Understanding Active Electrosensory Systems and Electrolocation Mechanisms Using Spatiotemporal Information in Weakly Electric Fish

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먼저 2 년 동안 끊임 없는 조언과 충고로 지도해 주신 김대은 교수님께 몇 마디 말로는 부족하지만 깊은 감사를 드립니다. 그리고 더 좋은 논문이 완성될 수 있도록 심사 과정에서 작은 부분까지 지적해주시고 아낌 없는 가르침을 주신 김동현 교수님과 Engelmann 박사님께도 깊은 감사를 드립니다. 진로 등의 상담으로 도움을 주신 손광훈 교수님, 박정욱 교수님, 황도식 교수님, 최정윤 교수님과 강의와 조언으로 도움 주신 전기전자공학부 모든 교수님들께 감사 드립니다. 지식적인 조언뿐 만이 아니라 미래에 대한 고민을 함께 해 주신 교수님들이 계셨기 때문에 부족하지만 학위논문으로 2 년의 결실을 보일 수 있었습니다.

언제 어디서나 제 걱정으로 많은 시간을 할애해 주는 가족들에게 깊은 영광을 돌리고 싶습니다. 멀리서도 응원과 격려를 아끼지 않는 이모, 이모부, 수진이, 영수 오빠에게 감사의 말을 전합니다.

그리고 1 년 동안 대학원 생활에 적응할 수 있도록 도와 준 지원 언니와 다른 한 해를 함께 해 준 승은이, 상욱이, 재홍이, 영서와 다른 곳에서 공학의 꿈을 펼치고 있은 승훈이 오빠, 준용이 오빠와 같은 공부를 하면서 도움이 되어 준 친구들과 선후배들에게 감사의 인사를 전하고 싶습니다.

Abstract

This dissertation deals with the unique sensory mechanisms of weakly electric fish. Weakly electric fish are very specialized to active electroreception. They generate an electric field through their own electric organs and detect the distortion of self-generated electric fields to localize a target object. We study the mechanisms of electrolocation in weakly electric fish and develop a model of electrosensory system using electric fields. There has been much research on how weakly electric fish identify a target object. Weakly electric fish sense the electric field perturbations due to neighboring objects. According to the research on electric images, there is a correlation between electric sensory image features and physical object features. We focused on the electrolocation using the relative slope known as distance measurement in the thesis.

So far the study of electrosensory system has focused on static electric images. In this thesis, we will consider both spatial and temporal structures of electric image for object recognition or distance estimation. There are three major purposes of the thesis; (1) suggestion of a new distance estimation method using tail-bending movements (2) proposal of a localization method of multiple target objects (3) comparative study of noise reduction method using low pass filter and cross-correlation in the spatiotemporal domain.

First, the temporal pattern generated by tail-bending movements of weakly electric fish can provide another cue for distance estimation. The normalized tail-bending pattern is independent of the size and conductivity of a target object. We suggest that weakly electric fish might use temporal tail-bending movements for electrolocation. The temporal patterns caused by tail bending do not need multiple electroreceptors and it is possible to estimate the distance with one or two electrosensors when a sweep of tail bending is used.

Second, the spatiotemporal electric images generated by the back-and-forth swimming provide us distance measurements for multiple objects. The relative slope is a useful distance measurement when there is one target object near a weakly electric fish. We provide a new model to estimate the distance, which can be applied to multiple target objects. A time-to-spatial slope uses the maximal amplitude in the time domain and maximum difference at the space domain. We can estimate the distances of multiple objects by the time-to-spatial slope regardless of varying rostrocaudal positions of objects.

Lastly, we adopt and use a low pass filter and cross-correlation to measure the distance of a target in noisy environments. Weakly electric fish generate electric organ discharge that has periodic characteristics. The cross-correlation is applied to two temporal signals, the waveform of electric organ discharge waveform and the sensed waveform caused by a target object and then the low pass filter is used in the spatial domain of electric image after the cross-correlation. When we use both low pass filter and cross-correlation, it is possible to measure the distance up to about $4.5cm$ while the distance can be hardly estimated without a de-noising method.

