to a constant release of the neurotransmitter glutamate. The absorption of a photon by the chromophore leads to a change of its configuration (from 11-cis to all-trans) catalysing the activation of the G-protein transducin. The activation of transducin starts a reaction cascade resulting in the closure of the sodium channels, which leads to a hyperpolarisation of the cell and thus a reduction or termination of the dark glutamate release (Fu, 2010; Kolb, 2011).

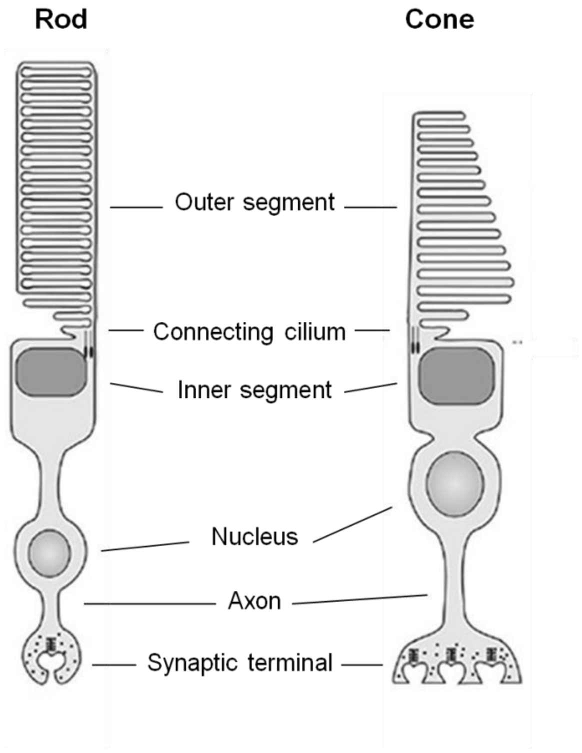

Figure 9: Schematic drawing of the morphology of a rod and a cone. Both photoreceptor types consist of an outer segment, containing the visual pigment, an inner segment containing the mitochondria, a nucleus, an axon and a synaptic terminal, with which the photoreceptors are connected to the retinal neurons. The main difference between rods and cones lies in the structure of the outer segments and in the visual pigments. The rod outer segments are longer and the discs containing the visual pigments are separated from the cell membrane whereas are build through folding of the cell membrane in cones. The only rod visual pigment is usually most sensitive to intermediate wavelengths (green), while cones might contain different types of visual pigments most sensitive to short, intermediate or long wavelengths. Changed after (Burns & Lamb, 2003).

In order to be able to react to changes in light intensity, the reaction cascade induced by light absorption has to be terminated and reversed again. Therefore, all activated proteins have to be inactivated again and the bleached all-trans chromophore has to be replaced by a new 11-cis chromophore from the pigment epithelium. The time necessary to reset all molecules within the reaction cascade determines the temporal resolution of the photoreceptor. The exchange of the chromophore is achieved via two different pathways in rods and cones. In cones Müller cells are involved in the chromophore exchange, which leads to a faster replacement and thus results in a higher temporal resolution compared to rods. Furthermore, these differences in chromophore regeneration time lead to the differences in light intensity tolerance between rods and cones. During bright light at day the chromophores within the rods cannot be replaced fast enough, which leads to complete bleaching of all visual pigments and thus an inactivity of the rods. Due to the different regeneration pathway the chromophores of the cones are replaced fast enough, allowing activity of the cones even in bright sunlight (Arshavsky, 2002; Mata, Radu, Clemmons, & Travis, 2002).

However, even in compete darkness the visual pigment undergoes spontaneous (thermal) activation, initiating the same reaction cascade as during light induced activation (dark noise). This spontaneous activation rate sets the ultimate limitation of light sensitivity (Aho, Donner, Hyden, Larsen, & Reuter, 1988; Barlow, 1956; Donner, 1992). A single toad rod has a spontaneous activation rate of ca. 0.021 events per second (Yau, Matthews, & Baylor, 1979). This high stability allows the maintain of a high sensitivity despite the great number of rhodopsin molecules within a single cell, which is necessary for increasing the probability of photon absorption. The spontaneous activation rate of the cones is with ca. 10 events per second per cone much higher than that of the rods, giving one reason, among several others, why rods are much more sensitive than cones (Fu, Kefalov, Luo, Xue, & Yau, 2008).

1.4.2.2. Neurons of the inner retina and retinal circuits

In addition to the photoreceptors there are five different neuron types located in the inner retina: the bipolar, amacrine, horizontal and interplexiform cells in the inner nuclear layer and ganglion cells in the ganglion cell layer (Figure 8). Of each of those neuron types several subtypes exist. Bipolar cells build synaptic connections from the photoreceptors to the ganglion cells. In humans, for example, there are 11 different subtypes, which differ in the size of their dendritic trees and thus the number of photoreceptors innervated and the type of synaptic contact and thus the response to the photoreceptor light signal. Depending on the synapse some bipolar cells react with a depolarisation (ON) and some with a hyperpolarisation (OFF) to the hyperpolarisation of the photoreceptor, building the fundament for the important ON and OFF-centre pathways.

As already indicated by the name, horizontal cells connect several photoreceptors (like different cone types or also rods and cones) and also bipolar cells horizontally within the outer plexiform layer and mediate lateral interactions, like e.g. feedback signalling. With these interactions horizontal cells provide the bipolar cells with a centre surround organisation. In most mammals there are two different subtypes of horizontal cells (in humans three) (Dowling, 1987; Dowling & Boycott, 1966; Kolb, 2007c; Werblin & Dowling, 1969).

Amacrine cells interconnect ganglion cells, bipolar cells and interplexiform cells within the inner plexiform layer. There are several different subtypes (e.g. at least 25 different in the human retina), which are categorised according to the size of their dendritic tree and their location (stratification level) within the inner plexiform layer. Some amacrine cells only connect bipolar and ganglion cells within the ON or OFF channel while others connect cells from the On and OFF channel. Thus amacrine cells are also involved in the ON- and OFF-centre processing.

Interplexiform cells have their dendritic origin in the inner plexiform layer receiving input from the amacrine cells and project to bipolar and horizontal cells within the outer plexiform layer. Thus these cells connect both plexiform layer in the opposite direction as the bipolar cells (Dowling & Ehinger, 1975).

The ganglion cells are the output neurons of the retina, which transmit the visual information received from the bipolar and horizontal cells in from of action potentials via the optic nerve into the brain. Again various subtypes of ganglion cells exist and at least 25 different types are found in the human retina. Ganglion cells either react with spikes to the presence (ON) or absence (OFF) of light and thus continue the ON- and OFF-centre pathway. Furthermore, they react in a centre surround fashion to differences in light intensity. Through the highly complex interaction with the other retinal neurons ganglion cells are already selectively tuned to certain image features such as colour, size and speed and direction of motion (Dowling, 1987; Dowling & Boycott, 1966; Kolb, 2007b; R. Nelson, 2007).

The information gathered by the ganglion cells are transmitted to the brain via the ganglion cell axons in the optic nerve. The optic nerves of the two eyes cross in the optic chiasm. Depending on the species either all axons cross to the contralateral side, like e.g. in lower vertebrates, or only parts cross, as in mammals (axons from the nasal part of the retina cross, while those of the temporal part do not cross) (Godement, Salaün, & Mason, 1990; Lázár, Libouban, & Szabo, 1984). In lower vertebrates the first stage of central processing of visual information is the optic tectum, which is homologous to the colliculus superior in mammals (Vanegas, 1984). The optic tectum is a laminated structure and often accounts for a quite big part of the brain (especially in birds and fish), indicating the importance of visual information for most animals.

1.4.3. Specialisations in vertebrate eyes

The visual system of an animal is usually adapted to the environmental conditions of the habitat and to the lifestyle of the animal. Such specialisation can be achieved via adaptations in the structure of the eye, specifications in the photoreceptor distribution across the retina and differences in the connection of the retinal neurons. The most specialisations are either for light sensitivity or for spatial resolution. These two extremes are not compatible, which means that a system is either very light sensitive with deficits in spatial resolution or a system has a high spatial resolution and is less light sensitive. However, compromises between both systems can be achieved through distinct areas of specialisation in the retina, like for example the fovea in the human eye. In the human retina rods and cones are not regularly distributed. While in total there are far more rods than cones allowing a decent light sensitivity, there is an extreme density of cones within the fovea allowing a good spatial acuity during day (Curcio, Sloan, Kalina, & Hendrickson, 1990; Dowling, 1987).

Probably the most prominent examples for specialisation on high spatial resolution is the visual system of eagles. The eagle retina consists to ca. 80% of cones which are densely packed. The ganglion cells receive input from only very few photoreceptors (nearly a ratio of 1:1) increasing the spatial resolution. The elongated form of the eye is also an adaptation to increase visual acuity (Reymond, 1985; Zeigler & Bischof, 1993). Specialists in light sensitivity, like for example owls, usually possess very big eyes with a retina strongly dominated by rods and additional reflecting systems like a tapetum lucidum. The ratio between ganglion cells and photoreceptors are often much smaller, which means that a given ganglion cell receives input from several receptor cells (Martin, 1982; Zeigler & Bischof, 1993).

An aquatic habitat requires specialisations to the different light spectrum and refraction properties under water. The eyes of some surface feeding fish, for example, are specialised on vision under and above water. In these fish the photoreceptors of different parts of the retina have different absorption maxima depending on the dominant wavelength above (intermediate wavelength) and under (longer wavelength) water (Owens, Rennison, Allison, & Taylor, 2012). In deep-sea fish, specialisations for light sensitivity are found as an adaptation to the extreme low light levels. The eyes of deep-sea fish are usually tuberous, with an upwards pointing visual axis and they possess enlarged lenses to enhance light collection. The retina of these fish is divided into subparts with individual photoreceptor organisations. While for example the anterior part of the main retina of these fish is similarly structured as the retinas of other vertebrates, the photoreceptors are grouped into bundles in the posterior part. In addition to this main retina which is located at the focal distance of the eye, there is an accessory retina, which is not within the focal distance and also possesses grouped photoreceptors (Locket, 1970, 1971). A grouped retina is also found in *G. petersii* and its organisation will be described in more detail in a following chapter.

1.5. The mechanosensory lateral line system

The mechanosensory lateral line system consists of mechanoreceptor organs called neuromasts, which are either located freely at the body surface or within subdermal fluid-filled canals along the visible lateral line and at the head. These neuromasts transduce water movement, relative to the body or fluid movement within the canal induced by pressure changes, into neuronal signals.

The existence of the mechanosensitive lateral line system was unknown until the middle of the 19th century. Until then the only clearly visible part of the lateral line system, the lateral line canal, was thought to be a mucus-producing organ, responsible for the slimy surface of fish (Coombs et al., 2012). The German anatomist Franz Leydig first discovered the existence of sensory organs within the canal in 1850 (Leydig, 1850) and eleven years later Franz Eilhard Schulze discovered the superficial neuromasts and first described their cupulae (Schulze, 1861). Schulze was also the first, to suggest that they are sensitive to water movement induced by low frequency vibrations such as sound waves (Schulze, 1870).

Due to the similarities with the inner ear, it was accepted for quite some time that the lateral line system was used for the perception of acoustic stimuli and another suggestion that it might be used for the perception of water currents in rivers remained unappreciated (Hofer, 1908). In a series of experiments in 1932, Karl von Frisch proved that the lateral line was not used for sound perception (von Frisch & Stetter, 1932). Following this finding there was a long debate about the adequate stimulus of the lateral line system. Extensive research finally led to the finding that the lateral line system is used as a "sense of touch at some distance" (Dijkgraaf, 1963), detecting moving objects such as predators, prey or conspecifics due to the water movements they induced as well as detecting stationary objects within existing or self-generated water currents (von Campenhausen, Riess, & Weissert, 1981). The lateral line system is involved in surface feeding, schooling, predator and obstacle avoidance and prey detection under water (Bleckmann, 1986; Bleckmann & Topp, 1981; Coombs et al., 2012; Dijkgraaf, 1963; Gregson & Burt de Perera, 2007; Kanter & Coombs, 2003; Montgomery, Coombs, & Halstead, 1995; Partridge & Pitcher, 1980; von Campenhausen et al., 1981).

1.5.1. Evolution and structure of the lateral line system

The lateral line system is an ancient feature of vertebrates, which is found in lamprey, fish and most larval and adult aquatic amphibians but was lost in terrestrial vertebrates (Coombs, Janssen, & Webb, 1988; Jørgensen, 1989). Simpler forms of lateral line neuromasts are found in hagfish and secondary mechanosensitive receptor cell organs (choronal organs) are found in urochordates. These choronal organs are suggested to be homologous to the lateral line system in vertebrates, suggesting that the lateral line system had already evolved in the chordate ancestors (Braun & Northcutt, 1997; Burighel et al., 2003).

The morphology of the lateral line system and its neuromasts differ strongly between species. While most cartilaginous and bony fish possess superficial neuromasts and a canal system, jawless vertebrates and amphibians only possess superficial neuromasts. Within the teleosts big variations are found in the structure and number of head canals and in the number and distribution of superficial neuromasts (Figure 10) (Coombs, Bleckmann, Fay, & Popper, 2014; Coombs et al., 2012).

Superficial neuromasts can be arranged singly, in pairs, rows or in clusters and they might sit flush with the skin, in pits or in grooves (mostly in non-teleost fish and amphibians, also called pit organs) or exposed on top of stalks, filaments or papillae (often found in deep sea or cave fish). Their function might be adapted to the habitat via additional non-sensory structures like papillae located next to the neuromast, which could act as protection and change the hydrodynamics. Such structures are often found in bottom-dwelling fish. The superficial neuromasts are directly exposed to the water and thus directly transduce the kinematic energy of water movement. Canal neuromasts, on the other hand, sit within the lateral line canals, located on the head and trunk, in between two canal pores. These pores can either be closed by a membrane or open. The movement of water particles close to a pore creates a pressure difference between the pores, which leads to a flow of the fluid within the canal away from the pore with the higher pressure. This movement of the fluid leads to a deflection of the neuromast. Therefore canal neuromasts transduce external water movements indirectly and react to slightly different parameters of the stimulus than the superficial neuromasts (Coombs et al., 1988; Webb, 2013). The morphology of the canals, especially on the head, is quite diverse and is broadly categorised according to their width in narrow and wide canals (Figure 10 B). The number of head canals varies within the teleosts, which might be an adaptation to the specific habitats of the fish, e.g. living in a pond with no or only very slow water currents puts other requirements on the lateral line system than life in fast running streams. It is assumed that the number of canals might be reduced and the number of superficial neuromasts might be increased with decreasing flow velocity of the habitat. While there are also slight morphological differences in the neuromast, the principle structure of teleost neuromasts is very similar and will be described in more detail in the next paragraph.

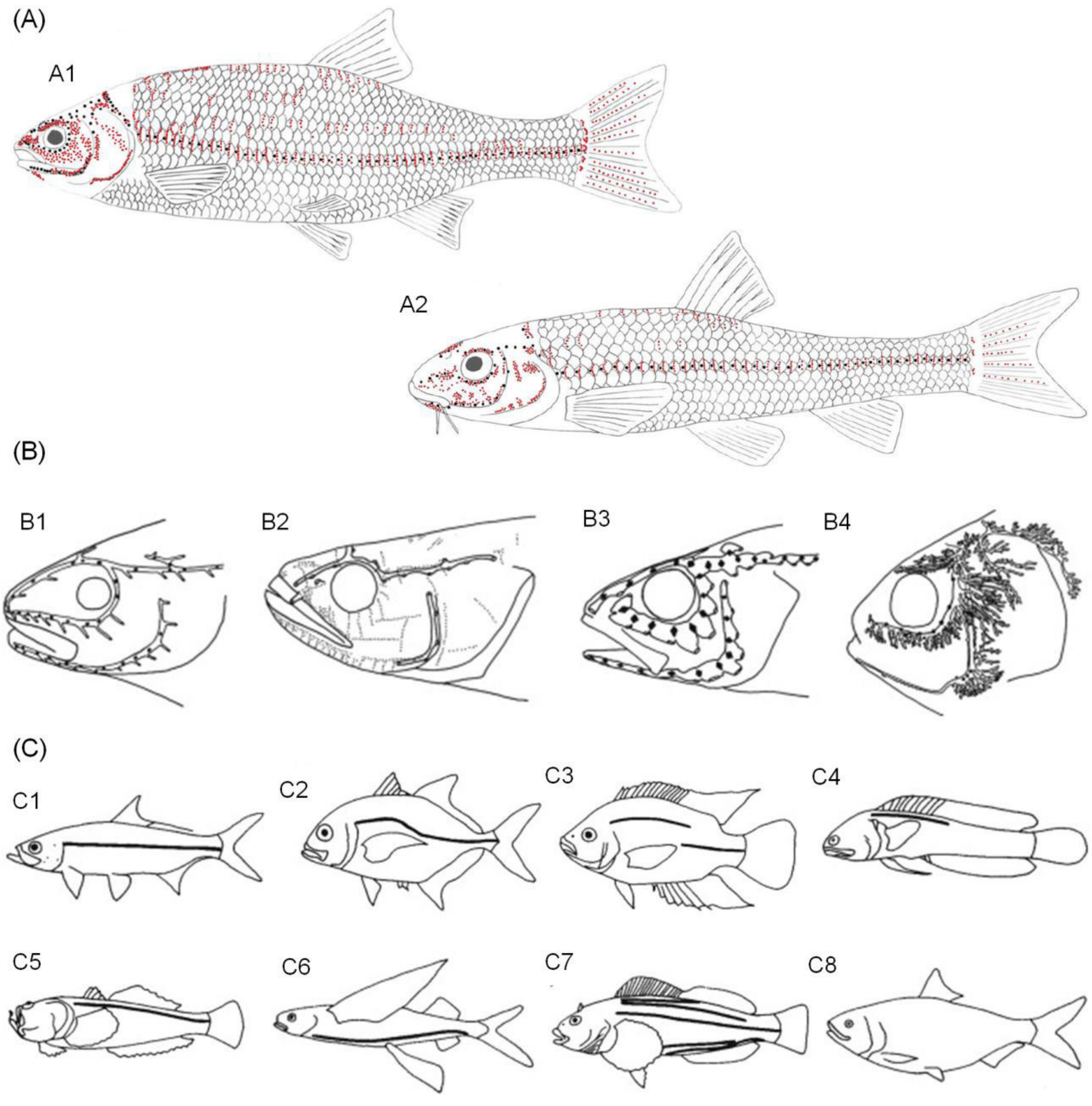

Figure 10: Structural diversity of the lateral line system. (A) Distribution of superficial neuromasts in leuciscus idus (ide) (A1) and gobio gobio (gudgeon). The red points indicate the location of superficial neuromasts and the black points indicate the position of canal neuromasts. (B) Different types of head canals: B1 narrow-simple canal system, B2 reduced canal system, B3 wide-simple canal system, B4 narrow-branched canal system. (C) Variations of the trunk lateral line system: C1 complete, straight; C2 complete, arched; C3 disjunct; C4 incomplete; C5 displaced dorsally; C6 displaced ventrally; C7 multiple and C8 absent. (A) changed after (Schmitz, Bleckmann, & Mogdans, 2014) and (B) and (C) changed after (Webb, 2011).

1.5.2. Neuromasts

The functional unit responsible for information transduction within the lateral line system is the neuromast, consisting of mechanosensitive hair cells and non-sensory cells (Figure 11 A, C). Each hair cell possesses a ciliary bundle with a long cilium (kinocilium) and several shorter microvilli (stereovilli) grading in length to one site of the kinocilium (Figure 11 B). The deflection direction of the stereovilli relative to the kinocilium determines the response of the receptor cell. In the undeflected state the receptor cell is firing at a constant tonic rate. Deflections of the stereovilli in direction of the kinocilium results in an excitatory increase of the firing, while deflections of the stereovilli away from the kinocilium has an inhibitory effect leading to a decrease of the firing rate (Coombs, Janssen, & Montgomery, 1992; Webb, 2013).

Within a single neuromast there are hair cells with different orientations, which usually develop in pairs with opposite directionality (Rouse & Pickles, 1991a). This paired arrangement increases the response of a neuromast to a deflection due to the opposing reactions of the paired hair cells (one increasing the other decreasing the firing rate). The number of hair cells per neuromasts varies between species and might also vary on different body parts within an individual.

To increase the effect of the water movements on the hair cells, a single gelatinous cupula covers the ciliary bundles of all hair cells within a neuromast. The cupula consists of a fibrillar core and two layers, a central layer covering the hair and support cells and an outer layer covering the mantel cells. The cupula grows continuously and thus can be repaired when damaged (Webb, 2013). The form and the length of the cupula varies between species and also between neuromasts of a single individual, which influences their function and determines the frequency response of the neuromast (Mukai, Yoshikawa, & Kobayashi, 1994; Van Trump & McHenry, 2008).

In addition to the sensory hair cells the neuromasts contain two types of non-sensory cells, support cells and mantel cells. Support cells are scattered between the sensory hair cells and reach from the surface down below the hair cells. They can differentiate into hair cells and thus are involved in hair cell turnover and regeneration (Hernández, Olivari, Sarrazín, Sandoval, & Allende, 2007; Namdaran, Reinhart, Owens, Raible, & Rubel, 2012; Williams & Holder, 2000). Mantel cells surround the hair and support cells of a neuromast and thus define its shape. They are responsible for the secretion of the cupula (Ghysen & Dambly-Chaudière, 2007; Rouse & Pickles, 1991b).

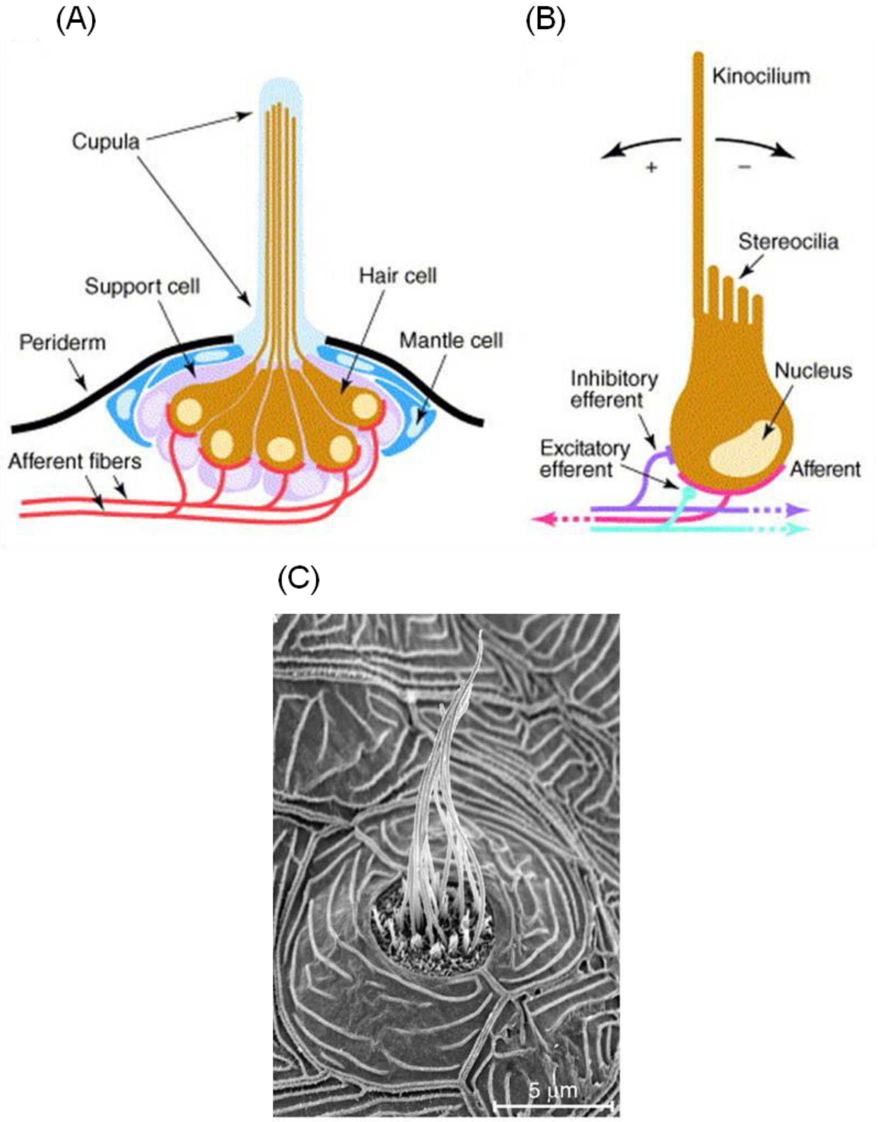

Figure 11: Morphology of the teleost neuromast. (A) Schematic drawing of a neuromast: The sensory hair cells are interspersed by support cells and surrounded by mantle cells. The ciliary bundles of the hair cells reach into a gelatinous cupula, which covers all hair and support cells of a neuromast and increases the effect of water movements on the receptors. (B) Schematic of a neuromast hair cell: The cilary bundle of the hair cell consists of a long kinocilium and shorter stereovilli. Deflection of the stereovilli in the direction of the kinocilium leads to an increase of the firing rate of the hair cell and a deflection away from the kinocilium leads to a decrease of the firing rate. The hair cell is innervated by primary afferent nerve fibres and receives input by efferent fibres. (C) A scanning electron micrograph of a zebrafish superficial neuromast located at the tail without the cupula. (A) and (B) changed after (Ghysen & Dambly-Chaudiere, 2004). (C) from (Gleason et al., 2009).

Like electroreceptors the mechanosensory hair cells of the lateral line system are secondary receptors. They are innervated by primary afferent neurons via excitatory glutamatergic synapses and additionally receive efferent input via choinergic synapses. The axons of the afferent neurons build the lateral line nerves. The anterior lateral line nerve (ALLN) innervates neuromasts at the head and the posterior lateral line nerve (PLLN) innervates neuromasts at the rest of the body. The mechanosensitive fibres of the lateral line nerves mainly terminate in the medial octavolateral nucleus (MON). Some lateral line projections also project to the Mauthner cells, which mediate an immediate flight responses called C-start response. Similarly to the central processing of electrosensory information, from this first processing stage in the MON secondary projections lead to several higher multisensory brain areas, which allows interaction with other sensory inputs (Bleckmann & Mogdans, 2014; Bodznick & Northcutt, 1980; McCormick, 1989; Wullimann & Grothe, 2014).

1.6. *Gnathonemus petersii*

The weakly electric fish *Gnathonemus petersii* (Günther 1862) is one of ca.195 species in the family Mormyridae, which is endemic to the African continent (Berra, 2001). Its common name elephantnose fish is inspired by its prominent moveable chin appendix also called *Schnauzenorgan* (Stendell, 1916). These typically grey-brown fish possess two characteristic white crescent-shaped markings between the dorsal and the anal fin and reach a length of up to 25 cm (Figure 12 A).

The geographic range of *G. petersii* itself is restricted to Central and West Africa (found at least in Benin, Cameroon, Nigeria, the Central African Republic, the Republic of Congo and the Democratic Republic of Congo (Arimoro & Osakwe, 2006; Moritz, 2010; Ogbeibu & Ezeunara, 2002; Ogbeibu & Oribhabor, 2002; Paugy, Traoré, & Diouf, 1994; Sullivan, Lavoue, & Hopkins, 2000; Wuraola & Adetola, 2011)) and its habitats are mainly turbid black water streams with a high flow velocity in dense moist forests (Figure 12 B and C) (Moritz, 2010). These fish are mainly active during night and dusk and dawn. During the day *G. petersii* spends most of its time hiding under roots, in holes or in dense vegetation of the rivers, moving only in the close proximity of their hiding space. During night however they move over a quite big range of up to hundreds of meters, regularly returning to their home shelter (Moller, 1995; Moller, Serrier, Belbenoit, & Push, 1979).

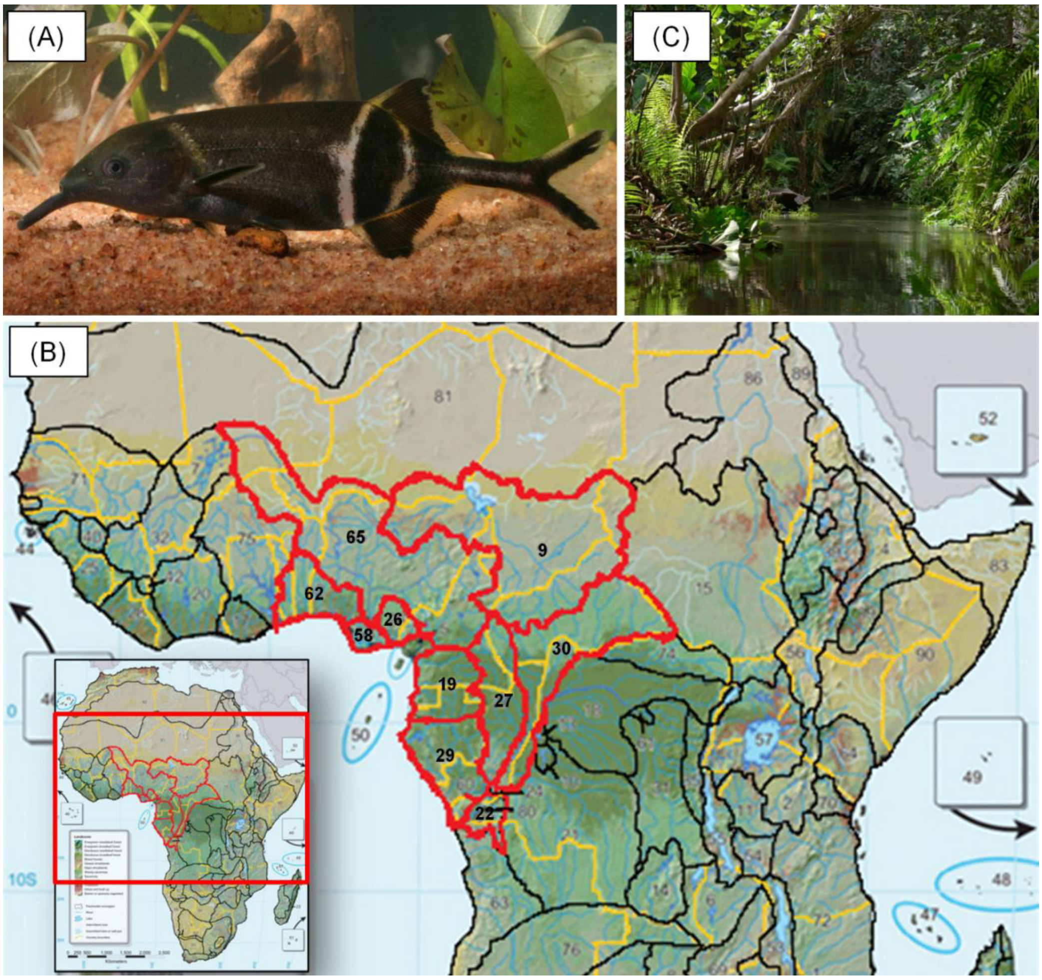

Figure 12: Habitus, distribution and habitat of *Gnathonemus petersii.* A) The habitus of *G. petersii* also known as elephantnose fish with the eponymic Schnauzenorgan, the narrow caudal peduncle and the white markings between dorsal and anal fin. B) Fresh water ecoregions of Africa, in which *G. petersii* was found (marked in red; changed after Thieme et al., 2005). Africa can be divided into 93 fresh water ecoregions, which are characterised by certain environmental conditions and contain a distinct assemblage of species (Thieme et al., 2005). *G. petersii* was found at least in ten of these ecoregions in Central and West Africa: the Lake Chad Catchment (9), characterised by floodplains, swamps and lakes, the Bight Costal ecoregion (62) and the Lower Niger-Benue (65) characterised by Savanna-dry forest rivers, the Niger Delta (58) characterised by big rivers and the Central, Northern and Southern West Costal Equatorial ecoregion (19, 26, 29), Lower Congo ecoregion (22), Sangha ecoregion (27) and Sudanic Congo ecoregion (30) characterised by moist forest rivers (Arimoro & Osakwe, 2006; Moritz, 2010; Ogbeibu & Ezeunara, 2002; Ogbeibu & Oribhabor, 2002; Paugy et al., 1994; Sullivan et al., 2000; Wuraola & Adetola, 2011). The black lines indicate the other freshwater ecoregions of Africa and the yellow lines indicate country borders. The inset shows which part of Africa was magnified in B. C shows a typical habitat of *G. petersii*, a moist forest stream (Benin) with turbid water (pictures in A and C from Gerhard von der Emde).

Studies investigating the stomach contents of wild individuals have shown that their main food source are insect larvae (Chironomidae), which live buried in the sediment of the rivers (Nwani, Odoh, Ude, & Okogwu, 2011). To find these hidden prey items as well as to orientate in its environment the sensory systems of *G. petersii* are especially adapted to the nocturnal or crepuscular live style as well as to the turbid waters of its environment. Like the other members of the Mormyridae *G. petersii* is capable of active electrolocation (Lissmann & Machin, 1958; Gerhard von der Emde & Horst Bleckmann, 1998) and they also possesses a highly specialised visual system with a grouped retina, which is also found in deep sea fish (Francke et al., 2014; Kreysing et al., 2012).

1.6.1. The sensory systems of *G. petersii*

The electroreceptor organs of *G. petersii* are distributed over almost the entire body surface and the only areas not to contain electroreceptor organs are the flanks (Figure 13 A). The density, however, varies between different body parts. The highest densities of electroreceptor organs are found at the Schnauzenorgan and in the nasal region (Hollmann, Engelmann, & von der Emde, 2008). This high density of receptor cells together with a considerable over-representation of these regions during central processing suggests that these two regions act as electric foveae, comparable to the visual fovea, the point of sharpest sight (Bacelo, Engelmann, Hollmann, von der Emde, & Grant, 2008). This is supported by passive pre-receptor mechanisms, focusing the electric field at the tip of the Schnauzenorgan (tip-effect) and leading to an even distribution of the voltage in the nasal region by funnelling the currents via the open mouth (funnelling-effect) (Pusch, 2013; Pusch et al., 2008). The Schnauzenorgan is of special importance during prey detection. During foraging *G. petersii* searches the ground using a swaying movement of the Schnauzenorgan to look for insect larvae dug in the sediment. At the same time the nasal region is aligned to a frontal direction focusing on the environment in front of the fish (Hollmann, 2008). In this way, the animal is able to utilise the high spatial accuracy of the two foveae for different tasks at the same time.

The electric organ of *G. petersii* consists of four columns of 70-170 flat disk-like electrocytes each (Figure 13 B) (Bruns, 1971; Westby, 1984). The innervation is achieved via stalks that penetrate the electrocytes and which are connected to the electromotorneuron via synapses. The EODs of *G. petersii* are biphasic pulses (Figure 13 C), which are emitted with a variable frequency depending on the behavioural state; during object recognition the EOD-frequency can reach up to 140 Hz, while during resting it might lay under 1 Hz (Moller, 1980; Schumacher, Burt de Perera, & von der Emde, 2016). Thus, the fish is able to reach a high temporal resolution if necessary but saves energy by reducing the number of costly EODs during resting. Furthermore, the variable EOD frequency can be used during communication with conspecifics (C. D. Hopkins, 1988; Moller & Bauer, 1973; Westby, 1981).

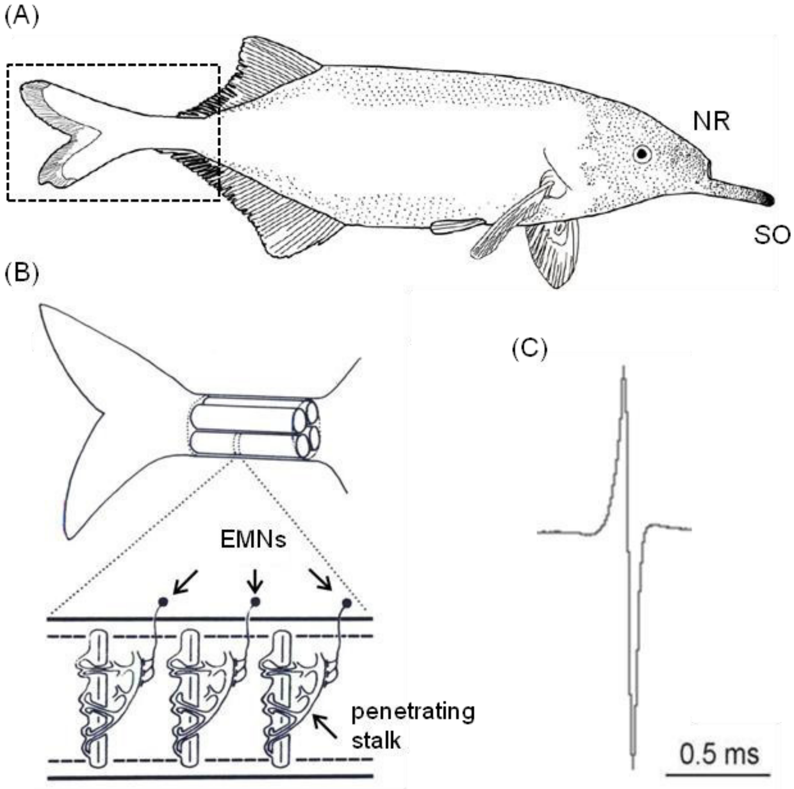

Figure 13: Schematic drawings of the active electric system in *Gnathonemus petersii*. (A) Distribution of the electroreceptor organs. Each dot indicates the position of a mormyromast. The highest density of mormyromasts is found at the Schnauzenorgan (SO) and in the nasal region (NR). The dashed square indicates the part enlarged in B. (B) Structure of the electric organ located in the caudal peduncle. The electric organ consists of electrocytes, which are arranged in series and are innervated by the elctromotorneurons via penetrating stalks. (C) Typical bi-phasic electric organ discharge (EOD) of *G. petersii*. (A) changed after (Hollmann et al., 2008); (B) and (C) changed after (Westby, 1984).

The visual system of *G. petersii* is specially adapted to its nocturnal and crepuscular activity and the turbid waters of its habitat. The structure of its retina is comparable to that of deep-sea fish. In this so-called grouped retina about 330 rods and 17-32 cones are packed into a bundle surrounded by a tapetum lucidum, forming a cup-like structure (Figure 14) (Francke et al., 2014; Kreysing et al., 2012; Landsberger et al., 2008). Within the light-adapted retina the outer segments of the cones are located at the bottom of the cup, while the rods lie underneath the cup within a light-scattering medium. Because of this organisation, the incoming light is focused on the outer segments of the cones via the cup-liked structure and the rods are protected from receiving too much light, preventing a complete bleaching of the visual pigment and allowing the rods to be active even under bright light. Thus in contrast to most other animals', the rods and cones of *G. petersii* are simultaneously active, which increases the spectral range of the otherwise monochromatic system. The single cone-type of *G. petersii* has an absorption maximum around 615 nm, which lies in the red light spectrum. The absorption maximum of the rods, on the other hand, lies with ca. 536 nm in the green light spectrum (Ciali, Gordon, & Moller, 1997; Kreysing et al., 2012).

In the dark adapted retina, the organisation changes drastically via retinomotor activity. The outer segments of the rods are drawn toward the location of the outer segments of the cones, so that the outer segments of both photoreceptor types are densely packed. This changes the shape of the cup, leading to a reduction of the focusing reflection (Landsberger et al., 2008).

All photoreceptors within a bundle project only to three or four ganglion cells and thus act as the smallest functional unit of the retina, which is also called the macroreceptor. This arrangement increases the light sensitivity of the ganglion cell but also seriously affects the spatial resolution of this visual system. The minimal visual angle of the grouped retina of *G. petersii* is ca. 3° and thus not suited for the detection of small objects (for comparison a thumb nail at arm's length has a visual angle of ca. 1° and the minimal visual angle of the human eye lies between ca. 5´ and 10´´ depending on the task, 1´ = 1/60° and 1´´=1/3600°). However, this rather poor spatial resolution provides an advantage in the turbid habitat of the fish. Visual noise, such as small particles in the water, is filtered by the system, so that visual object detection is only very slightly affected by the presence of visual noise (Kreysing et al., 2012; Landsberger et al., 2008; Schuster & Amtsfeld, 2002).

In contrast to the poor spatial resolution of the grouped retina, the system provides a high temporal resolution, allowing the detection of bigger fast moving object such as predators (Pusch, Kassing, et al., 2013).

In conclusion the experimental results show that the visual system of *G. petersii* is not specialised for visual accuracy and is also not adapted to optimal sensitivity. Instead it enhances light absorption in dim light and reduces visual noise in turbid water, which fits the natural conditions of the fish's habitat.

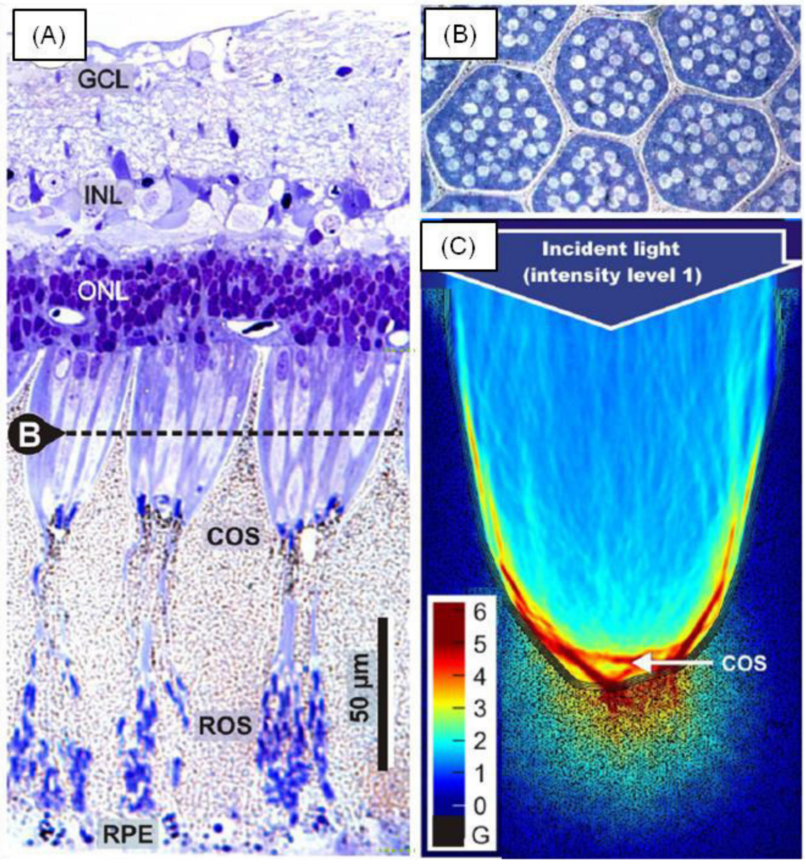

Figure 14: Structure of the grouped retina of *Gnathonemus petersii*: (A) Radial semi-thin section of the light adapted retina stained with toluidin blue. The outer segments of the cones (COS) lie at the bottom of a cup-like structure formed by the retinal pigment epithelium cells acting as a tapetum lucidum. The rod outer segments (ROS) are located beneath the cup. The outer nuclear layer (ONL) contains the inner segments of the photoreceptors. In contrast to the retinae of most other animals the inner retina with the inner nuclear layer (INL) and ganglion cell layer is much thinner than the photoreceptor layers. (B) Transverse section through the cup-like structures and the photoreceptor inner segments approximately at the level indicated with the dashed line in A. (C) Simulation of the light intensity distribution within the cup, based on the mirror features of the crystals. If light enters the cup it is focused at the bottom of the cup, where the outer segment of the cones are located. Thus the cone outer segments receive up to 500% of the incoming light intensity, while the rod outer segments receive only around 20%. Changed after (Kreysing et al., 2012).

There are very few studies dealing with the mechanosensory lateral line system of *G. petersii* or other weakly electric fishes. A few studies in both Gymnotiformes and Mormyriformes have shown that the mechanosensory lateral line system of weakly electric fish is involved in prey capture and shelter seeking and reactions to artificial stimuli were found (Bleckmann & Zelick, 1993; M. E. Nelson & Maciver, 1999; M. E. Nelson, MacIver, & Coombs, 2002; Rojas & Moller, 2002; Gerhard von der Emde & Horst Bleckmann, 1998; von der Emde & Prechtl, 1999; Walton & Moller, 2010). To my knowledge, so far no study has investigated the peripheral structure of the mechanosensory lateral line in *Gnathonemus* or any other mormyrid fish. In gymnotiform fish the distribution of neuromasts has been described for *Apteronotus albifrons* and *Eigenmannia sp* (Carr, Maler, & Sas, 1982; Vischer, 1989). In both species canal neuromasts and a small number of superficial neuromasts were found.

There are also some studies describing the central connections of the lateral line system in higher brain regions in *G. petersii*. They show that there are distinct sub-regions in the telencephalic nucleus dorsalis pars medialis (Dm) and in the anterior preglomerular nucleus (PGa) processing uni-modal mechanosensory lateral line information, while the mechanosensory information are processed in multisensory regions in the ventral preglomerular nucleus and in the pallium (Prechtl et al., 1998; von der Emde & Prechtl, 1999). Many open questions remain concerning the mechanosensory lateral line system in *Gnathonemus petersii*.