Declaration

I declare that this thesis was composed by myself, that the work contained herein is my own except where explicitly stated otherwise in the text, and that this work has not been submitted for any other degree or professional qualification except as specified.

(*Miyoung Sim*)

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Chapter 1

Introduction

Human beings and most of animals are highly dependent on vision. However, it is not easy to secure a clear view under water. We introduce the active electrolocation of weakly electric fish to develop an other sensory system for underwater environment.

When we think of the phrase ‘electric fish’, we usually think of fish like an electric eels. The electric eel is called a strongly electric fish. Usually the strongly electric fish can generate an electric discharge large enough to stun their prey or protect themselves from an enemy. There are three types of electric fishes; first, the strongly electric fish, such as the electric eel and ray; second, weakly electric fish; and third, elasmobranches, which can only detect the electric field. We will focus on the weakly electric fish, which is very specialized to electroreception. The weakly electric fish generate their own electric field for navigation, localization of a target, and communication. The electric discharge of weakly electric fish is less than 1 Volt and it is not enough to kill their prey or threaten predators. Instead of a weak electric discharge, weakly electric fish are very specialized to electrolocation.

In this thesis, we study electroreception of weakly electric fish to understand the mechanism of electrolocation. The study of weakly electric fish helps us to develop an other electrosensory system underwater. We use a spatiotemporal electric image with active body movements to understand the mechanism of electrolocation in weakly electric fish.

1.1 Why study weakly electric fish?

The ability of detecting an electric field is called electroreception. The electroreception is a unique electrosensory system of weakly electric fish. They perceive the varying electric fields and analyze for electrolocation and electrocommunication. To carry an electric discharge is easier in water than air because of the existence of electrolytes. This advantage provides the opportunity of electroreception to underwater creatures. Electric fish are the only creatures to use electric fields as an energy source due to their unique sensory system (Lissmann, 1974). The electric organ (EO) of strongly electric fish produces a stronger electric field than bioelectric fields of other nerve and muscle cells.

It is very interesting to study the electroreception procedure of electric fish. Electric fish generate an electric discharge and detect the distortion of their self-generated electric field to identify the target object, navigate and communicate with conspecifics. So far it is not a practical and common system using electric field as a source of sensory systems, such as an ultrasonic sensor that produces ultrasonic waves and acquire desired information from reflected waves. Most common uses of electroreception are to detect the overflow of an electric current of electric mechanism or bioelectric field of the human body. Since the electrolocation of electric fish discriminate not only a distance but also other characteristics of a target object, such as size, shape, and conductivity, active sensing systems using an electric field as a source of energy can be valuable for detecting surroundings.

Electric fish can be divided two groups; ‘weakly electric fish’ and ‘strongly electric fish’. Strongly electric fish have an electric organ that generates a strong enough electric field to hunt prey or protect themselves from an enemy. It is known that the amplitude of an electric discharge can range up to about 500 volts (Israel-Jacard and Kalant, 1965). Electric eels, rays, and catfish belong to the strongly electric fish group.

Weakly electric fish can’t use their electric discharges for prey capture or protection from enemies because of the weakness of the electric field. The electricity generated by weakly electric fish is less than one volt. However, weakly electric fish have gained more concern and attention than strongly electric fish since weak electric production provides us evolutionary information about electroreception (Lissmann, 1974). Elasmobranches can be included in classification of electric fish. There is no electric organ, but they have electroreceptors which detect bioelectric fields of other creatures.

The study of electric fish provides us the suitable sensory structure to extract novel information from the response of an electric field and inspiration for the practical application of electrosensory systems. This biologically inspired research is called “biomimetics”. This is introduced in the next section.

1.2 What is biomimetics?

Nature has provided a lot of solutions and respectable advice to make problems easier. For example, a camera is developed from the structure of human vision. The development of science makes it possible to fabricate inventions similar to the resources of nature. One such field of research is called ‘biomimetics’. This field of science is to study the model of methods, structures, and designs of nature (Bar-Cohen, 2006).

Biomimetics provides efficiency to both technology and biological arenas. Some animals are specialized to particular sensor mechanisms such as electric fish, who specialized in electroreception and electrolocation. The study of electric fish gives us the chance to understand the biological or neuroethological electroreception mechanism and utilize the active electric sensory system. Weakly electric fishes are especially specialized to active electrolocation, which is the identification of a target object by using a self-generated electric field. The understanding of the electrolocation process of weakly electric fish lends to the possibility of practical application in the electric field as an underwater sensing device and comprehension of the physiological mechanism of electroreception.

1.3 Understanding weakly electric fish

In this thesis, we focused on weakly electric fish. Weakly electric fish are very specialized to ‘active electrolocation’. They have efficient active sensory systems to identify target objects and navigate underwater. Peters’ elephantnose fish (Gnathonemus petersii) and the black ghost knifefish (Apteronotus albifrons) are the most studied and typical examples of weakly electric fish.

Weakly electric fish use both “active sensing” and “passive sensing” to detect their surroundings and capture prey (Nelson and MacIver, 1999; Nelson et al., 2000). There is also a mechanosensory system in weakly electric fish. We can suppose that weakly electric fish are highly dependent on the active sensory system than passive electroreception or mechanosensory systems because of the distribution of sensors and body movements of weakly electric fish. They have the largest number of receptors for active sensing.

A lot of researchers concentrate on the active sensing of weakly electric fish. Lissmann (1974) first used the concept of active sensing and suggested weakly electric fish identify the target object and detect surroundings and analyze sensor readings using “active electrolocation”. The term “active” manifests the use of a self-generated carrier (Bajcsy, 1988; Nelson and MacIver, 2006). Bajcsy (1988) defines the “active sensor” as a sensor that transmits, receives, and measures change of their own signals, such as ultrasonic waves, sonar, and microwaves. “Active sensing” is used for the representation of man-made systems that detect the reflected self-generated carrier using its own energy source and controlling the energy source to extract novel signals from background signals (Bajcsy, 1988; Nelson and MacIver, 2006). On the contrary, the “passive sensor” only detects the variation of an exterior energy without emitting certain sources.

Nelson and MacIver (2006) shows several examples of active sensory systems. Bats, dolphins, and mice can be typical examples of animals using active sensing for detecting target objects and navigation with different types of energy sources. The diversity of energy sources makes different sensing ranges as shown in Fig.1.1. Bat and dolphins use echolocation, and which use ultrasonic waves as an energy source, and mice use tactile sensing to detect their surroundings with active movement of their whiskers. According to their energy source, the sensing range is limited to a forward direction.

The electric perturbation decreases dramatically, when the target object moves far away from weakly electric fish. The sensing range of weakly electric fishes is very close to their body, but has an omni-directional sensing range due to the characteristics of electric fields. It is known that the sensing range of electrolocation is about one rostrocaudal length of the weakly electric fish (Nelson and MacIver, 1999; Nelson, 2005; Babineau et al., 2007). The small sensing range makes it possible to exploit swim movements to acquire accurate information (Budelli et al., 2002; Caputi, 2004). When an object becomes more distant, the modulation of the local image and the slope decrease rapidly. Further afield, the amplitude of modulation is in approximately inverse proportion to the cube of a distance (Nelson and MacIver, 1999; Nelson, 2005; Babineau et al., 2007). However, in the vicinity of the fish, this power scale reduction