1.6.2. Object recognition and navigation in *G. petersii*

The ability of *Gnathonemus petersii* to recognise and discriminate object using the active electric sense and also vision has been investigated in many studies. These fish are able to detect a wide range of object properties like the size, material, shape, distance, capacity and rotation of an object during active electrolocation (Behr, 2009; Fetz, 2005; Folde, 2006; Schumacher, 2011; Schumacher, Burt de Perera, & von der Emde, 2016; von der Emde et al., 2010; von der Emde & Fetz, 2007; von der Emde & Ringer, 1992; von der Emde et al., 1998). Furthermore, *G. petersii* is capable of figure-ground separation and moving backgrounds even enhance object recognition (Fechler, 2016; Fechler & von der Emde, 2013). The limits of active electrolocation were tested in several studies, showing that while the spatial resolution allows the detection of small gaps of about 1mm at close range, the perceptual range of the electric sense is quite small, allowing discrimination only in the range of 3-4 cm (Behr, 2009; Fechler et al., 2012; Moller, 1995; Schumacher, 2011; Schumacher, Burt de Perera, & von der Emde, 2016; von der Emde et al., 2010).

Some studies were also conducted to test the visual object recognition performance, showing that *G. petersii* is able to recognise bigger and fast moving objects using its visual sense (Kreysing et al., 2012; Schuster & Amtsfeld, 2002).

There is no experimental evidence, so far, that the lateral line system is involved in object recognition.

Although it is known that Gnathonemus travels quite large distances in its natural environment and thus has to rely on navigation, its navigational abilities have not been studied. A few experiments by Peter Cain and colleagues have shown that these fish are able to use electrical and hydrostatic cues to navigate at short range when trained to find a hole in a partition located at a certain height. Furthermore, they found out that in an unfamiliar environment Gnathonemus relied strongly on the electrosensory cues but when the environment became familiar, electrical cues were not necessary anymore and the fish relied on an internal representation and the hydrostatic information (Cain, 1995; Cain, Gerin, & Moller, 1994; Cain & Malwal, 2002). In the closely related *Mormyrus rume* studies have shown that these fish use electrical, visual and lateral line information synergistically during navigation in a meander maze. They use landmark based navigation in the presence of electrical cues but used egocentric information when only visual landmarks were available (Walton & Moller, 2010).

1.7. Aims of this thesis

To date, most studies concerning the sensory systems of *Gnathonemus petersii* have taken a uni-modal approach. The active electric sense and vision were mainly investigated individually and the mechanosensory lateral line system was completely neglected in most studies. However, under natural conditions all three senses are available at the same time and vision and electrolocation provide similar information about the environment (so far it is unknown how detailed the mechanosensory lateral line input is). Therefore, it is likely that these two senses are used for similar tasks and they should consequently interact in some way. This supposition is supported by previous studies, showing that during shelter seeking multisensory information is integrated leading to a synergetic effect (Moller, 2002;

Rojas & Moller, 2002). Similarly, during foraging tasks, multisensory information is used for prey detection (Gerhard von der Emde & Horst Bleckmann, 1998). However, little is known about the interaction of the sensory systems in *Gnathonemus petersii*. Furthermore, the fundamental mechanisms underlying multisensory integration have been revealed in only a few mammalian species (Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Fetsch et al., 2009; Sheppard et al., 2013). This leaves open the question of how multisensory integration is achieved in other vertebrates, like fish, which rely on less complex brain structures. The overarching aim of this thesis was to investigate multisensory interactions in the weakly electric fish *Gnathonemus petersii*, by using two different behavioural paradigms.

Under the headline "Multisensing" the first part of my thesis deals with the basic question how multisensory inputs are processed during object recognition. In detail I aimed to test the following:

- **Is *Gnathonemus petersii* able to transfer object related information from vision to the active electric sense and vice versa, i.e. is *G. petersii* capable of cross-modal object recognition?**
- **Is multisensory integration achieved via similar fundamental mechanisms known from mammals, i.e. is there dynamic weighting of sensory inputs in *G. petersii*?**
- **Is there a hierarchy of the sensory systems during object recognition, i.e. does one of the sensory systems dominate over the other?**
- **Are there advantages, such as synergy, redundancy or complementation, of using vision and electrolocation for similar tasks?**
- **Is the mechanosensory lateral line system involved in object recognition?**
- **How is the structure of the peripheral mechanosensory lateral line system of *G. petersii*, i.e. how are the superficial neuromasts distributed over the body, how is their morphological structure and how is the structure of the head canal system?**

To answer these questions, I used a two-alternative forced-choice procedure to train the fish to discriminate between two objects. By varying object properties and environmental conditions, the sensory input to the fish was manipulated, so that only specific senses could be used for the discrimination task. To investigate the structure of the lateral line system I used DASPEI staining and µCT.

In the second section titled "Navigation" I investigated the sensory influence on navigation. The main questions I wanted to answer in this project were:

- **Does the sensory system available during navigation influence route acquisition, i.e. does *G. petersii* learn a navigation task faster when trained with visual or electrical landmarks?**
- **Which navigational strategy uses *G. petersii* during navigation in a maze? Egocentric or allocentric navigation?**
- **Is the navigational strategy influenced by the sensory system available during navigation?**
- **Is *G. petersii* able to transfer landmark related information from vision to the active electric sense and vice versa, i.e. is there cross-modal landmark recognition in *G. petersii*?**

Here either visual or electrical landmarks were used to train fish in a navigational task to swim through a maze using the correct route. Again the sensory input was controlled by changing the object properties of the landmarks.

Together the results of this thesis will show how the sensory systems of *G. petersii* work together during different tasks and thus provide new insights in the mechanisms underlying multisensory processing in a non-mammalian vertebrate and the cognitive capabilities of these fish.

2. Multisensing

2.1 Cross-modal object recognition and dynamic weighting of sensory inputs in a fish

2. Multisensing

2.1. Cross-modal object recognition and dynamic weighting of sensory inputs in a fish

2.1.1. Abstract

Most animals use multiple sensory modalities to obtain information about objects in their environment. There is a clear adaptive advantage to being able to recognize objects cross-modally and spontaneously (without prior training with the sense being tested) as this increases the flexibility of a multisensory system, allowing an animal to perceive its world more accurately and to react more quickly to environmental changes. So far, spontaneous cross-modal object recognition has only been shown in a few mammalian species, raising the question as to whether such a high-level function may be associated with complex mammalian brain structures and therefore absent in animals lacking a cerebral cortex. Here we use an object discrimination paradigm based on operant conditioning to show, for the first time, that a non-mammalian vertebrate, the weakly electric fish *Gnathonemus petersii*, is capable of performing spontaneous cross-modal object recognition and that the sensory inputs are weighted dynamically during object discrimination. We found that fish trained to discriminate between two objects with either vision or the active electric sense, were subsequently able to accomplish the task using only the untrained sense. Furthermore we show that cross-modal object recognition is influenced by a dynamic weighting of sensory inputs. The fish weight object related sensory inputs according to their reliability, to minimize uncertainty and to enable an optimal multisensory integration. Our results show that spontaneous cross-modal object recognition and dynamic weighting of sensory inputs are present in a non-mammalian vertebrate.

2.1.2. Introduction

To behave adaptively, an animal must be able to perceive and react appropriately to environmental stimuli. Sensory information can often be obtained through multiple sensory channels and can interact in a number of ways before a behavioral output is produced. To increase the flexibility of a multisensory system, information about objects in the environment can be transferred between different senses. This enables some animals to use spatial information acquired with one particular sensory system to recognize objects with another one (cross-modal object recognition). In contrast to simple forms of cross-modal information transfer, which are based on the formation of direct associations between two specific stimuli (Guo & Guo, 2005; Proops, McComb, & Reby, 2009; Seraganian & Popova, 1976; Yehle & Ward, 1969), cross-modal object recognition requires additional and more complex conditions to be meet. These are: 1) The information provided by the two senses has to match in content, i.e., both senses have to provide information about the same characteristic object property (e.g. shape, surface structure). 2) The sensory inputs have to be encoded in a way that allows temporally disjointed information from two senses to be identified as identical, despite these senses relying on different physical stimuli. 3) Characteristic object features have to be stored in a neuronal representation that is accessible by multiple senses. So far, spontaneous cross modal object recognition has only been described in humans (Gaydos, 1956), apes (Davenport & Rogers, 1970), monkeys (Cowey & Weiskrantz, 1975), dolphins (Herman et al., 1998) and rats (Winters & Reid, 2010), and little is known about the neuronal structures that are involved in this process.

A reliable percept is fundamental for cross-modal object recognition. Although the interaction of multiple sensory channels offers many advantages, the integration of conflicting information from different senses could also lead to a decrease of the perceptual reliability. Therefore in order to obtain a reliable percept not all available senses contribute equally, and the observable behavioral output tends to be dominated by certain senses. Which sense dominates and the degree to which each sensory input contributes to the overall perception depends on the conditions and the task, and might be determined by the reliability of the different sensory inputs under the given conditions (Alais & Burr, 2004; Ernst & Banks, 2002; Sheppard et al., 2013; Young, Landy, & Maloney, 1993) and prior experience (Ernst & Bülthoff, 2004; Ernst & Di Luca, 2011). In humans, for example, vision is dominant during spatial tasks (Howard & Templeton, 1966b; Rock & Victor, 1964), while the acoustic or the haptic sense dominate over vision during tasks that require temporal assessments (Shams, Kamitani, & Shimojo, 2000, 2002). Since conditions may change rapidly, this “weighting” of sensory inputs has to be dynamically adjustable. Dynamic weighting of sensory inputs enables animals to integrate multisensory information optimally to obtain a reliable percept of the environment (Sheppard et al., 2013), but like cross modal object recognition has so far only been described in mammals (Alais, Newell, & Mamassian, 2010; Fetsch et al., 2009; Sheppard et al., 2013).

Weakly electric fish *Gnathonemus petersii* possess multiple senses, which could potentially be used for fine-scale spatial interrogation of their surroundings. These fish can discriminate between nearby objects using active electrolocation (von der Emde et al., 2010), a process during which object-evoked distortions in a self-generated electric field (electrical images) (Caputi, Budelli, Grant, & Bell, 1998; Rasnow, 1996) are perceived with special electroreceptor organs in the skin (Jorgensen, 2005). Active electrolocation is a near-field sense, which works only at short distances from the fish (von der Emde et al., 2010). In addition to this active electric sense, *G. petersii* possess a visual system with highly specialized eyes (Kreysing et al., 2012). The visual system is adapted to the crepuscular and nocturnal activity of the fish and their habitat, i.e., turbid black water streams in Central and West Africa. In the 'grouped retina' of their eyes, the photoreceptors are packed into bundles within a tapetum lucidum, which improves vision under dim light and in turbid waters (Kreysing et al., 2012). Previous studies have shown that the visual and electrosensory inputs can be integrated when sensing the surroundings (Moller, 2002), and both senses provide spatial information (matching content) about objects, making *G. petersii* a suitable model system to investigate cross-modal object recognition and dynamic weighting in a non-mammalian animal.

Here we used *G. petersii* to test for spontaneous cross-modal object recognition and dynamic weighing of sensory inputs. We applied a two-alternative forced-choice procedure, during which the fish were trained to discriminate between two objects using only vision or only their active electric sense and tested them subsequently with the untrained sense. Crucially, access to object information using the two senses was varied by altering features of the objects themselves without having to surgically manipulate the fish. This is an important approach as it reduces the uncontrolled effects of modifying animals' senses.

2.1.3. Methods

Ten naive *Gnathonemus petersii* were individually housed in tanks, which also served as the experimental arenas (Figure 15). Fish were trained in a two-alternative forced-choice procedure to swim through a gate with an object (Figure 16) that was positively associated with a food reward (a chironomid insect larva) and to avoid a second gate with a negative object, which was associated with a mild punishment (fish being chased back to start position). The position of the positive object was changed behind the gates pseudo-randomly after Gellermann (Gellermann, 1933). During training the objects were placed 1 cm behind the gates. In order to make sure that during training and testing the fish kept a certain minimal distance during object inspection, a so-called distance grid was placed directly behind each gate (Figure 15). Distance grids were made from thin cotton threads, with a mesh size of 15 mm (diagonal), which ensured unimpeded electrolocation through this mesh. The fish could pass the grids by pushing them aside.

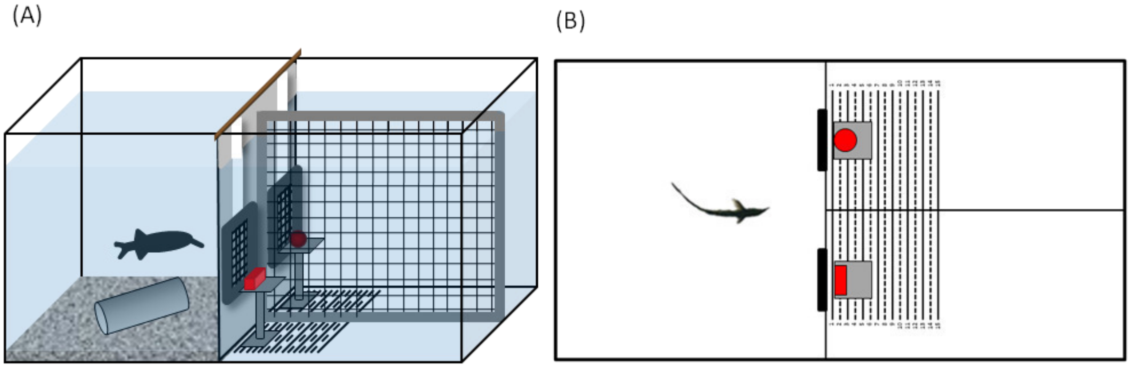

Figure 15: Experimental set-up. G. petersii were individually housed in 75 cm x 40 cm x 40 cm tanks, which also served as the experimental arenas ((A) schematic side view, (B) schematic top view). These were divided into two compartments (40 cm x 40 cm and 35 cm x 40 cm) by a partition with two closable gates behind which were positioned two objects (indicated in red) 1cm from gate. Distance grids, which were placed directly behind the gates and which could be passed by pushing them aside, made sure that the fish kept the correct minimal distance to the objects. The larger compartment (experimental area) was again divided into two compartments, one gate leading to each compartment.

All experiments, except the dark controls, were conducted at an ambient light level of 3-6 lx (measured just above the water surface) which lies in the optimal intensity range for visual object discrimination in *Gnathonemus petersii* (Schuster & Amtsfeld, 2002). The conductivity (95-110 µS/cm) and the temperature (25-27°C) of the water were kept constant.

Fish were divided into two training groups, which were either able to use vision or the active electric sense for object discrimination. Access via these senses was controlled by manipulating the objects or the ambient surroundings. Objects used in the visually trained group were constructed of electrically transparent, red coloured agarose (Figure 16 A, B). The conductivity of those objects was adjusted to the conductivity of the tank water (ca. 100 µS/cm); therefore they were “electrical invisible” to the fish (Heiligenberg, 1973)(see control tests). Red food colour (Lebensmittelpaste Rot, Deko Back, Waibstadt, Germany)) was added to deionised water (conductivity <10 µS) until a conductivity of 40 µS/cm was reached. By adding agarose powder (Agarose BP 160-100, Fisher Scientific, Fair Lawn, New Jersey, USA) (2g per 100ml) the conductivity was increased to ca. 100 µS/cm. This mixture was boiled and cast in moulds. After cooling down the agarose became stiff and the objects could be used in the discrimination experiments. Since it wasn´t possible to measure the conductivity of the stiffened agarose directly, the resistance of 250 ml stiff agarose within a beaker was compared with the resistance of 250 ml tank water using a multimeter (M-3650B, Voltcraft) to test whether their electrical properties were identical. For both measurements the measuring electrodes were positioned 5 cm apart. There was no measureable difference between the agarose and the tank water. Control tests ensured that the fish could not use electrical cues to discriminate between the objects (see control tests). Red colour was used because the cones of *G. petersii* are most sensitive to red light (absorption maximum: 615 nm (Kreysing et al., 2012)).

During training in the electrical group (group 2) aluminium objects were covered with hoods made of opaque, black cotton fabric to prevent influence of vision and the lateral line system on the discrimination performance (Figure 16 C,D,E). Since the cotton fabric was soaked with the tank water, the hoods themselves were electrically transparent. To ensure that the hoods had no influence on the discrimination performance, control tests were conducted (see Figure 21).

For all fish a sphere (Ø 3 cm) was used as the positive object (S+). In both groups, three fish (Fish No. 3, 4, 5, 6, 7 and 8) were trained with a cross (width: 4 cm, height: 4 cm, depth: 1.7 cm) and two fish (Fish No. 1, 2, 9 and 10) with a cuboid (4 cm x 2.2 cm x 1.7 cm) as negative object (S-). Since the volume and the material of S+ and all S- were the same, the fish could use only the shape to discriminate the objects.

After the preassigned learning criterion of at least 75% correct choices on three consecutive days was reached, test trials (s. below), which were neither rewarded nor punished, were introduced every third trial. After three to five days, the training to test trial ratio was increased to 2:2. With each test condition 30 trials were conducted with each fish. The number of training trials per fish ranged between 182 and 934.

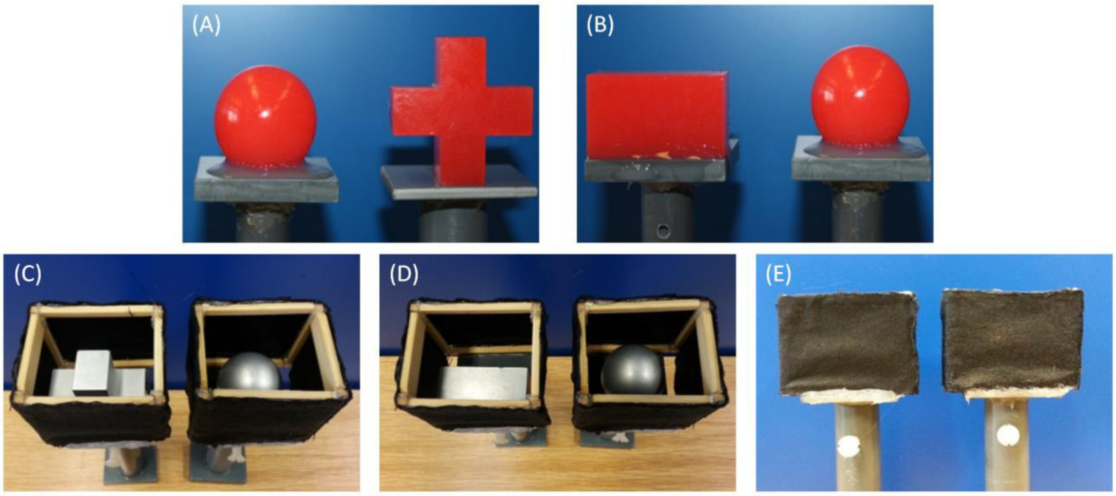

Figure 16: Training objects of the visual trained group (A + B) and the electrically trained group (C+D+E). To prevent electrical discrimination, the objects of the visually trained group were made of red colored electrically transparent agarose. For training with the electric sense, metal objects covered with hoods made of black cotton fabric were used. In all fish, a sphere was used as the positive object and either a cross (A, C) or a cuboid (B, D) served as negative object.

2.1.3.1. Transfer tests

During the transfer tests the fish could use only the previously untrained sense for the discrimination task. The fish of the visually trained group were tested in the dark at 1 cm distance with aluminium objects that were encased in cubes of electrically transparent agarose so that the positive and the negative object had the same outer shape and were only electrically distinguishable excluding vision and the lateral line system. The electrically trained group was tested visually with the red coloured, electrically transparent agarose objects placed 1 cm behind the gates.

2.1.3.2. Range tests

Four of the electrically trained fish were tested at different object distances (0.2 cm, 1 cm – 7 cm and 9 cm) with only the active electric sense available (aluminium objects covered with black cotton hood), with the visual sense available (red coloured, electrically transparent agarose objects) and with both senses available. For the latter, red coloured conductive agarose objects were used. These objects were produced in the same way as the electrically transparent agarose objects but instead of using deionised water a high conductive saline solution (> 10 S/m) was used. The tests with both senses available were conducted last to ensure that they would not influence the results of the visual tests. Besides that, the tested sense and object distances were chosen pseudo-randomly for each day. Tests with “electrically silenced” fish

For these tests four fish (Fish No. 6, 8, 9 and 10) of the electrically trained group were electrically silenced by cutting the spinal cord just anterior to the electric organ located in the caudal peduncle. Before the actual operation a sham operation was conducted. The fish were narcotized in a 100 mg/l solution of MS 222 (Acros Organics, Geel, Belgium), the operation site was locally anaesthetized with Xylocain Gel (AstraZeneca GmgH, 22876 Wedel) and the skin was penetrated with a dissecting needle. Afterwards the fish were tested electrically and visually with 1 cm object distance as a control (see supplementary data). For the real operation, fish were treated as in the sham operation described above but the dissecting needle was inserted dorsally into the vertebral canal to transect the spinal cord. After the fish were electrically silenced, visual tests were conducted with the red coloured electric neutral agarose objects at 1 cm distance. Since the electric input was missing for training trials, every third trial was rewarded independently of the choice made by the fish to maintain motivation.

2.1.3.3. Control tests

A series of control tests was conducted to exclude the influence of uncontrolled cues during the tests.

Control I: Exclusion of electrical or lateral line information during visual tests

During training in the visual trained group and during the transfer tests in the electrically trained group, red coloured agarose objects were used, which had approximately the same conductivity as the surrounding tank water. Even though the resistance of the objects was measured and matched that of the tank water, the fish might have been able to discriminate between these objects electrically using differences between the resistance of the objects compared to the tank water that were not technically measurable. Furthermore during the visual experiments an influence of the lateral line on the discrimination performance could not be excluded through the object design. Therefore to ensure that the fish used no other sensory cues than visual ones to discriminate between the red coloured, electrically transparent agarose objects, control tests at 1 cm and 3 cm distance were conducted before and after the fish were electrically silenced. The objects were presented in the dark (light intensity < 0.01 lx) excluding visual discrimination. In order to observe the outcome, the tank was illuminated with infrared light of 850 nm (IR Illuminator, S8030-3D-L-IR, ITAKKA, Wattens, Austria), which is invisible for *G. petersii* (Ciali et al., 1997), and was observed through an infrared sensitive camera (DCR-HC40E, Sony).

Control II: Exclusion of effects of the cotton hoods

A second control was conducted to test whether the black cotton hoods that were used during the training of the electrically trained group influenced the discrimination performance. During the tests with both senses available the performance of the electrically trained fish increased compared to the tests with only the electric sense available for object discrimination especially at longer distances (Figure 18 black curve). This could be explained by the additional visual input or it could have been an effect of the changes in the experimental condition. During tests with only the electric sense available, the objects were covered with hoods to prevent visual discrimination. These hoods were removed during the tests with both senses available, which could have lead to an increase in performance. Furthermore during the tests with both senses available red coloured agarose objects were used instead of the metal objects that were used during electrical tests. These were made of a high conductive saline solution (see description of range tests), so the different object material might have also influenced the performance. To exclude these factors, control tests with the conductive red coloured agarose objects were conducted in the dark at 2 cm resp. 3 cm distance.

Control III: Exclusion of influence of the experimenter

A double blind control under the training conditions was conducted to make sure that there was no influence of the experimenter on the decision of the fish. During this control, a person that had previous experience with the experimental procedure but had never worked with the tested fish before and did not know which object was positive, conducted the experiments.

Control IV: Exclusion of effects of the surgical procedure for electrical silencing

After the sham operation, a control was conducted to ensure that the principal surgical procedure had no influence on the performance. The fish were tested with only the electric sense and with only vision available.

Control V: Exclusion of effects of electrical input in electrically silenced fish and of passive electrical cues

After the surgery, control tests with the hood covered aluminium objects were conducted to test whether the “electrically silenced” fish were unable to discriminate between the objects electrically. Furthermore this control ensured that no additional electrical cues arising from the metal objects influenced the discrimination performance by stimulating the passive (ampullary) electrosensory system of the fish.

Control VI: Exclusion of effects of the electrically transparent agarose cubes

In the visually trained group aluminum objects encased in a cube of electrically transparent agarose were used in complete darkness during the electrical test in order to prevent influence of the lateral line system. To ensure that the agarose cubes did not influence the discrimination performance, control tests were conducted, during which the discrimination performance of the visually trained fish with and without the agarose cube were compared in the dark.

2.1.4. Results

To test for cross-modal object recognition, ten *Gnathonemus petersii* with no experimental experience were trained to discriminate between two objects of different shapes placed at a distance of 1 cm from the fish. By using objects made from different materials, either the visual sense only (red coloured electrically transparent agarose objects; group one, n=5) or the active electric sense only (metal objects covered by hoods; group two, n=5) provided information, which could be used for object discrimination. After the fish reached a preassigned learning criterion (75% correct choices on three consecutive training days), they were subjected to transfer tests, during which they could use only the untrained sense for the discrimination task; in the visually trained group the active electric sense (metal objects encased in a cube of electrically transparent agarose presented in the dark), and the visual sense in the electrically trained group (red coloured electrically transparent agarose objects). Control tests were performed to ensure that the fish could not use any other cues (e.g. electrical or lateral line input) to discriminate between the red coloured, electrically transparent agarose objects, and that the hoods did not influence the electrical performance during training or the tests (see control tests).

2.1.4.1. Transfer tests

After training, all fish of both training groups were able to discriminate between the objects with similar performances of 85% to 92% correct choices. However, when the objects were placed at a distance of 1 cm from the fish, the results of the two groups during the transfer tests differed (Figure 17). The discrimination performance of all fish in the visually trained group remained constant during transfer tests, during which only the electric sense was available for discrimination (**Figure 17** A), indicating that the fish were able to spontaneously discriminate between the objects electrically without previously being trained with this modality. In other words, they were capable of cross-modal object recognition. In contrast, only two out of five fish trained with only the active electric sense available reached a performance significantly different from chance-level when tested only with visual information available for object recognition. These two fish transferred information from the active electric sense to vision (Figure 17 B).

2.1.4.2. Range tests

We were unable to ascertain whether in the three unsuccessful fish (Fish No. 7, 8 and 10), transfer from the electric sense to vision failed to occur at the processing stage, or whether transfer did occur, but was masked by a dominance of the electric sense. During the tests when objects were only perceivable visually, the electrically trained fish were presented with conflicting information from the electric sense (providing the information that no object is present) and from vision (providing the information that an object is present)). Therefore the inability to discriminate between the objects in the visual transfer tests might have been driven by a reliability-based dominance of the electric sense at short distances. To investigate this, four fish (Fish No. 6, 8, 9, 10 (Fish 7 died)) from the electrically trained group were subsequently tested at different distances from the objects in three experimental situations: firstly, with only the active electric sense providing information about the objects (to provide a measure of the reliability of the electric sense at different distances); secondly, with only vision available (to test the transfer from the electric sense to vision) and thirdly with both senses available for object discrimination (a control).

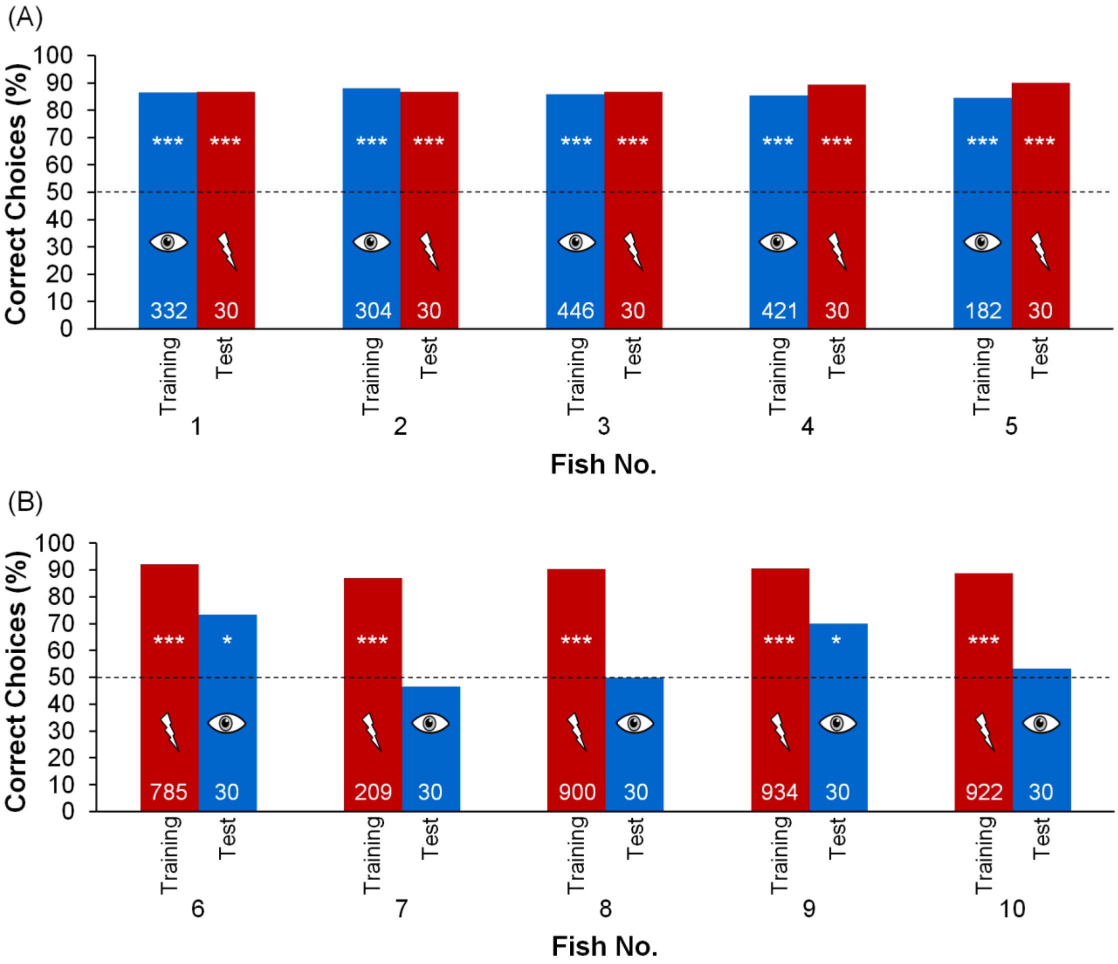

Figure 17: Visual (blue) and electrical (red) discrimination performance, under training conditions and during the transfer tests of (A) visually trained fish (Fish No. 1-5) and (B) electrically trained fish (Fish No. 6-10). All trials were conducted with two objects that only differed in shape placed at a distance of 1 cm behind the respective gates. The number of trials conducted with each condition is indicated within the bars. Training results include all training trials after reaching the learning criterion. The dashed line indicates the 50% chance level. A Chi^2-Test was conducted to test whether the performances were significantly different from chance level (* : $P \leq 0.05$; ** : $P \leq 0.01$; *** : $P \leq 0.001$).

At longer distances, the discrimination performance of the fish in the electrical tests decreased in line with decreasing reliability of the electric sense (Figure 18, red curves). However, the performance in the transfer tests, in which vision alone was available for object discrimination, increased with distance, eventually reaching a similar level as in the electrical training (Figure 18, blue curves). At even longer distances, the performances decreased again. These tests reveal that transfer must have occurred from the active electric sense to vision (there was no failure of transfer at the processing stage), but at short distances may have been masked in all but two fish at the point of the behavioural output.

When tested with both senses (vision and the electric sense) available for object discrimination, the information from both modalities corresponded, leading to a high discrimination performance at both short and long distances (Figure 18, black curves). Even at intermediate distances, where in both uni-modal cases the performances were near threshold-level (at a distance of about 2 cm), the fish now discriminated effectively between the objects. Control tests ensured that this effect was not due to differences in the experimental conditions (see Control tests).

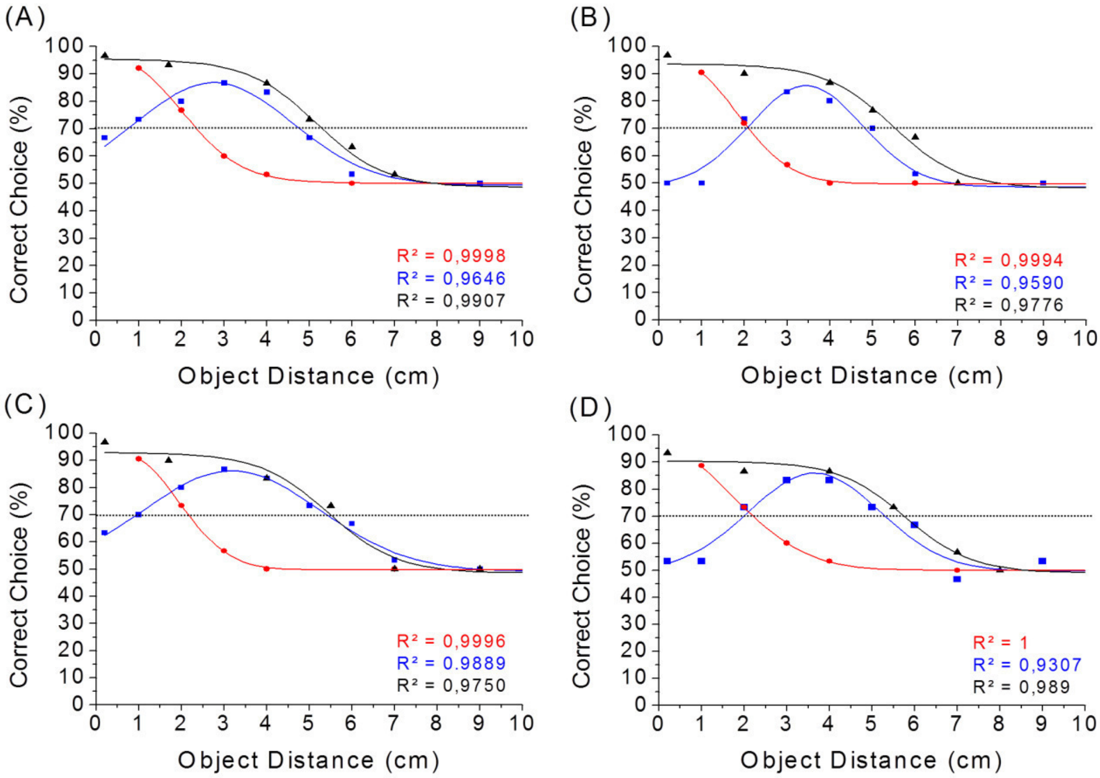

Figure 18: Discrimination performance of the electrically trained fish (Fish No. 6 (A), 8 (B), 9 (C) and 10 (D), same fish as in Figure 17 B) tested at different distances with only the electric sense (red circles), only vision (blue squares) and both senses (black triangles) available for object discrimination. At least 30 trials were conducted for each distance. The electrical (red line) and visual (blue line) results were fitted with a Gaussian fitting curve and a sigmoidal fit was used for the results of the tests with both senses available (black line). The R²-value is given in the corresponding colour for each curve in the figure. Results above the dotted line are significantly different from chance level (*P* ≤ 0.05, Chi²-test).

2.1.4.3. Tests with “electrically silenced” fish

To pursue this further and to test whether the inability to discriminate between the objects visually at short distances might be due to a non-functioning of the visual sense, the electric organ of each of the four electrically trained fish (Fish No. 6, 8, 9, 10) was surgically silenced. To do this, the spinal cord was sectioned anterior to the electric organ, which is located in the caudal peduncle (Rojas & Moller, 2002). Following this procedure, the performances in the visual transfer tests at short distance (1 cm) increased to a level similar to that during electrical training (Figure 19). This reveals that at short distances the eyes of the animals do provide information about object shape, and that in the absence of any electrical input the behavioural output is driven by the visual input. Control experiments after the tests at varying distances, before the fish were electrically silenced ensured that the changes in the discrimination performance were not due to experience gathered during the experiments with both senses (Figure 23).

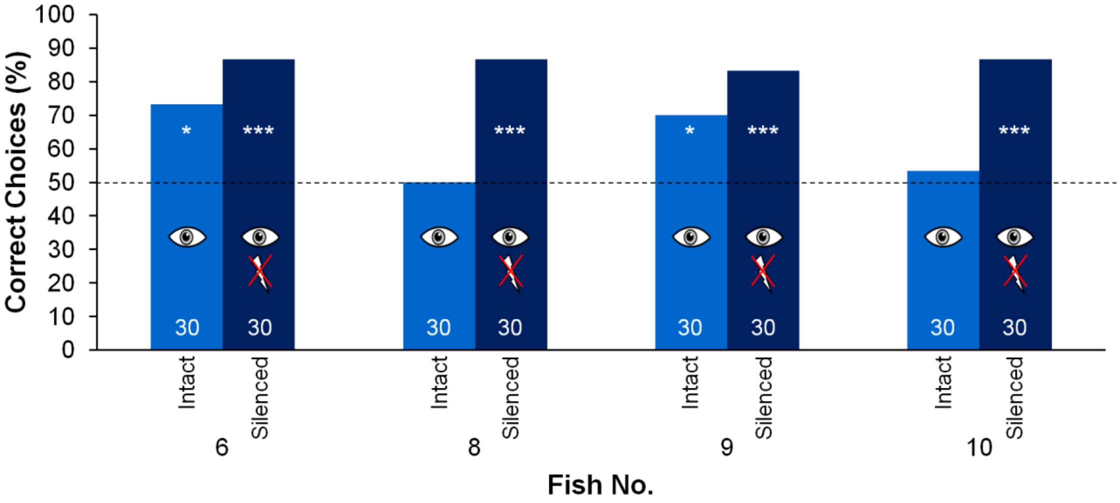

Figure 19: Discrimination performance at 1 cm object distances during the visual transfer tests of the electrically trained fish (Fish No. 6, 8, 9,10; same fish as in Figure 17 B and Figure 18) before (blue)(same data as in Figure 17 B) and after (dark blue) "electric silencing" (surgical deactivation of the electric organ). For further description see Figure 17.

2.1.4.4. Control tests

Control I: Exclusion of electrical or lateral line information during visual tests

A dark control was conducted during which the electrically transparent red coloured agarose objects were presented in complete darkness to test whether any other cues such as lateral line information or passive electric cues were used during visual tests. All fish of both training groups were unable to discriminate the objects during these control tests (Figure 20), showing that neither the lateral line system nor the electrical input was sufficient for the discrimination task, and that the fish used vision to discriminate between the objects during the training resp. the transfer tests with light.

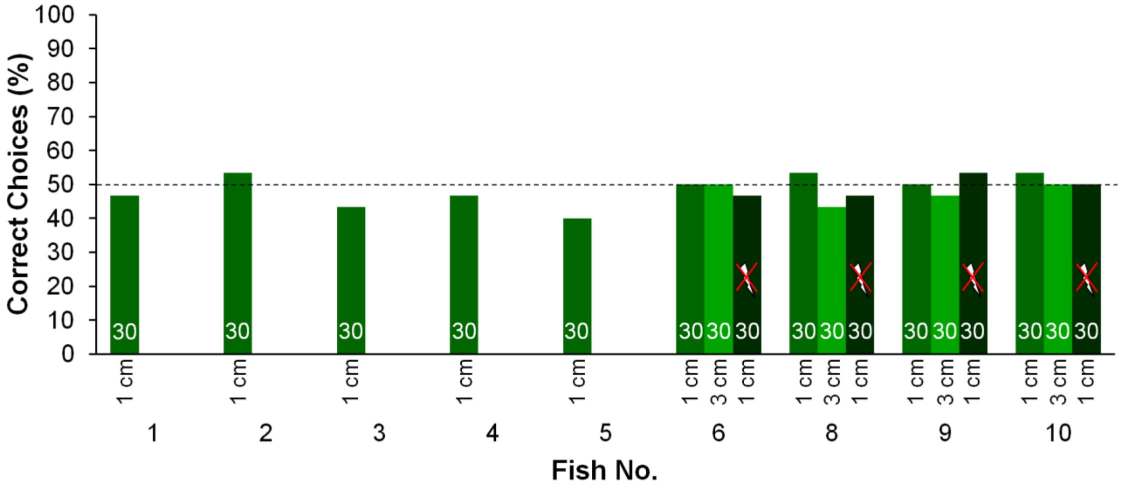

Figure 20: Discrimination performance during the dark control. These control tests were conducted to ensure that no additional cues were used to discriminate between the electrically transparent, red colored agarose objects. Tests were conducted at 1cm (green) and 3 cm (light green) object distance before and after electric silencing (dark green) with the visually trained fish (Fish No. 1-5) and four of the electrically trained fish (Fish No. 6, 8, 9, 10). A Chi²-test showed that none of the performances was significantly different from 50% chance-level ($P > 0.05$), indicating that the fish were not able to use additional cues such as electrical or lateral line input to discriminate between the objects. This shows that during the tests with light, only vision was used for discrimination. For further description see Figure 17.

Control II: Exclusion of effects of the cotton hoods

A control was conducted during which the performance during tests with conductive, red coloured agarose objects presented in complete darkness was compared with the performance during the standard electrical tests with hood covered metal objects to ensure that the differences in the experimental conditions did not influence the performance during tests with both senses. The results of these control tests were almost identical to the results of the tests with the hood covered metal objects (Figure 21), revealing that neither the hoods nor the different object material influenced the discrimination behaviour and leaving the additional visual input as an explanation for the performance increase in test with both senses available. The lack of influence of the cotton hoods furthermore supports the assumption that the cotton hoods were electrically transparent.

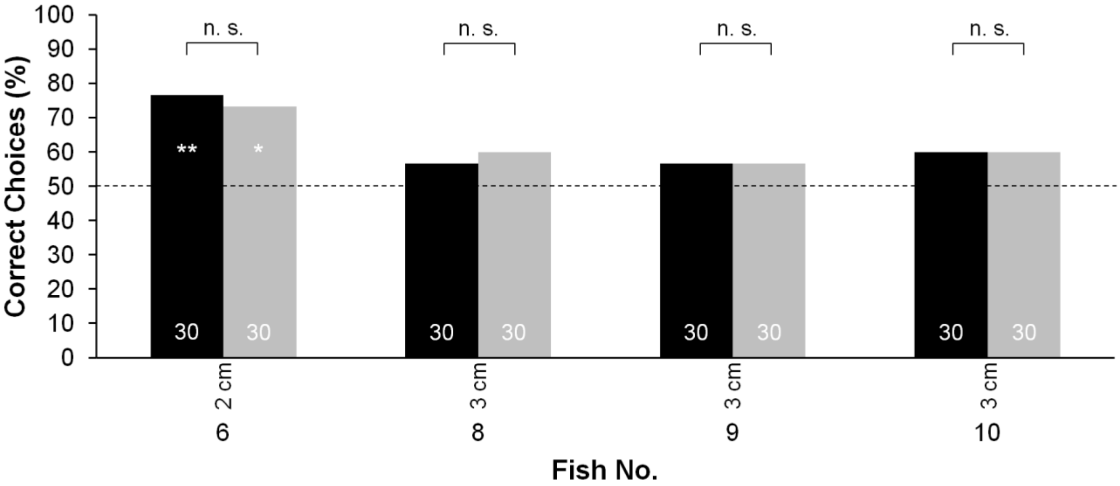

Figure 21: Discrimination performance of four of the electrically trained fish (Fish No. 6, 8, 9 and 10) during control tests which ensured that there was no influence of the hoods on the discrimination performance. Electrical tests were conducted with the hood-covered metal objects (black) and with conductive, red colored agarose objects in the dark (grey) at 2 cm resp. 3 cm object distance. The exact Fisher-test was used to test for significant differences between the performances (n .s.: $P > 0.05$). There were no significant differences between both conditions, showing that there was no influence of the hoods on the discrimination performance. Thus, performance differences between electrical tests and tests with the conductive red colored agarose objects in light (tests with both senses) (Figure 18 red and black curve) were not due to differences in the experimental conditions but originated from the additional visual input. For further description see Figure 17.

Control III: Exclusion of influence of the experimenter

Effects of the experimenter on the discrimination behaviour were controlled via a double blind control, during which a unknown experimenter conducted the experiments. The performance of the fish under these conditions was no different compared to the results with the original experimenter (Figure 22).

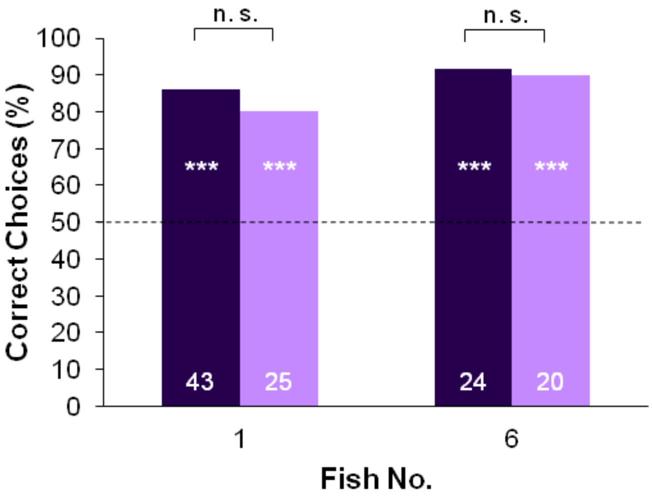

Figure 22: Discrimination performance of one fish of each training group (Fish No. 1 trained with vision and Fish No. 6 trained with the active electric sense) with the usual experimenter (dark purple) and with another experimenter during the double blind control (light purple). The tests aimed at excluding influences of the experimenter on the discrimination performance and were conducted under training conditions with both fish. The exact Fisher test showed no significant differences between both conditions (n. s. : $P > 0.05$). For further description see Figure 17.