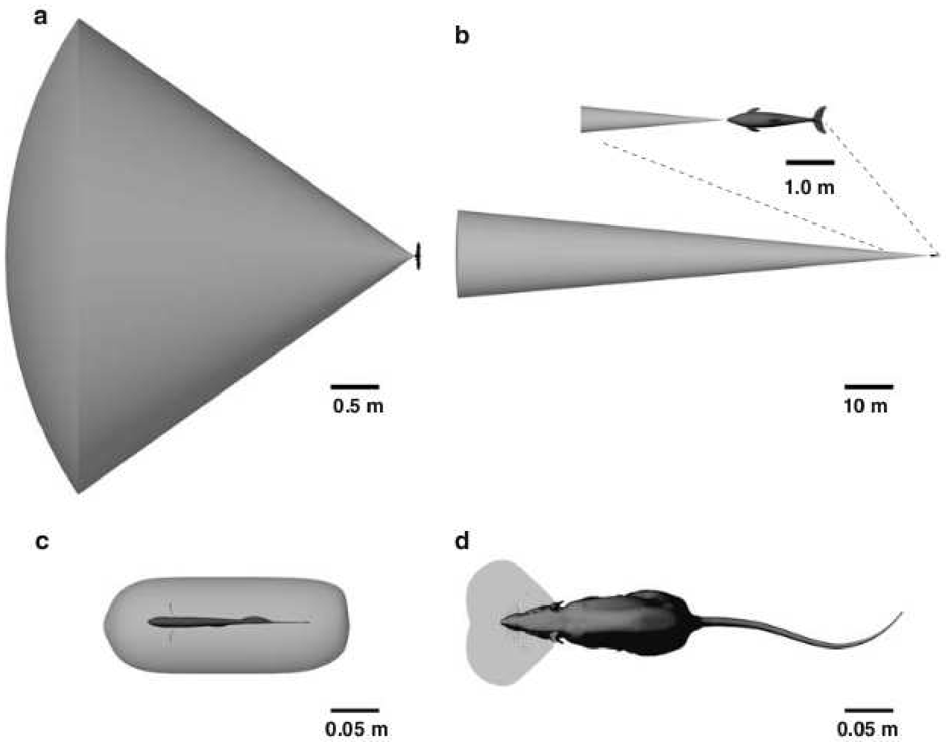


Figure 1.1: Emission ranges of different animals using active sensing (a) bat echolocation beam (b) dolphin echolocation (c) weakly electric fish (d) rat whisker system (reprinted from (Nelson and MacIver, 2006))

does not hold and a slower decline is observed.

Actually, there is another type of active sensory system using a manipulation of a motor. Aloimonos et al. (1988); Ballard (1991) use the term “active” to represent a system using active movements in vision. These active motions are found in weakly electric fish as swim movement. There is not any mechanism to take the focus to acquire exact novel signal in weakly electric fish (Heiligenberg, 1975). Therefore they have to be close to the target object, and this movement gives the result of far-field approximation, that means the generation of diminution of background effects.

We will focus on electrolocation mechanism using active body movements. When we consider active body movements, such as back-and-forth swimming and tail-bending movements, we can use spatiotemporal electric imaging. This spatiotemporal information can provide us more accurate distance estimation.

1.4 Motivation and objectives

This research is motivated by the unique sensory system of weakly electric fish. Weakly electric fish generate an electric field in every direction and have an omni-directional sensing range. This makes it possible to identify a target object all around the fish. Though electric imaging is simple for visual images, weakly electric fish identify not position alone, but also other characteristics of a target object, such as size, electrical property, or shape. The active sensory system does not need a light source, so it can be useful for underwater vehicles or aquatic robots.

We study the active electrosensory system with three notable objectives.

A distance measurement available with only a few sensors. When using electrosensory system for the electronic machine, it can be helpful to exploit small sensors for cost-reduction.

A distance measurement for multiple objects. When weakly electric fish swim back and forth, we can use spatiotemporal electric images. It has been observed that the spatiotemporal electric images provide us a more effective distance measurement for multiple objects.

An effective process to reduce the noise. It is typical to use a low pass filter to reduce noise in electric images. We use temporal information with cross-correlation.

The research will help with developments of electrosensory systems.