Control IV: Exclusion of effects of the surgical procedure for electrical silencing

A sham operation was conducted to exclude influence of the principal surgical procedure for electrical silencing on the discrimination behaviour. In all fish there was no significant change in performance during these tests compared to before the sham operation (Figure 23, intact vs. sham). This shows also that the performance changes after the real operation were not influenced by previous experiments with both senses available.

Control V: Exclusion of effects of electrical input in electrically silenced fish and of passive electrical cues

None of the electrically silenced fish was able to discriminate between the objects without visual cues and the performance of the fish decreased highly significantly compared to the performance of the intact fish (Figure 23, silenced).

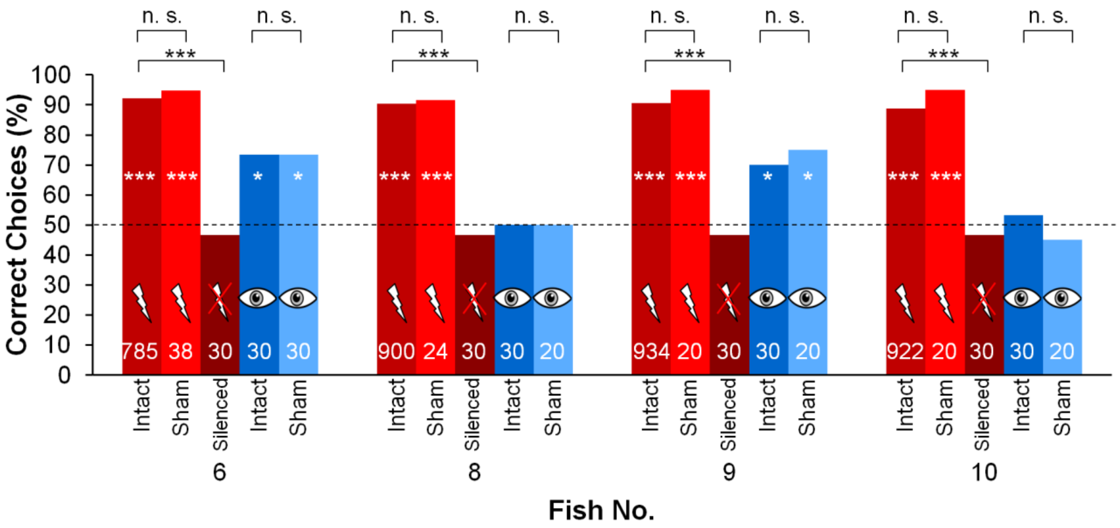

Figure 23: Discrimination performance of the electrically trained fish during control tests, which were conducted to exclude influences of the principal surgical procedure for electrical silencing on the discrimination performance. Electrical (red) and visual (blue) tests were conducted before the sham operation (intact, same data as in Figure 17), after the sham operation and after "electrically silencing" (only for the electrical tests). The exact Fisher-Test was used to test for significant differences between the performances of the intact fish compared to after the sham operation and after electric silencing (***: $P \leq 0.001$; n .s.: $P > 0.05$). For further description see Figure 17.

Control VI: Exclusion of effects of the electrically transparent agarose cubes

Tomake sure that the electrically transparent agarose cubes around the metal objects used during the electrical tests of the visually trained fish had no influence on the discrimination performance, tests under the same conditions without agarose cubes were conducted. These tests showed that the agarose cubes did not influence the discrimination behavior significantly (Figure 24).

2.1.4.5. Object inspection behaviour

During our experiments only the minimal distance of the fish to the objects was restricted and the fish could choose its distance to the gate freely. However observations of the behaviour of the fish while inspecting the objects showed that when approaching the gates all fish stopped in front of the gates/ distance grits and inspected the objects from this minimal distance, before swimming through the gate or swimming to the other gate. This behaviour did not change throughout the experiments suggesting, together with the results that the fish were unable to discriminate between the objects visually at short distance while being able to do so from a longer distance, that in this paradigm the fish made their decision at a more or less distinct location not applying information acquired before at longer distances.

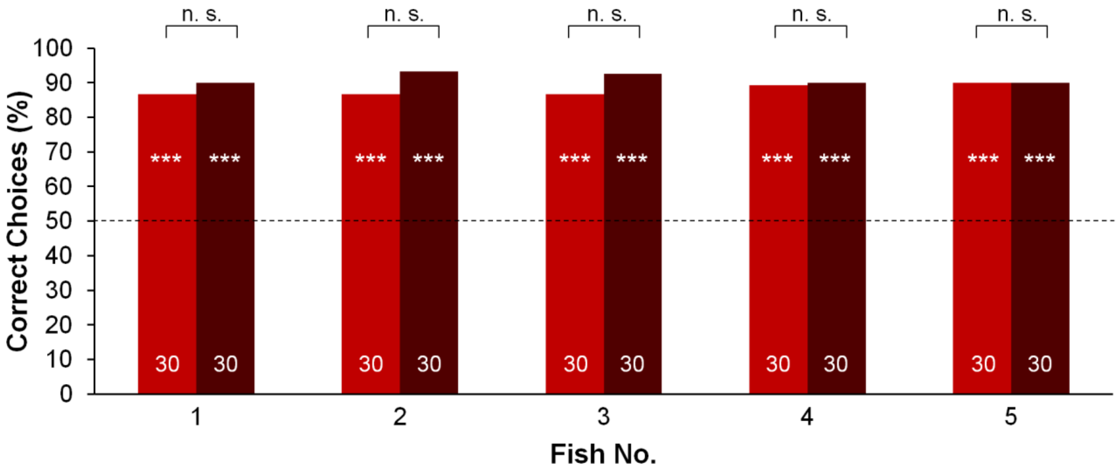

Figure 24: Discrimination performance of the visually trained fish (Fish No. 1-5) in complete darkness with (red) and without (dark red) agarose cubes encasing the aluminum objects. These control tests were conducted to exclude influences of the agarose cubes on the discrimination performance during the electrical tests. The exact Fisher test showed no significant differences between both conditions (n. s. : $P > 0.05$). For further description see Figure 17.

2.1.5. Discussion

Our results show that, similar to mammals, the weakly electric fish *Gnathonemus petersii* is capable of cross-modal object recognition (Figure 17). Cross-modal object recognition increases the flexibility of a multisensory system as it allows animals to recognize objects under varying conditions (e.g. day and night) and to exploit the advantages of their long range (vision) and short range (active electrolocation) sensory systems optimally. Since the senses have to provide information with matching content for cross-modal object recognition, in most mammals, this ability is restricted to vision and the haptic/tactile sense (Cowey & Weiskrantz, 1975; Davenport & Rogers, 1970; Gaydos, 1956; Winters & Reid, 2010). Similarly, dolphins are capable of performing cross-modal object recognition between vision and active echolocation (Herman et al., 1998). Here we show for the first time that cross-modal object recognition is also possible between vision and the active electric sense. Although the mechanosensitive lateral line system or the passive electric sense also could have provided object information and might influence object recognition in a natural environment, control experiments showed no involvement of these sensory systems in our experiments (Figure 20, Figure 23).

During our study, *G. petersii* used its active electric sense and vision to acquire information about the shape of the two objects to be discriminated. Thus, the animals had to recognise that the information provided by the two sensory systems about the same spatial object feature were identical, even though they were relying on different physical stimuli and the sensory information was arriving sequentially. This means that the sensory information had to be encoded in the brain in a way that allowed the two sensory channels to exchange information and compare and match object related inputs. This highly cognitive ability could be achieved in two different ways: Firstly, information about certain object features (in our experiment pertaining to shape) is encoded in a generic form, regardless of the input channel, i.e. both channels use a matching format of encoding. This would enable the fish to recognize objects cross-modally without any previous experience, in other words cross-modal object recognition would be an innate ability. Alternatively, information originating from multiple senses might not match in format. Instead, the fish could have learned to associate visual and electric inputs of basic features also common in other environmental objects when exposed to the features in the past. So, for example, a fish might have learned to associate a visual and electric image of a curved edge and/or a corner. Subsequently, these associations would have been generalized to new objects and new situations. In this case, cross-modal object recognition would be dependent on sensory experience and would not be innate. At present, we do not know which scenario is correct for *G. petersii*. Studies with humans have shown, however, that newborn infants are cable of cross-modal recognition of object shape and texture using touch and vision, suggesting that information is encoded generically (Sann & Streri, 2007; Streri, 2003; Streri & Gentaz, 2004). However, this has remained untested in any other animal.

In order to recognize objects cross-modally, information about characteristic object features has to be stored in some kind of neuronal representation, which is subsequently accessible by the other sense. This could be achieved either through a comparison of modality specific representations or through a single multimodal representation stored in a multisensory brain area (Ettlinger & Wilson, 1990; Lacey, Campbell, & Sathian, 2007; Winters & Reid, 2010). In mammals, cross-modal object recognition is associated with cortical structures such as the prefrontal cortex (Fuster, Bodner, & Kroger, 2000), the perirhinal or the posterior parietal cortex (Taylor, Moss, Stamatakis, & Tyler, 2006; Winters & Reid, 2010). Since fish lack an isocortex, the ability of cross-modal object recognition cannot depend on the existence of these mammalian brain structures per se. However, a recent study has shown a cryptic laminar and columnar organization of the dorsolateral pallium (DL) of a gymnotiform weakly electric fish which, together with other organizational structures, supports the hypothesis that there is a homology between the teleost DL and the mammalian cortex (Trinh, Harvey-Girard, Teixeira, & Maler, 2016). Furthermore the pallium of *G. petersii* is known to receive inputs from the auditory, the visual, the electrosensory and the lateral line systems (Prechtl et al., 1998), and lesion experiments in goldfish have shown that the teleost telencephalon is involved in spatial learning tasks (Broglio et al., 2005; Portavella, Vargas, Torres, & Salas, 2002; Rodrıguez et al., 2002), making it a prime candidate for the location of cross-modal object recognition *in G. petersii*. Other brain areas such as the tectum opticum, the torus semicirularis and the valvula cerebelli also receive multiple sensory inputs in *G. petersii* and therefore could also be involved in cross-modal transfers.

In *G. petersii,* cross-modal object recognition is influenced by dynamic weighting of the sensory inputs. The fish "weight" object related sensory inputs according to their reliability, to minimize uncertainty and to enable optimal multisensory integration. At short distances the active electric sense dominates the behavioural output during object discrimination. When the object was close by, the conflict between vision and the active electric sense (one sense providing the information that an object is present, the other sense providing the information that no object is present) was resolved in favour of the active electric sense, leading to an inability/decreased ability to discriminate between the objects visually in the intact electrically trained fish (**Figure 17**, Figure 18). However after being electrically silenced the identical fish were able to discriminate between the objects visually at short range at the same level as during electrical training (Figure 19). This suggests that in the absence of any electrical input, the visual information was no longer overwritten and the behavioural output was driven by the visual input, supporting the hypothesis that when intact the ability to discriminate between the objects visually was masked by the dominance of the active electric sense. At short range, the reliability of the electric sense exceeds that of the visual sense, which has a relatively low spatial resolution (minimal visual angle of about 3°) (Francke et al., 2014; Kreysing et al., 2012; Pusch, Wagner, von der Emde, & Engelmann, 2013). In contrast, active electrolocation provides the fish with fine scale three-dimensional spatial information and additionally informs the fish about the electrical properties of an object (von der Emde, 2006; von der Emde & Ronacher, 1994). The electric sense is very reliable at short distances because environmental factors like light level, turbidity or small suspended particles do not interfere with active electrolocation (in contrast to vision, which suffers e.g. from reflection, refraction, scattering, attenuation)(C. Hopkins, 2009). In addition, the observed dominance of the electric sense at short range might be based on the prior experience that in nature there are no nearby objects that cannot be perceived electrically. Because of the huge conflict between the visual and the electrical inputs during our experiments, integration might have even broken down (segregation), so that the visual information may have been discounted and the fish have ignored the objects even though they could be perceived by the visual sense (Ernst & Di Luca, 2011).

However, the results obtained after visual training of the fish show that the “weighting” of the sensory inputs can be adjusted through learning (Figure 17 A). The repetition and rewarding of the visual stimulus without electrical object input during visual training may have remapped the system so that the visual training was eventually successful. Also in experiments with humans and monkeys (Adams, Banks, & van Ee, 2001; Zaidel, Turner, & Angelaki, 2011) it was shown that it is possible to adapt to discrepancies in sensory inputs, if they are consistent and occur over many repetitions (Ernst & Di Luca, 2011).

At longer object distances, the reliability of the electric sense decreases rapidly due to its small working range (Pedraja, Aguilera, Caputi, & Budelli, 2014; von der Emde et al., 2010). Consequently, the dominance of the electric sense over vision decreases, and the conflict between vision and the electric sense is now solved in favour of the visual information (Figure 18). These results correspond well with findings in humans (Ernst & Banks, 2002), monkeys (Fetsch et al., 2009) and rats (Sheppard et al., 2013) and suggest that dynamic weighting of sensory inputs is a fundamental process necessary for multisensory integration, and is conserved across vertebrates. However, it is not known yet how the inputs of multiple senses are weighted and integrated in the brain. Multisensory information could, for example, be processed in a centralized or decentralized manner. In a centralised system information received through all sensory systems would be fed into a single integration centre, where the multiple inputs would be integrated (Magosso, Cuppini, Serino, Di Pellegrino, & Ursino, 2008; Ursino, Cuppini, Magosso, Serino, & Di Pellegrino, 2009). In contrast, in a decentralized system the integration would be achieved through the interconnection of many multisensory areas (W.-h. Zhang, Chen, Rasch, & Wu, 2016).

Here we show, for the first time, that cross-modal object recognition as well as dynamic weighting of sensory inputs exists not only in mammals but also in fish. This has important implications for our understanding of the mechanisms and the neuronal requirements underlying these functions, by revealing that the teleost brain, which is usually considered to be simple in relation to those of birds and mammals, is nonetheless capable of performing these complex cognitive tasks.

2.2 Electrosensory capture during multisensory discrimination of nearby objects in the weakly electric fish *Gnathonemus petersii*

2.2. Electrosensory capture during multisensory discrimination of nearby objects in the weakly electric fish *Gnathonemus petersii*

2.2.1. Abstract

Animal multisensory systems are able to cope with discrepancies in information provided by individual senses by integrating information using a weighted average of the sensory inputs. Such sensory weighting often leads to a dominance of a certain sense during particular tasks and conditions, also called sensory capture. Here we investigated the interaction of vision and active electrolocation during object discrimination in the weakly electric fish *Gnathonemus petersii*. Fish were trained to discriminate between two objects using both senses and were subsequently tested using either only vision or only the active electric sense. We found that at short range the electric sense dominates over vision, leading to a decreased ability to discriminate between objects visually when vision and electrolocation provide conflicting information. In line with visual capture in humans, we call this dominance of the electric sense *electrosensory capture*. Further, our results suggest that the fish are able to exploit the advantages of multiple senses using vision and electrolocation redundantly, synergistically and complementarily. Together our results show that by providing similar information about the environment on different spatial scales, vision and the electric sense of *G. petersii* are well attuned to each other producing a robust and flexible percept.

2.2.2. Introduction

The vast majority of studies in the field of sensory biology have been restricted to a single modality. However, objects and environments contain inherently multimodal information, therefore animals are likely to use information from multiple sensory channels to analyse features of their environment and to guide behaviour (Braun, Coombs, & Fay, 2002). A fundamental question in sensory biology is how multiple sensory systems operate together to produce an appropriate behavioural response. Here we aimed to investigate this question by using an object discrimination paradigm based on operant conditioning, to explore the interaction of the active electric sense and vision in the weakly electric fish *Gnathonemus petersii*.

In a multisensory system each sense provides an individual stream of information about the environment based on different physical stimuli. In order to form a robust and reliable overall percept these individual streams can be combined and integrated in different ways. The combination of different information sources can be used to increase the information input, and the integration of information from different senses about the same event or object can increase the reliability of the resulting percept (Ernst & Bülthoff, 2004). However, there is inherent noise within all sensory systems; so, even if different senses provide information arising from the same source, the informational content of the inputs varies slightly. For example, the visually perceived size of an object might differ slightly from the haptically perceived size of the same object. Instead of increasing the reliability of the percept through integration, these discrepancies between the inputs of different senses might lead to a decrease of reliability if combined equally.

To prevent this decrease and to obtain a coherent and reliable percept, not all senses contribute to the overall percept to the same degree. Instead the information from the different senses is integrated using a weighted average of the inputs. Studies in humans, monkeys and rats have found that this weighting depends on the reliability of the sensory inputs (Alais & Burr, 2004; Ernst & Banks, 2002; Fetsch et al., 2009; Sheppard et al., 2013) and is probably also based on prior experience (Ernst & Bülthoff, 2004; Ernst & Di Luca, 2011). As a result, the percept, and thus the observable behavioural output, is often dominated by a certain sense under certain conditions and during a certain task. Examples for such dominance of a sense can be seen in visual capture in humans during spatial tasks and in auditory capture during timing tasks. In humans, spatial decisions such as size estimation or source localisation are dominated by visual information, which can be observed when the sensory inputs of vision and the haptic or acoustic sense provide conflicting information (Howard & Templeton, 1966a; Rock & Victor, 1964). On the other hand, this dominance is reversed during tasks that require temporal decisions. For example during the identification of the number of presented light flashes and beeps, the number of presented beeps will affect the number of perceived flashes (Shams et al., 2000, 2002).

Although in these and other examples one sensory input dominates, the observed behaviour is still also influenced slightly by the input of the other senses. Therefore, drastic discrepancies between the different inputs might still lead to a decrease of the reliability of the overall percept. In order to prevent this loss of reliability, integration breaks down if the discrepancies between multisensory inputs are too large and the different inputs are processed separately (segregation)

(Ernst & Di Luca, 2011). The system is thus able to prevent the integration of information arising from two different events or objects.

The principles of integration through weighting of sensory inputs and segregation enable a multisensory system to obtain a robust percept and to exploit the advantages of possessing multiple information sources. For example, integration of multiple sensory inputs often leads to a *synergetic* effect, improving the behavioural response during multisensory trials compared to single sensory trials (Guo & Guo, 2005; Leonard & Masek, 2014; Stein, Meredith, Huneycutt, & McDade, 1989; L.-Z. Zhang, Zhang, Wang, Yan, & Zeng, 2014). Segregated information can be *complementary*, if the information streams are tuned to particular tasks or to components of a task (Agrawal, Safarik, & Dickinson, 2014). Furthermore, information from multiple senses could be used *redundantly*, where one sense can independently guide a behaviour but can be replaced by another if it becomes unavailable, for example at night when low light levels mean that vision cannot be used (Wilgers & Hebets, 2011).

Here, we aim to investigate these principles of multisensing by using the African weakly electric fish *Gnathonemus petersii* as a model. *G. petersii* is primarily known for its ability to orientate and communicate using its active electric sense. These fish are able to detect and discriminate objects by producing weak electric pulses in an electric organ located in the caudal peduncle (electric organ discharges (EODs)) (von der Emde, 2006; von der Emde & Fetz, 2007). Each EOD generates an electric field around the animal. Objects within this electric field distort the spreading of the field lines, creating an electric image (Caputi et al., 1998; Rasnow, 1996), and these distortions can be perceived by the fish using special cutaneous electroreceptor organs (Jorgensen, 2005). Electric images provide fine scale spatial information about the shape, size and location of nearby objects and they additionally provide information about the electrical properties of objects, such as their resistance and capacitance, which inform the fish whether these objects are animated or inanimate (von der Emde & Fetz, 2007).

Besides the prominent active electric sense, *G. petersii* possess a highly specialised visual system. As an adaptation to their crepuscular or nocturnal life style and their habitat in black water streams, these fish possess a so-called grouped retina, in which the photoreceptors are packed into bundles surrounded by a tapetum lucidum (Francke et al., 2014; Kreysing et al., 2012). This organisation of the photoreceptors improves vision under dim light and within turbid water but comes with the cost of a relatively low spatial resolution (minimal visual angle of about

3°) (Pusch, Wagner, et al., 2013). Since this visual system has a high temporal resolution (Pusch, Kassing, et al., 2013), it mainly functions to detect fast movement of bigger objects such as predators but it also enables the fish to discriminate between objects (Schumacher, Burt de Perera, Thenert, & von der Emde, 2016).

In an earlier study(Schumacher, Burt de Perera, Thenert, et al., 2016), we showed that *G. petersii,* which were trained to discriminate between two objects using either only the active electric sense or only vision, were capable of spontaneous cross-modal object recognition. Furthermore, when trained only with the active electric sense, electrolocation dominated over vision during object discrimination at short range. With increasing object distance this dominance of the active electric sense diminished, suggesting that the sensory inputs were weighted dynamically according to their reliability (Schumacher, Burt de Perera, Thenert, et al., 2016). During these experiments the fish could use only single senses to learn the task, which might have influenced the hierarchy of the senses through learning. The question remains as to how vision and the active electric sense operate together during an object discrimination task under more natural conditions when both senses can be used to acquire information about the object. Is there still a hierarchy of the senses or are vision and the electric sense weighted equally, when both senses could be used during training?

Here we extended this work by investigating sensory dominance, also known as sensory capture, with fish that were trained with both senses available, by subsequently comparing their performance during visual and electrical uni-modal tests. Furthermore, by investigating the performances of fish trained (1) with both senses, (2) only with vision (intact and electrically silenced), and (3) only with the active electric sense, we were able to study additional aspects of sensory weighting, such as remapping and the influence of sensory conflict, and whether there are any advantages of using both senses to solve similar tasks, including, redundancy, synergy and complementation. Together, our experiments indicate how the active electric sense and vision operate together to produce an appropriate behavioural response during object discrimination.

2.2.3. Methods

2.2.3.1. Subjects and set up

The subjects were eighteen naive *G. petersii* with a standard length of 9 – 14 cm. The fish were kept individually in 75 cm x 40 cm x 40 cm tanks, which also served as experimental tanks. Each tank was divided into two compartments (40 cm x 40 cm and 35 cm x 40 cm) by a partition containing two gates. The bigger compartment was used as the experimental area. It was again divided into two compartments, each of which was connected with the smaller section (living area) through one gate (Figure 25).

During the experiments objects were placed 1 cm behind the gates in the experimental area. Grids were placed behind the gates to make sure that the fish always kept the same minimum distance while inspecting the objects. These grids were made of a plastic frame stringed with cotton thread (diagonal mesh size 15 mm) and the fish had to push them aside in order to pass the gate. Most experiments were conducted under dim light conditions of 3-6 lx measured just above water level with a light probemeter (Extech instruments, Nashua, USA), which is within the range that allows optimal visual object recognition in *G. petersii* (Schuster & Amtsfeld, 2002). The experiments that required exclusion of visual input were conducted in complete darkness (<0.01 lx).

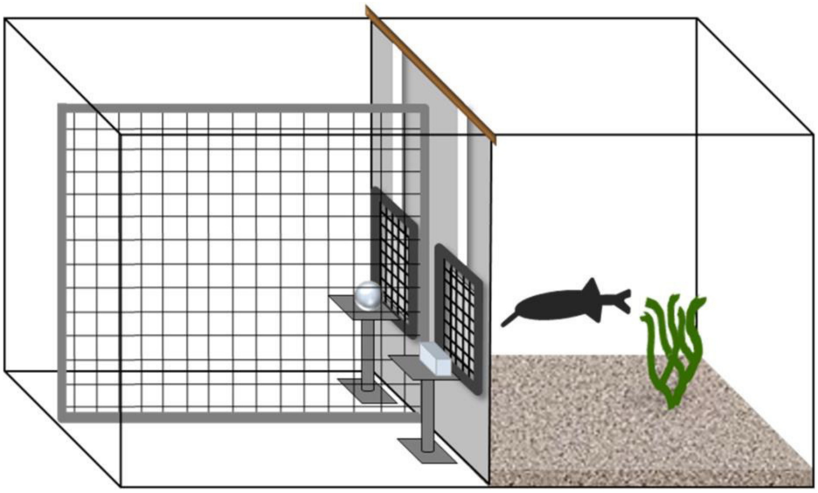

Figure 25: Schematic side view of the experimental tank.

2.2.3.2. Experimental procedure

The fish were trained in a two alternative forced choice procedure to discriminate between two objects that only differed in shape. At the start of each trial, the fish remained in the living area with closed gates, and the positive object (S+) and the negative object (S-) were placed behind the gates on the left or the right side of the experimental area according to a pseudorandom sequence (Gellermann, 1933). To start the trial, the gates were opened simultaneously, and the fish was able to inspect both objects through the gates. If the fish chose to swim through the gate with the S+ behind, it received a food reward (chironomid larva), while the selection of the S- was punished by chasing the fish back into the living area. After a correct decision, the fish was given approximately 1 min to return to the living area. If the fish did not swim back within this timeframe, it was carefully forced back into the living area (without inflicting stress). When the fish was back in the living area, the gates were closed and a new trial was prepared. Each fish conducted 15 – 44 trials per day.

Training was considered successful when the fish reached a pre-assigned learning criterion of > 75% correct choices on three consecutive training days. After the fish reached this criterion, tests were interspersed every third trial. This training to test ratio was increased to 2:2 after 3-5 days. During test trials fish were neither rewarded nor punished to prevent training effects during the tests.

2.2.3.3. Training groups and tests

Fifteen fish were divided into three training groups of five fish each, which could use either both vision and the active electric senses (B group; fish 1-5), only vision (V group; fish 6-10) or only the active electric sense (E group; fish 11-15) to discriminate between the objects. Additionally three fish were "electrically silenced" before being trained with only vision available (S group; fish 16-18).

During all experiments a sphere (Ø 3 cm) was used as the S+ (Figure 26 A). In the B, V and E training group three fish each were trained with a cross (width: 4 cm, height: 4 cm, depth: 1.7 cm; Figure 26 C1) and two with a cuboid (4 cm x 2.2 cm x 1.7 cm; Figure 26 B) as S-. In the S training group, the cross was used as S- for two fish and the cuboid for one.

To enable the fish to use both the active electric sense and vision to learn the discrimination task, the objects that were used during training in the B group were made of aluminium and were presented under light conditions.

For training in the V group as well as in the S group, electrically transparent agarose objects were used, which had approximately the same conductivity as the surrounding tank water, therefore they were "electrically invisible" to the fish. To improve the visual perceptibility, the objects were coloured with red food colour. Red was chosen because the absorption maximum of the cones of *G. petersii* is at a wave length of 615 nm (Kreysing et al., 2012). To produce the objects, red food colour (Lebensmittelpaste Rot, Deko Back, Waibstadt, Germany) was added to deionised water (conductivity: 8 µS/cm) until a conductivity of ca. 40 µS/cm was reached. Agarose powder was added in a ratio of 2g per 100 ml liquid (increasing the conductivity to ca, 100 µS/cm) and the mixture was boiled and cast in moulds. The objects were ready to use when the agarose became stiff.

To measure whether the electrical properties of the agarose objects matched those of the tank water, the resistances of 250 ml stiff agarose and 250 ml tank water were compared. For these measurements, the measuring electrodes of a multimeter (M-3650B, Voltcraft) were injected with 5 cm distance to each other in the agarose or water. There was no measurable difference between the resistance of the agarose and that of the tank water. Additional control test were conducted to ensure that the fish were unable to use electrical input for the discrimination task (see control tests).

In the E training group, aluminium objects were used that were covered with electrically transparent hoods made of opaque black cotton fabric ensuring that the positive and the negative objects had the same outer shape. This prevented discrimination with vision and also excluded a possible influence of the lateral line system on the performance.

In the V training group, it was not possible to exclude an influence of the lateral line system without also interfering with the visual discrimination. Hence, control tests were conducted to ensure that the lateral line system was not involved in the discrimination in the B, V and S training group (Control tests).

The three fish of the S training group underwent a surgical procedure before training, during which the spinal cord was sectioned anterior to the electric organ located in the caudal peduncle. The fish were narcotised in a 100 mg/l solution of MS 222 (Acros Organics, Geel, Belgium). Once the fish were unconscious, the operation side was locally anaesthetized with Xylocain Gel (AstraZeneca GmbH, Wedel, Germany) and a dissecting needle was inserted into the vertebral canal. With slight movements of the dissecting needle the spinal cord was sectioned, so that the electric organ no longer received command signals from the brain, hence the fish were unable to produce electric signals.

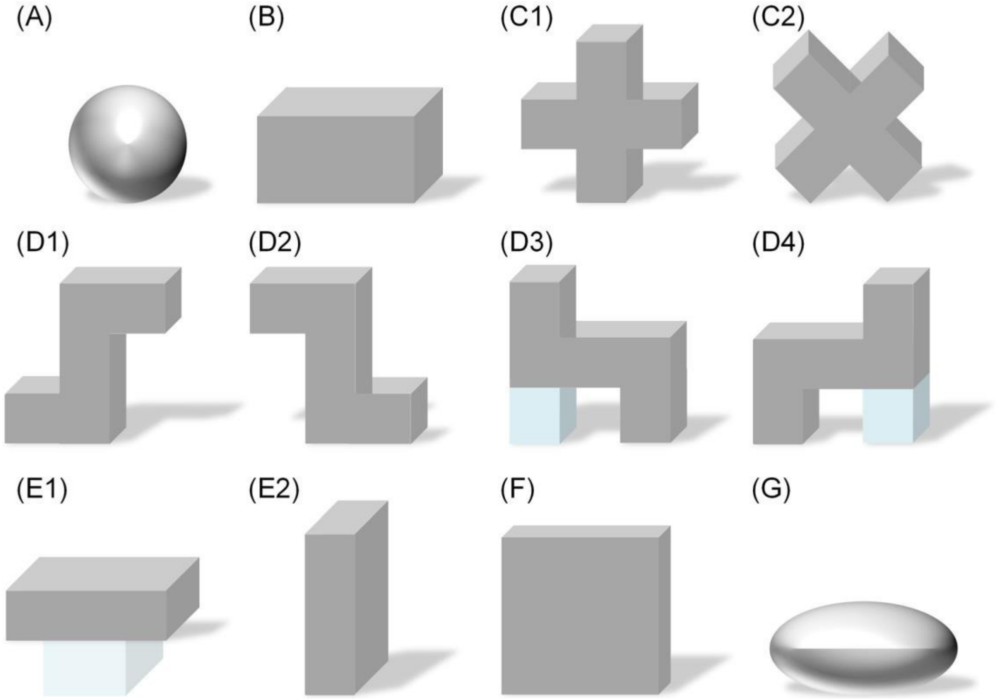

Figure 26: Shapes of objects used during training (A-C1) and during the feature recognition tests (C2-G). All objects had the same volume. The material of the objects differed for the different training groups. For the experiments with the B-group, which could use both vision and the electric sense for the discrimination task aluminium objects were presented in ambient light. For the training with only the electric sense (E group), the aluminium objects were covered with black cotton hoods. During vision only training and tests, the objects were made of red coloured electrically transparent agarose. The sphere (A) was used as the positive object during all experiments except for the tests with an exchanged positive object. The cuboid (B) and the cross (C1) were used as negative objects during training and during the uni-modal tests. Object D, E, F and G were neutral and never used in experiments with these fish before. To ensure that when using objects D3, D4 or E1 the horizontal bar was presented in the same height as in the cross, small cubes of electrically and visually transparent agarose were used to lift the objects.

2.2.3.3.1. Speed of task acquisition

To test whether the available sense influenced the speed of learning, the mean number of training days needed to reach the pre-assigned learning criterion of 75% correct choices on three consecutive training days was compared for the four different training groups. A Kolmogorov-Smirnov-test was conducted to test whether the training durations of each group was normally distributed. Afterwards a One-Way-ANOVA and a post-hoc-test with a Bonferoni-correction were conducted to compare the results of the different groups.

2.2.3.3.2. Accuracy of response

To test whether there were any effects of the available sense on the accuracy with which the fish solved the task, the performances of the different groups under their training conditions were compared at asymptote-level. The percentage of correct choices during all training trials after reaching the learning criterion was calculated for each fish. To allow statistical analyses, the percentage data were transformed using the Arcsine transformation. The results of each group were tested for normal distribution with the Kolmogorov-Smirnov-test and the groups were compared using a One-Way-ANOVA and a post-hoc-test with a Bonferoni-correction. The mean and the standard error of the mean were calculated for each group, transformed back and plotted in bar charts.

2.2.3.3.3. Uni-modal tests

After training, the fish trained with both vision and the active electric sense (B training group) were tested in uni-modal tests, during which the fish could use either only vision or only the electric sense to discriminate between the objects. During the tests, the fish were neither rewarded nor punished. The vision only tests were conducted with the red coloured electrically transparent agarose objects presented in light. To test the discrimination performance when only the active electric sense provided information about the objects and to prevent influence of other sensory systems, aluminium objects were encased in cubes of electrically transparent agarose and presented in complete darkness.

After all tests (increased conflict, feature detection, memory test and control tests) were completed, two of the fish trained with both senses (fish 2 and 5) were electrically silenced. Since these fish were used during the memory tests beforehand (see below), fish 2 had to be retrained again before it was silenced. Fish 5 never reached a performance below 70 %, therefore retraining was unnecessary. Before the actual operation, a sham operation was conducted, following the same procedure as the real operation described above for the S training group, but instead of inserting the dissecting needle into the vertebral canal, only the skin was penetrated, so that the ability to produce electrical signals was not impaired. The fish were then tested again with the metal objects and with the electrically transparent red coloured agarose objects in light, to ensure that the surgical procedure had no effect on the discrimination performance. Because this was the case in all fish, the fish were then electrically silenced and tested again with only vision (red coloured electrically transparent agarose objects in light) available for the discrimination task.

With each test condition at least 30 trials were conducted. The performance of each fish during the different tests was plotted in a bar chart and tested for significant differences to the 50%-chance level using a Chi^2-test. Exact Fisher-Tests were used to compare the performance under the different conditions for each fish.

2.2.3.3.4. Conflict between senses

During the uni-modal visual tests, vision and the active electric sense provide conflicting information about the objects (vision giving the information that objects are present and the electric sense giving the information that there are no objects). To test how the conflict between vision and the electric sense affects the discrimination performance, the intact fish of the B group, the fish of the V group and two fish of the B group (fish 2 and 5) after being electrically silenced were tested visually with visually transparent plastic screens (5 cm x 8 cm, 0.1 cm thick) placed in front of the red coloured electrically transparent agarose objects. During these tests the visual sense still provided information about the shape of the objects, while the electric sense provided information about the shape of the plastic screens, thus increasing the conflict between both senses compared to the visual tests without plastic screens. The screens were placed directly in front of the objects, so that the distance of the fish to the object and the screen was almost identical. With each fish at least 30 test trials were conducted and a Chi^2-test was conducted to test whether the performance was significantly different from chance level. To test whether there were significant differences between the performances of the two fish trained with both senses before and after they were electrically silenced the exact Fisher-test was used.

2.2.3.3.5. Feature detection

To investigate whether vision and the electric sense are tuned to particular aspects of object discrimination, we tested which features of the objects the fish used to discriminate between them under different sensory conditions. First we tested whether both objects were used to fulfil the discrimination task or whether the discrimination task only depended on one of the objects (either the S+ or the S-). To do this, two fish of the B group (fish 1 and 2) and two fish of the V group (fish 8 and 9) (all four fish were trained with the cross as negative object) were tested with: 1) the known positive object vs. a different shaped unknown neutral object (ellipsoid,

Figure 26, object G) and 2) with the known negative object vs. the ellipsoid. Since all fish were able to fulfil the task when the positive object was exchanged but none of the fish was able to do so when the negative object was exchanged (see results), the further feature detection tests were conducted by exchanging the negative object.

The feature detection tests were again conducted with fish 1 and 2 of the B group and fish 8 and 9 of the V group. During these tests, the S- was replaced by three additional unknown objects (Figure 26 D-F), which all had the same volume as the known negative object (cross, C1). Object D consisted of the same basic elements as the cross and was presented at four different perspectives (D1-4). Depending on the perspective, the object had certain identical features as the cross, e.g. the horizontal bar or the vertical bar, with relocated features, for example, the upper and lower arm or the right and the left arm. Object E consisted only of a single bar of the cross and was presented either horizontally or vertically (E 1, 2). Object F was a cuboid with the same length and height (4 cm x 4 cm) as the cross. The known negative object (cross, C1) was also presented with a rotation of 45° (C2). Thus there were eight different test conditions that were compared with the results of the training trials with the cross. 20 trials were conducted with each condition. The percentages of correct choices with the different objects were plotted in bar charts and a Chi^2- test was used to test whether the performance was significantly different from chance level.

2.2.3.3.6. Robustness of performance

To test for how long the fish were able to perform the learned discrimination task, three fish of the B group (fish 1, 2 and 5) and two fish of the V group (fish 6 and 7) were tested after four weeks without any training and subsequently once a week under the same conditions that they were trained with (except fish 5, which was tested after 6 weeks and then once every 4 weeks). On each test day, 20 trials were conducted, during which the fish received a food reward every third trial no matter which decision was made in order to maintain motivation. No punishment was used during these tests. When the fish reached a performance of less than 70% correct choices on three consecutive weeks, it was assumed that the fish were no longer able to perform the task and the tests were stopped.

2.2.4. Results

During training, 15 intact and 3 electrically silenced (S group) naive *G. petersii* were trained to discriminate between two differently shaped objects under different sensory conditions. Either they could use both vision and the active electric sense (B group; metal objects), only vision (V and S group; electrically transparent agarose objects) or only the active electric sense (E group; metal objects covered with opaque cotton hoods) to discriminate between the objects.

2.2.4.1. Speed of task acquisition

All fish, no matter which senses they could use during training, learned the discrimination task and reached the pre-assigned learning criteria of 75% correct choices on three consecutive training days. The speed of learning however differed significantly depending on the senses available (Figure 27). The five fish of the V training group learned the discrimination task on average in 31.5 (29-36) training days, which was significantly slower than the five fish of the B training group with an average of 12.5 (4-28) training days and the five fish of the E training group with an average of 16.2 (10-23) training days. When trained under the same conditions, the three electrically silenced fish, which were not able to produce any electric signals, reached the learning criterion significantly faster than the intact V group. With an average training duration of only 6 (5-7) days these fish also learned the task slightly faster than the fish of the B and the E training groups.

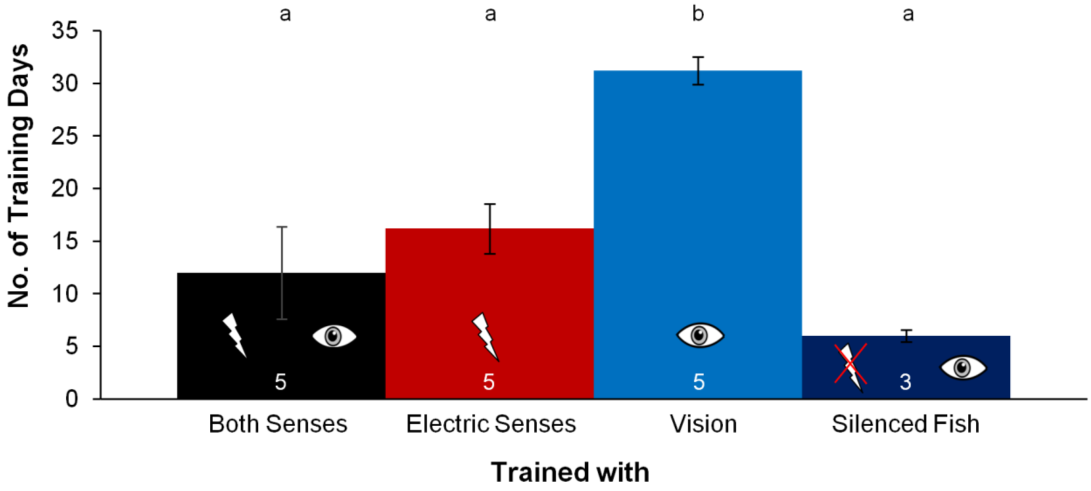

Figure 27: Mean number of training days the different training groups needed to reach the pre-assigned learning criterion. The error bars indicate the standard errors of mean. To test for normal distribution, the Kolmogorov-Smirnov-test was used (P > 0.05 for all groups). A One-

Way-ANOVA (P < 0.001, F = 13.123) and a post-hoc-test with Bonferroni-correction were conducted to compare the different groups. The letters above the bars indicate the results of the post-hoc-test. Bars which do not differ significantly are indicated by the same letter above the bars (P > 0.05). A different letter above the bar indicates a significant difference in performance (P ≤ 0.05). The number of fish in each group is shown within the bars.

2.2.4.2. Accuracy of response

After reaching the learning criterion, the accuracy of all of the fish increased up to at least 84 % correct choices (Figure 28). The highest accuracy at asymptote level was reached by the fish of the B training group with an average of 94.5% (90.4% - 99.2%), which was significantly higher than the accuracy of the V training group and the S training group. With an average accuracy of 89.8% (87.1% - 92.1%) the performance of the E training group was not significantly different from the results of the B group (P = 0.058) but a similar trend to a reduced performance could be observed. The accuracy of the V training group (Ø 86.2% (84.6% - 88.2%)) and the electrically silenced fish trained under the same conditions (Ø 85.3% (84.1 % - 86.0%)) were very similar.

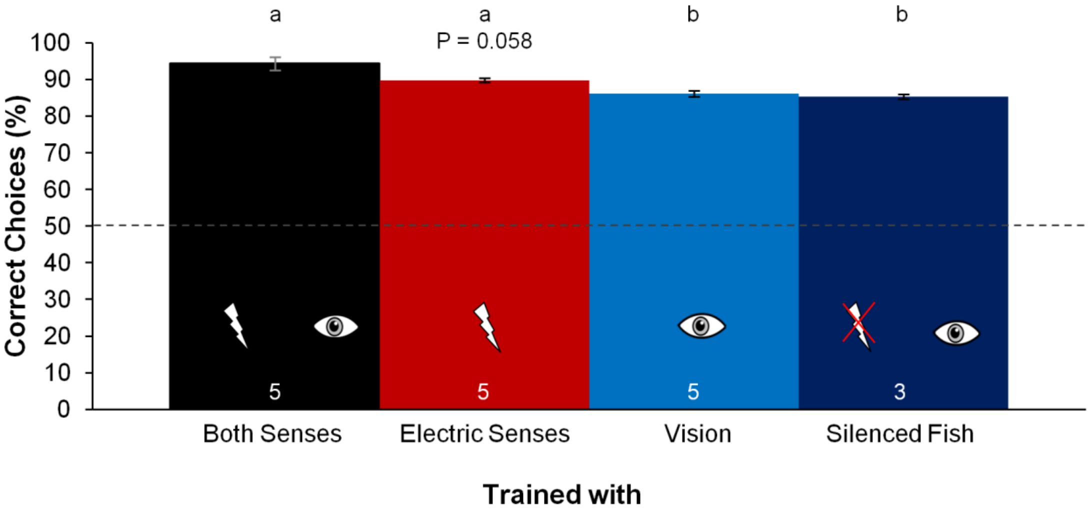

Figure 28: Mean accuracy of the different training groups during the training trials of the object discrimination experiments. The percentage of correct choices was calculated for each fish including all training trials after the fish reached the learning criterion. For the statistical analyses the data was arcsine transformed. The Kolmogorov-Smirnov-test was used to test for normal distribution (P > 0.05 for all groups). To compare the results of the different groups a One-Way-ANOVA (P = 0.001, F = 8.908) and post-hoc-tests with Bonferroni-correction were conducted. The mean and standard error of mean (indicated by the error bars) were calculated and back transformed. The dashed line indicates the 50% chance-level. For further description see Figure 27.

2.2.4.3. Uni-modal tests

After training, the fish of the B training group were tested in uni-modal tests, during which they could use only the active electric sense or only vision.

All of the five fish of the B group were able to discriminate between the two objects using only the active electric sense with an accuracy of over 93% correct choices, significantly above the 50% chance level (Figure 29). In tests, during which the fish could use only the visual sense, the performance of the individuals differed. Three (fish 2, 4 and 5) of the five fish were not able to discriminate between the objects in these tests performing just at chance level (40.7 % - 53.3 %). However two of the fish (fish 1 and 3) reached an accuracy significantly above chance level (74.2 % and 68 %) and were thus able to discriminate between the objects even though the accuracy was significantly lower than in training.

During the visual tests with the electrically transparent agarose objects there was a conflict between vision (providing information about the object) and the electric sense (providing the information that no object was present). The visual discrimination could have failed in the three unsuccessful fish either because the fish had not learned to use visual information for the task or because the conflict between the sensory inputs was solved in favour of the electric sense. To test between these alternatives, two of these unsuccessful fish were subsequently electrically silenced, which excluded electrical input. When subsequently tested visually under the same conditions as before, the fish reached a performance significantly above chance level (80 %, 82%) and thus were now able to discriminate between the objects using only vision (Figure 29). This means that the information for discriminating between the objects using vision must have been available but wasn't used as long as the electric sense was working.

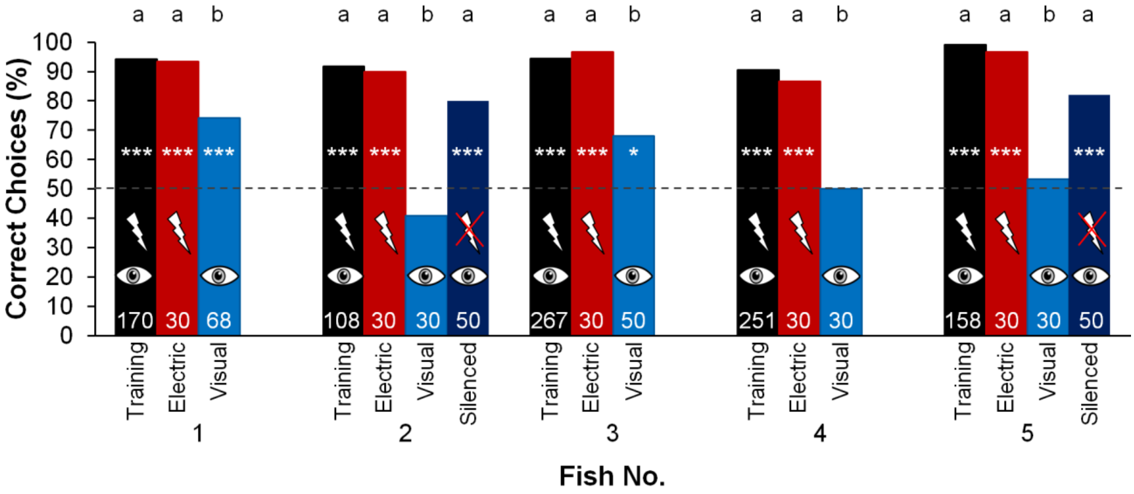

Figure 29: Discrimination performance of the fish trained with both senses (fish 1-5) during training (black), during uni-modal test with the active electric sense only (red) and with vision only (blue) and during visual test after being electrically silenced (fish 2 and 5; dark blue). The number of trials conducted with each condition is given within the bars. The 50%-chance level is indicated by the dashed line. To test whether the performances were significantly different from chance level, Chi²-tests were conducted (* : $P \leq 0.05$; ** : $P \leq 0.01$; *** : $P \leq 0.001$). Fisher-tests were used to compare the performances under the different conditions for each fish. Bars which do not differ significantly are indicated by the same letter (a) above the bars ($P > 0.05$). A different letter (b) above the bar indicates a significant difference in performance ($P \leq 0.05$).

2.2.4.4. Conflict between senses

To test whether the degree of conflict between vision and the active electric sense during the visual tests influences the discrimination performance, a test with a large conflict between the two senses was conducted by putting a clear plastic screen in front of the red coloured electrically transparent agarose objects. The plastic screens increased the conflict between vision and the electric sense compared to the visual tests without screens, because the fish electrically perceived the shape of the screen, while seeing the shape of the agarose objects.

During these tests, none of the intact fish of the B group were able to discriminate between the objects (Figure 30 A, light blue bars). Even the two fish (fish 1 and 3), which were able to discriminate between the objects during the visual test, did not reach a performance significantly different from chance level. However after fish 2 and 5 were electrically silenced, the performance during the tests with an increased conflict significantly rose to a level significantly different from chance level (green bars). These fish were now able to discriminate between the objects.

The performance of the fish of the V group during the tests with an increased conflict however did not differ from those during the visual tests and all five fish reached a performance significantly different from chance level (Figure 30 B).

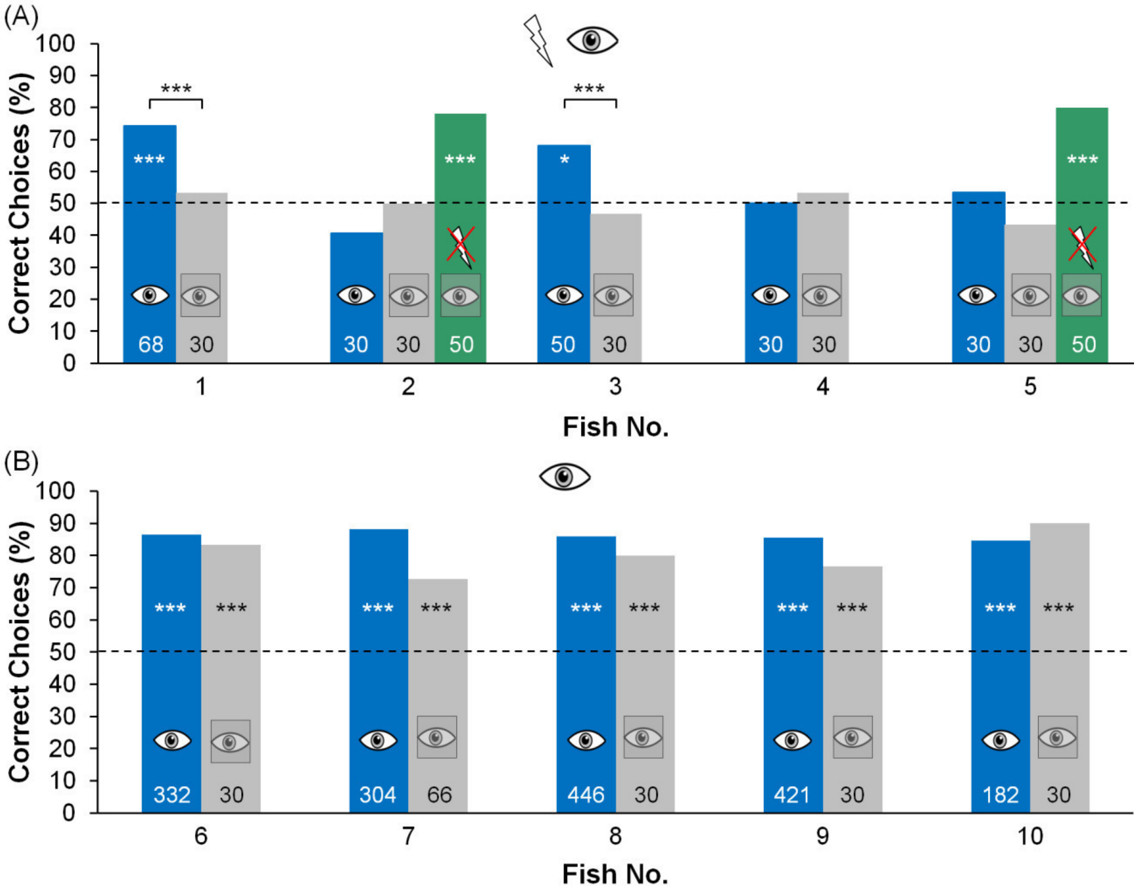

Figure 30: Discrimination performance of the fish trained with both sense (A) and the fish trained only with vision (B) during tests with an increased conflict between the visual and the electrical object information provided (grey). During these tests, a visually transparent plastic screen was placed in front of the red coloured electrically transparent agarose objects. Thus vision provided information about the shape of the objects, while the active electric sense provided information about the plastic screen, creating a stronger conflict between the sensory inputs compared to visual tests without plastic screens. Fish 2 and 5 were tested again after being electrically silenced (green). For reference, the performance of the fish during the visual tests is shown (blue; A same data as in Figure 29, B data from Schumacher et al 2016). An exact Fisher-Test was conducted to compare the performance during the visual tests and the test with increased conflict and the performance before and after being silenced. For further description see Figure 29.

2.2.4.5. Feature detection

To test which features the fish used to discriminate between the objects, we first tested whether the fish had learned both objects, only the positive or only the negative object. All fish, no matter whether trained with both senses or trained only with vision, reached a performance significantly different from chance level when the positive object was exchanged with a neutral object (Figure 31, dark bars). Thus they were able to fulfil the discrimination task although the known positive object was missing. However when tested with a neutral object replacing the negative object, the performance of all tested fish dropped to chance level, showing that the fish were unable to fulfil the task without the negative object present (Figure 31, lighter bars). This suggests that the presence of the negative object is vital for the discrimination task.

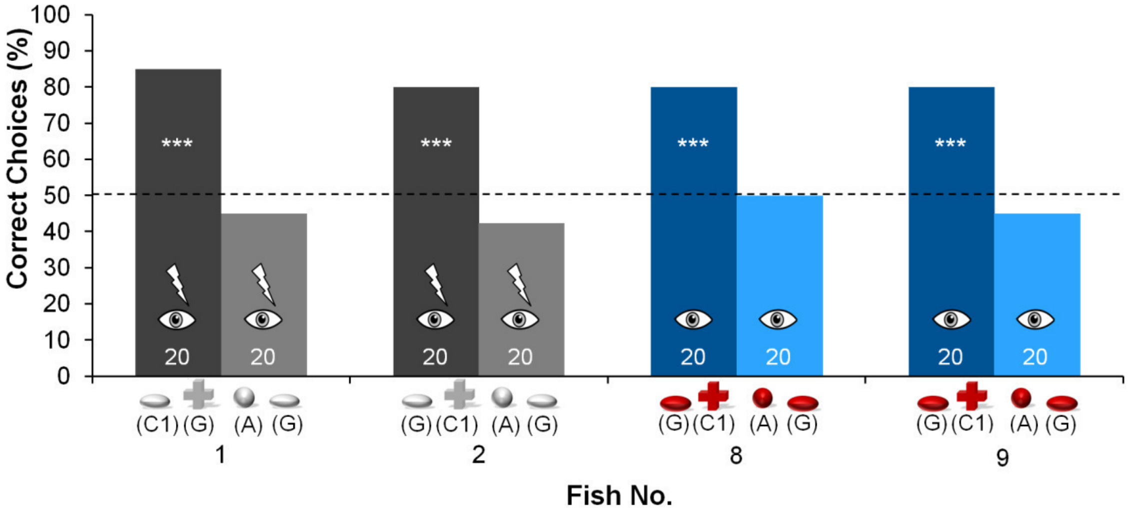

Figure 31: Discrimination performance of two fish trained with both senses (fish 1 and 2) and two fish trained with vision (fish 8 and 9) during test where either the positive object (dark bars) or the negative object (lighter bars) was exchanged by a neutral object. For further description see Figure 29.

In the next test, the negative object was changed to test which features of the object the fish used to recognise it. All four tested fish, no matter whether trained with both senses or only with vision, were able to fulfil the task not only when the known negative object (C1) was present but also reach performances significantly different from chance level with some of the other objects, suggesting that the fish recognised certain features of the negative objects (Figure 32). The objects the fish recognised as negative differed between the fish. Both fish of the B group were unable to fulfil the task, when only the vertical bar of the cross was present (E2) or when only the very basic dimensions of the object matched those of the cross (F), suggesting that both features together were not sufficient for the fish to recognise the objects as their negative object. While fish 2 was also unable to discriminate between the objects when only the horizontal bar was present (E1), fish 1 reached a performance significantly different from chance level with this object, suggesting that the horizontal bar was necessary for fish 1 to recognise the object. This is supported by the ability of this fish to fulfil the task when object D3 and D4 were presented instead of the cross. In both objects the horizontal bar was also unchanged. Furthermore, this fish was unable to discriminate between the objects when object D2 without an intact horizontal bar was presented. However, fish 1 also reached a performance significantly different from chance level with object D1 replacing the cross, suggesting that the presence of the right arm was crucial for the fish. Fish 2 was only able to fulfil the task when object D1 and D4 were presented. Thus, this fish might have learned a certain combination of the right arm and the upper arm.

The two fish of the V group reached a performance of at least 70% correct choices in all test except for the tests with object E1 and 2 and thus were probably able to recognise features of the known negative object. Due to the small N, a performance of 70% correct choices was not significantly different from chance level but still it is likely that the fish were able to fulfil the task. Both fish were still able to fulfil the task when an object, which only matched the cross in its basic dimensions (F), was presented but did not reach a performance different from chance level when objects with very different dimensions (E1 and 2) replaced the negative object. This leads to the suggestion that the visually trained fish had learned the basic outer dimensions of the S- rather than a certain feature of the cross.

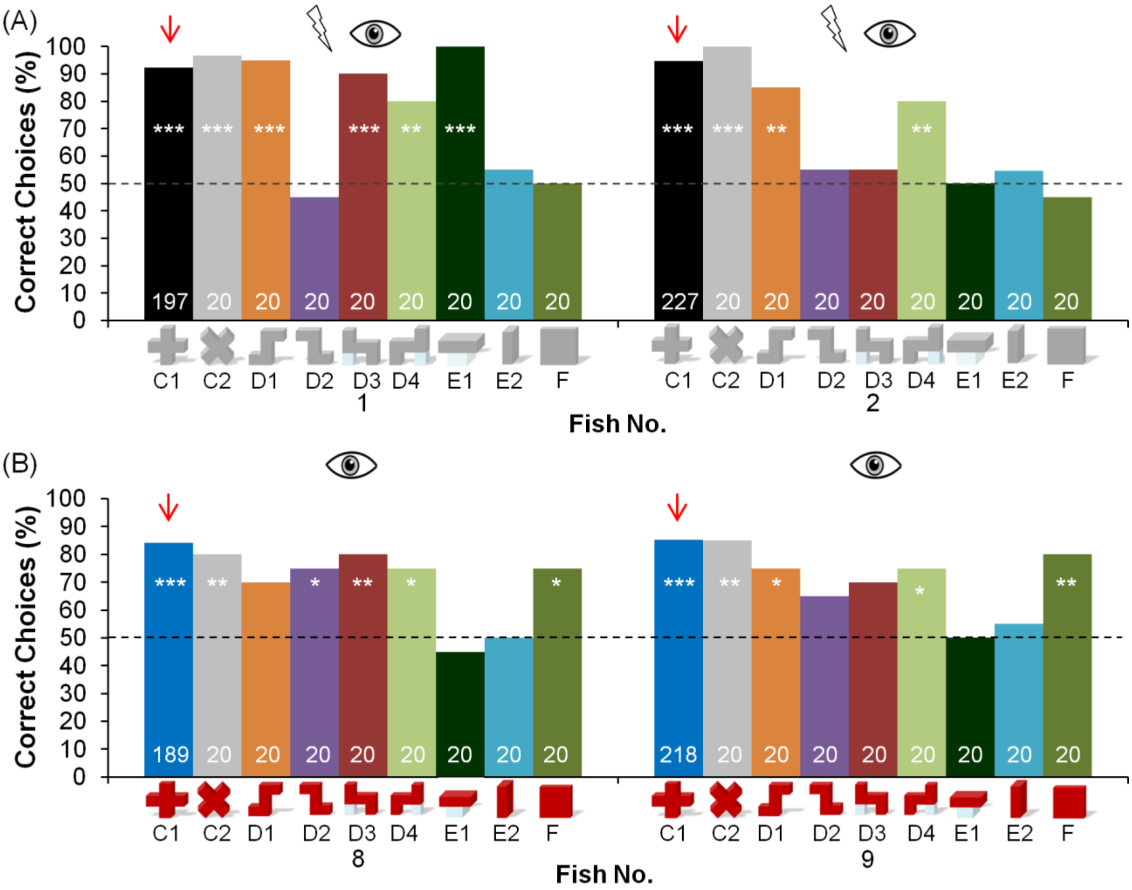

Figure 32: Discrimination performance of two fish trained with both senses (A) and two fish trained only with vision (B) during tests during which the negative object (cross, C1) was exchanged with an unknown object. The performance during training trials is shown as reference indicated by the red arrow above the bar. All objects had the same volume and were made of the same material (aluminium in A, red-coloured electrically transparent agarose in B) as the negative object. Which object was used is shown beneath the bars. For further description see Figure 29.

2.2.4.6. Robustness of performance

To test for how long the fish were able to perform the discrimination task without further training, three fish of the B group and two fish of the V group were tested four weeks after the last training day and thereafter once per week.

All three fish of the B group reached a performance of at least 70% correct choices up to week 17 after the last training (Figure 33 A). The performance of fish 1 and 2 dropped below 70% correct choices after 18/17 weeks. Fish 5 never reached a performance below 75% correct choices and was still able to fulfil the discrimination task after 26 weeks without training. The performance of the two fish of the V group dropped below 70% already after week 10 respectively 9 (Figure 33 B). Thus the fish trained with both senses were able to fulfil the task for nearly twice as long (or longer in case of fish 5) as the fish trained with vision alone. The comparison of the fish trained with both senses and the fish trained only with vision shows that while the performance of the fish of the B group decreased steadily with increasing time without training, the performance of the fish of the V group decreased more rapidly.

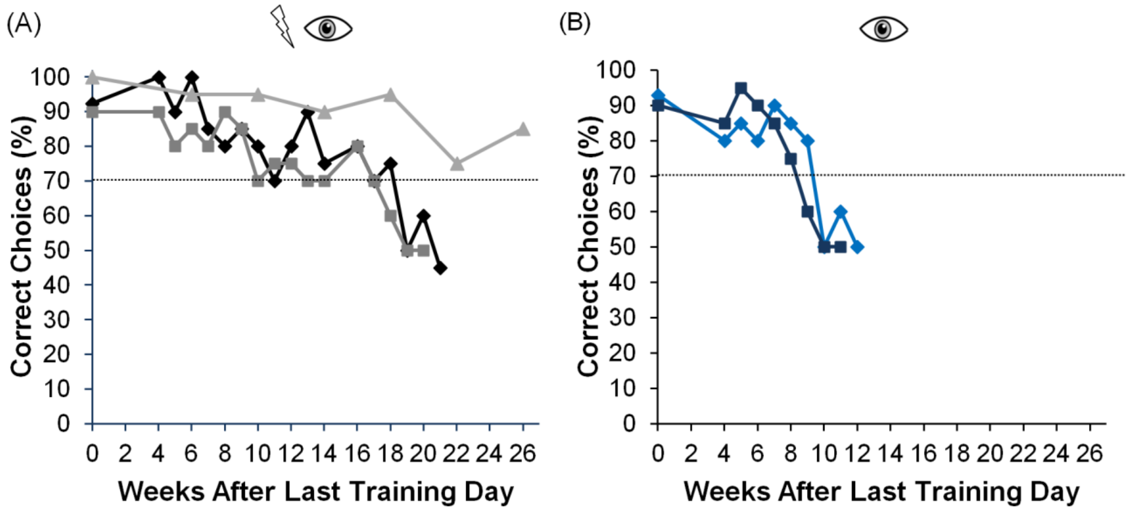

Figure 33: Discrimination performance of three fish (fish 1 (black), fish 2 (grey) and fish 5 (light grey)) trained with both senses (A) and two fish (fish 6 (blue) and fish 7 (dark blue)) trained only with vision (B) during tests of the robustness of performance. Fish 1, 2, 6 and 7 were tested with their trained senses after four weeks without training and thereafter once a week. Fish 5 was tested with after 6 weeks without training and from there on every four weeks. On each test day 20 trials were conducted with each fish. During test every third trial was rewarded, no matter which decision the fish made, and no punishment was applied. If the fish did not reach a performance above 70% correct choices on three consecutive test days, it was assumed that the fish had forgotten the task and tests were stopped. The dotted line indicates the threshold of 70% correct choices.

2.2.4.7. Control tests

To exclude that other cues like electrical or lateral line input influenced the results during the visual tests, a control test was conducted during which the electrically transparent agarose objects were presented in complete darkness. None of the tested fish no matter whether intact or electrically silenced was able to fulfill the discrimination task when vision was unavailable for the discrimination task (Figure 34). The performance of all fish was close to chance level under these conditions, showing that the fish could not use other cues to discriminate between the agarose objects.

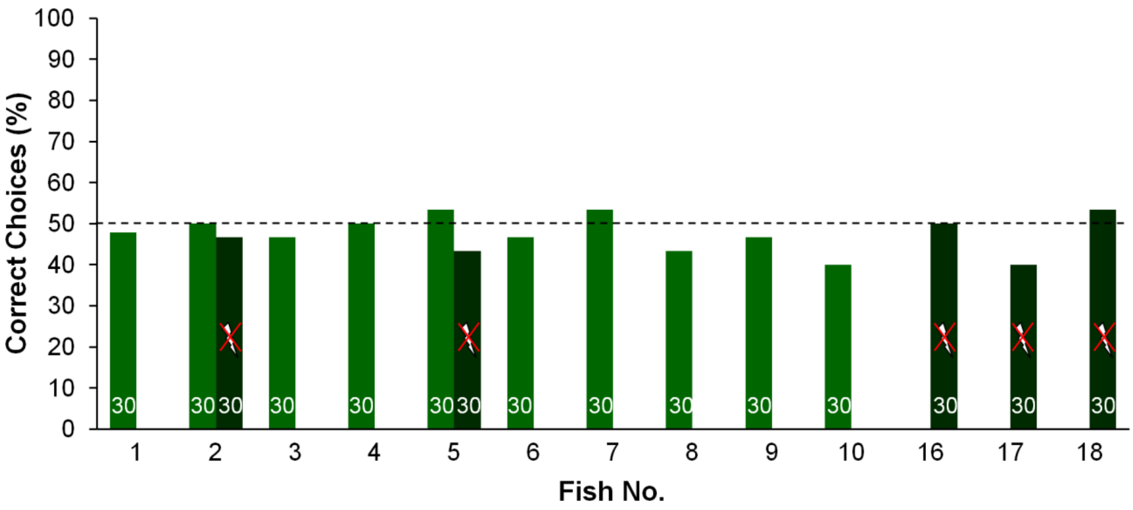

Figure 34: Discrimination performance of the intact fish trained with both senses (fish 1-5), fish 2 and 5 after being electrically silenced, the fish trained only with vision (fish 6-10, data from Schumacher et al. 2016) and the electrically silenced fish trained with vision (fish 16-18) during the dark control. To ensure that no other cues than those that were visual were used to discriminate between the red coloured electrically transparent agarose object, these trials were completed in complete darkness. For further description see Figure 29.

As a second control test a double blind control was conducted with an unknown experimenter, to exclude that the experimenter influenced the discrimination performance. Both tested fish were able to fulfil the task under these conditions, and there was no significant difference in the performance compare to the training with the known experimenter. This showed that the ability of the fish to discriminate between the objects was independent of the experimenter (Figure 35).

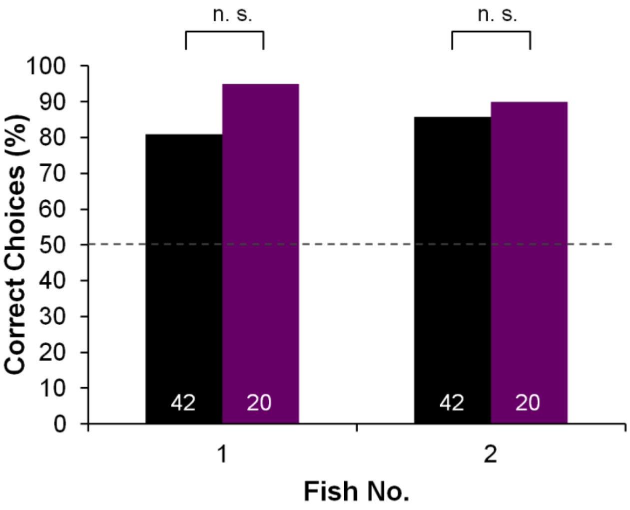

Figure 35: Discrimination performance of two fish trained with both senses (fish 1 and 2) during the double blind control with an unknown experimenter (purple). The experimenter had previous

experience with the experimental procedure but did not know which object was positive and which negative. For comparison the performance with the known experimenter is given (black). An exact Fisher-test was conducted to compare the performances (n.s.: P > 0.05). For further description see Figure 29.

2.2.5. Discussion

The presence of multiple senses allows an animal to obtain a full and flexible representation of the world. Streams of information are acquired through multiple sensory channels and are integrated at the neural level allowing the animal to respond appropriately to environmental challenges. Here, we considered the advantages of multisensing by examining the interaction of vision and the active electric sense in the weakly electric fish *G. petersii*.

2.2.5.1. Electrosensory capture

Our results show that, at short range (1 cm distance of the objects), the active electric sense dominates over vision during an object discrimination task even if the fish were able to learn the task with both senses. In line with visual or acoustic capture in humans, we call this dominance of the active electric sense *electrosensory capture*. While all five fish trained with both senses were able to discriminate the objects electrically during the uni-modal tests at the same level of accuracy as during training with both senses, the uni-modal visual performance of those fish was significantly worse than during training. Three of the five fish were not able to discriminate between the objects at all when using only vision (Figure 29). However, after two of those fish were electrically silenced, they were able to discriminate between the objects when using only vision. This shows that the reason that the intact fish were unable to discriminate during the visual tests (where vision alone was available for object discrimination) was not because of a general inability of the visual system to fulfil the task. Instead, this supports the hypothesis that the limited visual performance was produced by a masking effect caused by the dominance of the electric sense. During the visual test the perceptual conflict between vision (which gave the information that there was an object) and the electric sense (which gave the information that there was no object) was solved in favour of the electric sense. This led to the fish being unable, or less able to discriminate between the objects during these tests. After the fish were electrically silenced, the electric sense did not provide any information about the surrounding environment. Without any electrical input, which might overwrite the visual information, vision could be used to discriminate between the objects.

The uni-modal tests correspond with the results of fish that were trained only with the active electric sense (Schumacher, Burt de Perera, Thenert, et al., 2016). Thus, electrosensory capture is independent of possible training effects, which might have influenced the results of the electrically trained fish. In the fish that were trained only with the active electric sense, the dominance of the electric sense might have been an effect of an overrepresentation of the electrical information during training, i.e., it might have been a training effect (remapping). However this study shows that the dominance of the electric sense remained present under more natural conditions, when the fish could use both senses to acquire and store information about the objects. This is consistent with studies on mammalian species (such as humans, monkeys and rats) that reveal that sensory inputs are weighted, which often leads to a dominance of certain senses during particular situations and tasks (Alais & Burr, 2004; Ernst & Banks, 2002; Fetsch et al., 2009; Sheppard et al., 2013). These results are consistent with studies in South American weakly electric fish (Gymnotidae), which also showed a dominance of the electric sense over vision during refuge-tracking and object discrimination (Dangelmayer, Benda, & Grewe; Sutton, Demir, Stamper, Fortune, & Cowan, 2016).

There are a number of potential functional explanations for the dominance of the electric sense. The active electric sense is well adapted for object discrimination. It provides detailed three-dimensional information about objects within a very short temporal scale (von der Emde et al., 2010), making it a well-suited sense for object detection and discrimination. Properties like the distance or the size of an object can be extracted from only one EOD (von der Emde, 2006; von der Emde et al., 1998). With an EOD frequency of about 30 – 140 Hz (during swimming and object inspection) (Moller, 1980; Schumacher, Burt de Perera, & von der Emde), the temporal resolution of the electric sense exceeds that of the visual sense (Pusch, Kassing, et al., 2013), and the fish are able to analyse their environment effectively even during fast swimming using active electrolocation. Furthermore, the electric sense is not restricted to the presence of light and is therefore available throughout day and night, which is of special importance for a nocturnal animal such as *G. petersii*. The dominance of the active electric sense might also be based upon experience. In a natural environment, it would be extremely unlikely that objects have the same conductivity as the surrounding water. Therefore, it would be unlikely that objects exist that are within the working range of the electric sense but could not be perceived electrically.

The dominance of the electric sense can also be inferred from neuroanatomical observations. A large part of the brain is occupied by areas that process the input from the electric sense (ELL, Torus semicircularis, Valvula, a.o.) while the optic tectum is reduced in comparison to other fish (von der Emde & Ruhl, 2016). These immense structural differences in the brain suggest strongly that the electric sense has a central role during perception of the environment.

2.2.5.1.1. Conflict between senses

The effect of the conflict between vision and the electric sense is shown by the results of the fish that were trained with both senses, and subsequently tested with a large conflict (in comparison to the previous uni-modal visual tests) (Figure 30 A). During the visual tests without plastic screens, the conflict between vision and the electric sense lay in vision providing information about the objects while the electric sense provided the information that no object was present. These bits of information were conflicting but not irreconcilable, because there are natural condition e.g. when an object is far away, during which also only vision provides information about an object. During these tests without plastic screens, the visual information did not appear to be completely discarded and vision therefore still influenced the behaviour. When using the plastic screens, however, the electric sense and vision provided contradictory shape information. The visual sense provided the shape information of the objects and electrolocation provided shape information arising from the plastic screens (rectangular shape). The information of both senses was therefore incompatible (one object cannot have two different shapes, e.g. a cross and a rectangle, at the same time). The results show that under these conditions, all of the intact fish trained with both senses were unable to discriminate between the objects visually. Thus the increased conflict might have led to sensory segregation and a complete discarding of the visual information or at least to a further down rating of the visual information. As before, the ability of the silenced fish to fulfil the same task shows that this effect cannot be explained by a failure of the visual system.

2.2.5.1.2. Remapping

The differences in the training durations show that the dominance of the active electric sense might also influence the training performance. While the fish trained with both senses and with only the active electric sense learned the task in a similar time, the fish trained only with vision needed significantly longer to learn the task (Figure 27). Due to the dominance of the active electric sense, visual information could have been overwritten at the start of training, which would have led to the fish being unable to discriminate between the objects when only visual object information was available. The fish could therefore not learn the task. However, due to the constant repetition of the consistent discrepancy between vision (which gave the information that there was an object) and the active electric sense (which gave the information that there was no object) during training, the system seems to be able to adjust the hierarchy of the senses (which is termed, remapping) (Ernst & Di Luca, 2011). The system could have been trained to rely on the visual information instead of relying on the usually dominant electrical input via the repeated presentation of the visual object information without any electrical object information. After the system was remapped, the visual information could have been used to learn the discrimination task. This hypothesis is supported by the results of the fish of the S group, which were trained under the same conditions as the visually trained fish after being electrically silenced. These fish learned the task significantly faster than the fish of the V group. This shows that *G. petersii* is in principal able to learn the discrimination task visually as fast as electrically and suggests that the significantly longer training duration of the visually trained intact fish might result from the additional time the system needed to be remapped.

This remapping in the visually trained fish does not seem to have been restricted to the particular conflict in information created by the red coloured electrically transparent agarose objects but seems to have led to a more general dominance of the visual sense at short range in these fish. During the tests with an increased conflict, the performance of the visually trained fish did not change compared to training (Figure 30 B). Hence the system did still rely on the visual information although the conflict was different.

The robustness of performance might also be influenced by the remapping of the system. The visually trained fish were unable to fulfil the discrimination task after 9 or 10 weeks without further training. In contrast, the fish trained with both senses were able to do so nearly twice as long or even longer (Figure 33). This could either be explained through differences in the storage of the information or through a re-remapping of the system in the visually trained fish. Without further visual training, the everyday experience of the electric sense being more reliable at short range might have re-remapped the system so that visual discrimination at close range might have been masked again by the regained dominance of the electric sense. This hypothesis is supported by the abruptness by which the visually trained fish suddenly became unable to discriminate between the objects. Once the system was re-remapped, the fish would have been unable to fulfil the task without a constant decrease of performance. However, further experiments are necessary to test this hypothesis.

The ability to remap the weighting of the sensory inputs increases the flexibility of a multisensory system and emphasises the importance of the influence of prior experience on the weighting of sensory inputs. It allows the animal to adjust to new conditions and maintain multisensory integration at an optimal level in a variable environment.

2.2.5.2. Multisensing: Redundancy, synergy and complementation

In addition to electrosensory capture and the flexibility within a multisensory system provided by remapping, this study shows that *G. petersii* exploits the advantages of possessing two sensory systems that can be used to solve similar tasks. We have shown that the fish are able to use the active electric sense and vision redundantly (one sense can be used as a backup for the other), synergistically (performance can be improved through multisensory integration) and complementarily (senses are tuned to particular tasks).

While the electric sense dominates during close-range object discrimination, vision can be used as a backup and is sufficient to fulfil the task alone, if the active electric sense is inoperable as was the case in the electrically silenced fish (Figure 27, Figure 28, Figure 29). This redundancy has a clear adaptive value, for example if the electric organ is damaged. With its location in the caudal peduncle damages to the electric organ are possible without being lethal, and therefore the ability to use vision as a backup is highly beneficial.

The comparison of the accuracy of the discrimination performance of the four training groups suggests that there is a synergetic effect between vision and the active electric sense, since the fish trained with both senses available reached a higher discrimination accuracy than the other groups (Figure 28). As the level of discrimination was already highly accurate when only single senses were available, this synergetic effect is rather small. However, under conditions where the discrimination performance with the single senses is near threshold level, this synergetic effect might be more important. In this way, multisensory integration would enable the fish to recognise environmental objects under suboptimal conditions and would therefore enable the fish to operate successfully under a broad spectrum of environmental settings. These results align with earlier studies that show synergetic effects during foraging and shelter seeking in *G. petersii* (Rojas & Moller, 2002; G von der Emde & H Bleckmann, 1998).

The results of the feature detection tests suggest that vision and the electric sense can also complement one another in some situations. While the fish that could use the electric sense for the discrimination task seemed to have used specific features of the objects for recognition of the negative object, the visually tested fish recognised the objects as negative as long as the general outer dimensions matched those of the known negative object (Figure 32). These results correspond with the visual template matching described by Schuster and Amtsfeld (Schuster & Amtsfeld, 2002) and the electrical feature detection described by von der Emde and Fetz(von der Emde & Fetz, 2007). This suggests that in intact fish, the visual sense is probably not used for recognition of fine scale object information because of the low spatial resolution of the visual system (Pusch, Wagner, et al., 2013). Instead, acquisition of fine scale information is better provided by the active electric sense. However, due to its small working range(von der Emde et al., 2010) electrical fine scale inspection of the environment is restricted to an area within the close vicinity of the fish. Thus, the visual sense might be used instead, to perceive an overview of the surroundings. This would enable the electrical information to be placed within a spatial context and would allow the fish to locate possible predators from afar. With this specific task division of vision and the active electric sense, *G. petersii* is able to use the advantages of both far and close ranging senses optimally.

2.2.5.3. Conclusion

Together our results show that there is electrosensory capture during object discrimination at short range in *Gnathonemus petersii*. Even if the fish are able to use both senses to acquire and learn information about an object, the electric sense dominates over vision under conditions, during which both senses provide conflicting information. Nevertheless, by using both senses redundantly and complementarily and by integrating information from the senses synergistically, these fish exploit the advantages of possessing two senses, which provide similar information about the environment on different spatial scales.

2.3. Morphology of the peripheral mechanosensory lateral line system of the weakly electric fish *Gnathonemus petersii*

2.3. Morphology of the peripheral mechanosensory lateral line system of the weakly electric fish *Gnathonemus petersii*

2.3.1. Abstract

The mechanosensory lateral line system of teleost fish, consists of superficial neuromasts (SNs) and canal neuromasts (CNs) within a subepidermal canal system and it mediates the perception of water movements. The number and distribution of SNs as well as the structure of the canal system varies greatly between species. Weakly electric fish, like *Gnathonemus petersii*, additionally possess an electrosensory lateral line system, consisting of three different types of electroreceptor organs. While the electrosensory system is well studied, little is known about the morphology of the peripheral mechanosensory system of these fish. Here we investigated the distribution and morphology of the SNs and the structure of the head canal system of *G. petersii* using DASPEI staining, a preparation of the canal system, and micro computed tomography (µCT) scans. We found that these fish possess only a limited number of SNs and that their morphology is reduced, consisting only of 1 - 6 hair cells. The results of the µCT scans show that while the head canal system of *G. petersii* consists of seven cranial canals, which is typical for teleosts, these canals are reduced to open canals or simply a groove-like structure. Together, our results show a reduction of the complete peripheral mechanosensory lateral line system, which suggests a restricted function, perhaps as a result of the presence of the electrosensory system.

2.3.2. Introduction

Fish and amphibians are able to perceive water movements and pressure changes using the mechanosensory lateral line system (Bleckmann & Zelick, 2009; Coombs et al., 2014; Dijkgraaf, 1963). The functional unit of the lateral line system is the neuromast, which consist of several hair cells covered by a single gelatinous cupula. The cilliary bundles of the hair cells, consisting of a single long kinocilium and several shorter stereovilli, project into the cupula. A deflection of the cupula, induced by movement of the surrounding medium, leads to a deflection of the cillary bundle, which results in a response of the hair cells (Flock, 1967; Van Trump & McHenry, 2008). The hair cells of the neuromasts are secondary receptor cells and are synaptically innervated by the anterior (all neuromasts at the head) or posterior (all neuromasts at the trunk) lateral line nerve (Bleckmann & Mogdans, 2014; McCormick, 1989; Northcutt, 1989).

In teleost fish the neuromasts are either located at the body surface in direct contact to the surrounding water (superficial neuromasts, SNs) or they are located within a subepidermal fluid-filled canal (canal neuromasts, CNs). These canals are connected to the surrounding water via a series of pores, whereby usually one neuromast is located in between two pores. The CNs respond to movements of the canal fluid induced by pressure gradients between two pores and thus respond indirectly to external stimuli. Most fish possess a canal at the trunk, building the eponymous visible lateral line, and a canal system at the head (cranial canal system) (Coombs et al., 1988; Webb, 1989). The development of the canals starts with a presumptive canal neuromast at the surface. In later stages of development a bony groove is built around the presumptive CN, which is later enclosed by soft tissue walls, building an epithelial canal. In the last stage of canal development the bony walls fuse together building a complete canal (Webb & Shirey, 2003).

The number and distribution of superficial neuromasts as well as the structure and complexity of the head canal system varies greatly between species, which might be an adaptation to the environmental conditions (Coombs et al., 1992; Coombs et al., 1988; Webb, 2013). Most fish living in still waters, such as lakes, possess relatively high numbers of superficial neuromasts with a reduced canal system, while fish living in fast running rivers tended to show a reduction of the superficial neuromasts with a more complex canal system (Bassett, Carton, & Montgomery, 2006; Bleckmann & Münz, 1990; Engelmann, Hanke, & Bleckmann, 2002; Engelmann, Kröther, Bleckmann, & Mogdans, 2003; Merriless & Crossman, 1973a, 1973b).

In addition to this mechanosensory lateral line system, some fish possess an electrosensory lateral line system. The electroreceptor organs of this system probably derives from the mechanosensory neuromasts and it mediates passive electroreception. In combination with an electric organ it also enables active electrolocation in two groups of teleost fish (mormyriformes and gymnotiformes) (Baker et al., 2013).

The mormyrid weakly electric fish *Gnathonemus petersii* lives in turbid fast running rivers in Central and West Africa and uses active electrolocation for orientation and communication with conspecifics (Lissmann & Machin, 1958; Moller & Bauer, 1973; Moritz, 2010; von der Emde, 2006). To do so, these fish produce weakly electric pulses with their electric organ located in the caudal peduncle and perceive object evoked changes in the resulting electrical field (Lissmann & Machin, 1958; von der Emde, 1990). Like all members of the mormyriformes, *G. petersii* possesses three different types of epidermal electroreceptor organs, which are distributed over the whole surface of the head and at the dorsal and ventral parts of the trunk, leaving only an area of ca. 2 cm around the visible lateral line without electroreceptor organs (Hollmann et al., 2008; Jorgensen, 2005). Like the mechanosensory neuromasts, the electroreceptor organs are innervated by the anterior or posterior lateral line nerve. However, the electrosensory fibres terminate in a specific brain area called the electrosensory lateral line lobe (ELL) (Bell & Maler, 2005).

While some studies have shown that the mechanosensory lateral line system of *G. petersii* is involved in foraging and shelter seeking (Rojas & Moller, 2002; Gerhard von der Emde & Horst Bleckmann, 1998), no involvement of the lateral line system was found during object recognition in these fish (Schumacher, Burt de Perera, Thenert, et al., 2016; Schumacher, Burt de Perera, & von der Emde, 2017). This raises the question to which extent *G. petersii* is able to perceive information using the lateral line system and how the peripheral lateral line system of these fish is constituted.

To investigate the morphological structure of the peripheral lateral line system of *G. petersii*, we used the fluorescent dye DASPEI to stain the superficial neuromasts and a preparation of the head canal system as well as micro computed tomography (µCT) to find out whether there is a head canal system and if so, how it is structured.

2.3.3. Methods

Six individuals of the species *Gnathonemus petersii* with a standard length of 9.5 - 12 cm were used for the DASPEI staining. Two of those fish with a standard length of 9.5 and 12 cm were subsequently used for the preparation of the head canal system and another one with a standard length of 10 cm for the µCT scans. A seventh individual with a standard length of 15,5 cm was additionally used for the preparation. The fish were wild caught in Africa and bought in a local store, therefore sex and age were unknown. All fish were kept individually at least four weeks prior to the staining to ensure that the superficial neuromasts were not damaged by fights between fish and that there was enough time for neuromast regeneration (Hernández et al., 2007). Four of the six fish were previously used during behavioural experiments and kept individually for ca. two years.

2.3.3.1. Distribution and morphology of superficial neuromasts

To investigate the number and distribution of superficial neuromasts, fish were incubated in a 0.1 mmol/l solution of 2-[4-dimethylaminostyryl]-N-ethylpyridinium iodide (DASPEI; Sigma-Aldrich, Taufkirchen, Germany) for 30 min with constant oxygen supply. Subsequently, the fish were euthanized with an overdose of 200mg/l MS 222 (Tricaine-methansulfonat, Acros Organics, Geel, Belgium). The fish were then examined using a fluorescence microscope (blue spectrum 460-480 nm; Leica Leitz, DRBE) and the location of superficial neuromasts was recorded. After the examination the fish were preserved in a 70% ethanol solution or in a 4% paraformaldehyde solution.Structure of the head canal system.

2.3.3.2. Structure of the head canal system

The structure of the head canal system in *G. petersii* was investigated via a preparation and using µCT scans. For the preparation two ethanol preserved fish from the DASPEI staining were used. The head canal system was prepared starting at the position where the visible lateral line ends at the skull, following the course of the canals. A third fish was euthanized with an overdose of 200mg/l MS 222 and the head canal system was prepared in the freshly killed fish. A 0.1 % solution of methylene blue was injected in the canal at the last pore of the trunk canal and at the postotic canal.

For the µCT scans the fish was fixated in paraformaldehyde for three days and subsequently transferred to a 70% ethanol solution using an ascending ethanol series starting with 10%. For the scans the fish was fixed in a plastic tube. The scans were conducted at the Steinmann Institute of the University of Bonn (phoenix v|tome|x s 180/240). The resulting data was analysed and visualised using the programs phoenix datos|x and VGStudio MAX (Volume Graphics).

2.3.4. Results

2.3.4.1. Distribution and morphology of superficial neuromasts

The DASPEI staining showed that *G. petersii* possess only a very limited number of superficial neuromasts. In all six examined fish SNs were found singly or in pairs along the visible lateral line canal at the trunk (Figure36 A, red dots). Pairs (Figure 36 B) were mainly found at the caudal peduncle. In some individuals, additional pairs were found in a more rostral location, the position slightly varying between individuals (blue dots). In four of the six examined individuals three to four SNs were found at the base of the dorsal fin and six to eight SNs were found at the base of the anal fin. A cluster of four SNs was found at the operculum in four of the six fish and a single neuromast was found at the same place in a fifth individual. In three individuals a row of three SNs was found above the eye. The total number of SNs varied between 28 and 48.

The morphological analyses showed that the SNs of *G. petersii* are relatively small. Most SNs possessed only four or two hair cells (Figure 36 B-D) and while there were a few neuromasts with six hair cells in the tail region there were also some with only a single hair cell especially at the base of the dorsal and anal fin. Consequently the neuromasts were only 20 µm or less in size.

2.3.4.2. Structure of the head canal system

The preparation of the head canal system as well as the µCT scans of the skull show that the head canal system of *G. petersii* is similar to the typical teleost lateral line system with seven cranial canals (Figure 37, Figure 38 and Figure 39): infraorbital (IO; black), supraorbital (SO; white), preopercular (PR; blue), mandibular (MD; yellow), otic (OT; red), postotic (PO; dark red) and supratemporal (ST; violet). However, in contrast to most other teleost fish there is no connection between the OT canal and the SO canal, which is clearly visible in the µCT scans (Figure 39 A) and was also found in the preparation. The transverse section through the scans of the rostral end of the OT canal shows that here its bony structure was incomplete and rather resembled a groove (Figure 39 B, upper magnification). This was again confirmed by the preparation.