1.5 Structure of dissertation

In this section, we introduced the concept of bio-inspired research and electroreception in weakly electric fish briefly. In the next chapter, we will review general information of weakly electric fish. Weakly electric fish have special organs for the transmission and reception of electric fields that are called electric organ and electroreceptor respectively. We will introduce these two organs and electrosensory system. In previous studies, electric images were used to understand the mechanisms of electrolocation electric images are used. We present the electric images in Chapter 2. From Chapter 3 to Chapter 6, we will study and simulate the electrosensory system. In Chapter 3, the study of localization mechanisms using spatial structures will be discussed. Chapter

4 presents the distance measurement using temporal information of electric images. When weakly electric fish bend their tail, temporal patterns are generated and this pattern provides us with another distance measure. Chapter 5 introduces the spatiotemporal structure to estimate distances of multiple objects. In this chapter, we will study how weakly electric fish identify a target object in complex scenes with background objects. In the last chapter, the spatial and temporal process will be studied for accurate distance estimation in a noisy environment. When we apply a noise reduction process in spatiotemporal electric images, we can remove noise more effectively.

Chapter 2

Active electrosensory system of weakly electric fish

This chapter introduces general information about weakly electric fish, their electric organ, electroreceptors, and basic concept of electrolocation and electroreceptors. The electrosensory system can be composed of three components, the electric organ, receptors, and distance measurement system. Weakly electric fish have an electric organ (EO) to generate an electric field and many electroreceptors on the skin surface for electroreception. The electric image has been used to understand the electrosensory mechanism. It is known that the electric organ can be modeled as a collection of electric poles and we can derive the transdermal potential at an electroreceptor mathematically (Chen et al., 2005). When a target object is near weakly electric fish, the electric potential changes and it can be translated into an electric image. It is possible to estimate the location and characteristics of a target object by analysis of an electric image. This thesis concentrates on the localization of a target object and will be discussed in next chapter.

Chapter 2 will provide background knowledge to understand the electrolocation system of weakly electric fish. The electric field model is based on the wave-type weakly electric fish, especially Gymnotiformes (Babineau et al., 2006; Chen et al., 2005). The purpose of this thesis is to understand how the electrosensory mechanism is used so that weakly electric fish can identify a distance of a target object based on computer-based simulation and a suggestion of using the distance estimation method. The experiments will be based on analysis of an electric image studied in this chapter.

2.1 Electric organ

Bennett (1971), Zimmermann (1985), and Bass (1986) studied and Kramer (1996) reviews the electric organ of weakly electric fish. The EO is the internal organization modified from nerve and muscle cells (Kramer, 1996). EO is discriminately derived from different cells according to species. Fig. 2.1 shows several electric fish and their electric organs. As in Fig. 2.1, there are various type of EOs and they have different sizes, shapes, and locations in electric fish. Torpedo (Fig. 2.1), a strongly electric ray, has an electric organ in its head that has been modified from the branchial muscle (Kramer, 1996). The weakly electric fish, for example the Raja in Fig. 2.1, has its electric organ in its long, thin tail.

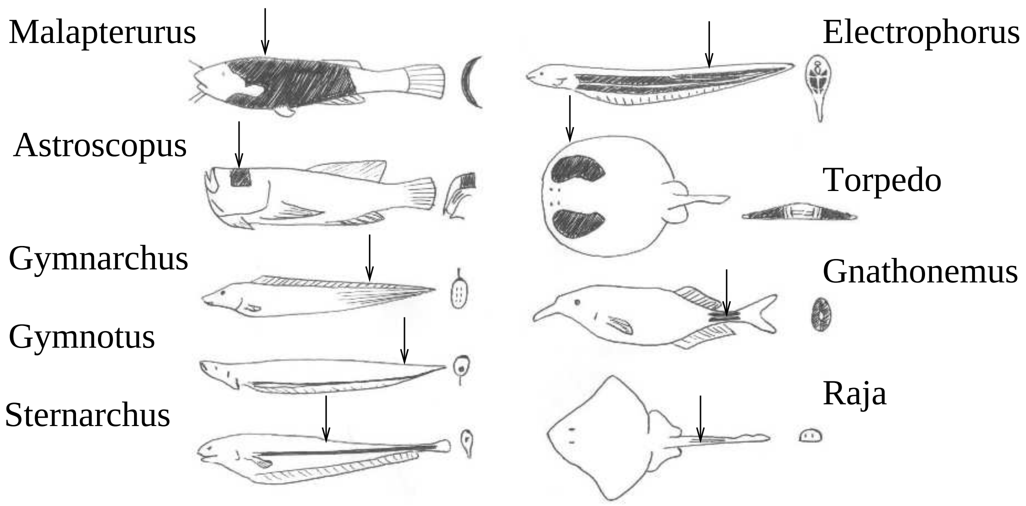


Figure 2.1: Some electric fish and their electric organs; the top four figures (Malapterurus, Electrophorus, Astroscopus, and Torpedo) are strongly electric fishes and the others show weakly electric fishes (arrows indicate electric organs and figures next to electric fishes show cross sections of electric organs) (modified from (Kramer, 1996))

Strongly electric fish generate a pulse discharge which has monopolar characteristics (Kramer, 1996). It appears to make a powerful electric pulse to capture the prey. On the contrary, weakly electric fish produces multipolar or bipolar discharges.

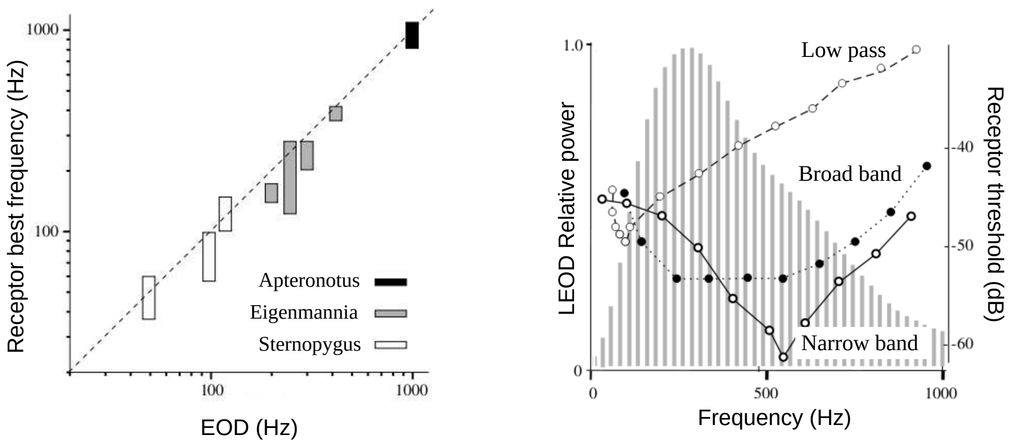
The EO is composed of electrolytes and it generates an electric organ discharge (EOD) (Kramer, 1999). EODs usually have waveform characteristics. There are two types of waveform characteristics; pulse and wave. It is known that most of Gymnotiformes and Mormyriformes generate a pulse waveform which has large interval between short pulses. *Gymnarchus niloticus*, which is one of Gymnotiformes, and most South American freshwater electric fish are of the wave-type EOD waveform (Kramer, 1999). In Chapter 6, we will focus on the characteristics of the EOD waveforms. The advantage of periodic characteristics of EOD waveform provides another chance to reduce noise in electric images. Strictly, the EOs and electric field models of two species, the pulse-type and wave-type, are different as shown in Fig. 2.1. In this thesis, the electric field model is based on the wave EOD species, Gymnotiformes, for all the experiments (Rasnow, 1996; Chen et al., 2005). Chapter 6 will handle the temporal structure of the electrosensory system due to EODs. It is assumed that the electric field model of pulse EOD species can be represented as the similar model of wave-type electric fish (von der Emde et al., 2009). Six different EOD models will be used and applied to the basic electric field model (introduced in section 2.4). Though the assumption can make a difference with a realistic model, the study can show how different EOD characteristics affect the noise reduction method using cross-correlation in the time domain.