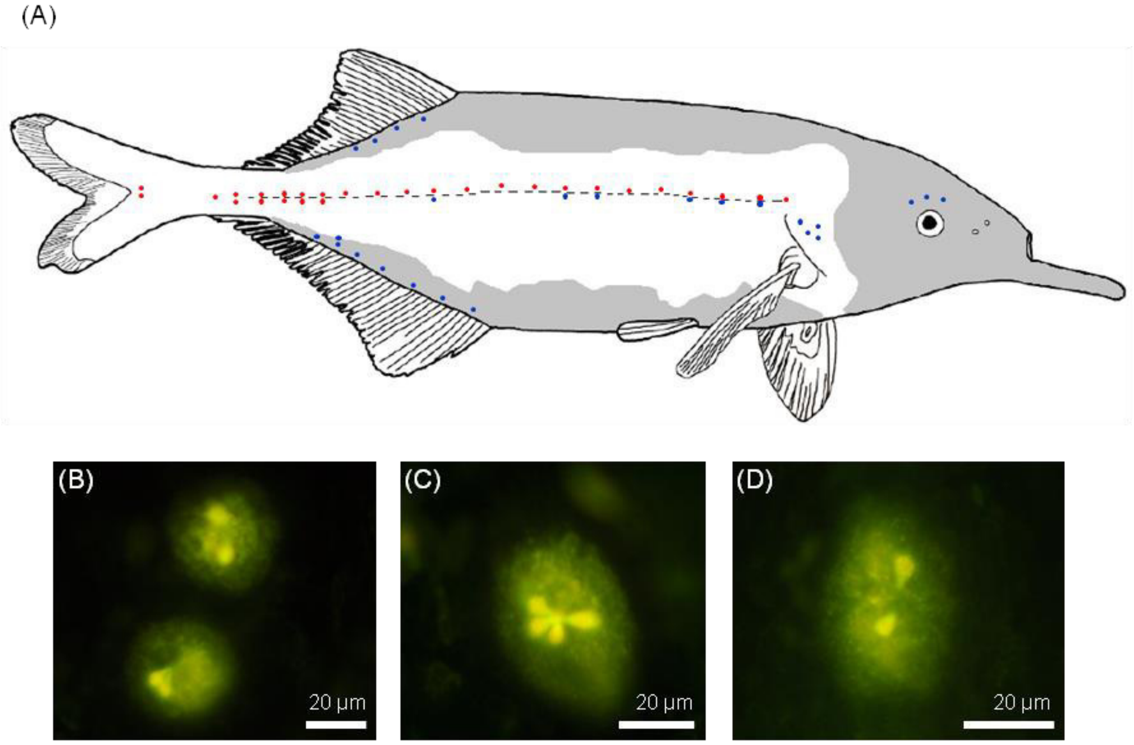

Figure 36: Distribution and morphology of superficial neuromasts. (A) In all six examined fish superficial neuromasts were found along the visible lateral line (indicated by the dashed line) in double rows (example shown in B) or singly (examples in C and D) (red dots). In some individual superficial neuromasts were additionally found above the eye, at the operculum and at the root of the dorsal and anal fin (blue dots). In grey indicated is the area where electroreceptor organs were found by Hollmann et al (Hollmann et al., 2008). (B-D) The found neuromasts were relatively small (ca. 20-25 µm) and consisted of only six to one hair cells (most often four (C) or two (D)).

Furthermore, the µCT scans show that the PR and MD canal possess a few small branches and the section through the scan shows that these canals have a tube-like structure with a narrow vent, which probably connects the canal with the skin (Figure 39 B, lower magnification). Without any contrast in the nearly clear structure of the canal and due to the limited magnification of a binocular, the vent was not clearly visible in the preparation (Figure 37 E).

The scans also suggest that the structure of most parts of the SO and IO canals vary between both structures described above. However, caudal to the eye the canal seems to be completely closed and the preparation suggests that there is at least one, probably two pores in this part of the canal. Apart from those, pores were only found in the trunk canal (Figure 37 D).

The injection with methylene blue was not successful. The dye spread only in the very near field of the injection side. However, clearly visible through the staining is a branched system at the transition from the trunk to the head canal system (Figure 38 C).

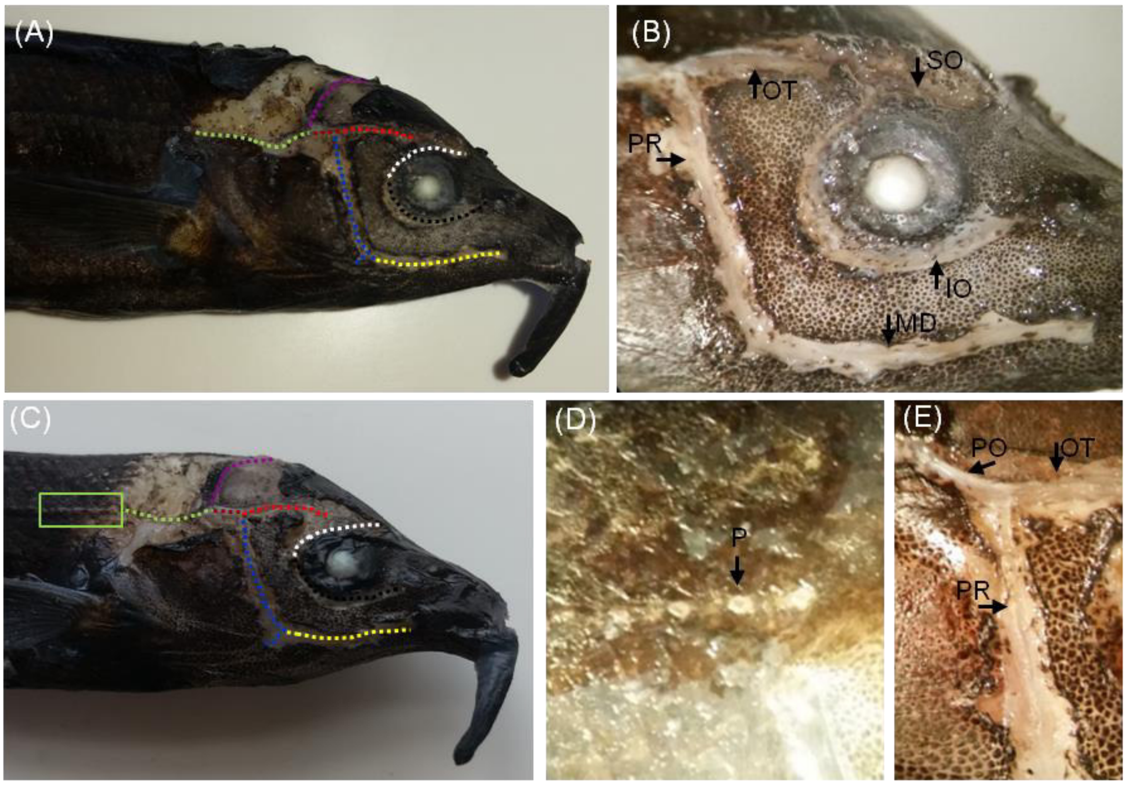

Figure 37: Preparation of the lateral line head canal system in two individuals of *G. petersii* (A+B and C-D). The preparation was started at the junction of the trunk canal with the head canal system. (A and C) *G. petersii* possess a more or less typical teleost head canal system with seven different canal, which are indicated colour-coded by the dotted lines: supratemporal (ST; violet), postotic (PO; dark red), otic (OT; red), supraorbital (SO; white), infraorbital (IO; black), preopercular (PR; blue) and the mandibular (MD; yellow) canals at the head (indicated by the dotted lines). Indicated in green is the trunk canal system. B shows a magnification of A. D and E are magnifications of C, D showing the canal pores of the trunk canal (exposed by removal of the covering scales), E showing the PR and parts of the PO and OT.

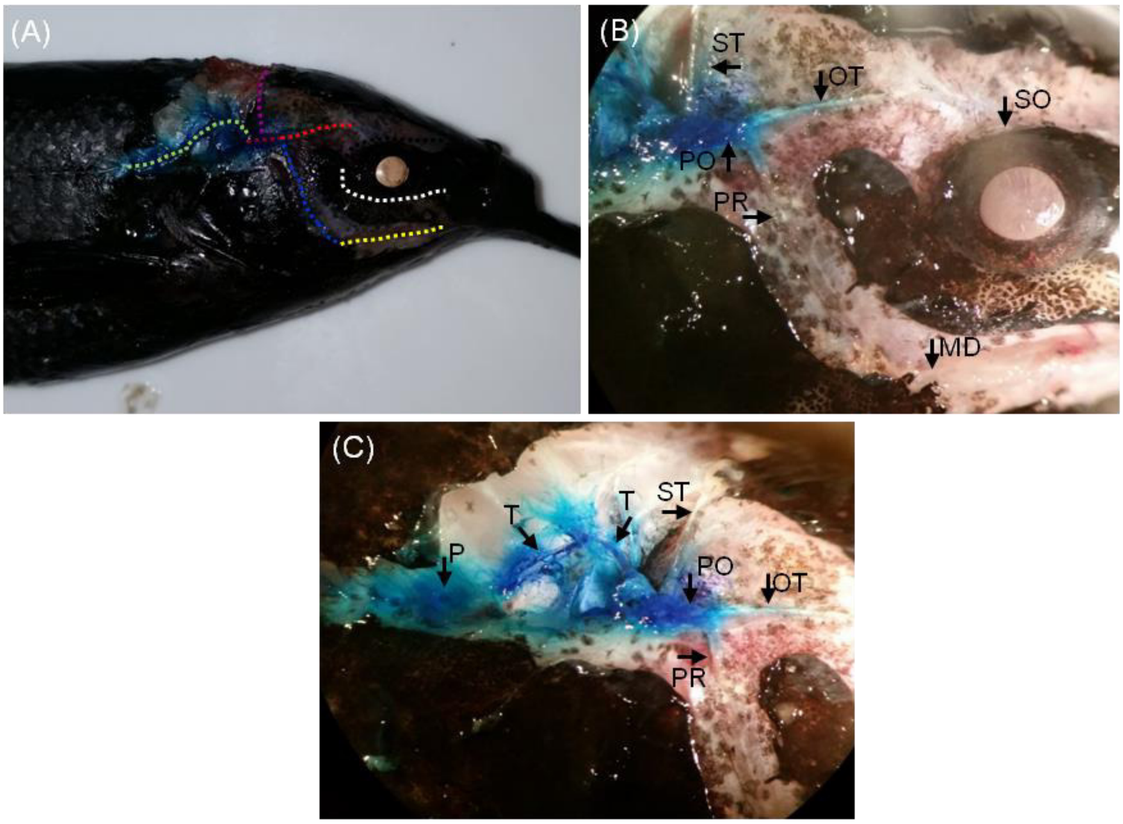

Figure 38: Preparation of the lateral line head canal system of *G. petersii* injected with methylene blue. The methylene blue dye spread only in the range of a few millimetres around the injection side. (A) Overview of the lateral line canal system (for description of the coloures see Figure 37). (B) Magnification of the head canal system. (C) Magnification of the transition from the trunk to the head canal system (for description of the abbreviations see Figure 37)

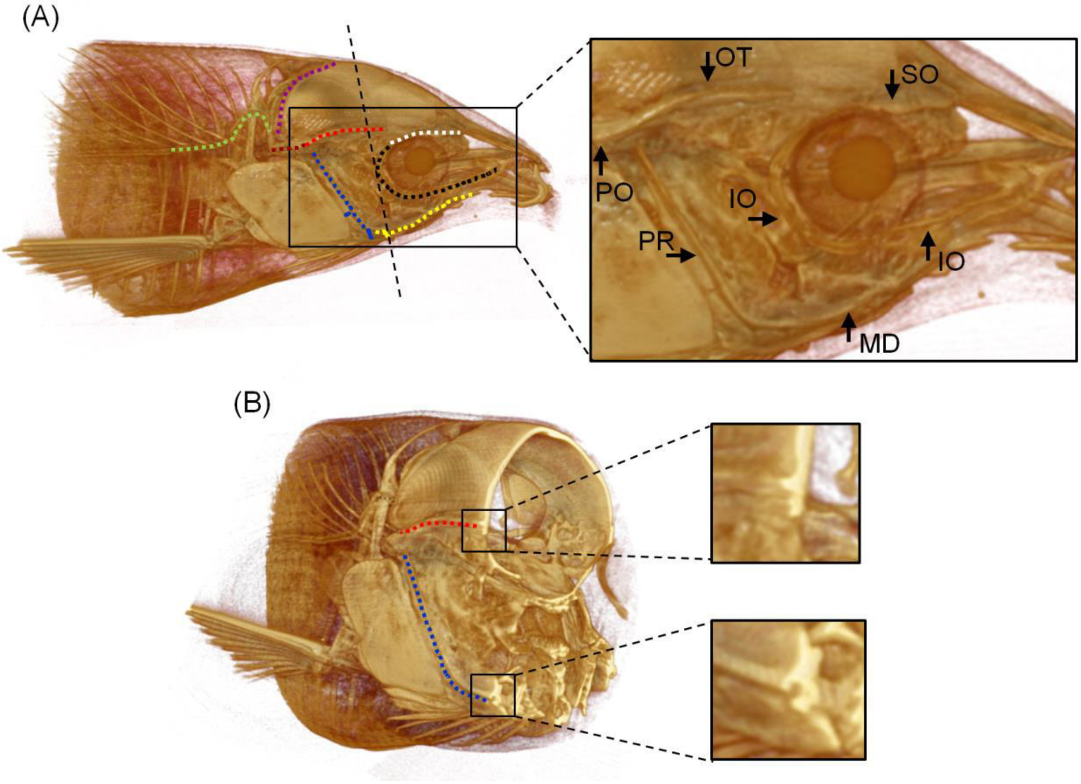

Figure 39: Micro computed tomographic scans of the skull of *G.petersii.* (A) Lateral view: Visible are the same canals also found in the preparation: supratemporal (violet, ST), postotic (dark red, PO), otic (red, OT) supraorbital (SO, white), infraorbital (IO, black), preopercular (PR, blue) and the mandibular (MD, yellow) canals at the head (indicated by the dotted lines). Indicated in green is the trunk canal. The magnification shows the canals without indication. (B) Transverse section through the skull just posterior of the eye (position indicated by the dashed line in A). The magnifications show the sections through the rostral end of the otic canal (upper) and through the propercular/mandibular canal (lower). While there is a clear canal structure in the mandibular canal the otic canal is quite reduced.

2.3.5. Discussion

Gnathonemus petersii is known for its ability to use active electrolocation and consequently its electrosensory system has been studied intensively. However, little is known about the mechanosensory lateral line system of these fish. Here we investigated the morphological structure of the peripheral mechanosensory system by examining the distribution and morphology of superficial neuromasts and we determined the structure of the head canal system.

2.3.5.1. Distribution and morphology of superficial neuromasts

The results of the DASPEI staining show that *G. petersii* possesses only very few superficial neuromasts, which are both reduced in size and in the number of hair cells (Figure 36). The maximum number of SNs found was 48. For comparison the goldfish (*Carassius auratus*) possesses 1800-2000 SNs and the minnow (*Phoxinus phoxinus),* a cyprinid fish living in fast running European rivers, possesses ca. 900 SNs (Schmitz, Bleckmann, & Mogdans, 2008; Schmitz et al., 2014). The small number of SNs is consistent with findings in gymnotiform weakly electric fish and is also similar to the cichlid fish *Astatotilapia burtoni*, which lives in a comparable habitat as *G. petersii* (African tropical rivers and lakes) (Butler & Maruska, 2015; Szabo, 1965; Vischer, 1989). While in contrast to *G. petersii*, *A. burtoni* possesses a higher number of SNs in the head region, the distribution of the SNs around the trunk canal in pairs or singly is similar to the one we found in *G. petersii*. The even smaller number of SNs found e.g. in the gymnotiform fish Hypopomus were also arranged in a longitudinal line but in contrast to *G. petersii,* this line is located at the dorsal part of the trunk.

The small number of SNs mainly located in a longitudinal line in *G. petersii* might be an adaptation to its habitat (fast running rivers), which might explain the similarities in SN distribution to the not closely related *A. burtoni* and gymnitiform fish living in similar habitats. The permanent strong currents of such rivers provide a very noisy environment and therefore probably reduce the efficiency of SNs (Engelmann et al., 2002; Engelmann et al., 2003). Another explanation for the small number of SNs, especially at the head, might be the presence of a very high number of electroreceptor organs, mediating active and passive electrolocation (Hollmann et al., 2008). The head possesses only a limited area of skin surface and, like all mormyrid fish, *G. petersii* possesses three different types of electroreceptor organs, which compete with the SNs for that area. This might have led to a reduction of SNs in favour of the more important electroreceptor organs. This would explain why SNs are mainly found in regions where no (visible lateral line and operculum) or only a limited number (base of dorsal and anal fin) of electroreceptor organs are located (Figure 36 A).

In addition to the restricted surface area, another aspect of electrolocation might affect the mechanosensory lateral line system. The area, where electroreceptor organs are located, is covered with a mucus layer, which is thickest at the head (Figure 40) (Szabo, 1965). This thick slimy layer at the head would prevent direct contact of the SNs with the surrounding water and thus probably influence their response properties.

The individual differences in SN numbers between the six examined fish might be explained by differences in examination time rather than morphological differences. In the first two examined fish only the neuromasts along the lateral line were found. During these two examinations it took considerable time to find and photograph the stained neuromasts because the staining was relatively weak and could only be seen in high magnification (the examination was started at the tail lateral line). The DASPEI staining lasts only for 30 - 60 min, therefore it is well possible that the staining in neuromasts at other body parts was already faded out before they were found in these first attempts.

Besides the reduction of the number of SNs we also found a reduction in size and number of hair cells (Figure 36 B-D). The SNs possessed only two to six hair cells and in some cases even only a single hair cell. In comparison, the number of hair cells in goldfish and minnows varies between ca. 14 and 38 and in the blind cave fish (*Astyanax mexicanus)*, a lateral line specialist, a single neuromast can possess up a hundred hair cells (Schmitz et al., 2008, 2014; Teyke, 1990; Yoshizawa, Gorički, Soares, & Jeffery, 2010).

This reduction of hair cells probably drastically affects the sensitivity of the SNs. Hair cells of neuromasts are usually arranged in pairs with opposite directionality to increase the response of the neuromast (Rouse & Pickles, 1991a). A single hair cell is therefore much less sensitive. Furthermore individual hair cell pairs within a neuromast usually slightly vary in the direction of maximum response allowing a more accurate perception of the direction of water movement (Song & Northcutt, 1991). With only up to three pairs of hair cells the sensitivity of direction perception is probably also reduced.

Figure 40: Mucus layer covering the area where electroreceptor organs are located in an ethanol fixated *G. petersii*. In living fish this mucus layer is clear and slimy and covers all areas where electroreceptor organs are located (A, for comparison see Figure 36 or (Hollmann et al., 2008)). In the fixated fish the mucus becomes milky and forms a more solid layer, which can be removed (B).

2.3.5.2. Structure of the head canal system

Our results show that in general, the structure of the head canal system of *G. petersii* corresponds with the typical teleost cranial system, consisting of seven canals (Northcutt, 1989; Webb, 1989, 2013). However, in comparison to this typical teleost canal system, the canals are reduced (Figure 37, Figure 38 and Figure 39). The connection between the OT and SO canal is missing and the µCT scans show that the rostral end of the OT is reduced to a groove-like structure, like it is usually found during canal development (Webb & Shirey, 2003). Furthermore, the position of the superficial neuromasts above the eye found during the DASPEI staining correlates with the position where the connection between OT and SO is missing. This might suggest that these found neuromasts are not primary SNs but replacement neuromasts (presumptive CNs remaining on the surface due to reduction of the canal) (Webb, 2013). This would suggest that there is a complete loss of SNs at the head in *G. petersii*. As described above this loss might be a result of the competition with the electrosensory system.

Except for a small part of the IO canal caudal to the eye, the cranial canals are also reduced as they are not completely closed, which also explains the absence of pores. The reduction of the cranial canals might indicate that in *G. petersii,* canal development stops at an earlier incomplete stage (epithelial canal), suggesting an ongoing evolutionary reduction of the mechanosensory lateral line system in these fish. However, since the fish that was used for the µCT scans was relatively small (10 cm; fully grown fish can reach a size over 20 cm), canal development might have been not completed yet in this fish (note, however, that the fish was more than two years old) and a detailed examination of the canal structure was not possible in the preparation. It is be possible that the bony canal would have closed over in time. However, in the preparation of the 15.5 cm long fish no additional pores were found in the head canal system and no obvious differences were found in comparison to the smaller fish, pointing against an ongoing development of the canal system with further growth in adult fish. To ensure that there are no structural differences in the cranial canal system between small and large fish and thus the canal structure remains on an early developmental stage independent of size, further µCT scans with larger fish are necessary.

Like for the SNs the reduction of the cranial system might be induced by the presence of the electrosensory system and the thick mucus layer covering the head. Even if pores were present, the mucus layer would prevent direct contact with the surrounding water, which would probably result in a drastically decrease of the sensitivity of the canal system. This impaired function might have led to the reduction of the head canal system.

The open structure of the canal and the absence of pores has further implications for the function of the canal system. CNs usually detect fluid movements in the canal induced by pressure gradients between two pores. Without pores, and in an open canal, the transduction of pressure changes is much more difficult, which probably results in a considerable decrease of sensibility of CNs. This is supported by the unsuccessful injection of methylene blue into the canal (Figure 38). In studies with other species an injection of methylene blue into cranial pores resulted in blue staining of the whole canal system (Butler & Maruska, 2015; Maruska & Tricas, 1998; Vischer, 1990). In our experiments the blue stain only spread in the trunk canal and its transition to the head canal system, when injected in the last pore of the trunk canal. Also when injected in the postotic canal the dye spread only in the range of a few millimetres in parts of the preopercular, otic and supratemporal canal, which were seemingly completely closed. The open structure of most parts of the canal might have prevented further transport of the stain, possibly due to missing capillary forces. This indicates strong effects of the open structure on fluid movements in the canal. However, additional investigations on the morphology and number of CNs in the cranial canals as well as in the trunk canal are necessary to draw more detailed conclusions about the function of the canal system.

2.3.6. Conclusion

Our examinations show that the whole peripheral mechanosensory lateral line system (superficial neuromasts and canal system) of *G. petersii* is reduced in comparison to most other teleost fish. This probably has serious implications for the function of this system. While some studies have shown that the lateral line system is involved in some behavioural tasks (Rojas & Moller, 2002; Gerhard von der Emde & Horst Bleckmann, 1998), the sensory limits and the behavioural importance of this sense are still unknown. Nevertheless, some predictions can be made based on the morphological structure of the system:

The arrangement of the SNs in a longitudinal line together with the trunk canal system probably allows the perception of flow velocity, despite the reduction of hair cells within the neuromasts. This would for example allow the fish to use rheotaxis during navigation in the environment. The small number of SNs and their small number of hair cells probably reduce the sensitivity of the system especially in respect to directional information and within the noisy natural environment of the fish. The open structure of the cranial canals probably allows only a restricted function of the head canal system.

From an adaptational point of view, the reduction of the lateral line system of *G. petersii* might be influenced by the habitat, e.g. the arrangement of the SNs in a longitudinal line, but is probably mostly driven by the takeover of the electrosensory lateral line system, which provides more detailed information about the environment and thus might have superseded the mechanosensory system during many tasks like during social interactions and foraging. In contrast to other senses, such as the visual system, the mechanosensory and the electrosensory system are in direct competition in relation to their positioning on the body surface and they also compete in terms of their central capacities. The competition of two sensory systems, which are used for similar tasks, consequently leads to the reduction of the less efficient system, in this case the mechanosensory lateral line.

While the anatomical competition between the electrosensory and mechanosensory lateral line system might have led to a reduction of the mechanosensory system, the available inputs of both systems might functionally interact. Neuroanatomical studies show that mechanosensory input from the lateral line system is processed in multisensory brain areas like the torus semicircularis or the pallium (Bell & Maler, 2005; Prechtl et al., 1998; von der Emde & Prechtl, 1999). This strongly suggests that lateral line information is integrated with electrical and also visual information and thus synergistically contributes to the multisensory system of *G. petersii.*

3. Navigation

3.1 Sensory influence on navigation in the weakly electric fish Gnathonemus petersii

3. Navigation

3.1. Sensory influence on navigation in the weakly electric fish *Gnathonemus petersii*

3.1.1. Abstract

Most animals possess multiple sensory systems, which can be used during navigation. Different senses obtain environmental information on different spatial scales and thus provide a different basis for efficient navigation. Here we used the weakly electric fish *Gnathonemus petersii* to investigate how different sensory inputs influence the navigational strategy and whether landmark information can be transferred flexibly between two sensory systems. Fish were trained to swim through a maze using a particular route indicated by either visual landmarks, electrical landmarks or without any landmarks. In subsequent tests, egocentric (internal cues, such as motion patterns) and allocentric cues (external cues like landmarks) were put in conflict by relocating the local landmarks. We found that all fish, independent of the available sensory input, chose the egocentric over the allocentric route. However, visual landmarks significantly improved the training duration compared to the other groups, suggesting an involvement of allocentric visual cues during route acquisition. In a second experimental series, fish were trained to use either visual or electrical landmarks for navigation and were subsequently tested in sensory transfer tests. Fish trained with visual landmarks were able to learn this allocentric navigation task and were capable of cross-modal landmark recognition, although navigation based on electrical landmarks was less efficient. The fish trained with electrical landmarks did not learn the task at all, suggesting that the short perceptual range of the electric sense prevented learning of allocentric navigation. Together our results show that the type of sensory input influences the efficiency of allocentric navigation in *G. petersii* and that these fish are able to use egocentric and allocentric strategies flexibly to navigate successfully under varying environmental conditions.

3.1.2. Introduction

The ability to navigate successfully is vital for most actively moving organisms and is therefore widely spread amongst animals. A range of different navigation strategies are known that allow animals to return to food sources, mating sites or refuges across different spatial scales (Able, 1980; Benhamou, Sauvé, & Bovet, 1990; Bingman & Cheng, 2005; T. S. Collett & Rees, 1997; Etienne, Maurer, et al., 1998; Etienne, Maurer, & Séguinot, 1996; Rüdiger Wehner, 1998; Rüdiger Wehner, Michel, & Antonsen, 1996). While navigation is well studied in many species, little is known about how sensory input shapes the strategy that animals use, and how information can be used flexibly by different senses to navigate through their environment. Here we investigate these questions by using the weakly electric fish *Gnathonemus petersii*.

In order to navigate through space, animals must perceive information about their surroundings using sensory systems. Among other factors, the sensory equipment and the quantity and quality of sensory input determines whether an organism is only capable of performing simple phototaxis orientating towards or away from a light source (e.g. bacteria relying on simple photoreceptors (Häder, 1987; Jékely, 2009)) or whether it is capable of navigating successfully halfway around the world during migration (e.g. birds or mammals equipped with an array of complex sensory system (Alerstam, Gudmundsson, Green, & Hedenström, 2001; Gagliardo, 2013; Mouritsen, 2015; R. Wiltschko & Wiltschko, 2009). Besides influencing this basic navigational framework, the sensory input might also affect the navigational strategy within a single individual. Most animals possess multiple sensory systems, which can be used combined, redundantly or complementarily and provide different potentials which navigation strategy could be used efficiently (Able, 1991; Braithwaite & De Perera, 2006; Ernst & Bülthoff, 2004; Hebets et al., 2014; Sutherland, Holbrook, & Burt De Perera, 2009; R. Wiltschko & Wiltschko, 2009).

A key factor affecting which navigational strategy is applied might be the perceptual range of the sensory system that is used to gather information about the environment (Able, 1991; Prevedello, Forero-Medina, & Vieira, 2010; Schooley & Branch, 2005; Sutherland et al., 2009). Depending on the sense that is employed and the limits of its perceptual range, an animal might obtain information only from its very near surroundings or at a greater distance (C. U. M. Smith, 2008).

While navigation always involves an interaction with the surroundings and thus always requires sensory input, the degree to which individual navigation strategies depend on environmental information varies greatly. Egocentric navigation, for example, is based on internal cues such as learned motion sequences and is therefore less dependent on external information (Benhamou et al., 1990; Etienne, Berlie, Georgakopoulos, & Maurer, 1998; Etienne, Maurer, et al., 1998; Healy, 1998; Klatzky, 1998). A prominent example of egocentric navigation is path integration (in mammals also called dead reckoning). For instance, after extensive food searching walks, the desert ant *Cataglyphis fortis* is able to return to its nest on a straight direct path by integrating internal information on direction and distance that are based upon internal cues such as proprioception and odometry (Müller & Wehner, 1988; Wittlinger, Wehner, & Wolf, 2006). Similar mechanisms are also found in humans and other mammals (Etienne & Jeffery, 2004; Etienne, Maurer, et al., 1998; Loomis, Klatzky, Golledge, & Philbeck, 1999; M. -L. Mittelstaedt & Mittelstaedt, 1980; Marie-Luise Mittelstaedt & Mittelstaedt, 2001). An egocentric strategy provides the advantage that it is robust to changes in the environment. However, it is restricted to a defined known route and external cues are required to give information about the start point or for calibrating the current location (Benhamou et al., 1990), for example, the in addition to using egocentric cues, the desert ant uses visual, olfactory and tactile cues to optimise path integration (Buehlmann, Hansson, & Knaden, 2012; T.S. Collett, Collett, & Wehner, 2001; Seidl & Wehner, 2006; Rudiger Wehner, 2003; Rüdiger Wehner et al., 1996). On the other hand, allocentric navigation relies on external information such as landmarks to return to a goal location. For example, pigeons are famously known to rely on visual landmarks when navigating within a familiar environment (Biro, Guilford, & Dawkins, 2003; Burt, Holland, & Guilford, 1997). During such allocentric navigation strategies, landmarks can be used in various ways, for example, they can directly indicate a goal (beacon), or many landmarks can be combined together in a map-like system (Braithwaite & De Perera, 2006; Healy, 1998; López, Broglio, Rodríguez, Thinus-Blanc, & Salas, 1999; Odling-Smee & Braithwaite, 2003; Rodriguez, Duran, Vargas, Torres, & Salas, 1994; Schluessel & Bleckmann, 2005). Allocentric navigation strategies will be most efficient when landmarks can be perceived from a longer distance (Pe'er & Kramer-Schadt, 2008). From this, it can be hypothesised that the available sensory input might determine which navigation strategy is employed. For example, the availability of a far range sense, such as vision, might promote allocentric navigation and the restriction to short range sensory input, might favour the use of an egocentric strategy.

Here we used the African weakly electric fish *Gnathonemus petersii* as a model to investigate the influence of sensory input on navigation. With its active electric sense and a highly specialised visual system these fish possess two sensory systems that provide similar information about the environment on different spatial scales.

During active electrolocation, *G. petersii* is able to perceive its surroundings by detecting distortions in a self-generated electric field. These fish produce weak electrical pulses also called electric organ discharges (EOD) with an electric organ located in the caudal peduncle (Lissmann, 1958; Lissmann & Machin, 1958). With each EOD, a 3-dimensional electric field is built up around the fish, which is perceived with epidermal electroreceptor organs (Jorgensen, 2005). According to their electrical properties, objects within this electric field distort the spreading of the field lines, which leads to a local change of the perceived amplitude and waveform of the EOD (Lissmann & Machin, 1958; von der Emde, 1990; von der Emde et al., 2010). Using these object evoked distortions of the electrical field, *G. petersii* is able to detect and recognise objects within its environment (Graff, Kaminski, Gresty, & Ohlmann, 2004; Schumacher, Burt de Perera, & von der Emde, 2016; von der Emde & Fetz, 2007). However, the perceptual range of the active electric sense is restricted to approximately one or two fish length (ca. 10 - 20 cm) when detecting objects and to only a few centimetres during object recognition (Fechler & von der Emde, 2013; Moller, 1995; von der Emde et al., 1998)

The visual system of *G. petersii* relies on a so-called grouped retina, which enhances light absorption under dim light conditions and reduces visual noise in turbid water (Kreysing et al., 2012; Landsberger et al., 2008). Thus it is perfectly adapted to the fishes' crepuscular (main activity during dusk and dawn) or nocturnal life style and their habitat in black water streams in Central and West Africa. Within this grouped retina, the photoreceptor cells are packed into bundles and are located at the bottom of a cup like structure formed by reflective retinal pigment epithelial cells (tapetum lucidum), which focuses incoming light on the outer segments of the cones (Francke et al., 2014; Kreysing et al., 2012; Landsberger et al., 2008). This organisation of the retina, however, results in a relatively low spatial resolution of the visual system of *G. petersii* (minimal visual angle of about 3°)(Kreysing et al., 2012; Schuster & Amtsfeld, 2002). Despite this poor spatial resolution these fish are able to use visual information for object recognition, applying template matching to do so (Schumacher et al., 2017; Schuster & Amtsfeld, 2002).

Previous studies have shown that *G, petersii* is able to integrate information from vision and the active electric sense and that both senses can be used to recognise objects in the near field of the fish (Moller, 2002; Rojas & Moller, 2002; Schumacher, Burt de Perera, Thenert, et al., 2016; Schumacher et al., 2017). Furthermore, *G. petersii* is capable of cross-modal object recognition, i.e. object information acquired and learned with one of the senses can be used by the other for object recognition (Schumacher, Burt de Perera, Thenert, et al., 2016). Both senses have a high temporal resolution which allows detailed perception of the environment even during fast swimming (Moller, 1980; Pusch, Kassing, et al., 2013; Schumacher, Burt de Perera, & von der Emde, 2016). Together, this means that both sensory systems are able to provide the information necessary for allocentric navigation. However due to the short perceptual range of the active electric sense, navigation based on the perception of landmarks might be inefficient.

So far little is known about how *Gnathonemus petersii* navigates in its environment and which senses they use primarily to do so. Studies have shown that during a vertical navigation task, *G. petersii* is able to use electrical and hydrostatic pressure cues for short range navigation (Cain, 1995; Cain et al., 1994; Cain & Malwal, 2002). In their natural environment *G. petersii* is known to possess home territories, which they leave to forage and where they regularly return to (Moller et al., 1979). In order to do this, they must be able to navigate successfully in their environment across a considerable range.

Here we investigate how the use of vision or the active electric sense affects the navigation strategy in *G. petersii* by training individual fish to swim through a maze using a particular route indicated by either visual landmarks, electrical landmarks or without landmarks. By putting egocentric and landmark-based allocentric cues into conflict, we tested whether the fish employed an egocentric or an allocentric strategy. In a second experimental series we explored whether the use of landmarks could be transferred between the senses, by testing visually trained fish with electrical landmarks and vice versa. Together our experiments inform us how the perceptual range of sensory systems influences navigation and how flexible navigation strategies can be employed within a species.

3.1.3. Methods

3.1.3.1. Subjects and set up

During this study we used 17 *G. petersii*, with a standard length of 8.5 - 13 cm as subjects. The fish were bought in a local store in Oxford (The Goldfish Bowl Oxford) and were imported, wild caught from Africa. The age and sex of the fish were unknown. The fish were housed individually in housing tanks with the dimensions 60 cm x 35 cm x 40 cm. The experiments were conducted in a separate experimental tank (130 cm x 45 cm x 45 cm), which was divided into five compartments (Figure 41). The outermost compartments acted as the start and goal area. They were divided from the other compartments with a partition containing one door and were, in contrast to the inner compartments, equipped with gravel on the floor. The other three compartments had the same size (30 cm) and were divided by partitions containing two gates, so that in order to get from the start area to the goal area the fish had to choose twice between two gates. A cage made of a plastic framework covered with fly screen net was attached to each gate. At each partition there was one open cage and one closed cage, therefore the passage into the next compartment was only possible if the fish chose the gate with the open cage behind. The cages were used in order to prevent the possibility of the fish detecting the difference between an open and a closed gate from afar. The cages could be taken off, and since the setup was symmetrical, the experiments could be conducted in both directions by relocating the cages to the other side of the partition. In other words, the goal area of the first trial was used as the start area of the second trial and vice versa.

The temperature, the pH-value and the conductivity of the water in the experimental as well as in the housing tanks were kept constant at 24±1°C, 6-7 and 100±10 µS/cm.

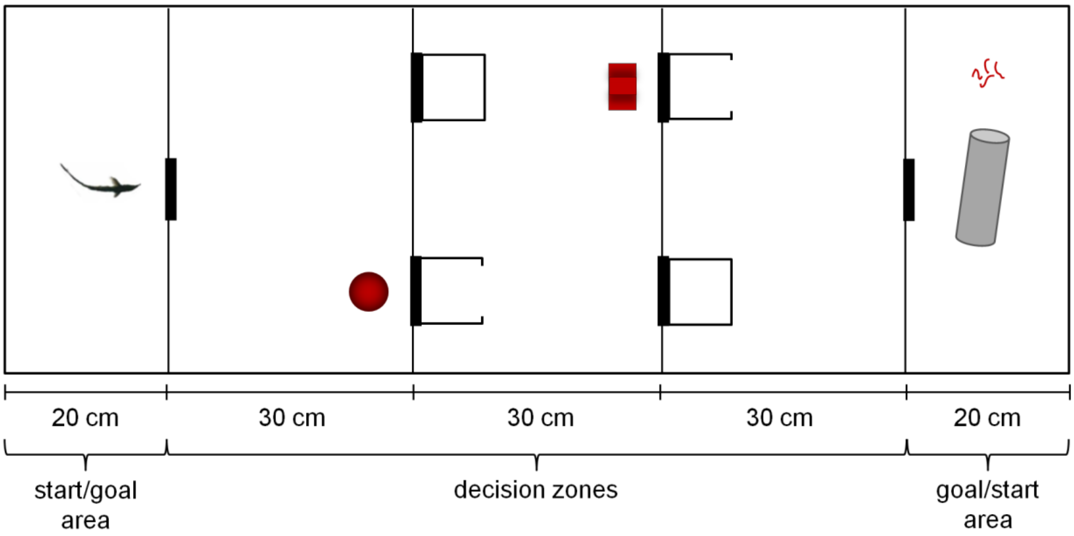

Figure 41: Top view of the experimental tank with a symmetrical two-directional design. Start and goal area switched after each trial as the fish either had to swim from left to right or from right to left. The correct landmark indicated route allowed passage via open cages, whereas incorrect doors denied passage via closed cages (dead end). To maintain motivation the goal area was equipped with a refuge (plastic tube) and a food reward (bloodworms).To minimise uncontrolled external cues a black curtain was placed around the setup.

3.1.3.2. General procedure

Before the first trial was started, the door of the start area was closed and the door of the goal area opened. The goal area contained a plastic tube as a hiding place and a food reward in the form of a small amount of bloodworm (Chironomidae larvae). Both motivated the fish to swim into the goal area.

The fish was carefully netted, taken from its home tank and placed in the start area of the experimental tank. After a short habituation phase of two minutes, the door of the start area was opened. When the fish had left the start area, the door was closed in order to prevent a return of the fish. The fish was given 10 minutes to swim into the goal area. If it did not enter the area in this time the trial was aborted and the fish was placed back into the start area. If the fish did swim into the goal area the door was closed and the fish was given 3 minutes to feed and hide. In the meantime, the cages were replaced on the other side of the partitions and the new goal area was equipped with the food reward and a plastic tube. Before the new trial was stared the plastic tube was removed from the new start area.

3.1.3.3. Sensory influence on navigation

3.1.3.3.1. Training

Before the training started, pre-training sessions were conducted, during which the fish were trained to swim from the start area to the goal area without the two partitions in between. As described above the food reward and the hiding place were placed in the goal area to motivate the animals to perform. Once the fish had learned to swim directly from the start area to the goal area (after 2 - 3 days) the partitions with the cages were introduced.

To test the sensory influence on navigation during the first experimental series, the open cages were positioned in a pre-assigned order. For example, on the first partition (first decision) the open cage was attached to the right gate and on the second partition (second decision) it was placed behind the left gate, forcing the fish to swim a right - left route in order to reach the goal area. An object (landmark) was placed 3 cm in front of each correct gate with the open cage behind. For the first decision a sphere with a diameter of 5 cm was used as the landmark and a cross with the same volume was used for the second decision. The number of training trials conducted per day varied between two and eight trials per fish (only even numbers to avoid overrepresentation of one of the swimming directions in the two-directional design), all fish conducting the same number of trials each day..

The fish were divided into four training groups composed of five or four in each. In all training groups three or two fish were trained to the route, right - left and two to the route, left - right. The training groups were exposed to objects that were made from different materials, which influenced the senses that could be used to detect the objects:

1) The first training group (visual group, fish 1 - 5) could only use vision to detect the objects. This was achieved by making the objects from red coloured electrically transparent agarose. These objects had approximately the same conductivity as the tank water and were therefore electrically "invisible". To produce these objects, red food colour was added to deionised water until the conductivity of the mixture reached a value of ca. 40 µS/cm. Red colour was used because the cones of *G. petersii* are most sensitive to red light (absorption maximum: 615 nm (Kreysing et al., 2012)). By adding agarose powder (Agarose BP 160-100, Fisher Scientific, Fair Lawn, New Jersey, USA) (2g per 100ml) the conductivity was increased to ca. 100 µS/cm. This mixture was boiled and cast in moulds. After cooling down the agarose became stiff and the objects could be used. Since it was not possible to measure the conductivity of the stiffened agarose directly, the resistance of 250 ml stiff agarose within a beaker was compared with the resistance of 250 ml tank water using a multimeter (M-3650B, Voltcraft) to test whether their electrical properties were identical. For both measurements the measuring electrodes were positioned 5 cm apart. There was no measureable difference between the agarose and the tank water.

2) The second group (plastic group, fish 6 - 9) could use only their active electric sense to perceive the objects. In this case, visual detection of the landmark was prevented by covering plastic objects (detectable by the active electric sense) with hoods made of opaque, black cotton fabric. Identical hoods containing no landmark, were placed in front of the doors with the closed cages behind, therefore the fish had to use electrolocation to detect the navigational landmark.

3) Since the effect of plastic on the electrical field of the fish is relatively small, a third group (metal group, fish 10 - 13) was trained with metal objects covered by the cotton hoods instead of the plastic objects.

4) As a control a fourth group (control group, fish 14 - 17) was trained without any landmarks at all. The aim of this was to test whether the objects had an uncontrolled effect and whether these objects acted as positive or negative

reinforcers on the training duration and the accuracy with which the fish navigated through the maze.

During training, the fish learned to swim from the start to the goal area on the pre-assigned route without directional errors. Directional errors were counted when the fish either swam into the dead-end of a closed cage or when the fish swam back through an open cage in the direction of the start area. The probability of completing this task without any errors at random was 16.67% (first decision: right or left gate (50:50), second decision: right, left or backwards (1/3:1/3:1/3)).

The number of errors as well as the trial duration, from leaving the start area to entering the goal area, were documented. Training was considered successful when the fish reached the pre-assigned learning criterion of 21 correct trials out of 24 (87.5 %).

To compare the training performance of the four different training groups, we plotted the number of trials taken to reach the learning criterion (e.g. a fish making errors only in three trials between trial 32 and 55 reached the criterion after 55 trials) in box plots, and we conducted a Kurskal Wallis test and a post hoc test. We calculated the mean trial duration, the mean number of errors and the percentage of correct trials of 8 trial intervals for each group and plotted them in learning curves. To compare the within-subjects effects of trial number and the interaction of trial number x training group as well as the between-subjects effect of training group, we conducted a mixed-design ANOVA with post-hoc-tests (Bonferroni correction) for trial duration, number of errors and percentage of correct trials. We arcsine-transformed the percentage of correct trials and back-transformed the mean and the standard error for plotting the learning curves.

3.1.3.3.2. Egocentric vs. allocentric navigation

After the fish had reached the preassigned learning criterion, probes were introduced every fifth trial, to test whether the fish learned the egocentric route or whether they learned to navigate by using the landmarks (allocentric route). To achieve this, the egocentric and the allocentric information were put into conflict by moving the landmarks. For these tests, all cages were opened and the objects were placed in front of the gates that were closed during training; e.g. in tests with fish that were trained to the route right - left, the objects were placed left - right. In the group trained without landmarks only, all cages were opened to control whether the closed cages had any effect on the performance. In order to prevent a training effect during the tests, no food reward or hiding place was placed in the goal area. Ten test trials were conducted with each fish.

We calculated the percentage of trials during which the fish chose the previously trained to route (egocentric route) for all training trials after the fish had reached the learning criterion and for the test trials for each fish and conducted a Chi^2-test to test whether the performance was significantly different from the 16.66% chance-level. To test whether there was a significant difference between the performances during training and tests and between the different training groups we arcsine-transformed the data and conducted a mixed design ANOVA. Subsequently we calculated the mean and the standard error and transformed the data back to percentage and plotted them in bar charts.

3.1.3.4. Cross-modal landmark recognition during navigation

3.1.3.4.1. Training

After the first experimental series a second set of experiments was conducted with the group trained with visual landmarks and the group trained with plastic landmarks, in which the fish were forced to use the landmarks for navigation instead of following a pre-assigned route. To do this, the positions of the correct gates with the open cages were changed pseudo-randomly every trial using the four possible combinations (right - right, right - left, left - left, left - right). As in the first experimental series the correct gates were indicated by the visual/plastic landmarks (red coloured electric transparent agarose objects/ plastic objects covered with cotton hoods and empty cotton hoods).

Since none of the fish trained with plastic landmarks showed a training effect after 96 trials, the plastic objects were replaced by metal objects. This was done because metal has a stronger effect on the electrical field and therefore is easier to detect and can be perceived from a greater distance. The learning criterion for this experimental series was set to 17 correct trials out of 25 (68%).

We plotted the number of trials to criterion for those fish that reached the learning criterion. For all fish the percentage of correct trials of the last 25 training trials was calculated (either the fish reached the learning criterion or the training was considered unsuccessful and stopped). We used a Chi^2-test to test whether the performance was significantly different from the 16.67% chance level. We plotted the mean trial duration, the mean number of errors and the mean percentage of correct trials of 8 trial intervals for each group and conducted a mixed-design

ANOVA with post hoc-tests (Bonferroni correction) to analyse the within-subjects effects of trial number and the interaction of trial number x training group as well as the between-subjects effect of training group for trial duration, number of errors and percentage of correct trials. To do this the percentage of correct trials was arcsine-transformed and the mean and the standard error were back-transformed for plotting the learning curves.