2.2 Electroreceptors

Weakly electric fish have three types of receptors; tuberous electroreceptor, ampullary electroreceptor, and mechanosensory lateral line (Kramer, 1996; Nelson and MacIver, 1999; Nelson et al., 2000; von der Emde and Fetz, 2007). Tuberous electroreceptors and ampullary organs are similar to mechanoreceptors in the sense that response to external stimuli and delivery of sensor readings to the brain, except that these stimuli are not physical stimuli, but electric potential.

Ampullary organs are mainly found in elasmobranches, such as sharks, rays, and skates which possess only the ability of detecting changes in electric field. They use passive sensing to capture prey. The bio-electric fields are generated from nerve and muscle cells because of the control of the ionic balance in all live creatures (Kramer, 1996). Ampullary electroreceptors are able to detect very weak variation of the electric field. It has been mentioned in previous research that ampullary organs sense about $5nV/cm$ in fishes living in the sea and from $1\mu V/cm$ to $5\mu V/cm$ in freshwater fish (Zakon, 1986; Kalmijn, 1988; Bretschneider and Peters, 1992; Kramer, 1996). These ampullary electroreceptors are specialized to perceive low frequency electric field of bio-electric signals.

Tuberous electroreceptors are specialized for active sensing and sensitive to high-frequency signals (Zakon, 1986; Kalmijn, 1988; Bretschneider and Peters, 1992; Kramer, 1996). It is said that only a few teleosts (Mormyroide and Gymnotiformes) have tuberous electroreceptors (Bennett, 1971; Zakon, 1986; Kramer, 1996). Tuberous organs that respond to high frequencies seem to have characteristics of a band pass filter.



(a) (b)

Figure 2.2: Response of electroreceptors (A) Wave gymnotids emit a sine-wave like EOD and exhibit electroreceptors tuned to its main frequency (Data from (Hopkins, 1976)) (B) Pulse gymnotids local electric organ discharge (LEOD) covers a broader band spectrum and exhibit different types of electroreceptors sensing different aspects of the spectrum (reprinted from (Caputi, 2004), data from (Watson and Bastian, 1979; Aguilera and Caputi, 2003))

Fig. 2.2 shows different responses to electric organ discharges (EODs) (Caputi, 2004). Wave gymnotids show a very small bandwidth of receptors and these receptors are tuned to this specific range of frequency. It is noted that there is a tuning process in the mechanism to extract desired information. Weakly electric fish generate carriers and tune the receptor to the carrier to improve the signal-to-noise ratio. This receptor tuning process makes it possible to extract different information from complex electric images. It can be useful in drawing the target object signal in a complex natural environment. Contrary to wave gymnotids, pulse gymnotids, use a broader bandwidth. There are four types of receptors in pulse gymnotids; some respond to the total energy of stimuli and have a broad bandwidth, and some have a narrow bandwidth and have preferred frequencies. The different types of electroreceptors in the active sensory system are determined by both motor and sensory aspects.

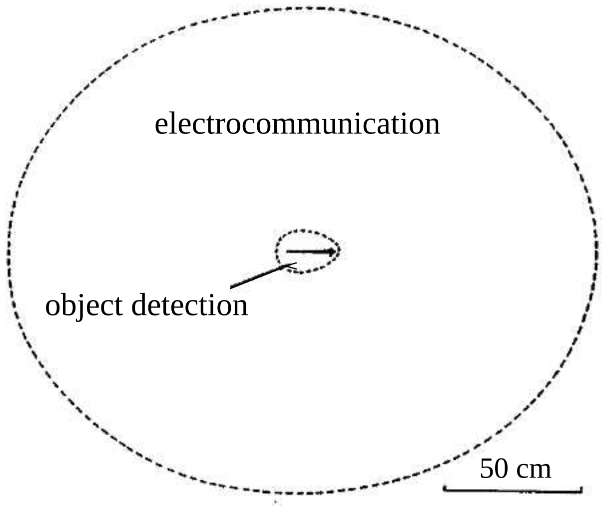


Figure 2.3: Range for the electrolocation and electrocommunication (reprinted from (Kramer, 1996))