3.1.3.4.2. Transfer tests

After the fish had reached the learning criterion, we tested whether the ability to recognise the landmarks and use them for navigation was transferable between the senses. To do this, the training landmarks used by the visually trained fish were replaced by electrical landmarks (metal objects covered with hoods) and vice versa. During these tests all cages behind the gates were open and no reward was used. A total of 20 probe trials were interspersed into training every fifth trial.

We calculated the percentage of correct trials for each fish for all training trials after the fish had reached the learning criterion and for the test trials. To test whether the performance was significantly different from chance level we used a Chi^2-test and with exact Fisher-tests we compared the performance during training and tests for each fish. Furthermore, we compared the performance with electrical landmarks of the group trained with visual landmarks during the transfer tests and the group trained with electrical landmarks during training using a Mann-Whitney-U-test.

3.1.3.4.3. Analyses of decision behaviour

To record the decision behaviour of the fish during training and transfer test trials, a camera was placed above the tank. For each fish 22-35 training trials and 20 test trials were recorded and analysed. We observed the direction in which the fish swam after leaving the start area/ after passing the first barrier (right or left) and whether it changed the swimming direction. Training and test trials as well as correct and incorrect decisions were analysed separately. We plotted the mean relative frequency of decisions, during which the fish swam in the individual favoured direction (direction chosen with a relative frequency of more than 50%; the favourite direction was separately assigned for the first and the second decision for each fish) and of decision during which the fish changed direction (swimming towards one gate and at a distance of ca. 5 cm in front of the gate turning towards the other gate without entering the first) for the correct and the incorrect decisions during training and transfer tests. To analyse the main effects of training/transfer and correct/incorrect and the interaction of both factors (training/transfer x correct/incorrect) we arcsine-transformed the data and conducted a two-way repeated measures ANOVA with subsequent post hoc-tests (Bonferroni correction) for favourite direction and changed direction. For the plots the mean and the standard error were back-transformed into percentage data.

3.1.4. Results

3.1.4.1. Sensory influence on navigation

To test whether the navigation strategy of *G. petersii* is influenced by the sensory system available for landmark detection, we trained the fish to swim through a maze using a defined route, which was indicated by landmarks that could be perceived only with vision (electrically transparent agarose objects) or only with the active electric sense (plastic or metal objects) or no landmarks were present.

3.1.4.1.1. Route acquisition

All fish from the four training groups reached the pre-assigned learning criterion of 21 correct trials out of 24 and therefore learned to swim from the start area to the goal area using the defined route. However the number of trials the fish needed to learn the task differed between the groups (Figure 42). The fish, which were trained with the visual landmarks, learned the navigation task significantly faster than all the other groups (Kurskal-Wallis-test: $H_3 = 11.504$, $P = 0.009$), reaching the learning criterion with a median number of 55 training trials. The training duration of the other three groups did not differ significantly. These results suggest that the visual landmarks had a positive influence on the training, while the electrical landmarks (plastic and metal) had no significant influence compared to the control group without landmarks.

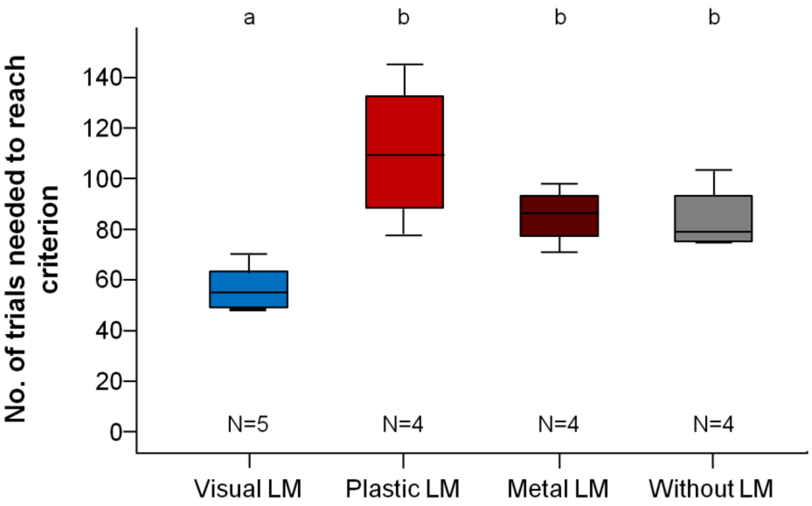

Figure 42: Box plots of the number of training trials the different training groups needed to reach the pre-assigned learning criterion of 21 correct trials out of 24. The fish were trained to swim from the start area to the goal area using a pre-assigned landmark indicated combination of gates (either right - left or left - right). The number of fish within each group is indicated in the figure. The lines of the box plot indicate the lower quartile (25 %), the median (50%) and the upper quartile (75 %) and the whiskers indicate the minimum and maximum values. A Kurskal Wallis-test and a post hoc test was conducted to ascertain whether the training duration of the groups differed significantly (KW: H_3 = 11.504, P=0.009). The letters above the box plots indicate which training durations are significantly different. Groups with the same letter do not differ significantly ($P > 0.05$). Groups with different letters are significantly different ($P \leq 0.05$).

In line with the significantly shorter training duration a comparison of the learning curves of the four different training groups also indicates that the performance of the group trained with visual landmarks improved faster than that of the other groups (Figure 43). While there was no significant difference in trial latency or number of errors between the four training groups (mixed-design ANOVA: between-subjects effects of training group: $F_{3,13}$ = 1.257; P = 0.33 (trial latency); $F_{3, 13}$ = 2.250 ; P= 0.131 (No. of errors); interaction No. of trials x group: $F_{4.687, 20.310}$ = 0.625; P = 0.673 Greenhouse-Geisser correction $\varepsilon = 0.195$ (trial duration); $F_{5.982, 25.924}$= 0.807; P = 0.574 Greenhouse-Geisser correction $\varepsilon = 0.195$ (No. of errors)), the percentage of correct trials differed between the groups over the training period (mixed-design ANOVA: interaction trial No. x training group: $F_{24, 104}$= 2.09; P = 0.006). On trials No.41-48, 49-56 and 57-64 the visually trained group reached a significantly higher performance than the other groups, suggesting that during this training period the visual landmarks positively influenced the training performance.

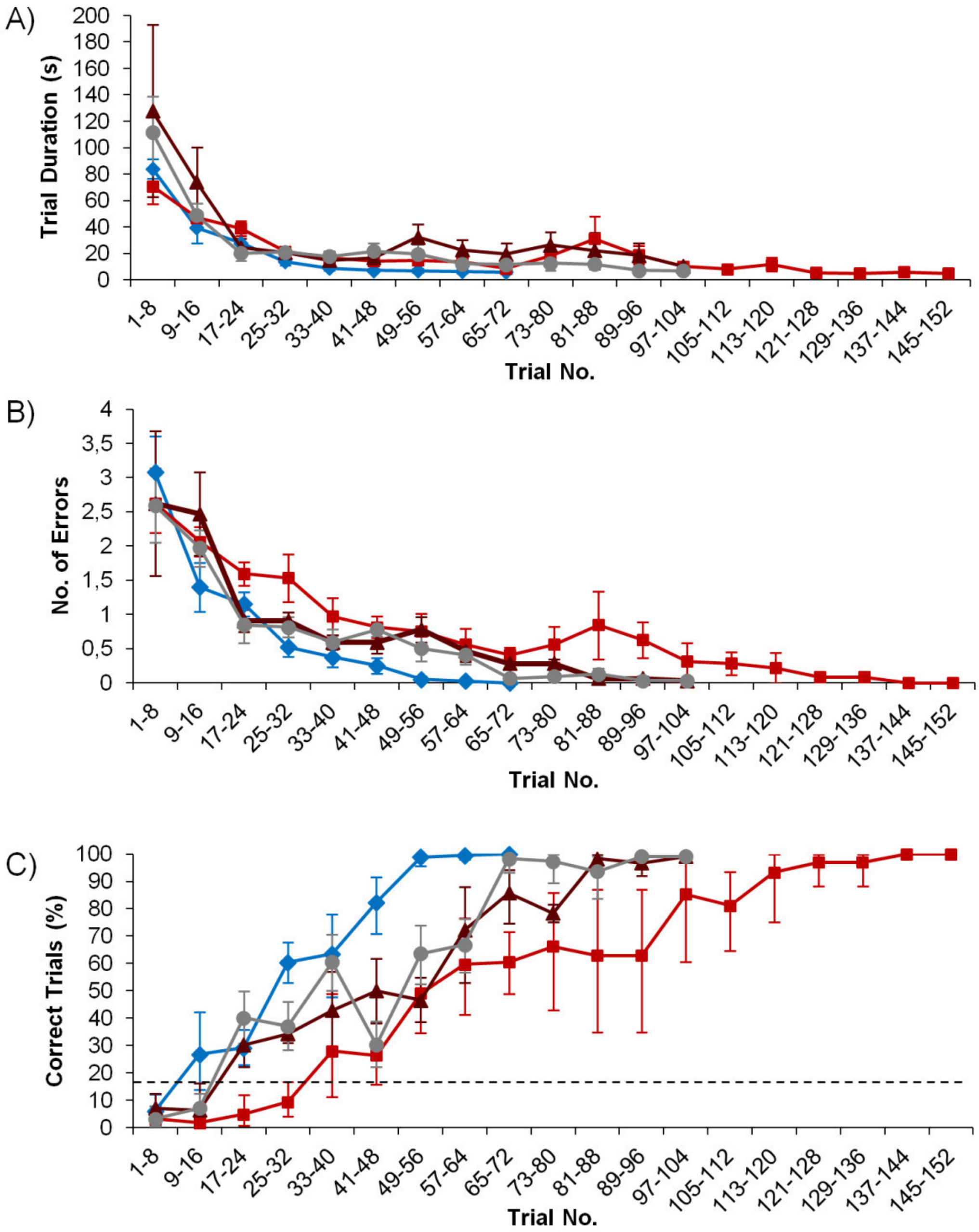

Figure 43: Learning curves of the four different groups trained with visual landmarks (blue), plastic landmarks (red), metal landmarks (dark red) and without landmarks (grey). Mean trial duration (A), mean number of errors (B) and mean percentage of correct trials (C) of 8 trials of each group. The trial duration was measured from the moment the fish left the start area to the moment it entered the goal area. It was counted as an error when the fish swam into a dead end of the incorrect gate or swam back in the direction of the start through an open gate. During a correct trial the fish swam from the start to the goal area without any errors. The error bars indicate the standard error within each group. The dashed line in C indicates the chance level of 16.67% which results from a 50% chance for the first decision (correct or incorrect gate) and a 33.33% chance for the second decision (correct, incorrect or backwards).

3.1.4.1.2. Egocentric vs. allocenric navigation

After the fish reached the learning criterion, we tested whether they had learned the egocentric route or whether they had learned to rely on the landmarks by putting these navigational strategies in conflict.

During the conflict tests all fish chose the previously learned egocentric route over the landmark indicated allocentric route in at least 9 of 10 test trials (Chi^2-test: $P < 0.001$). The comparison of the performance during tests and training shows that in all four groups the fish chose the egocentric route during tests with the same accuracy as during training (mixed design ANOVA, within-subjects effects: $F_{1,\ 13} = 0.93$, $P = 0.352$, interaction group x training/test: $F_{1,\ 13} = 0.993$, $P = 0.427$) (Figure 44). Furthermore, there was no difference in the performances of the different training groups (mixed design ANOVA, between-subjects effects: $F_{3,\ 13} = 1.11$, $P = 0.381$), revealing that the fish chose the egocentric route no matter which sense was used for landmark detection.

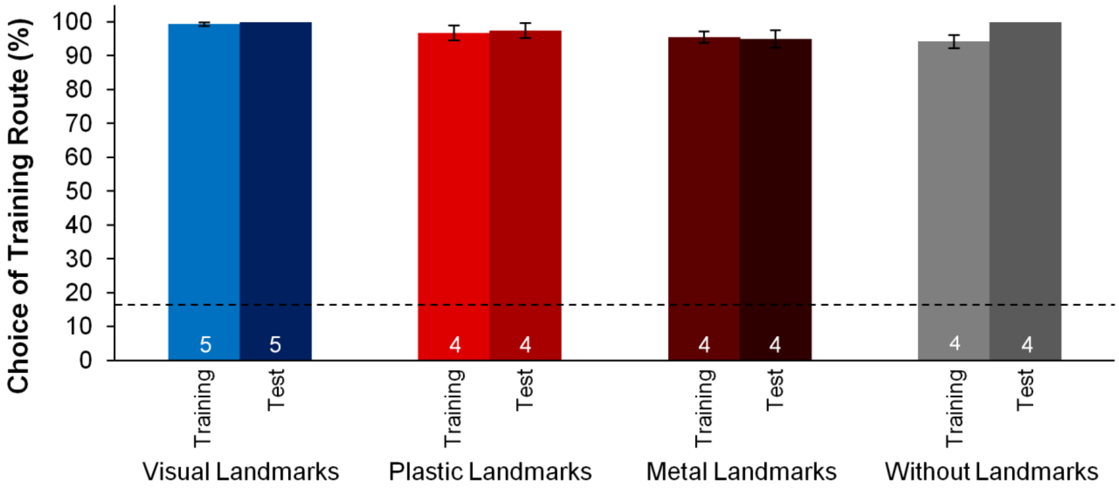

Figure 44: Mean choice of the training route of the four different groups trained with visual landmarks (blue), plastic landmarks (red), metal landmarks (dark red) and without landmarks (grey) during training (lighter bars) and during tests where egocentric and landmark cues were put in conflict (darker bars). The error bars indicate the standard error and the number of tested fish is given within the bars. The chance level of 16.67% is marked by the dashed line.

3.1.4.2. Cross-modal landmark recognition during navigation

To test whether *G. petersii* is able to navigate using landmarks that are transferred across two senses, we trained the fish from the visual and the plastic groups to use allocentric local landmark cues for navigation. To do this the landmark indicated correct route was altered pseudo-randomly every trial. After the fish had reached the pre-assigned learning criterion of 17 correct trials out of 25, we tested the fish with the previously untrained sense.

3.1.4.2.1. Training

In the group trained with visual landmarks four of the five fish reached the learning criterion. On average they needed 136 trials to do so (Figure 45 A) and thus needed more than twice as many trials to learn the navigation task as during the first experimental series. After 168 trials, the fifth fish of this group showed a slight learning effect and reached a level of 40% correct trials within the last 25 trials, which is significantly above the chance level of 16.67% but it did not reach the learning criterion (Chi^2-test: $P = 0.002$).

After 96 training trials none of the fish trained with plastic landmarks showed any training effect, therefore we replaced the plastic objects with metal objects. This was done because metal has a much stronger effect on the electric field than plastic and is therefore easier to detect for the fish. However even with the metal landmarks, none of the fish reached the pre-assigned learning criterion, so that the training was considered unsuccessful and was stopped after a minimum of 168 training trials. Within the last 25 training trials, none of the fish reached an accuracy of over 24% correct trials which is not significantly different from chance level (Chi^2-test: $P > 0.05$) (Figure 45 B).

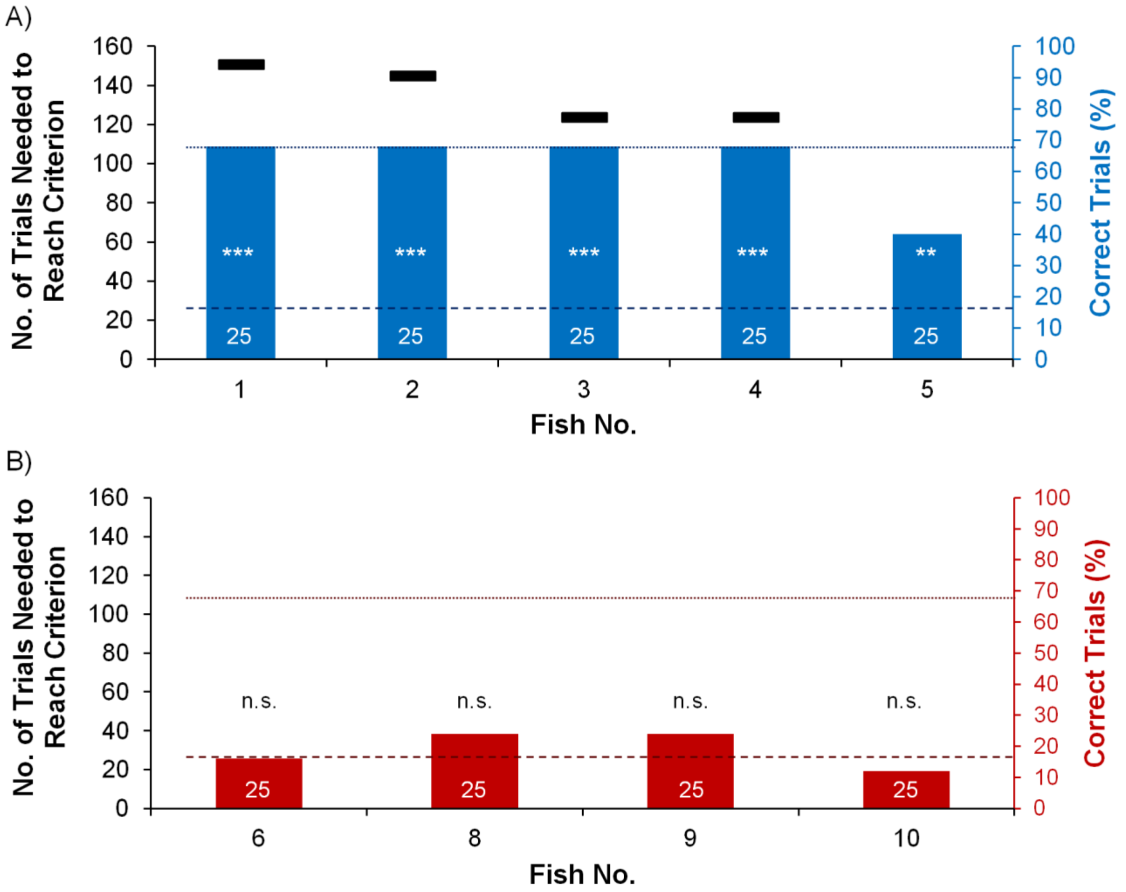

Figure 45: Training performance of the fish trained with visual landmarks (A) and the fish trained with electrical landmarks (B) during the experiments where the fish were trained to use an allocentric navigation strategy. To do this, the correct route indicated by the landmarks was changed pseudo-randomly every trial. The black bars on the primary y-axis (left) show the number of training trials the fish needed to reach the learning criterion of 17 correct trials out of 25 (68%). If the fish did not reach the criterion no bar is shown. The blue/red columns on the secondary y-axis (right) show the percentage of correct trials the fish reached within the last 25 trials of training before the fish reached the learning criterion or before training was stopped. To test whether the performance of the fish was significantly different from the 16.67% chance level, Chi^2-tests were conducted (n.s.: $P > 0.05$, *: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$). The dashed line indicates chance level and the dotted line indicates the learning criterion.

The learning curves (Figure 46) show that while there was no significant difference in the decrease of trial duration between the visual and the electrical group (mixed-design ANOVA: within-subjects effect of training group: $F_{1,\ 7} = 1.151$, $P = 0.319$, trial No. x training group: $F_{3.992,\ 27.942} = 1.307$, $P = 0.292$ Greenhouse-Geisser correction $\varepsilon = 0.210$), the number of errors and the percentage of correct trials differed significantly between the groups from trial No. 121-128 unti the end of training at trial No. 161-168 (mixed-design ANOVA: trial No. x training group:

$F_{4.883,\ 34.179} = 2.908$, $P = 0.028$ Greenhouse-Geisser correction $\varepsilon = 0.257$ (No. of errors) , $F_{4.537,\ 31.762} = 3.163$, $P = 0.023$ Greenhouse-Geisser correction $\varepsilon = 0.239$ (correct trials) post-hoc-tests with Bonferroni correction $P < 0.05$). This reveals that the visually trained fish learned the task better than the electrically trained group. The learning curves (Figure 46 B and C) also show that there was no training effect over the entire training period in the electrical landmark group (red lines). There was no significant difference in the mean number of errors or in the mean percentage of correct trials between trials No. 1-8 and any other trial interval (mixed-designed ANOVA: trial No. x training group: $F_{4.883,\ 34.179} = 2.908$, $P = 0.028$ Greenhouse-Geisser correction $\varepsilon = 0.257$ (No. of errors), $F_{4.537,\ 31.762} = 3.163$, $P = 0.023$ Greenhouse-Geisser correction $\varepsilon = 0.239$ (correct trials) post-hoc-tests with Bonferroni correction $P > 0.05$). In contrast, the performance of the fish trained with visual landmarks significantly improved over time. After trial 64, the number of mistakes steadily decreased and the percentage of correct trials increased in line (mixed-designed ANOVA: trial No. x training group: $F_{4.883,\ 34.179} = 2.908$, $P = 0.028$ Greenhouse-Geisser correction $\varepsilon = 0.257$ (No. of errors), $F_{4.537,\ 31.762} = 3.163$, $P = 0.023$ Greenhouse-Geisser correction $\varepsilon = 0.239$ (correct trials) post-hoc-tests with Bonferroni correction $P < 0.05$). However in comparison to the first experimental series, where the fish were trained to use a defined route, the mean percentage of correct trials was much poorer and never exceeded 73%.

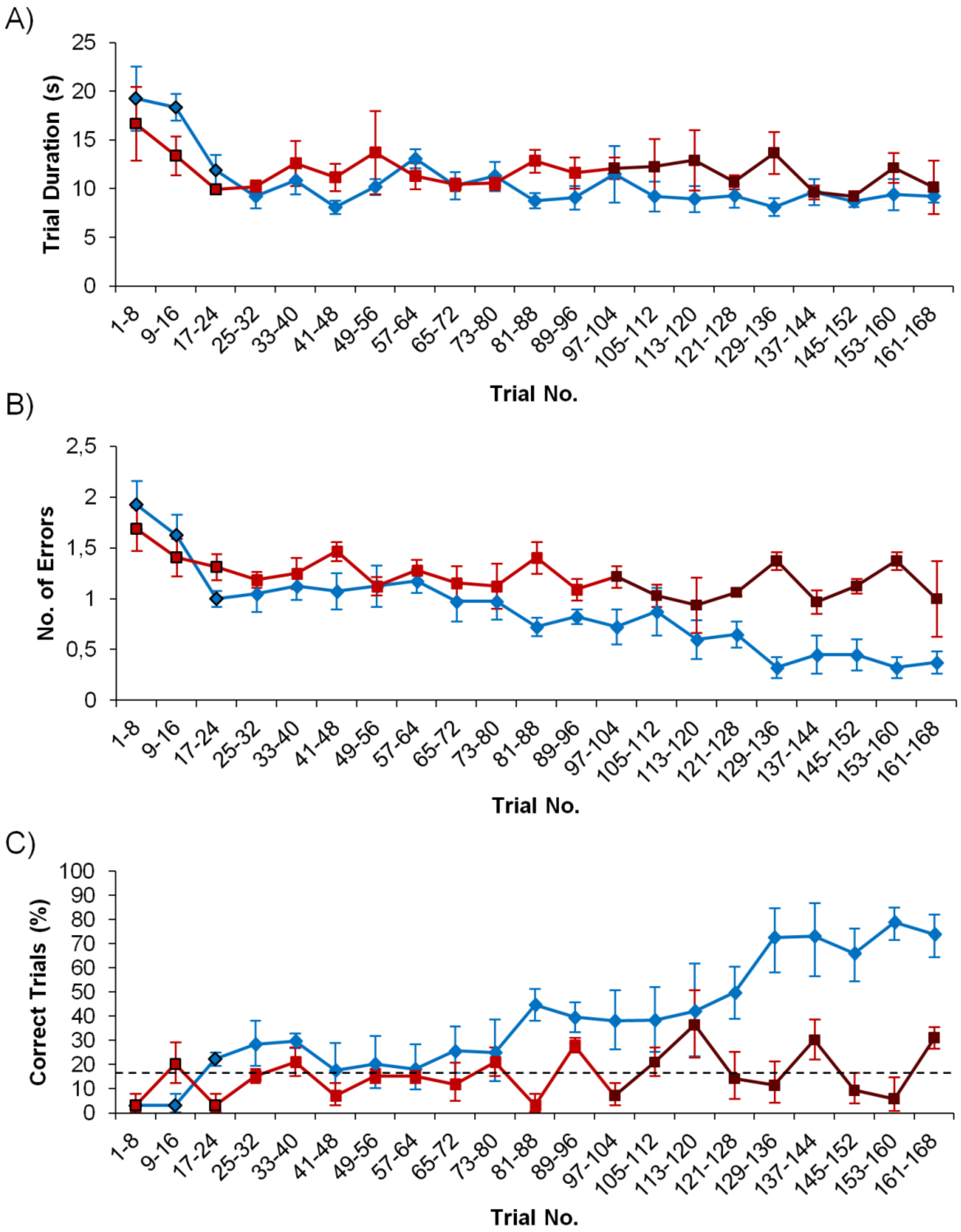

Figure 46: Learning curves of the groups trained with visual landmarks (blue) and with electrical landmarks (red). Mean trial duration (A), mean number of errors (B) and mean percentage of correct trials (C) of 8 trials of each group. Within the first 24 trials the route the fish were previously trained to (right - left or left - right) was not used during training (black framed data points). Subsequently all four possible routes were shuffled pseudo-randomly and were used with the same frequency. After 96 trials there was still no consistent trainings effect in all fish trained with plastic landmarks, therefore the plastic objects were replaced by metal objects from trial 97 on (dark red). For further description see Figure 43.

3.1.4.2.2. Transfer tests

Subsequent to training, the four fish of the group trained with visual landmarks were tested in transfer tests, during which the visual landmarks were replaced by electrical landmarks (metal objects covered with electrically transparent cotton hoods in front of one gate and empty hoods in front of the other gate).

During the transfer test, all four tested fish reached a performance significantly different from the 16.67% chance level (Chi²-test: $P \leq 0.05$; Figure 47). However, in all fish the transfer performance with the electrical landmarks (38.75 + 2.39) was significantly worse than the training performance with the visual landmarks (70.87 + 1.1) (exact Fisher-test: $P < 0.001$). The comparison of the performance during the transfer tests with the training performance of the group trained with the electrical landmarks after at least 168 training trials shows that the visually trained group reached a significantly better performance during navigation with the electrical landmarks without any training with these landmarks (Mann-Whitney-U-test: $U = -2.337$, $N_1 = N_2 = 4$, $P = 0.029$; Figure 48). This suggests that while the fish seemed to be able to transfer the use of the landmarks, the electrical input might not be sufficient for efficient allocentric navigation.

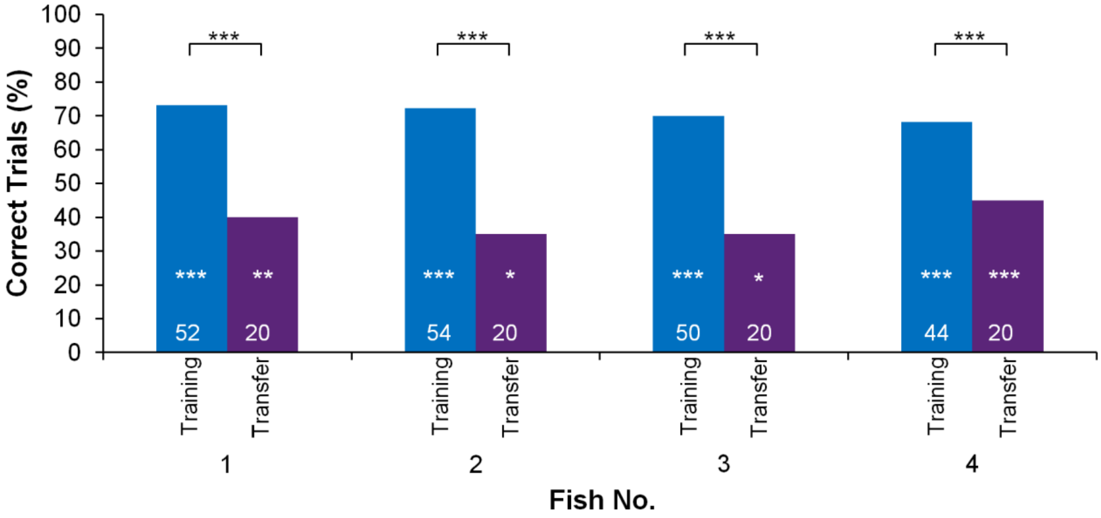

Figure 47: Percentage of correct trials of the four fish trained with visual landmarks that reached the learning criterion during training (blue) and during transfer tests with electrical landmarks (purple). The training performance was calculated for each fish using all training trials after the fish had reached the learning criterion. Chi^2-tests were conducted to test whether the performances were significantly different from the 16.67% chance level. The results are indicated by the asterisks within the bars (*: $P \leq 0.05$; **: $P \leq 0.01$; ***: $P \leq 0.001$). To test whether there was a significant difference between the performance during training and during the transfer tests exact Fisher-tests were conducted (***: $P \leq 0.001$).

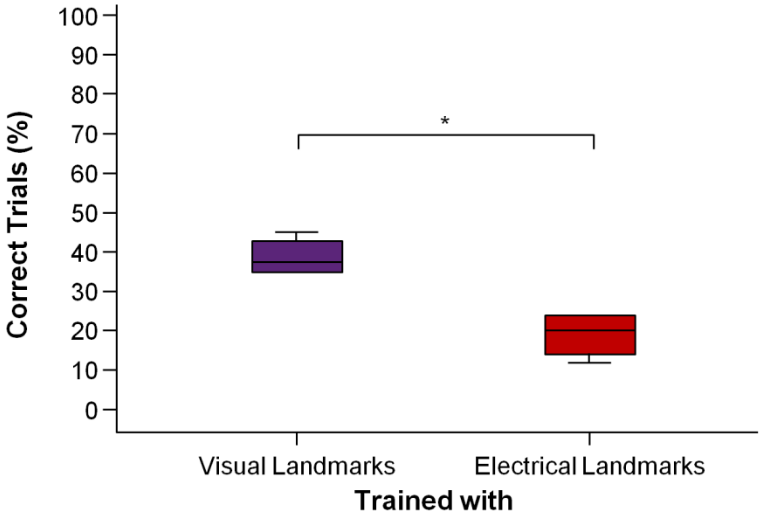

Figure 48: Box plots of the percentage of correct trials of the group trained with visual landmarks during transfer tests with electrical landmarks and of the group trained with electrical landmarks during training. For each fish of the group trained with visual landmarks the percentage of correct trials was calculated from the 20 transfer test trials. For the fish trained with electrical landmarks, the last 25 trials before the training was stopped were analysed. A Mann-Whitney-U-test was conducted to test whether there was a significant difference between the performances (U = -2.337, $N_1 = N_2 = 4$, P = 0.029).

3.1.4.2.3. Decision behaviour

The analysis of the recorded trials shows that each fish tended to swim in an individually preferred direction during most decisions (Figure 49). This preferred direction did not depend on the direction the fish was trained to in the first experimental series. The fish chose this individually preferred direction on average in 62.4 % (training) and 68.6 % (transfer tests) of the correct decisions and in 78.7 % (training) and 81.7 % (transfer tests) of the incorrect decisions, indicating a non-significant trend towards choosing the favourite direction more often during incorrect trials (two-way repeated measures ANOVA: main effect correct/incorrect: $F_{1,3}$ = 5,947, P = 0.093 Greenhouse-Geisser correction $\varepsilon = 1.000$).

Furthermore during the correct decisions, the fish changed directions (swimming in one direction and changing direction shortly before (ca. 5cm) entering the gate) on average in 43.25% of the training decisions and in 53.74% of the transfer decisions. In comparison, during the incorrect decisions the fish changed directions with an average 6.39% of the training decisions and 7.24% of the transfer decisions significantly less often (two-way repeated measures ANOVA: main effect correct/incorrect: $F_{1,3}$ = 2021.877; P < 0.001 Greenhouse-Geisser correction $\varepsilon = 1.000$). This suggests that during correct trials the fish changed the direction towards the correct gate when noticing the absence of the landmark on an initially incorrect route and tended to swim less often in the individually preferred direction maybe in favour of swimming towards the landmark.

During both decision behaviours (favourite direction and changed direction), there was no significant difference between training and test (two-way repeated measures ANOVA: main effect training/transfer: $F_{1,3} = 0.671$, $P = 0.473$ (favourite direction); $F_{1,3} = 3.646$, $P = 0.152$ (changed direction)) and no significant interaction between training/transfer and correct/incorrect (two-way repeated measures ANOVA: training/transfer x correct/incorrect: $F_{1,3} = 0.530$, $P = 0.833$ (favourite direction); $F_{1,3} = 0.250$, $P = 0.651$ (changed direction) Greenhouse-Geisser correction $\varepsilon = 1.000$) .

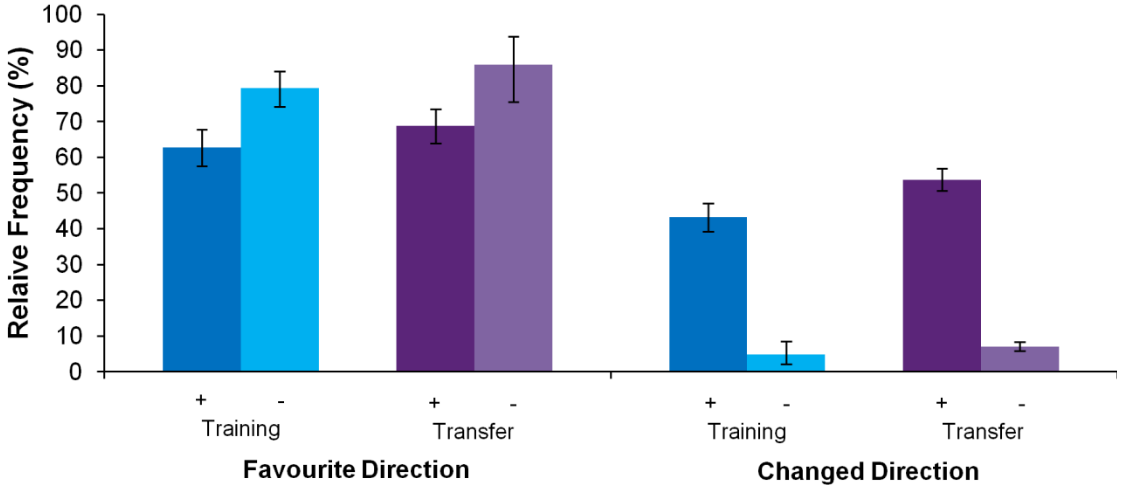

Figure 49: Mean relative frequency of decisions (two decisions per trial), during which the fish swam in its favoured direction and changed directions during training (blue) and during the transfer tests of the four fish trained with visual landmarks that reached the learning criterion. Correct (+) and incorrect (-; lighter bars) decisions were analysed separately. The favourite direction is defined as the direction the fish chose with a frequency of more than 50% and it was assigned for each fish for both decisions separately. The fish changed direction when swimming in the direction of one of the gates but then swam in the direction of the other gate before entering the first gate. For each fish, 22-35 training trials after reaching the criterion (44-70 decisions, 34-55 correct decisions, 10-25 incorrect decisions) and 20 transfer test trials (40 decisions, 20-24 correct decisions, 16-20 incorrect decisions) were analysed. The percentage data was arcsine transformed and a two-way repeated measures ANOVA was conducted independently for the favourite direction and for changed direction. The mean and the standard error (error bars) were back transformed into percentage data.

3.1.5. Discussion

3.1.5.1. Sensory Influence on navigation

3.1.5.1.1. Route acquisition

Our results show that *G. petersii* is able to learn a determined route highly accurately. All fish, no matter whether trained with visual landmarks, electrical landmarks or without landmarks, were able to navigate through the maze with an accuracy of nearly 100% correct trials after training (Figure 44). However, the performance during training shows that task acquisition was influenced by the available sensory input (Figure 42 and Figure 43). The fish trained with visual landmarks learned the task significantly faster than all other groups. These fish were probably able to see the visual landmarks in front of the correct doors from their start position or after swimming through the first partition, therefore the visual landmarks might have affected the decision in which direction to swim, improving route acquisition.

The electrical landmarks (plastic and metal objects) had no significant influence on the training duration compared to the group trained without landmarks. Because of the short perceptual range of the electric sense and the distance of ca. 27 cm between the door and the objects, the fish could not perceive the electrical landmarks from their start position. In this case, the landmarks were unlikely to guide the directional decision, and thus had no influence on task acquisition. This does not correspond with the results of studies of Cain et al. showing that in a vertical navigation task *G. petersii* did use electrical cues during task acquisition (Cain, 1995; Cain et al., 1994; Cain & Malwal, 2002). These differences might be explained by differences in the navigational task and differences in the experimental setup. During the experiments of Cain et al the fish had to find a hole in a partition located at a certain height, vertically navigating in the range of ca. 20 cm, while during our experiments the fish had to swim a specific more complex route, navigating over a total range of 90 cm (from start area to goal area). During a very short range navigation task such as that used in the studies by Cain et al., the electric sense seems to be much more efficient than in our experiments.

However, our results might also be influenced by a systematic difference in landmark presentation of the visual and the electrical cues. During the experiments with the visual landmarks there was only one object present for each decision. In contrast, during the experiments with the electrical landmarks, the hoods were placed in front of both gates. The presence of visually detectable hoods in front of both doors while only one of them contained an electrically detectable object, introduced an additional conflict between the visual and electrical information, which might have made the electrical landmarks less reliable.

3.1.5.1.2. Egocentric vs. allocentric navigation

The results of the test in which egocentric and allocentric cues were put in conflict reveal that all fish no matter which landmarks were available preferred the previously learned egocentric route over the use of landmarks (Figure 44). This suggests that there is an inherent dominance of the egocentric navigation strategy in *G. petersii* when navigating on a familiar route, which is not influenced by the availability of certain senses. This corresponds with findings in fruit bats (*Rousettus aegyptiacus*) showing a very similar dominance of an egocentric representation of space over displaced local landmarks during a familiar navigation task independent of whether the bats used vision or echolocation for landmark detection (Holland, Winter, & Waters, 2005). Together with studies in pigeons and hummingbirds this indicates the importance of egocentric representation of space (Hurly & Healy, 1996; Strasser & Bingman, 1996). Egocentric navigation is more robust against changes in the environment and is therefore the more reliable strategy in a variable environment. The natural habitats of *G. petersii* are rivers in West and Central Africa, which provide a highly variable environment (Moller, 1995). Because of the water current of rivers, local landmarks are likely to be relocated and seasonal changes of the water level (rainy and dry seasons) will additionally affect the structure of the fish´s habitat. Within such unstable environments, allocentric navigation based on local landmarks is probably less reliable than egocentric navigation, especially if the route is very well known and used repeatedly. Therefore river fish might be more likely to use an egocentric strategy than fish that live in more stable habitats like lakes or ponds, as for example shown in sticklebacks (Girvan & Braithwaite, 1998; Odling-Smee & Braithwaite, 2003). Our results, however, do not correspond with maze studies in the closely related African weakly electric fish *Mormyrus rume*, which used landmark based navigation when electrical landmarks were available and only chose egocentric navigation in the presence of visual landmarks (Walton & Moller, 2010). The experimental setup and landmark presentation were very different in this study so that the results are not directly comparable.

An additional factor, which might have influenced our results, is that we might have created a conflict between local and global landmark as we not only put egocentric and allocentric cues in conflict but we also changed the position of the local landmarks within the tank. While we minimised global cues by shielding the tank from the outside and by using the setup in two directions, the availability of uncontrolled cues cannot be completely excluded. Such global landmarks might have supported the egocentric navigation strategy and reduced the reliability of the local landmarks.

3.1.5.2. Cross-modal landmark recognition during navigation

3.1.5.2.1. Training

The training results of the second experimental series show that while the fish preferred the egocentric route in the first series, *G. petersii* is able to use visual landmarks for allocentric navigation (Figure 45). However, with an accuracy of ca. 70% correct trials and a more than twice as long training duration, this allocentric navigation was much less efficient than the egocentric strategy. This might result from the possible conflict between the local landmarks and global cues. Under natural conditions using objects for navigation, which vary their position relative to unchanging global cues, probably would not be efficient. Therefore it was proposed that a conflict between local and global cues is solved based on the perceived stability (a priori reliability) of the cues (Biegler & Morris, 1996). Since in our experiments only the local landmarks changed their position and the rest of the setup stayed constant throughout the experiments, the local landmarks were probably perceived as less reliable. Hence to learn the task, the fish might first had to learn to rely on the local cues.

Caution should be taken, however, as the training performances during the first and the second experimental series are not independent. The previous experience of the first experimental series, during which the fish were trained using one defined route, might have influenced the training of the second experimental series. The fish were already familiar with the setup and knew that they had to swim from the start area to the goal area, which might have positively influenced the training performance. This positive effect is shown in the trial duration (Figure 43 A and Figure 46 A). While at the start of the second experimental series the trial duration slightly increased compared to the end of the first series, the fish were much faster than at the start of the first series. Alternatively, the previous experience might also have had a negative influence on training. The new task contradicted with the previously learned information, hence to learn the new task the previously learned task had to be overwritten. It is therefore possible that naive fish would have learned the allocentric navigation task faster.

The difference in the training performance of the fish trained with visual landmarks and the fish trained with electrical landmarks is probably based on the difference in perceptual range of both senses (Figure 45 and Figure 46). As described above the fish could not perceive the electrical landmarks from their start position or directly after they had passed the first barrier. Therefore, the fish could have made the decision in which direction to swim before they could detect the electrical landmarks and thus did not associate the decision and its consequences with the landmark.

The visual landmarks, on the other hand, could be perceived from a greater distance, so the fish might have been more likely to associate the landmark with the directional decision and thus to learn the task. However, the analysis of the swimming behaviour of the fish trained with visual landmarks shows that these fish also tended to swim in a preferred direction independently of whether this direction was indicated by a landmark or not (Figure 49). This was especially the case when they made an incorrect decision, suggesting that in these cases the fish swam in their preferred direction without attending to the landmarks. During trials in which correct decisions were made, the fish seem to have used the landmarks in two different ways. In 56.75% of the correct training decisions the fish directly swam in the direction of the correct landmark indicated direction, suggesting that the fish might have used the landmarks for guiding the decision. In the other 43.25% of the correct decision, the fish first swam in the direction of the incorrect gate and then changed the direction, suggesting that the fish noticed the absence of the landmark when swimming in the direction of the incorrect gate and reacted with a change of direction.

3.1.5.2.2. Transfer tests

The results of the transfer tests with electrical landmarks show that all four visually trained fish tested reached a performance significantly different from chance level (Figure 47). However, with only 35% - 45% correct trials the performance was significantly worse than during training with visual landmarks and navigation was not very efficient. The comparison of this test performance with the training performance of the group trained with electrical landmarks shows that under the same conditions the visually trained fish without any training with the electrical landmarks reached a significantly higher performance than the electrically trained group after more than 160 training trials (Figure 48). This suggests that the visually trained fish were able to transfer the use of landmarks from vision to the electric sense, however, the short working range of the electric sense made the landmark recognition ineffective. During the transfer tests with the electrical landmarks, the hoods and thus some visual cues were present in front of both gates. From this, the fish received ambiguous visual information, which made the task more difficult to solve. The fact that despite this ambiguous visual input the fish reached a performance significantly different from chance level, might suggest that the fish had not just learned to swim to any visible object but recognised the landmarks more specifically and were able to transfer this information from vision to the electric sense. This corresponds with the findings of an earlier study that *G. petersii* is capable of cross-modal object recognition (Schumacher, Burt de Perera, Thenert, et al., 2016).

The comparison of the recorded decision behaviour during training and transfer tests supports the hypothesis that the fish were able to transfer the use of the landmarks but that navigation was impaired, because of the small perceptual range of the electric sense. The decision behaviour during training and test was very similar but during the transfer test the fish chose slightly more often the favoured direction and changed the direction slightly more often (Figure 49). During the transfer trials the fish could not perceive the landmarks from their start position but could only detect their presence or absence when close to the gate and therefore might have changed the direction more often than during the trials with visual landmarks.

3.1.5.3. Conclusion

Our results show that *G. petersii* is able to navigate highly efficiently in a familiar environment using egocentric cues. After learning the navigational task, an egocentric strategy, perhaps supported by global landmarks, dominated over an allocentric strategy, independently of the available sensory system. Nevertheless, our results suggest that navigation is influenced by the employed sensory system in subtle ways. In contrast to electrical landmarks, visual landmarks significantly improved task acquisition and allowed allocentric navigation. This suggests that there might be a task division of allocentric and egocentric navigation. *G. petersii* might tend to use allocentric cues during route acquisition in less familiar environments whereas the egocentric strategy might be employed when following familiar routes. This hypothesis is supported by the results of Cain et al. showing that *G. petersii* used electrical cues during acquisition of a short range vertical navigation task and relied on an egocentric representation when the fish were familiarised with the task (Cain, 1995; Cain et al., 1994). Furthermore, our results in conjunction with the above cited results from Cain et al. and previous studies showing a dominance of the electric sense at close range (Schumacher, Burt de Perera, Thenert, et al., 2016; Schumacher et al., 2017), suggest that there is also a task division between vision and the active electric sense. Vision might be used for detecting larger landmarks from some distance, which aids longer range navigation, whereas active electrolocation is probably used to perceive fine-scale information about its close surroundings, orientating at very close range.

The results of the allocentric training and the transfer tests show that, although egocentric navigation seems to be inherently dominant during navigation in a familiar environment, *G. petersii* is able to adjust its navigation strategy if necessary, and is able to use cross-modal landmark recognition to further increase the flexibility of the navigational system. These results, together with previous research in other taxa, underpin the importance of navigation mechanisms being flexible in order to cope with environmental challenges (T. S. Collett & Graham, 2004). A flexible multisensory system allows an animal to navigate successfully within the environment under varying conditions in diverse environments, providing a clear adaptive advantage.

4. General Discussion

4. General Discussion

The perception of the environment via combination and integration of multiple sensory inputs provides several adaptive advantages (Ernst & Bülthoff, 2004). Consequently, not only the individual senses but rather the whole multisensory system is adapted to optimise information input within a given habitat. Through cognitive abilities. such as learning, this perceptually gained information can be used flexibly to fulfil complex tasks like object recognition and navigation. Thus perception and cognition are essential features allowing successful interaction with the environment. In this thesis I investigated how the sensory systems of the weakly electric fish *Gnathonemus petersii* operate together, forming a multisensory system that is specially adapted to the environmental conditions of its habitat and its nocturnal live style. The results reveal some of the fundamental mechanisms underlying multisensory processing and underline the high cognitive abilities of these non-mammalian vertebrates.

4.1. Perception: Sensory ecology of the multisensory system

Both vision and the active electric sense are well studied on a uni-modal basis in *G. petersii*, whereas little is known about the mechanosensory lateral line system of these fish. However, under natural conditions the three senses are not used independently but are, together with the acoustic, tactile, olfactory and gustatory sense, part of a complex multisensory system, in which the information from several senses can be combined and integrated (Moller, 2002). From an adaptational point of view this is an important consideration as constraints of one sensory system might be compensated by another, increasing the chance of survival in a competitive and predator-rich environment such as the natural habitat of *G. petersii* (Alais et al., 2010). These fish live in species-rich rivers in Central and West Africa, where up to 43 different fish species were found at a single sampling station (for comparison, in the whole river Rhein 39 different fish species live and for a single sampling station the maximum a number of 30 species was found; and in Bonn only 15 different species were found (Brenner, Korte, & Schneider, 2002)) and where especially during the dry-season the density of fish is quite high (Moritz, 2010; Ogbeibu & Ezeunara, 2002; Wuraola & Adetola, 2011).

All three senses examined in this thesis are in general able to provide spatial information about the environment and objects within it (Hassan, 1989; Lissmann & Machin, 1958; Schuster & Amtsfeld, 2002; von Campenhausen et al., 1981). This raises the question as to why *G. petersii* possesses all three of them when they might be used for the same tasks. The behavioural results of the multisensory interactions between vision and the active electric sense as well as the anatomical data about the mechanosensory lateral line systems presented in this thesis, indicate two contrary ways of how evolutionary adaptation worked on these seemingly redundant senses. While vision and active electrolocation are highly specialised and well adapted to the environmental conditions and are well tuned to each other, the results of chapter 2.3. show that a drastic morphological reduction of the peripheral mechanosensory lateral line system occurred in *G. petersii*.

The active electric sense is most certainly an adaptation to nocturnal activity, as both mormyrid and gymnotiform weakly electric fish are mainly active during the night (Henninger, Benda, & Krahe, 2012; Moller, 1980; Moller et al., 1979; Westby, 1988; Winemiller & Adite, 1997). Active electrolocation allows the perception of detailed information about the environment independently of the presence of light. It thus allows successful nocturnal foraging, while avoiding an increased predation pressure during day (Moller et al., 1979). However, the active electric sense is energetically very costly. In gymnotiform wave- and pulse-type fish up to 30% of the total energy consumption is associated with active electrolocation (Salazar et al., 2013). In the presence of such a costly sense, one might ask why these fish still invest in additional senses, which provide similar information. For example, some other animals, such as the Mexican blind cave fish (*Astyanax mexicanus*) or the olm (*Proteus anguinus*), completely reduced their eyes as an adaptation to their extreme low light environments in caves and instead use their specialised mechanosensory lateral line system and, in case of the olm, the passive electric system for orientation (Jeffery, 2005; Roth & Schlegel, 1988; Uiblein, Durand, Juberthie, & Parzefall, 1992; Yoshizawa et al., 2010). However, in contrast to these animals, *G. petersii* lives in habitats, where even at night low light levels are present and with a much higher predation pressure. With its small working range the active electric sense is unable to provide information from afar, which would certainly increase the predation risk due to delayed predator detection in an uni-modal active electric system (Fechler & von der Emde, 2013; von der Emde et al., 2010; Westby, 1984). Therefore an additional far ranging sense such as vision provides an adaptational advantage.

With its grouped retina G. petersii possesses a specially adapted visual system. The grouped retina was first found in deep sea fish and thus was thought to be a pure adaptation to low light levels (Brauer, 1908). However, since then this retinal structure was also found in several shallow water fish and the spatial low-pass filter properties found in *G. petersii* suggest that it is additionally an adaptation to the fish´s turbid habitat (Francke et al., 2014; Kreysing et al., 2012; Pusch, 2013). The visual system of *G. petersii* with its grouped retina and high temporal but poor spatial resolution allows the detection of bigger and fast moving objects from afar reducing predation risk, whilst additionally reducing visual noise in the turbid environment (Pusch, Kassing, et al., 2013; Pusch, Wagner, et al., 2013). However, within an uni-modal visual system the poor spatial resolution would prevent the detection of its typical small food items especially since they are mainly hidden in the ground (Kreysing et al., 2012; Nwani et al., 2011; Schuster & Amtsfeld, 2002). Thus the active electric sense provides an additional foraging strategy by searching for food in the sediment, which decreases food competition with other non-electrosensory fish.

These advantages and constraints of both senses are perfectly balanced in the multisensory system reflected by the results of this thesis. My results show that the spatial information provided by vision and electrolocation can be used in different advantageous ways: 1) They can be used redundantly in case one sense is unavailable, as shown in the electrically silenced fish during object recognition, 2) they can be used complementarily for slightly different tasks as indicated by the results during object recognition, where the electric sense is dominant, and navigation, where visual landmarks improved route acquisition and 3) they can be used synergistically when integrated as shown by the improved multisensory performance during object recognition compared to the uni-modal performances.

Thereby the differences in perceptual range are reflected by the dynamic weighting of the sensory inputs described in chapter 2.1. During object recognition at close range, the advantages of the active electric sense are best utilised via a dominance of the electrical over the visual input. Here the electric sense provides fine-scale spatial information about an object such as distance, size and shape and additionally provides important information about material properties and thus informs whether an object is animate or not (von der Emde, 1993; von der Emde et al., 2010; von der Emde & Fetz, 2007; von der Emde & Ringer, 1992). These pieces of information allow the fish to detect and recognise food items even when buried in the sediment and are important when collecting information about environmental objects in the close proximity (Regett, 2016a, 2016b). The results of the feature detection test in chapter 2.2., during which the fish used specific features of the objects for electric but the general shape for visual object recognition, suggest that electrolocation provides more detailed information about the object, which can be used for the recognition task.

This electrosensory capture is comparable to the visual capture found in humans during spatial tasks, during which vision provides the most reliable and accurate information (Howard & Templeton, 1966b). Sensory illusions like the well-know ventriloquism effect, during which sounds from the ventriloquist appear to be coming from the moving mouth of the puppet, result from this visual dominance and are necessary to form a coherent multisensory percept (Alais & Burr, 2004).

The results of chapter 2.1. show that sensory weighting is dynamic and adjustable over distance in *G. petersii*. The same electrosensory capture, which is beneficial during multisensory integration at close range, would be fatal at longer range, where the electric sense provides no or only unreliable information. Consequently, the hierarchy is reversed at greater distances, utilising the longer perceptual range of the visual sense optimally. Visual object information from a greater distance can be used to aid navigational tasks as shown in chapter 3.1. During such tasks the use of more general object features for landmark detection as described in this thesis and by Schuster and Amtsfeld might even be beneficial (Schuster & Amtsfeld, 2002). Detailed object features are harder to detect from greater distances and might be view-dependent. Learning the more general outlines of an object might thus allow landmark-based navigation without relying on defined features. Some insects, for example, use template matching for navigation, a strategy, during which a more general template of a landmark is used to find back to the place, where the template was acquired (Cheng, 1999; Rüediger Wehner, Cheng, & Cruse, 2014). Similar mechanisms are also used for successful landmark-based navigation in mobile robots (Abe, Shikano, Fukuda, Arai, & Tanaka, 1998; Balkenius & Kopp, 1997).

The dynamic weighting found here in *G. petersii* is again comparable to mechanisms found in mammals where the hierarchy of the sensory inputs is adjusted according to their reliability (Ernst & Banks, 2002; Fetsch et al., 2009; Raposo, Sheppard, Schrater, & Churchland, 2012; Sheppard et al., 2013).

On the other hand, the anatomical data of the mechanosensory lateral line system indicate that here evolution led to a reduction of the system probably as an adaptation to the environment and the redundancy with the electric system. Whereas vision provides compensation for the short working range of active electrolocation, the mechanosensory lateral line system itself is also restricted to a short range (Hassan, 1985, 1989). The noisy environment of the natural habitat of *G. petersii*, fast running rivers, probably prevents the detection of detail information like e.g. the position of moving predators or prey using lateral line information (Engelmann et al., 2002; Engelmann et al., 2003). Furthermore in comparison to some surface feeding fish, which use the prey evoked water movements for prey localisation, the lateral line system is less appropriate for detecting the main food source of *G. petersii*, Chironomidae larvae, when buried in the sediment and therefore do not evoke many water movements (Bleckmann, 1986; Bleckmann & Topp, 1981). The additional competition about surface area and brain capacity between the electrosensory and the mechanosensory lateral line system therefore might have led to the reduction of the mechanosensory system in favour of the more valuable electrosensory system. Comparative anatomical studies between river-dwelling and lake-dwelling weakly electric fish might reveal in more detail, whether the reduction of the peripheral mechanosensory lateral line system is an adaptation to the noisy habitat, to the competition with the electric system or both.

Despite the morphological reduction, some behavioural evidence suggests that the mechanosensory lateral line input contributes synergistically to the multisensory system and the here presented anatomical data may also suggest a possible rheotactical use (Pluta & Kawasaki, 2008; Gerhard von der Emde & Horst Bleckmann, 1998). Thus the reduction could also be seen as a kind of specialisation of the lateral line system on the more basic features of hydrodynamic stimuli.

Together the results of my thesis show that all three senses are not just well adapted to the environmental conditions but also form a well adapted but flexible multisensory systems, in which each sense occupies a slightly different niche and still provides advantages through integration and compensation.

4.2. Cognition: Multisensory processing and cognitive abilities

While perception provides important external information, the information and thus the corresponding receptor organ provides only a selection advantage, if it influences the behavioural output of the animal. In order to do so sensory information needs to be processed and may be shaped through cognitive processes like learning and memory, resulting in a distinct behaviour, which provides the actual adaptive value for the animal (Alais et al., 2010). Consequently, the way how sensory input is processed and the cognitive abilities of an animal are as much part of the evolutionary selection process as is the peripheral structure of the receptor organs.

Processing multisensory information is highly complex as each sense provides slightly different information due to physical constrains of the different stimuli and receptors. While vision and electrolocation both provide spatial information about the environment, they do so in different ways and each sense provides bits of information that cannot be obtained by the other. As described above the active electric sense provides information only from the near field, whereas vision provides additional information from longer distances. On the other hand electrolocation is omnidirectional, providing information from all directions around the body, whereas the visual system of *G. petersii* is restricted to cone-shaped visual fields on both sides of the fish´s head, which slightly overlap in the front (Pusch, 2013). Furthermore, the active electric sense provides 3-dimentional information about objects even if they are visually covered, e.g. by other objects, and provides additional information about material and capacity, which are not provided by vision (Fechler & von der Emde, 2013; von der Emde, 1993; von der Emde & Ringer, 1992). In return, the visual system, although monochromatic, provides unique information about light intensity and the light reflection properties of objects (Kreysing et al., 2012). These differences between the individual inputs pose big challenges on the system, as congruent information has to be extracted from incongruent, in order to allow efficient multisensory integration (Ernst & Di Luca, 2011).

The integration of multiple sensory inputs is further complicated by the fact that even inputs obtained from the same source slightly differ in content due to inherent noise in all sensory system (Ernst & Bülthoff, 2004). The dynamic weighting of sensory inputs, demonstrated in some mammalian species and here for the first time in *G. petersii*, provides a tolerance against resulting discrepancies in sensory inputs, allowing the formation of a robust multisensory percept (Ernst & Banks, 2002; Fetsch et al., 2009; Sheppard et al., 2013). The more reliable a sensory input is, the more it will contribute to the overall percept, increasing the chance to receive reliable and accurate information from the environment (Ernst & Bülthoff, 2004).

Further inferences about how multisensory information is processed in these fish can be made based on the results of chapter 2.1. by showing that *G. petersii* is capable of spontaneous cross-modal object recognition. In order to fulfil this highly complex task, individual sensory inputs need to be processed in a way that allows flexible transfer of information between the senses. This allows information acquired and learned with one sense to be used by another sense and sets high requirements on the system (Cloke, Jacklin, & Winters, 2015). Temporally disjoint information from different senses, relying on different physical stimuli, have to be recognised as identical. Vision and electrolocation provide very different images of the environment, from which the object information has to be extracted and matched. As described in the discussion of chapter 2.1. this might be achieved in different ways: either through a matching format of the individual sensory inputs or via a generalisation of previously learned associations between the different inputs. The results of the feature detection tests in chapter 2.2. might slightly hint for the use of generalisation in *G. petersii*, as the fish seem to store very different aspects of the object during electrical and visual object recognition. During generalisation the detailed electrical information might be matched to the more general visual information based on previously learned association. However, further research is necessary to reveal the detailed processing mechanism underlying this cross-modal object recognition.

Both the robustness against discrepant inputs as well as the transferability of information between senses provide clear adaptive advantages as they allow the formation of a coherent but still flexible multisensory system and thus provide the foundation for a efficient use of multisensory information. The occurrence of similar processing mechanisms in mammals and in a fish raises the question whether these forms of multisensory processing evolved convergently in both groups or whether they are fundamental features of vertebrates and if similar mechanisms also occur in invertebrates.

The robustness against inherent discrepancies in sensory inputs is essential for a successful multisensory integration and thus processing mechanisms preventing a loss of reliability like the dynamic weighting of sensory inputs could be widely conserved across animals. For example, many insect species are known to use multisensory integration (Leonard & Masek, 2014; Wessnitzer & Webb, 2006) and similar weighting mechanisms were found e.g. during navigational tasks in desert ants, which weight and integrate conflicting celestial and terrestrial cues to determine their homing direction (Legge, Wystrach, Spetch, & Cheng, 2014).

Simpler forms of information transfer between senses were also found in some insects (Guo & Guo, 2005). However, these forms of multisensory transfer rely on direct associations built between two stimuli and thus on different processing mechanisms as the here described mechanisms fundamental for cross-modal object recognition. Since spontaneous cross-modal object recognition is processed in higher brain areas (at least in mammals) (Cloke et al., 2015; Taylor et al., 2006), it is less likely that this ability is conserved across invertebrates and vertebrates. To determine how far these or similar processing mechanisms are spread among animals, further comparative studies in vertebrates and invertebrates are necessary.

The adaptive value of such a multisensory system is further increased through cognitive abilities such as learning and memory, which increase the flexibility of the system. They allow sensory information to be stored and used at any time and thus enable an animal to fulfil complex tasks like object recognition and navigation. Furthermore, learning provides a means to adjust the system flexibly to changes of the environmental conditions.

The results of my thesis clearly underline the high cognitive abilities of *G. petersii*. The ability to recognise objects and associate them with positive or negative stimuli provides a clear selection advantage, as it allows the animal to avoid negative consequences or to identify food sources. Previous studies have shown that *G. petersii* is able to recognise objects based on a wide range of object properties using active electrolocation and vision (Schuster & Amtsfeld, 2002; von der Emde et al., 2010).

My results show additionally that these fish are capable of spontaneous cross-modal object recognition, a high cognitive function previously only known from a few mammalian species. This ability further increases the flexibility of the multisensory system and allows successful object recognition under a variety of environmental conditions. The effect of this ability might be increased, when information can be transferred between a short and a long range sense such as the active electric sense and vision. For example, it allows the fish to use information visually acquired from a greater distance on short range with the active electric sense and thus may help to put electrically gained information in a spatial context. This is supported by the results of the cross-modal landmark recognition tests in chapter 3.1. During these tests the fish were unable to learn the allocentric navigation task based on electrical landmarks, however, when previously trained with visual landmarks they were also able to use electrical landmarks. Thus this cross-modal landmark recognition also increases the flexibility of the system during navigational tasks. Navigation itself is a quite fundamental ability of actively moving animals and is thus widely spread among animals (T. S. Collett & Graham, 2004; Mouritsen, 2001). It allows an animal to actively interact with its surroundings and still be able to return to food sources, hiding places or mating sites.

While sensory information provides the fundament of such cognitive tasks, learning in return influences the way how sensory input is processed. This is shown, for example, by the results of the visually trained fish in chapter 2.2.. Through constant repetition the visual training remapped the weighting of the sensory inputs, so that after successful training the visual information dominated over the electrical input at close range. This remapping shows that learning and previous experience influence the weighting of sensory inputs, allowing flexible adjustment of the system to the current environmental conditions. The ability to adapt to changing conditions is of special importance in a highly variable environment such as the natural habitat of *G. petersii*. Drastic seasonal changes of the water levels, in addition to permanent strong currents in their home rivers, lead to an ever-changing habitat, which requires a flexible system, which might have led to a promotion of high cognitive abilities in these fish.

To better understand the convergent evolution of high cognitive abilities Emery and Clayton as well as Marino have compared the cognitive abilities of corvids or cetaceans with those of apes and humans and described some factors promoting the evolution of high cognitive abilities as well as physical requirements and some common abilities (Emery & Clayton, 2004; Marino, 2002). While a direct comparison of the cognitive abilities of *G. petersii* with those of humans, crows or cetaceans would be a stretch, some of the described mechanisms can be also found in these fish.

Besides the above mentioned variability of the environment both reviews mention that perishable food sources and social interactions promote high cognitive abilities. Both factors are at least partly applicable to *G. petersii*. Studies investigating the stomach contents of *G. petersii* have found that ca. 40 % of the caught fish had an empty stomach, suggesting that food is not freely available but has to be actively searched on the ground (Nwani et al., 2011). Furthermore, several studies show that, although adult *G. petersii* probably do not live in social groups under natural conditions, they interact and communicate with conspecifics, and groups kept in captivity form social hierarchies (Moller, 1980, 1995; Moller & Bauer, 1973; Moller et al., 1979; Neusel, 2014).

Furthermore, both reviews describe brain size as a fundamental factor restricting the cognitive abilities of an animal and state that crows and cetaceans have enlarged brains in comparison to other birds or mammals (Marino, 1998; Rogers &

Kaplan, 2012). This requirement is also met by the massively enlarged brain of *G. petersii* in comparison to other fish. The brain of *G. petersii* is responsible for a total of 60% of the body O_2 consumption (in comparison the human brain is responsible for about 20% of the O_2 consumption and in most other mammals this value does not exceed 8%) (Nilsson, 1996). When regarding the ratio of brain to body weight *G. petersii* actually has one of the biggest brains of all animals even slightly exceeding humans (Bell & Szabo, 1986; Meek & Joosten, 1989; Nieuwenhuys & Nicholson, 1967). While the size of the brain is not the only thing that matters, brain enlargement is an indicator for higher cognitive abilities.

In their review Emery and Clayton furthermore suggest a "cognitive toolkit" for corvids, apes and humans on which their "intelligent behaviour" is based. This toolkit consists of four cognitive tools: casual reasoning, flexibility, imagination and prospection. Without going into further detail casual reasoning, imagination and prospection probably do not apply to *G. petersii*. Flexibility on the other hand, which they define as the flexible use of learned information based on generalisations, is comparable to mechanisms underlying cross-modal object recognition described in this thesis. On a lower level, these similarities might suggest that comparable and maybe convergent to corvids in birds and cetaceans and primates in mammals, *G. petersii* evolved higher cognitive abilities in fish.

In conclusion, based on behavioural experiments this thesis provides new insights in the fundamental mechanisms underlying multisensory interactions in *G. petersii*, which enhance our understanding of the cognitive abilities of fish and which inform about the neuronal requirements underlying such abilities.

References

Abe, Y., Shikano, M., Fukuda, T., Arai, F., & Tanaka, Y. (1998). *Vision based navigation system by variable template matching for autonomous mobile robot.* Paper presented at the Robotics and Automation, 1998. Proceedings. 1998 IEEE International Conference on.

Able, K. P. (1980). Mechanisms of orientation, navigation and homing. *Animal migration, orientation and navigation*, 283-373.

Able, K. P. (1991). Common themes and variations in animal orientation systems. *American Zoologist*, 157-167.

Adams, W. J., Banks, M. S., & van Ee, R. (2001). Adaptation to three-dimensional distortions in human vision. *Nature neuroscience, 4*(11), 1063-1064.

Agrawal, S., Safarik, S., & Dickinson, M. (2014). The relative roles of vision and chemosensation in mate recognition of Drosophila melanogaster. *The Journal of experimental biology, 217*(15), 2796-2805.

Aho, A. C., Donner, K., Hyden, C., Larsen, L. O., & Reuter, T. (1988). Low retinal noise in animals with low body temperature allows high visual sensitivity. *Nature, 334*(6180), 348-350.

Alais, D., & Burr, D. (2004). The ventriloquist effect results from near-optimal bimodal integration. *Current Biology, 14*(3), 257-262.

Alais, D., Newell, F. N., & Mamassian, P. (2010). Multisensory processing in review: from physiology to behaviour. *Seeing and perceiving, 23*(1), 3-38.

Albert, J. S., & Crampton, W. G. (2006). Electroreception and Electrogenesis. In D. H. Evans & J. B. Clairborne (Eds.), *The physiology of fishes*. Boca Raton, FL: CRC Press.

Alerstam, T., Gudmundsson, G. A., Green, M., & Hedenström, A. (2001). Migration along orthodromic sun compass routes by arctic birds. *Science, 291*(5502), 300-303.

Alonso, J. M., & Stepanova, A. N. (2004). The Ethylene Signaling Pathway. *Science, 306*(5701), 1513-1515. doi:10.1126/science.1104812

Arendt, D. (2003). Evolution of eyes and photoreceptor cell types. *International Journal of Developmental Biology, 47*(7-8), 563-571.

Arendt, D., & Wittbrodt, J. (2001). Reconstructing the eyes of Urbilateria. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 356*(1414), 1545-1563. doi:10.1098/rstb.2001.0971

Arimoro, F. O., & Osakwe, E. I. (2006). The influence of sawmill wood wastes on the distribution and population of macroinvertebrates at Benin River, Niger Delta Area, Nigeria. *Chemistry & biodiversity, 3*(5), 578-592.

Arshavsky, V. Y. (2002). Like night and day: rods and cones have different pigment regeneration pathways. *Neuron, 36*(1), 1-3.

Ayala, F. J. (2007). Darwin's greatest discovery: Design without designer. *Proceedings of the National Academy of Sciences, 104*(suppl 1), 8567-8573. doi:10.1073/pnas.0701072104

Bacelo, J., Engelmann, J., Hollmann, M., von der Emde, G., & Grant, K. (2008). Functional foveae in an electrosensory system. *Journal of Comparative Neurology, 511*(3), 342-359.

Baker, C. V., Modrell, M. S., & Gillis, J. A. (2013). The evolution and development of vertebrate lateral line electroreceptors. *Journal of Experimental Biology, 216*(13), 2515-2522.

Balkenius, C., & Kopp, L. (1997). Elastic template matching as a basis for visual landmark recognition and spatial navigation. *Lund University Cognitive Science*, 1-10.

Barlow, H. B. (1956). Retinal noise and absolute threshold. *JOSA, 46*(8), 634-639.

Bassett, D. K., Carton, A. G., & Montgomery, J. C. (2006). Flowing water decreases hydrodynamic signal detection in a fish with an epidermal lateral-line system. *Marine and Freshwater Research, 57*(6), 611-617.

Bear, M. F., Connors, B. W., & Paradiso, M. A. (2007). *Neuroscience* (Vol. 2): Lippincott Williams & Wilkins.

Behr, K. (2009). *Entfernungsabhängige Objektunterscheidung und räumliches Auflösungsvermögen während der aktiven Elektroortung beim schwachelektrischen Fisch Gnathonemus petersii.* (Diplomarbeit), Universität Bonn, Bonn.

Bell, C. C., & Maler, L. (2005). Central neuroanatomy of electrosensory systems in fish *Electroreception* (pp. 68-111): Springer.

Bell, C. C., & Szabo, T. (1986). Electroreception in mormyrid fish: central anatomy. *Electroreception*, 375-421.

Benhamou, S., Sauvé, J.-P., & Bovet, P. (1990). Spatial memory in large scale movements: efficiency and limitation of the egocentric coding process. *Journal of Theoretical Biology, 145*(1), 1-12.

Berra, T. M. (2001). *Freshwater fish distribution*: Academic Press.

Biegler, R., & Morris, R. (1996). Landmark stability: studies exploring whether the perceived stability of the environment influences spatial representation. *Journal of Experimental Biology, 199*(1), 187-193.

Bingman, V. P., & Cheng, K. (2005). Mechanisms of animal global navigation: comparative perspectives and enduring challenges. *Ethology Ecology & Evolution, 17*(4), 295-318. doi:10.1080/08927014.2005.9522584

Biro, D., Guilford, T., & Dawkins, M. S. (2003). Mechanisms of visually mediated site recognition by the homing pigeon. *Animal Behaviour, 65*(1), 115-122. doi:https://doi.org/10.1006/anbe.2002.2014

Bleckmann, H. (1986). Role of the lateral line in fish behaviour *The behaviour of teleost fishes* (pp. 177-202): Springer.

Bleckmann, H., & Mogdans, J. (2014). Central Processing of Lateral Line Information. In S. Coombs, H. Bleckmann, R. R. Fay, & A. N. Popper (Eds.), *The Lateral Line System* (pp. 253-280). New York, NY: Springer New York.

Bleckmann, H., & Münz, H. (1990). Physiology of lateral-line mechanoreceptors in a teleost with highly branched, multiple lateral lines. *Brain, behavior and evolution, 35*(4), 240-250.

Bleckmann, H., & Topp, G. (1981). Surface wave sensitivity of the lateral line organs of the topminnow Aplocheilus lineatus. *Naturwissenschaften, 68*(12), 624-625.

Bleckmann, H., & Zelick, R. (1993). The responses of peripheral and central mechanosensory lateral line units of weakly electric fish to moving objects. *Journal of Comparative Physiology A, 172*(1), 115-128.

Bleckmann, H., & Zelick, R. (2009). Lateral line system of fish. *Integrative Zoology, 4*(1), 13-25. doi:10.1111/j.1749-4877.2008.00131.x

Bodznick, D., & Northcutt, R. G. (1980). Segregation of electro- and mechanoreceptive inputs to the elasmobranch medulla. *Brain research, 195*(2), 313-321. doi:http://dx.doi.org/10.1016/0006-8993(80)90067-0

Braam, J. (2005). In touch: plant responses to mechanical stimuli. *New Phytologist, 165*(2), 373-389. doi:10.1111/j.1469-8137.2004.01263.x

Braithwaite, V., & De Perera, T. B. (2006). Short-range orientation in fish: how fish map space. *Marine and freshwater behaviour and physiology, 39*(1), 37-47.

Brauer, A. (1908). Die Tiefseefische. II. Anatomischer Teil. In C. Chun (Ed.), *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer “Valdivia" 1898-1899*. Jena: Fischer.

Braun, C. B., Coombs, S., & Fay, R. R. (2002). What is the nature of multisensory interaction between octavolateralis sub-systems? *Brain, behavior and evolution, 59*(4), 162-176.

Braun, C. B., & Northcutt, R. G. (1997). The lateral line system of hagfishes (Craniata: Myxinoidea). *Acta Zoologica, 78*(3), 247-268.

Brenner, T., Korte, E., & Schneider, J. (2002). *Rheinfischfauna 2000: was lebt zwischen dem Rheinfall bei Schaffhausen und der Nordsee* Internationale Kommission zum Schutze des Rheins (IKSR).

Broglio, C., Gomez, A., Duran, E., Ocana, F., Jiménez-Moya, F., Rodriguez, F., & Salas, C. (2005). Hallmarks of a common forebrain vertebrate plan: specialized pallial areas for spatial, temporal and emotional memory in actinopterygian fish. *Brain research bulletin, 66*(4), 277-281.

Bruns, V. (1971). Elektrisches Organ vonGnathonemus (Mormyridae). *Zeitschrift für Zellforschung und mikroskopische Anatomie, 122*(4), 538-563.

Buehlmann, C., Hansson, Bill S., & Knaden, M. (2012). Path Integration Controls Nest-Plume Following in Desert Ants. *Current Biology, 22*(7), 645-649. doi:https://doi.org/10.1016/j.cub.2012.02.029

Bullock, T. H. (1973). Seeing the World through a New Sense: Electroreception in Fish: Sharks, catfish, and electric fish use low-or high-frequency electroreceptors, actively and passively, in object detection and social communication. *American Scientist, 61*(3), 316-325.

Bullock, T. H., Bodznick, D. A., & Northcutt, R. G. (1993). The phylogenetic distribution of electroreception: evidence for convergent evolution of a primitive vertebrate sense modality *How do Brains Work?* (pp. 581-602): Springer.

Bullock, T. H., Hopkins, C. D., & Fay, R. R. (2006). *Electroreception* (Vol. 21): Springer Science & Business Media.

Burighel, P., Lane, N. J., Fabio, G., Stefano, T., Zaniolo, G., Carnevali, M. D. C., & Manni, L. (2003). Novel, secondary sensory cell organ in ascidians: in search of the ancestor of the vertebrate lateral line. *Journal of Comparative Neurology, 461*(2), 236-249.

Burns, M. E., & Lamb, T. D. (2003). Visual transduction by rod and cone photoreceptors. *The visual neurosciences*, 215-233.

Burt, T., Holland, R., & Guilford, T. (1997). Further evidence for visual landmark involvement in the pigeon's familiar area map. *Animal Behaviour, 53*(6), 1203-1209. doi:https://doi.org/10.1006/anbe.1996.0389

Butler, J. M., & Maruska, K. P. (2015). The mechanosensory lateral line is used to assess opponents and mediate aggressive behaviors during territorial interactions in an African cichlid fish. *The Journal of experimental biology, 218*(20), 3284-3294. doi:10.1242/jeb.125948

Cain, P. (1995). Navigation in familiar environments by the weakly electric elephantnose fish, Gnathonemus petersii L.(Mormyriformes, Teleostei). *Ethology, 99*(4), 332-349.

Cain, P., Gerin, W., & Moller, P. (1994). Short-range Navigation of the Weakly Electric Fish, Gnathonemus petersii L.(Mormyridae, Teleostei), in Novel and Familiar Environments. *Ethology, 96*(1), 33-45.

Cain, P., & Malwal, S. (2002). Landmark use and development of navigation behaviour in the weakly electric fish Gnathonemus petersii (Mormyridae; Teleostei). *Journal of Experimental Biology, 205*(24), 3915-3923.

Caputi, A., Budelli, R., Grant, K., & Bell, C. (1998). The electric image in weakly electric fish: physical images of resistive objects in Gnathonemus petersii. *Journal of Experimental Biology, 201*(14), 2115-2128.

Carr, C. E., Maler, L., & Sas, E. (1982). Peripheral organization and central projections of the electrosensory nerves in gymnotiform fish. *The Journal of Comparative Neurology, 211*(2), 139-153.

Cassin, B., Solomon, S., & Rubin, M. L. (1984). *Dictionary of eye terminology*: Triad Pub. Co.

Chandrashekar, J., Hoon, M. A., Ryba, N. J., & Zuker, C. S. (2006). The receptors and cells for mammalian taste. *Nature, 444*(7117), 288-294.

Cheng, K. (1999). Landmark-based spatial search in honeybees. I. *Animal Cognition, 2*(2), 73-78. doi:10.1007/s100710050026

Ciali, S., Gordon, J., & Moller, P. (1997). Spectral sensitivity of the weakly discharging electric fish Gnathonemus petersi using its electric organ discharges as the response measure. *Journal of Fish Biology, 50*(5), 1074-1087. doi:10.1111/j.1095-8649.1997.tb01631.x

Clarke, D. (2015). *Electro-reception in bumblebees.* University of Bristol.

Cloke, J. M., Jacklin, D. L., & Winters, B. D. (2015). The neural bases of crossmodal object recognition in non-human primates and rodents: A review. *Behavioural brain research, 285*, 118-130. doi:http://dx.doi.org/10.1016/j.bbr.2014.09.039

Cohen, A. I. (1963). Vertebrate retinal cells and their organization. *Biological Reviews, 38*(4), 427-459.

Collett, T. S., Collett, M., & Wehner, R. (2001). The guidance of desert ants by extended landmarks. *Journal of Experimental Biology, 204*(9), 1635-1639.

Collett, T. S., & Graham, P. (2004). Animal navigation: path integration, visual landmarks and cognitive maps. *Current Biology, 14*(12), R475-R477.

Collett, T. S., & Rees, J. A. (1997). View-based navigation in Hymenoptera: multiple strategies of landmark guidance in the approach to a feeder. *Journal of Comparative Physiology A, 181*(1), 47-58. doi:10.1007/s003590050092

Coombs, S., Bleckmann, H., Fay, R. R., & Popper, A. N. (2014). *The lateral line system*: Springer.

Coombs, S., Görner, P., & Münz, H. (2012). *The Mechanosensory Lateral Line: Neurobiology and Evolution*: Springer New York.

Coombs, S., Janssen, J., & Montgomery, J. (1992). Functional and Evolutionary Implications of Peripheral Diversity in Lateral Line Systems. In D. B. Webster, A. N. Popper, & R. R. Fay (Eds.), *The Evolutionary Biology of Hearing* (pp. 267-294). New York, NY: Springer New York.

Coombs, S., Janssen, J., & Webb, J. F. (1988). Diversity of lateral line systems: evolutionary and functional considerations *Sensory biology of aquatic animals* (pp. 553-593): Springer.

Cowey, A., & Weiskrantz, L. (1975). Demonstration of cross-modal matching in rhesus monkeys, Macaca mulatta. *Neuropsychologia, 13*(1), 117-120.

Curcio, C. A., Sloan, K. R., Kalina, R. E., & Hendrickson, A. E. (1990). Human photoreceptor topography. *The Journal of Comparative Neurology, 292*(4), 497-523. doi:10.1002/cne.902920402

Czech-Damal, N. U., Liebschner, A., Miersch, L., Klauer, G., Hanke, F. D., Marshall, C., . . . Hanke, W. (2011). Electroreception in the Guiana dolphin (Sotalia guianensis). *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20111127.

Dangelmayer, S., Benda, J., & Grewe, J. Weakly electric fish learn both visual and electrosensory cues in a multisensory object discrimination task. *Journal of Physiology-Paris*. doi:http://dx.doi.org/10.1016/j.jphysparis.2016.10.007

Darwin, C. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.

Davenport, R. K., & Rogers, C. M. (1970). Intermodal equivalence of stimuli in apes. *Science*.

Dijkgraaf, S. (1963). The functioning and significance of the lateral-line organs. *Biological Reviews, 38*(1), 51-105.

Donner, K. (1992). Noise and the absolute thresholds of cone and rod vision. *Vision research, 32*(5), 853-866. doi:http://dx.doi.org/10.1016/0042-6989(92)90028-H

Doty, R. L. (2015). *Handbook of olfaction and gustation*: John Wiley & Sons.

Dowling, J. E. (1987). *The retina: an approachable part of the brain*: Harvard University Press.

Dowling, J. E., & Boycott, B. (1966). Organization of the primate retina: electron microscopy. *Proceedings of the Royal Society of London B: Biological Sciences, 166*(1002), 80-111.

Dowling, J. E., & Ehinger, B. (1975). Synaptic organization of the amine-containing interplexiform cells of the goldfish and Cebus monkey retinas. *Science, 188*(4185), 270-273. doi:10.1126/science.804181

Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science, 306*(5703), 1903-1907.

Engelmann, J., Hanke, W., & Bleckmann, H. (2002). Lateral line reception in still and running water. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 188*(7), 513-526.

Engelmann, J., Kröther, S., Bleckmann, H., & Mogdans, J. (2003). Effects of running water on lateral line responses to moving objects. *Brain, behavior and evolution, 61*(4), 195-212.

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature, 415*(6870), 429-433.

Ernst, M. O., & Bülthoff, H. H. (2004). Merging the senses into a robust percept. *Trends in cognitive sciences, 8*(4), 162-169.

Ernst, M. O., & Di Luca, M. (2011). Multisensory perception: from integration to remapping. *Sensory cue integration*, 224-250.

Etienne, A. S., Berlie, J., Georgakopoulos, J., & Maurer, R. (1998). Role of dead reckoning in navigation *Spatial representation in animals* (pp. 54-68). New York, NY, US: Oxford University Press.

Etienne, A. S., & Jeffery, K. J. (2004). Path integration in mammals. *Hippocampus, 14*(2), 180-192. doi:10.1002/hipo.10173

Etienne, A. S., Maurer, R., Berlie, J., Reverdin, B., Rowe, T., Georgakopoulos, J., & Seguinot, V. (1998). Navigation through vector addition. *Nature, 396*(6707), 161-164.

Etienne, A. S., Maurer, R., & Séguinot, V. (1996). Path integration in mammals and its interaction with visual landmarks. *The Journal of experimental biology, 199*(1), 201-209.

Ettlinger, G., & Wilson, W. (1990). Cross-modal performance: behavioural processes, phylogenetic considerations and neural mechanisms. *Behavioural brain research, 40*(3), 169-192.

Falke, J. J., & Hazelbauer, G. L. (2001). Transmembrane signaling in bacterial chemoreceptors. *Trends in biochemical sciences, 26*(4), 257-265.

Fechler, K. (2016). *Die Analyse komplexer Szenen während der aktiven Elektroortung bei Gnathonemus petersii: Objekterkennung, räumliches Auflösungsvermögen und lokomotorisches Verhalten.* (Dissertation), Universität Bonn, Bonn.

Fechler, K., Holtkamp, D., Neusel, G., Sanguinetti-Scheck, J., Budelli, R., & von der Emde, G. (2012). Mind the gap: the minimal detectable separation distance between two objects during active electrolocation. *Journal of Fish Biology, 81*(7), 2255-2276.

Fechler, K., & von der Emde, G. (2013). Figure–ground separation during active electrolocation in the weakly electric fish, Gnathonemus petersii. *Journal of Physiology-Paris, 107*(1), 72-83.

Fernald, R. D. (1997). The evolution of eyes. *Brain, behavior and evolution, 50*(4), 253-259.

Fernald, R. D. (2000). Evolution of eyes. *Current Opinion in Neurobiology, 10*(4), 444-450.

Fetsch, C. R., Turner, A. H., DeAngelis, G. C., & Angelaki, D. E. (2009). Dynamic reweighting of visual and vestibular cues during self-motion perception. *The Journal of Neuroscience, 29*(49), 15601-15612.

Fetz, S. (2005). *Dreidimensionale Objekterkennung bei Gnathonemus petersii.* (Diplomarbeit), Universität Bonn, Bonn.

Fine, B. S., & Zimmerman, L. E. (1962). Miiller's cells and the" middle limiting membrane" of the human retina. *Invest. Ophth, 1*, 304.

Firestein, S. (2001). How the olfactory system makes sense of scents. *Nature, 413*(6852), 211-218.

Flock, Å. (1967). Ultrastructure and function in the lateral line organs. *Lateral line detectors, 12*, 163-197.

Folde, C. (2006). *Erkennung der Form und Größe von Objekten durch aktive Elektroortung bei Gnathonemus petersii.* (Diplomarbeit), Universität Bonn, Bonn.

Forrester, J. V., Dick, A. D., McMenamin, P. G., Roberts, F., & Pearlman, E. (2015). *The eye: basic sciences in practice*: Elsevier Health Sciences.

Francke, M., Kreysing, M., Mack, A., Engelmann, J., Karl, A., Makarov, F., . . . Pusch, R. (2014). Grouped retinae and tapetal cups in some Teleostian fish: Occurrence, structure, and function. *Progress in retinal and eye research, 38*, 43-69.

Fu, Y. (2010). Phototransduction in Rods and Cones by Yingbin Fu *The Organization of the Retina and Visual System*: Webvision.

Fu, Y., Kefalov, V., Luo, D.-G., Xue, T., & Yau, K.-W. (2008). Quantal noise from human red cone pigment. *Nat Neurosci, 11*(5), 565-571.

Fuster, J. M., Bodner, M., & Kroger, J. K. (2000). Cross-modal and cross-temporal association in neurons of frontal cortex. *Nature, 405*(6784), 347-351.

Gagliardo, A. (2013). Forty years of olfactory navigation in birds. *Journal of Experimental Biology, 216*(12), 2165-2171.

Gallant, J. R., Traeger, L. L., Volkening, J. D., Moffett, H., Chen, P.-H., Novina, C. D., . . . Pinch, M. (2014). Genomic basis for the convergent evolution of electric organs. *Science, 344*(6191), 1522-1525.

Gaydos, H. F. (1956). Intersensory transfer in the discrimination of form. *The American journal of psychology*, 107-110.

Gebhardt, K., Böhme, M., & von der Emde, G. (2012). Electrocommunication behaviour during social interactions in two species of pulse-type weakly electric fishes (Mormyridae). *Journal of Fish Biology, 81*(7), 2235-2254.

Gehring, W. J. (2004). Historical perspective on the development and evolution of eyes and photoreceptors. *International Journal of Developmental Biology, 48*(8-9), 707-717.

Gehring, W. J., & Ikeo, K. (1999). Pax 6: mastering eye morphogenesis and eye evolution. *Trends in Genetics, 15*(9), 371-377.

Gellermann, L. W. (1933). Chance orders of alternating stimuli in visual discrimination experiments. *The Pedagogical Seminary and Journal of Genetic Psychology, 42*(1), 206-208.

Ghysen, A., & Dambly-Chaudiere, C. (2004). Development of the zebrafish lateral line. *Current Opinion in Neurobiology, 14*(1), 67-73.

Ghysen, A., & Dambly-Chaudière, C. (2007). The lateral line microcosmos. *Genes & development, 21*(17), 2118-2130.

Girvan, J. R., & Braithwaite, V. A. (1998). Population differences in spatial learning in three–spined sticklebacks. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 265*(1399), 913-918. doi:10.1098/rspb.1998.0378

Gleason, M. R., Nagiel, A., Jamet, S., Vologodskaia, M., López-Schier, H., & Hudspeth, A. (2009). The transmembrane inner ear (Tmie) protein is essential for normal hearing and balance in the zebrafish. *Proceedings of the National Academy of Sciences, 106*(50), 21347-21352.

Godement, P., Salaün, J., & Mason, C. A. (1990). Retinal axon pathfinding in the optic chiasm: divergence of crossed and uncrossed fibers. *Neuron, 5*(2), 173-186.

Gomelsky, M., & Hoff, W. D. (2011). Light helps bacteria make important lifestyle decisions. *Trends in microbiology, 19*(9), 441-448.

Graff, C., Kaminski, G., Gresty, M., & Ohlmann, T. (2004). Fish perform spatial pattern recognition and abstraction by exclusive use of active electrolocation. *Current Biology, 14*(9), 818-823.

Gregson, J., & Burt de Perera, T. (2007). Shoaling in eyed and blind morphs of the characin Astyanax fasciatus under light and dark conditions. *Journal of Fish Biology, 70*(5), 1615-1619.

Guo, J., & Guo, A. (2005). Crossmodal interactions between olfactory and visual learning in Drosophila. *Science, 309*(5732), 307-310.

Häder, D. (1987). Photosensory behavior in procaryotes. *Microbiological reviews, 51*(1), 1.

Hassan, E. S. (1985). Mathematical analysis of the stimulus for the lateral line organ. *Biological Cybernetics, 52*(1), 23-36.

Hassan, E. S. (1989). Hydrodynamic imaging of the surroundings by the lateral line of the blind cave fish Anoptichthys jordani *The Mechanosensory Lateral Line* (pp. 217-227): Springer.

Healy, S. E. (1998). *Spatial representation in animals*: Oxford University Press.

Hebets, E. A., Aceves-Aparicio, A., Aguilar-Argüello, S., Bingman, V. P., Escalante, I., Gering, E. J., . . . Segura-Hernández, L. (2014). Multimodal sensory reliance in the nocturnal homing of the amblypygid Phrynus pseudoparvulus (Class Arachnida, Order Amblypygi)? *Behavioural Processes, 108*, 123-130.

Hecht, S., Shlaer, S., & Pirenne, M. H. (1942). Energy, quanta, and vision. *The Journal of general physiology, 25*(6), 819-840.

Heegaard, S., Jensen, O., & Prause, J. (1986). Structure and composition of the inner limiting membrane of the retina. *Graefe's archive for clinical and experimental ophthalmology, 224*(4), 355-360.

Heiligenberg, W. (1973). Electrolocation of objects in the electric fishEigenmannia (Rhamphichthyidae, Gymnotoidei). *Journal of comparative physiology, 87*(2), 137-164.

Heiligenberg, W. (1987). Central processing of sensory information in electric fish. *Journal of Comparative Physiology A, 161*(4), 621-631.

Henninger, J., Benda, J., & Krahe, R. (2012). *Undisturbed long-term monitoring of weakly electric fish in a small stream in Panama.* Paper presented at the Front Behav Neurosci Conference Abstract: Tenth International Congress of Neuroethology. doi: 10.3389/conf. fnbeh.

Herman, L. M., Pack, A. A., & Hoffmann-Kuhnt, M. (1998). Seeing through sound: Dolphins (Tursiops truncatus) perceive the spatial structure of objects through echolocation. *Journal of Comparative Psychology, 112*(3), 292.

Hernández, P. P., Olivari, F. A., Sarrazín, A. F., Sandoval, P. C., & Allende, M. L. (2007). Regeneration in zebrafish lateral line neuromasts: Expression of the neural progenitor cell marker sox2 and proliferation-dependent and-independent mechanisms of hair cell renewal. *Developmental neurobiology, 67*(5), 637-654.

Hofer, B. (1908). Studien über die Hautsinnesorgane der Fische I. *Die Funktion der Seitenorgane bei den Fischen. Ber Kgl Bayer Biol Versuchsstation München, 1*, 115-168.

Holland, R. A., Winter, P., & Waters, D. A. (2005). Sensory systems and spatial memory in the fruit bat Rousettus aegyptiacus. *Ethology, 111*(8), 715-725.

Hollmann, M. (2008). *Die elektrorezeptiven Foveae von Gnathonemus petersii: Rezeptorverteilung, Rezeptormorphologie und Futtersuchverhalten.* (Dissertation), Universität Bonn, Bonn.

Hollmann, M., Engelmann, J., & von der Emde, G. (2008). Distribution, density and morphology of electroreceptor organs in mormyrid weakly electric fish: anatomical investigations of a receptor mosaic. *Journal of Zoology, 276*(2), 149-158.

Hopkins, C. (2009). Electrical perception and communication. *Encyclopedia of neuroscience, 3*, 813-831.

Hopkins, C. D. (1988). Neuroethology of electric communication. *Annual review of neuroscience, 11*(1), 497-535.

Howard, I. P., & Templeton, W. B. (1966a). *Human spatial orientation*. London; New York: Wiley.

Howard, I. P., & Templeton, W. B. (1966b). Human spatial orientation.

Hurly, A. T., & Healy, S. D. (1996). Memory for flowers in rufous hummingbirds: location or local visual cues? *Animal Behaviour, 51*(5), 1149-1157.

Jeffery, W. R. (2005). Adaptive evolution of eye degeneration in the Mexican blind cavefish. *Journal of Heredity, 96*(3), 185-196.

Jékely, G. (2009). Evolution of phototaxis. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1531), 2795-2808.

Jorgensen, J. M. (2005). Morphology of electroreceptive sensory organs. *Springer Handbook of Auditory Research, 21*, 47.

Jørgensen, J. M. (1989). Evolution of Octavolateralis Sensory Cells. In S. Coombs, P. Görner, & H. Münz (Eds.), *The Mechanosensory Lateral Line: Neurobiology and Evolution* (pp. 115-145). New York, NY: Springer New York.

Kaas, J. H. (2004). The evolution of the visual system in primates. *The visual neurosciences, 2*, 1563-1572.

Kalloniatis, M., & Luu, C. (2015). Color perception *The organization of the retina and visual system*: Webvision.

Kalmijn, A. J. (1966). Electro-perception in sharks and rays. *Nature, 212*(5067), 1232-1233.

Kanter, M. J., & Coombs, S. (2003). Rheotaxis and prey detection in uniform currents by Lake Michigan mottled sculpin (Cottus bairdi). *Journal of Experimental Biology, 206*(1), 59-70.

Klatzky, R. L. (1998). *Allocentric and egocentric spatial representations: Definitions, distinctions, and interconnections.* Paper presented at the Spatial cognition.

Kolb, H. (2007a). Gross anatomy of the eye *The Organization of the Retina and Visual System* Webversion.

Kolb, H. (2007b). Inner plexiform layer *The Organization of the Retina and Visual System*: Webvision.

Kolb, H. (2007c). Outer plexiform layer *The Organization of the Retina and Visual System*: Webvision.

Kolb, H. (2011). Photoreceptors *The Organization of the Retina and Visual System.* : Webvision.

Kreysing, M., Pusch, R., Haverkate, D., Landsberger, M., Engelmann, J., Ruiter, J., . . . Francke, M. (2012). Photonic crystal light collectors in fish retina improve vision in turbid water. *Science, 336*(6089), 1700-1703.

Lacey, S., Campbell, C., & Sathian, K. (2007). Vision and touch: multiple or multisensory representations of objects? *Perception-London, 36*(10), 1513-1522.

Lamb, T. D., Collin, S. P., & Pugh, E. N. (2007). Evolution of the vertebrate eye: opsins, photoreceptors, retina and eye cup. *Nature Reviews Neuroscience, 8*(12), 960-976.

Land, M. F., & Fernald, R. D. (1992). The evolution of eyes. *Annual review of neuroscience, 15*(1), 1-29.

Landsberger, M., von der Emde, G., Haverkate, D., Schuster, S., Gentsch, J., Ulbricht, E., . . . Wagner, H.-J. (2008). Dim light vision–morphological and functional adaptations of the eye of the mormyrid fish, Gnathonemus petersii. *Journal of Physiology-Paris, 102*(4), 291-303.

Lavoué, S., Miya, M., Arnegard, M. E., Sullivan, J. P., Hopkins, C. D., & Nishida, M. (2012). Comparable ages for the independent origins of electrogenesis in African and South American weakly electric fishes. *PLoS one, 7*(5), e36287.

Lázár, G., Libouban, S., & Szabo, T. (1984). The mormyrid mesencephalon. III. Retinal projections in a weakly electric fish, Gnathonemus petersii. *Journal of Comparative Neurology, 230*(1), 1-12.

Legge, E. L. G., Wystrach, A., Spetch, M. L., & Cheng, K. (2014). Combining sky and earth: desert ants (Melophorus bagoti) show weighted integration of celestial and terrestrial cues. *The Journal of experimental biology, 217*(23), 4159-4166. doi:10.1242/jeb.107862

Leonard, A. S., & Masek, P. (2014). Multisensory integration of colors and scents: insights from bees and flowers. *Journal of Comparative Physiology A, 200*(6), 463-474.

Leydig, F. (1850). Ueber die Schleimkanäle der Knochenfische. *Mull Arch Anat Physiol*, 170-181.

Lihoreau, M., & Raine, N. E. (2013). Bee positive: the importance of electroreception in pollinator cognitive ecology. *Frontiers in psychology, 4*.

Lissmann, H. (1951). Continuous Electrical Signals from the Tail of a Fish, Gymnarchus niloticus Cuv. *Nature, 167*(4240), 201-202.

Lissmann, H. (1958). On the function and evolution of electric organs in fish. *Journal of Experimental Biology, 35*(1), 156-191.

Lissmann, H., & Machin, K. (1958). The mechanism of object location in Gymnarchus niloticus and similar fish. *Journal of Experimental Biology, 35*(2), 451-486.

Locket, N. A. (1970). Deep-sea fish retinas. *British medical bulletin, 26*(2), 107-111.

Locket, N. A. (1971). Retinal Anatomy in Some Scopelarchid Deep-sea Fishes. *Proceedings of the Royal Society of London. Series B. Biological Sciences, 178*(1051), 161-184. doi:10.1098/rspb.1971.0059

Loomis, J. M., Klatzky, R. L., Golledge, R. G., & Philbeck, J. W. (1999). Human navigation by path integration. *Wayfinding behavior: Cognitive mapping and other spatial processes*, 125-151.

López, J. C., Broglio, C., Rodríguez, F., Thinus-Blanc, C., & Salas, C. (1999). Multiple spatial learning strategies in goldfish (Carassius auratus). *Animal Cognition, 2*(2), 109-120.

Magosso, E., Cuppini, C., Serino, A., Di Pellegrino, G., & Ursino, M. (2008). A theoretical study of multisensory integration in the superior colliculus by a neural network model. *Neural Networks, 21*(6), 817-829.

Mainz, T., Schmitz, A., & Schmitz, H. (2004). Variation in number and differentiation of the abdominal infrared receptors in the Australian ‘fire-beetle’Merimna atrata (Coleoptera, Buprestidae). *Arthropod structure & development, 33*(4), 419-430.

Marino, L. (1998). A comparison of encephalization between odontocete cetaceans and anthropoid primates. *Brain, behavior and evolution, 51*(4), 230-238.

Marino, L. (2002). Convergence of complex cognitive abilities in cetaceans and primates. *Brain, behavior and evolution, 59*(1-2), 21-32.

Martin, G. R. (1982). An owl's eye: Schematic optics and visual performance inStrix aluco L. *Journal of comparative physiology, 145*(3), 341-349. doi:10.1007/bf00619338

Martinac, B., Delcour, A., Buechner, M., Adler, J., & Kung, C. (1992). Mechanosensitive ion channels in bacteria *Comparative Aspects of Mechanoreceptor Systems* (pp. 3-18): Springer.

Maruska, K. P., & Tricas, T. C. (1998). Morphology of the mechanosensory lateral line system in the Atlantic stingray, Dasyatis sabina: the mechanotactile hypothesis. *Journal of morphology, 238*(1), 1-22.

Mata, N. L., Radu, R. A., Clemmons, R. S., & Travis, G. H. (2002). Isomerization and Oxidation of Vitamin A in Cone-Dominant Retinas: A Novel Pathway for Visual-Pigment Regeneration in Daylight. *Neuron, 36*(1), 69-80. doi:http://dx.doi.org/10.1016/S0896-6273(02)00912-1

McCormick, C. A. (1989). Central Lateral Line Mechanosensory Pathways in Bony Fish. In S. Coombs, P. Görner, & H. Münz (Eds.), *The Mechanosensory Lateral Line: Neurobiology and Evolution* (pp. 341-364). New York, NY: Springer New York.

Meek, J., & Joosten, H. (1989). Distribution of serotonin in the brain of the mormyrid teleost Gnathonemus petersii. *Journal of Comparative Neurology, 281*(2), 206-224.

Merriless, M., & Crossman, E. (1973a). Surface pits in the family Esocidae. I. Structure and types. *Journal of morphology, 141*(3), 307-320.

Merriless, M., & Crossman, E. (1973b). Surface pits in the family Esocidae. II. Epidermal dermal interaction and evidence for aplasia of the lateral line sensory system. *Journal of morphology, 141*(3), 321-343.

Mittelstaedt, M.-L., & Mittelstaedt, H. (1980). Homing by path integration in a mammal. *Naturwissenschaften, 67*(11), 566-567. doi:10.1007/bf00450672

Mittelstaedt, M.-L., & Mittelstaedt, H. (2001). Idiothetic navigation in humans: estimation of path length. *Experimental Brain Research, 139*(3), 318-332. doi:10.1007/s002210100735

Molenaar, G. J. (1992). Anatomy and physiology of infrared sensitivity of snakes. *Biology of the Reptilia, 17*, 367-453.

Moller, P. (1980). Electroreception and the behaviour of mormyrid electric fish. *Trends in Neurosciences, 3*(5), 105-109.

Moller, P. (1995). *Electric fishes: history and behavior* (Vol. 17): Chapman & Hall.

Moller, P. (2002). Multimodal sensory integration in weakly electric fish: a behavioral account. *Journal of Physiology-Paris, 96*(5), 547-556.

Moller, P., & Bauer, R. (1973). 'Communication'in weakly electric fish, Gnathonemus petersii (Mormyridae) II. Interaction of electric organ discharge activities of two fish. *Animal Behaviour, 21*(3), 501-512.

Moller, P., Serrier, J., Belbenoit, P., & Push, S. (1979). Notes on ethology and ecology of the Swashi River mormyrids (Lake Kainji, Nigeria). *Behavioral Ecology and Sociobiology, 4*(4), 357-368.

Montgomery, J., Coombs, S., & Halstead, M. (1995). Biology of the mechanosensory lateral line in fishes. *Reviews in Fish Biology and Fisheries, 5*(4), 399-416.

Moritz, T. (2010). Fishes of Iguidi River—a small forest stream in South-East Benin. *Ichthyological Exploration of Freshwaters, 21*(1), 9.

Mouritsen, H. (2001). Navigation in birds and other animals. *Image and Vision Computing, 19*(11), 713-731.

Mouritsen, H. (2015). Magnetoreception in birds and its use for long-distance migration. *Sturkie's Avian Physiology*, 113-133.

Mukai, Y., Yoshikawa, H., & Kobayashi, H. (1994). The relationship between the length of the cupulae of free neuromasts and feeding ability in larvae of the willow shiner Gnathopogon elongatus caerulescens (Teleostei, Cyprinidae). *Journal of Experimental Biology, 197*(1), 399-403.

Müller, M., & Wehner, R. (1988). Path integration in desert ants, Cataglyphis fortis. *Proceedings of the National Academy of Sciences, 85*(14), 5287-5290.

Murray, R. (1960). Electrical sensitivity of the ampullae of Lorenzini. *Nature, 187*(4741), 957-957.

Namdaran, P., Reinhart, K. E., Owens, K. N., Raible, D. W., & Rubel, E. W. (2012). Identification of modulators of hair cell regeneration in the zebrafish lateral line. *Journal of Neuroscience, 32*(10), 3516-3528.

Nelson, M. E., & Maciver, M. A. (1999). Prey capture in the weakly electric fish Apteronotus albifrons: sensory acquisition strategies and electrosensory consequences. *Journal of Experimental Biology, 202*(10), 1195-1203.

Nelson, M. E., MacIver, M. A., & Coombs, S. (2002). Modeling electrosensory and mechanosensory images during the predatory behavior of weakly electric fish. *Brain, behavior and evolution, 59*(4), 199-210.

Nelson, R. (2007). Visual responses of Ganglion cells *The Organization of the Retina and Visual System*: Webvision.

Neusel, G. (2014). *Electrocommunication and social behaviour in groups of the weakly electric fish Gnathonemus petersii (Mormyridae, Teleostei).* (Masterarbeit), Universität Bonn, Bonn.

Nieuwenhuys, R., & Nicholson, C. (1967). Cerebellum of mormyrids. *Nature, 215*(5102), 764-765.

Nilsson, G. (1996). Brain and body oxygen requirements of Gnathonemus petersii, a fish with an exceptionally large brain. *The Journal of experimental biology, 199*(3), 603-607.

Northcutt, R. G. (1989). The phylogenetic distribution and innervation of craniate mechanoreceptive lateral lines *The mechanosensory lateral line* (pp. 17-78): Springer.

Nwani, C. D., Odoh, G. E., Ude, E. F., & Okogwu, O. I. (2011). Food and feeding habits of Gnathonemus petersii (Osteichthyes: Mormyridae) in Anambra River, Nigeria. *Int Aquat Res, 3*, 45-51.

Odling-Smee, L., & Braithwaite, V. A. (2003). The influence of habitat stability on landmark use during spatial learning in the three-spined stickleback. *Animal Behaviour, 65*(4), 701-707.

Odling-Smee, L., & Braithwaite, V. A. (2003). The role of learning in fish orientation. *Fish and Fisheries, 4*(3), 235-246.

Ogbeibu, A., & Ezeunara, P. (2002). Ecological impact of brewery effluent on the Ikpoba River, Nigeria, using the fish communities as bio-indicators. *Journal of Aquatic sciences, 17*(1), 35-44.

Ogbeibu, A., & Oribhabor, B. (2002). Ecological impact of river impoundment using benthic macro-invertebrates as indicators. *Water research, 36*(10), 2427-2436.

Owens, G. L., Rennison, D. J., Allison, W. T., & Taylor, J. S. (2012). In the four-eyed fish (Anableps anableps), the regions of the retina exposed to aquatic and aerial light do not express the same set of opsin genes. *Biology letters, 8*(1), 86-89.

Partridge, B. L., & Pitcher, T. J. (1980). The sensory basis of fish schools: relative roles of lateral line and vision. *Journal of comparative physiology, 135*(4), 315-325.

Paterson, M. (2007). *The senses of touch: Haptics, affects and technologies*: Berg.

Paugy, D., Traoré, K., & Diouf, P. (1994). *Faune ichtyologique des eaux douces d'Afrique de l'Ouest.* Paper presented at the Annales du Musée Royal d'Afrique Centrale. Sciences Zoologiques.

Pe'er, G., & Kramer-Schadt, S. (2008). Incorporating the perceptual range of animals into connectivity models. *Ecological Modelling, 213*(1), 73-85. doi:https://doi.org/10.1016/j.ecolmodel.2007.11.020

Pedraja, F., Aguilera, P., Caputi, A. A., & Budelli, R. (2014). Electric imaging through evolution, a modeling study of commonalities and differences.

Pluta, S. R., & Kawasaki, M. (2008). Multisensory enhancement of electromotor responses to a single moving object. *Journal of Experimental Biology, 211*(18), 2919-2930.

Portavella, M., Vargas, J., Torres, B., & Salas, C. (2002). The effects of telencephalic pallial lesions on spatial, temporal, and emotional learning in goldfish. *Brain research bulletin, 57*(3), 397-399.

Prechtl, J. C., von der Emde, G., Wolfart, J., Karamürsel, S., Akoev, G. N., Andrianov, Y. N., & Bullock, T. H. (1998). Sensory processing in the pallium of a mormyrid fish. *The Journal of Neuroscience, 18*(18), 7381-7393.

Prevedello, J. A., Forero-Medina, G., & Vieira, M. V. (2010). Movement behaviour within and beyond perceptual ranges in three small mammals: effects of matrix type and body mass. *Journal of Animal Ecology, 79*(6), 1315-1323. doi:10.1111/j.1365-2656.2010.01736.x

Proops, L., McComb, K., & Reby, D. (2009). Cross-modal individual recognition in domestic horses (Equus caballus). *Proceedings of the National Academy of Sciences, 106*(3), 947-951.

Proske, U., Gregory, J., & Iggo, A. (1998). Sensory receptors in monotremes. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 353*(1372), 1187-1198.

Pusch, R. (2013). *Environmental imaging with two sensory systems in Gnathonemus petersii.* (Dissertation), Universität Bonn, Bonn.

Pusch, R., Kassing, V., Riemer, U., Wagner, H.-J., von der Emde, G., & Engelmann, J. (2013). A grouped retina provides high temporal resolution in the weakly electric fish Gnathonemus petersii. *Journal of Physiology-Paris, 107*(1), 84-94.

Pusch, R., von der Emde, G., Hollmann, M., Bacelo, J., Nöbel, S., Grant, K., & Engelmann, J. (2008). Active sensing in a mormyrid fish: electric images and peripheral modifications of the signal carrier give evidence of dual foveation. *Journal of Experimental Biology, 211*(6), 921-934. doi:10.1242/jeb.014175

Pusch, R., Wagner, H. J., von der Emde, G., & Engelmann, J. (2013). Spatial Resolution of an Eye Containing a Grouped Retina: Ganglion Cell Morphology and Tectal Physiology in the Weakly Electric Fish Gnathonemus petersii. *Journal of Comparative Neurology, 521*(17), 4075-4093.

Raposo, D., Sheppard, J. P., Schrater, P. R., & Churchland, A. K. (2012). Multisensory decision-making in rats and humans. *The Journal of Neuroscience, 32*(11), 3726-3735.

Rasnow, B. (1996). The effects of simple objects on the electric field of Apteronotus. *Journal of Comparative Physiology A, 178*(3), 397-411.

Rasnow, B., & Bower, J. M. (1997). Imaging with Electricity *Computational Neuroscience* (pp. 795-800): Springer.

Regett, S. (2016a). *Detektion von im Kies vergrabenen Beutetieren durch aktive Elektroortung beim schwach elektrischen Fisch Gnathonemus petersii.* (Projektarbeit), Universität Bonn, Bonn.

Regett, S. (2016b). *Objektdetektion im Substrat beim schwach elektrischen Fisch Gnathonemus petersii.* (Bachelorarbeit), Universität Bonn, Bonn.

Reymond, L. (1985). Spatial visual acuity of the eagle Aquila audax: a behavioural, optical and anatomical investigation. *Vision research, 25*(10), 1477-1491.

Rock, I., & Victor, J. (1964). Vision and touch: An experimentally created conflict between the two senses. *Science, 143*(3606), 594-596.

Rodriguez, F., Duran, E., Vargas, J. P., Torres, B., & Salas, C. (1994). Performance of goldfish trained in allocentric and egocentric maze procedures suggests the presence of a cognitive mapping system in fishes. *Animal Learning & Behavior, 22*(4), 409-420.

Rodrıguez, F., López, J., Vargas, J., Broglio, C., Gómez, Y., & Salas, C. (2002). Spatial memory and hippocampal pallium through vertebrate evolution: insights from reptiles and teleost fish. *Brain research bulletin, 57*(3), 499-503.

Rogers, L. J., & Kaplan, G. (2012). *Comparative vertebrate cognition: are primates superior to non-primates?* : Springer Science & Business Media.

Rojas, R., & Moller, P. (2002). Multisensory contributions to the shelter-seeking behavior of a mormyrid fish, Gnathonemus petersii Günther (Mormyridae, Teleostei): the role of vision, and the passive and active electrosenses. *Brain, behavior and evolution, 59*(4), 211-221.

Roth, A., & Schlegel, P. (1988). Behavioral evidence and supporting electrophysiological observations for electroreception in the blind cave salamander, Proteus anguinus (Urodela). *Brain, behavior and evolution, 32*(5), 277-280.

Rouse, G., & Pickles, J. (1991a). Paired development of hair cells in neuromasts of the teleost lateral line. *Proceedings of the Royal Society of London B: Biological Sciences, 246*(1316), 123-128.

Rouse, G., & Pickles, J. (1991b). Ultrastructure of free neuromasts of Bathygobius fuscus (Gobiidae) and canal neuromasts of Apogon cyanosoma (Apogonidae). *Journal of morphology, 209*(1), 111-120.

Salazar, V. L., Krahe, R., & Lewis, J. E. (2013). The energetics of electric organ discharge generation in gymnotiform weakly electric fish. *The Journal of experimental biology, 216*(13), 2459-2468. doi:10.1242/jeb.082735

Sanes, J. R., & Zipursky, S. L. (2010). Design Principles of Insect and Vertebrate Visual Systems. *Neuron, 66*(1), 15-36. doi:http://dx.doi.org/10.1016/j.neuron.2010.01.018

Sann, C., & Streri, A. (2007). Perception of object shape and texture in human newborns: evidence from cross-modal transfer tasks. *Developmental Science, 10*(3), 399-410.

Scheich, H., Langner, G., Tidemann, C., Coles, R. B., & Guppy, A. (1986). Electroreception and electrolocation in platypus. *Nature, 319*(6052), 401-402.

Schlegel, P. (1975). Elektroortung bei schwach elektrischen fischen: verzerrungen des elektrischen feldes von Gymnotus carapo und Gnathonemus petersii durch gegenstände und ihre wirkungen auf afferente aktivitäten. *Biological Cybernetics, 20*(3-4), 197-212.

Schluessel, V., & Bleckmann, H. (2005). Spatial memory and orientation strategies in the elasmobranch Potamotrygon motoro. *Journal of Comparative Physiology A, 191*(8), 695-706.

Schmitz, A., Bleckmann, H., & Mogdans, J. (2008). Organization of the superficial neuromast system in goldfish, Carassius auratus. *Journal of morphology, 269*(6), 751-761.

Schmitz, A., Bleckmann, H., & Mogdans, J. (2014). The lateral line receptor array of cyprinids from different habitats. *Journal of morphology, 275*(4), 357-370.

Schooley, R. L., & Branch, L. C. (2005). Limited perceptual range and anemotaxis in marsh rice ratsOryzomys palustris. *Acta theriologica, 50*(1), 59-66.

Schulze, F. E. (1861). Ueber die Nervenendigung in den sogenannten Schleimkanälen der Fische und ueber entsprechende Organe der durch Kiemen atmenden Amphibien. *Arch Anat Physiol Lpz*, 759-769.

Schulze, F. E. (1870). Ueber die sinnesorgane der seitenlinie bei fischen und amphibien. *Archiv für mikroskopische Anatomie, 6*(1), 62-88.

Schumacher, S. (2011). *Einfluss von elektrischen Störsignalen und von Objektformen auf die Objekterkennung wärend der aktiven Elektroortung beim schwach elektrischen Fisch Gnathonemus petersii* (Diplomarbeit), Universität Bonn, Bonn.

Schumacher, S., Burt de Perera, T., Thenert, J., & von der Emde, G. (2016). Cross-modal object recognition and dynamic weighting of sensory inputs in a fish. *Proceedings of the National Academy of Sciences*, 201603120.

Schumacher, S., Burt de Perera, T., & von der Emde, G. Object discrimination through active electrolocation: Shape recognition and the influence of electrical noise. *Journal of Physiology-Paris*. doi:http://dx.doi.org/10.1016/j.jphysparis.2016.11.008

Schumacher, S., Burt de Perera, T., & von der Emde, G. (2016). Object discrimination through active electrolocation: Shape recognition and the influence of electrical noise. *Journal of Physiology-Paris*.

Schumacher, S., Burt de Perera, T., & von der Emde, G. (2017). Electrosensory capture during multisensory discrimination of nearby objects in the weakly electric fish Gnathonemus petersii. *Scientific reports, 7*, 43665.

Schuster, S., & Amtsfeld, S. (2002). Template-matching describes visual pattern-recognition tasks in the weakly electric fish Gnathonemus petersii. *Journal of Experimental Biology, 205*(4), 549-557.

Schwarz, S. (2000). *Gnathonemus petersii: three-dimensional object shape detection and geometry of the self-produced electric field.* (Dissertation), Universität Bonn, Bonn.

Seidl, T., & Wehner, R. (2006). Visual and tactile learning of ground structures in desert ants. *Journal of Experimental Biology, 209*(17), 3336-3344. doi:10.1242/jeb.02364

Seraganian, P., & Popova, Y. I. (1976). Cross modal transfer of a conditional flexion response in dogs. *The Pavlovian journal of biological science: official journal of the Pavlovian, 11*(3), 162-174.

Shams, L., Kamitani, Y., & Shimojo, S. (2000). What you see is what you hear. *Nature*.

Shams, L., Kamitani, Y., & Shimojo, S. (2002). Visual illusion induced by sound. *Cognitive Brain Research, 14*(1), 147-152.

Sheppard, J. P., Raposo, D., & Churchland, A. K. (2013). Dynamic weighting of multisensory stimuli shapes decision-making in rats and humans. *Journal of Vision, 13*(6), 4.

Shettleworth, S. J. (2010). *Cognition, evolution, and behavior*: Oxford University Press.

Smith, C. U. M. (2008). *Biology of sensory systems*: John Wiley & Sons.

Smith, H. (2000). Phytochromes and light signal perception by plants[mdash]an emerging synthesis. *Nature, 407*(6804), 585-591.

Song, J., & Northcutt, R. G. (1991). Morphology, Distribution and Innervation of the Lateral-Line Receptors of the Florida Gar, Lepisosteus platyrhincus; pp. 24–37. *Brain, behavior and evolution, 37*(1), 24-37.

Stebbins, W. C. (1983). *The acoustic sense of animals*: Harvard University Press.

Stein, B. E., Meredith, M. A., Huneycutt, W. S., & McDade, L. (1989). Behavioral indices of multisensory integration: orientation to visual cues is affected by auditory stimuli. *Journal of Cognitive Neuroscience, 1*(1), 12-24.

Stendell, W. (1916). Die schnauzenorgane der mormyriden. *Zeit wiss Zool, 115*, 650-670.

Strasser, R., & Bingman, V. P. (1996). The relative importance of location and feature cues for homing pigeon (Columba livia) goal recognition. *Journal of Comparative Psychology, 110*(1), 77.

Streri, A. (2003). Cross-modal recognition of shape from hand to eyes in human newborns. *Somatosensory & motor research, 20*(1), 13-18.

Streri, A., & Gentaz, E. (2004). Cross-modal recognition of shape from hand to eyes and handedness in human newborns. *Neuropsychologia, 42*(10), 1365-1369.

Sullivan, J. P., Lavoue, S., & Hopkins, C. D. (2000). Molecular systematics of the African electric fishes (Mormyroidea: Teleostei) and a model for the evolution of their electric organs. *Journal of Experimental Biology, 203*(4), 665-683.

Sutherland, L., Holbrook, R. I., & Burt De Perera, T. (2009). Sensory System Affects Orientational Strategy in a Short-Range Spatial Task in Blind and Eyed Morphs of the Fish, Astyanax fasciatus. *Ethology, 115*(5), 504-510.

Sutton, E. E., Demir, A., Stamper, S. A., Fortune, E. S., & Cowan, N. J. (2016). Dynamic modulation of visual and electrosensory gains for locomotor control. *Journal of The Royal Society Interface, 13*(118), 20160057.

Szabo, T. (1965). Sense organs of the lateral line system in some electric fish of the Gymnotidae, Mormyridae and Gymnarchidae. *Journal of morphology, 117*(2), 229-249.

Taylor, K. I., Moss, H. E., Stamatakis, E. A., & Tyler, L. K. (2006). Binding crossmodal object features in perirhinal cortex. *Proceedings of the National Academy of Sciences, 103*(21), 8239-8244.

Teyke, T. (1990). Morphological differences in neuromasts of the blind cave fish Astyanax hubbsi and the sighted river fish Astyanax mexicanus. *Brain, behavior and evolution, 35*(1), 23-30.

Thieme, M. L., Abell, R., Burgess, N., Lehner, B., Dinerstein, E., & Olson, D. (2005). *Freshwater ecoregions of Africa and Madagascar: a conservation assessment*: Island Press.

Trinh, A. T., Harvey-Girard, E., Teixeira, F., & Maler, L. (2016). Cryptic laminar and columnar organization in the dorsolateral pallium of a weakly electric fish. *Journal of Comparative Neurology, 524*(2), 408-428.

Uiblein, F., Durand, J. P., Juberthie, C., & Parzefall, J. (1992). Predation in caves: the effects of prey immobility and darkness on the foraging behaviour of two salamanders, Euproctus asper and Proteus anguinus. *Behavioural Processes, 28*(1), 33-40. doi:http://dx.doi.org/10.1016/0376-6357(92)90046-G

Ursino, M., Cuppini, C., Magosso, E., Serino, A., & Di Pellegrino, G. (2009). Multisensory integration in the superior colliculus: a neural network model. *Journal of computational neuroscience, 26*(1), 55-73.

Van Trump, W. J., & McHenry, M. J. (2008). The morphology and mechanical sensitivity of lateral line receptors in zebrafish larvae (Danio rerio). *Journal of Experimental Biology, 211*(13), 2105-2115. doi:10.1242/jeb.016204

Vanegas, H. (1984). *Comparative neurology of the optic tectum*: Plenum Pub Corp.

Vischer, H. A. (1989). The Development of Lateral-Line Receptors in Eigenmannia (Teleostei, Gymnotiformes). I. The Mechanoreceptive Lateral-Line System (Part 1 of 2). *Brain, behavior and evolution, 33*(4), 205-213.

Vischer, H. A. (1990). The morphology of the lateral line system in 3 species of Pacific cottoid fishes occupying disparate habitats. *Cellular and Molecular Life Sciences, 46*(3), 244-250.

von Campenhausen, C., Riess, I., & Weissert, R. (1981). Detection of stationary objects by the blind Cave Fish Anoptichthys jordani (Characidae). *Journal of comparative physiology, 143*(3), 369-374.

von der Emde, G. (1990). Discrimination of objects through electrolocation in the weakly electric fish, Gnathonemus petersii. *Journal of Comparative Physiology A, 167*(3), 413-421.

von der Emde, G. (1992). Electrolocation of capacitive objects in four species of pulse-type weakly electric fish: II. Electric signalling behaviour. *Ethology*.

von der Emde, G. (1993). Capacitance discrimination in electrolocating, weakly electric pulse fish. *Naturwissenschaften, 80*(5), 231-233.

von der Emde, G. (2006). Non-visual environmental imaging and object detection through active electrolocation in weakly electric fish. *Journal of Comparative Physiology A, 192*(6), 601-612.

von der Emde, G., Behr, K., Bouton, B., Engelmann, J., Fetz, S., & Folde, C. (2010). 3-Dimensional scene perception during active electrolocation in a weakly electric pulse fish. *Frontiers in behavioral neuroscience, 4*.

von der Emde, G., & Bleckmann, H. (1998). Finding food: senses involved in foraging for insect larvae in the electric fish gnathonemus petersii. *The Journal of experimental biology, 201*(7), 969-980.

von der Emde, G., & Bleckmann, H. (1998). Finding food: senses involved in foraging for insect larvae in the electric fish Gnathonemus petersii. *Journal of Experimental Biology, 201*(7), 969-980.

von der Emde, G., & Fetz, S. (2007). Distance, shape and more: recognition of object features during active electrolocation in a weakly electric fish. *Journal of Experimental Biology, 210*(17), 3082-3095.

von der Emde, G., & Prechtl, J. C. (1999). Anatomical connections of auditory and lateral line areas of the dorsal telencephalon (Dm) in the osteoglossomorph teleost, Gnathonemus petersii. *Brain research, 818*(2), 355-367.

von der Emde, G., & Ringer, T. (1992). Electrolocation of Capacitive Objects in Four Species of Pulse-type Weakly Electric Fish I. Discrimination Performance. *Ethology, 91*(4), 326-338.

von der Emde, G., & Ronacher, B. (1994). Perception of electric properties of objects in electrolocating weakly electric fish: two-dimensional similarity scaling reveals a City-Block metric. *Journal of Comparative Physiology A, 175*(6), 801-812.

von der Emde, G., & Ruhl, T. (2016). Matched Filtering in African Weakly Electric Fish: Two Senses with Complementary Filters *The Ecology of Animal Senses* (pp. 237-263): Springer.

von der Emde, G., & Schwarz, S. (2000). Three–dimensional analysis of object properties during active electrolocation in mormyrid weakly electric fishes (Gnathonemus petersii). *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 355*(1401), 1143-1146.

von der Emde, G., & Schwarz, S. (2001). How the electric fish brain controls the production and analysis of electric signals during active electrolocation. *Zoology, 103*(3-4), 112-124.

von der Emde, G., & Schwarz, S. (2002). Imaging of objects through active electrolocation in Gnathonemus petersii. *Journal of Physiology-Paris, 96*(5), 431-444.

von der Emde, G., Schwarz, S., Gomez, L., Budelli, R., & Grant, K. (1998). Electric fish measure distance in the dark. *Nature, 395*(6705), 890-894.

von Frisch, K., & Stetter, H. (1932). Untersuchungen zum Sitz des Gehörsinns bei der Elritze. *Z Vergl Physiol, 17*, 686-801.

Wald, G. (1958). The significance of vertebrate metamorphosis. *Science, 128*(3337), 1481-1490.

Walton, A. G., & Moller, P. (2010). Maze Learning and Recall in a Weakly Electric Fish, Mormyrus rume proboscirostris Boulenger (Mormyridae, Teleostei)1. *Ethology, 116*(10), 904-919. doi:10.1111/j.1439-0310.2010.01807.x

Webb, J. F. (1989). Gross Morphology and Evolution of the Mechanoreceptive Lateral-Line System in Teleost Fishes (Part 1 of 2). *Brain, behavior and evolution, 33*(1), 34-43.

Webb, J. F. (2011). HEARING AND LATERAL LINE | Lateral Line Structure *Encyclopedia of Fish Physiology* (pp. 336-346). San Diego: Academic Press.

Webb, J. F. (2013). Morphological diversity, development, and evolution of the mechanosensory lateral line system *The lateral line system* (pp. 17-72): Springer.

Webb, J. F., & Shirey, J. E. (2003). Postembryonic development of the cranial lateral line canals and neuromasts in zebrafish. *Developmental dynamics, 228*(3), 370-385.

Wehner, R. (1998). Navigation in context: grand theories and basic mechanisms. *Journal of Avian Biology*, 370-386.

Wehner, R. (2003). Desert ant navigation: how miniature brains solve complex tasks. *Journal of Comparative Physiology A, 189*(8), 579-588.

Wehner, R., Cheng, K., & Cruse, H. (2014). Visual navigation strategies in insects: lessons from desert ants. *The new visual neurosciences. MIT Press, Cambridge*, 1153-1164.

Wehner, R., Michel, B., & Antonsen, P. (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *Journal of Experimental Biology, 199*, 129-140.

Werblin, F. S., & Dowling, J. E. (1969). Organization of the retina of the mudpuppy, Necturus maculosus. II. Intracellular recording. *Journal of Neurophysiology, 32*(3), 339-355.

Wessnitzer, J., & Webb, B. (2006). Multimodal sensory integration in insects: towards insect brain control architectures. *Bioinspiration & Biomimetics, 1*(3), 63.

Westby, G. M. (1981). Communication and jamming avoidance in electric fish. *Trends in Neurosciences, 4*, 205-210.

Westby, G. M. (1984). Electroreception and communication in electric fish. *Science progress, 69*(274), 291.

Westby, G. M. (1988). The ecology, discharge diversity and predatory behaviour of gymnotiforme electric fish in the coastal streams of French Guiana. *Behavioral Ecology and Sociobiology, 22*(5), 341-354.

Wilgers, D. J., & Hebets, E. A. (2011). Complex courtship displays facilitate male reproductive success and plasticity in signaling across variable environments. *Current Zoology, 57*(2), 175-186.

Williams, J., & Holder, N. (2000). Cell turnover in neuromasts of zebrafish larvae. *Hearing research, 143*(1), 171-181.

Wiltschko, R., & Wiltschko, W. (2009). Avian navigation. *The Auk, 126*(4), 717-743.

Wiltschko, W., & Wiltschko, R. (2005). Magnetic orientation and magnetoreception in birds and other animals. *Journal of Comparative Physiology A, 191*(8), 675-693.

Winemiller, K. O., & Adite, A. (1997). Convergent evolution of weakly electric fishes from floodplain habitats in Africa and South America. *Environmental Biology of Fishes, 49*(2), 175-186.

Winters, B. D., & Reid, J. M. (2010). A distributed cortical representation underlies crossmodal object recognition in rats. *The Journal of Neuroscience, 30*(18), 6253-6261.

Wittlinger, M., Wehner, R., & Wolf, H. (2006). The Ant Odometer: Stepping on Stilts and Stumps. *Science, 312*(5782), 1965-1967. doi:10.1126/science.1126912

Wullimann, M. F., & Grothe, B. (2014). The Central Nervous Organization of the Lateral Line System. In S. Coombs, H. Bleckmann, R. R. Fay, & A. N. Popper (Eds.), *The Lateral Line System* (pp. 195-251). New York, NY: Springer New York.

Wuraola, O. B., & Adetola, J.-O. (2011). Assessment of Fish Biodiversity in Oni River, Ogun State, Nigeria. *International Journal of Agricultural Management and Development (IJAMAD), 1*(3).

Yau, K.-W., Matthews, G., & Baylor, D. (1979). Thermal activation of the visual transduction mechanism in retinal rods. *Nature, 279*(5716), 806-807.

Yehle, A. L., & Ward, J. P. (1969). Cross-modal transfer of a specific discrimination in the rabbit. *Psychonomic Science, 16*(5), 269-270.

Yoshizawa, M., Gorički, Š., Soares, D., & Jeffery, W. R. (2010). Evolution of a Behavioral Shift Mediated by Superficial Neuromasts Helps Cavefish Find Food in Darkness. *Current Biology, 20*(18), 1631-1636. doi:http://doi.org/10.1016/j.cub.2010.07.017

Young, M. J., Landy, M. S., & Maloney, L. T. (1993). A perturbation analysis of depth perception from combinations of texture and motion cues. *Vision research, 33*(18), 2685-2696.

Zaidel, A., Turner, A. H., & Angelaki, D. E. (2011). Multisensory calibration is independent of cue reliability. *The Journal of Neuroscience, 31*(39), 13949-13962.

Zeigler, H. P., & Bischof, H.-J. (1993). *Vision, brain, and behavior in birds*: MIT Press.

Zhang, L.-Z., Zhang, S.-W., Wang, Z.-L., Yan, W.-Y., & Zeng, Z.-J. (2014). Cross-modal interaction between visual and olfactory learning in Apis cerana. *Journal of Comparative Physiology A, 200*(10), 899-909.

Zhang, W.-h., Chen, A., Rasch, M. J., & Wu, S. (2016). Decentralized Multisensory Information Integration in Neural Systems. *The Journal of Neuroscience, 36*(2), 532-547.

Zupanc, G. K., & Bullock, T. H. (2005). From electrogenesis to electroreception: an overview *Electroreception* (pp. 5-46): Springer.

Danksagung

An erster Stelle bedanke ich mich bei Herrn Prof. Dr. Gerhard von der Emde für die Möglichkeit, dass ich meine Arbeit in seiner Arbeitsgruppe anfertigen konnte, und die hilfreiche und stets freundliche Betreuung während der gesamten Zeit der Doktorarbeit sowie bereits zuvor. Desweiteren gilt mein Dank Dr. Theresa Burt de Perera für die Übernahme des Korreferats, für die freundliche Aufnahme in ihre Arbeitsgruppe während meiner Zeit in Oxford und die vielfältige Unterstützung bei der Erstellung dieser Arbeit.

Prof. Dr. Lukas Schreiber und Prof. Dr. Jes Rust danke ich für ihre Bereitschaft als Gutachter meiner Arbeit zu fungieren.

Bei Dr. Anke Schmitz und Dr. Hendrik Herzog bedanke ich mich für ihre Hilfe während der anatomischen Versuche zum Seitenliniensystem.

Die Erstellung dieser Arbeit wurde mir auch ermöglicht durch das Promotionsstipendium der Universität Bonn und das Kurzstipendium für Doktoranden des Deutschen Akademischen Austauschdienstes.

Ganz herzlich möchte ich mich auch bei der gesamten Arbeitsgruppe Neuroethologie/ Sensorische Ökologie bedanken und hier im Besonderen bei meinen Mitdoktoranden Martin Gottwald und Martin Worm für die inspirierenden fachlichen und die sehr unterhaltsamen fachfremden Gespräche, die mir die Arbeit sicherlich erleichtert haben. Außerdem gilt ein besonderer Dank den beiden Technischen Assistentinnen Bärbel Bauch und Ute Grundner, die mir immer mit gutem Rat zur Seite gestanden haben.

Ebenso möchte ich mich bei der Animal Navigation Group in Oxford bedanken, die mich in meiner Zeit dort sehr nett aufgenommen und vor allem auf die Navigationsversuche durch ihren Rat positiv eingewirkt haben.

Meinen Freunden sowie meinem Bruder Marcus danke ich von ganzem Herzen, dass sie auch in schwereren Zeiten immer an meiner Seite waren und immer ein offenes Ohr für mich hatten. Besonders bedanke ich mich hier bei Eva Wierschem für das Korrekturlesen meiner Arbeit.

Zu guter Letzt gilt der größte Dank meinen Eltern. Ihr habt mir das Biologiestudium überhaupt erst ermöglicht, mir die Möglichkeit geboten nach Oxford zu gehen, mich bei wichtigen Entscheidungen immer unterstützt und so meine Karriere entscheidend geprägt. Ihr habt mir immer den Rücken gestärkt und mir das nötige Selbstvertrauen gegeben, um meine Ziele zu erreichen. Ohne euch hätte ich es nicht so weit geschafft. Vielen Dank!

Erklärung

Hiermit erkläre ich an Eides statt, dass die vorliegende Dissertation mit dem Titel "From perception to cognition: Multisensory object recognition and navigation in the weakly electric fish *Gnathonemus petersii*" – abgesehen von den ausdrücklich bezeichneten Hilfsmitteln – persönlich, selbständig und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt wurde;
die aus anderen Quellen direkt oder indirekt übernommenen Daten und Konzepte unter Angabe der Quelle kenntlich gemacht sind;
die vorgelegte Arbeit oder ähnliche Arbeiten nicht bereits anderweitig als Dissertation eingereicht worden ist bzw. sind;
für die inhaltlich-materielle Erstellung der vorgelegten Arbeit keine fremde Hilfe, insbesondere keine entgeltliche Hilfe von Vermittlungs- bzw. Beratungsdiensten in Anspruch genommen wurde, sowie keinerlei Dritte vom Doktoranden unmittelbar oder mittelbar geldwerte Leistungen für Tätigkeiten erhalten haben, die im Zusammenhangmit dem Inhalt der vorgelegten Arbeit stehen.

Bonn den

Sarah Schumacher