The roles of tuberous electroreceptors are divided into two parts, the detection of objects and electrocommunication with conspecifics. Fig. 2.3 shows a different range of electroreception to identify the neighbor object and electrocommunicate. When the tuberous electroreceptors detect their own EOD, weakly electric fish can identify a target object in the near-field by detecting the distortion of electric fields. It is also possible to detect the EOD of other conspecifics for electrocommunication.

In Mormyroidei and Gymnotiformes, both ampullary organs and tuberous electroreceptors are found (Fig. 2.4). They have mechanosensory lateral lines also, this receptor responds to physical pressure. The movements of the prey or predator stimulate mechanoreceptors. Nelson et al. (2000) suggest a model to combine the electrosensory and mechanosensory images. In *Apteronotus albifrons* (Gymnotiformes), there are about $14,000$ tuberous electroreceptors, 700 ampullary electroreceptors, and 200 mechanoreceptors over the surface. Fig. 2.5 shows the responses of each receptors when the fish captures the prey.

Nelson's model shows that these three types of receptors are affected by the movements of a target object and contribute to localize the target object. All three sensory systems have a short sensing range. However, the tuberous sensory system can be the best solution for detecting a novel signal near weakly electric fish since there is a drastic decrease of response, which provides a simpler stimulus image. In addition, the tuberous electroreceptor has the highest density on the surface of the fish. It provides

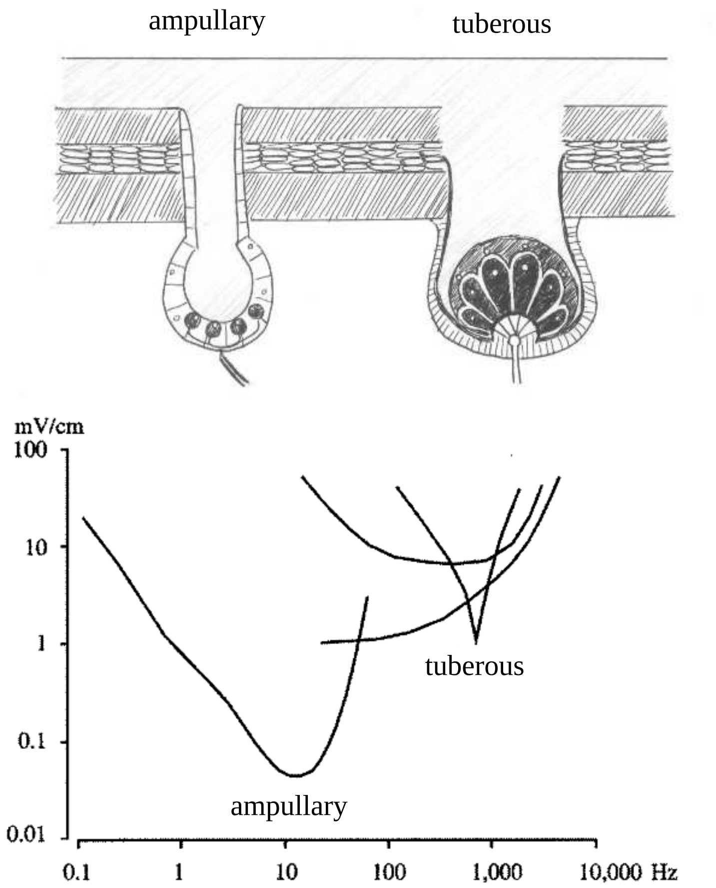


Figure 2.4: Two types of electroreceptors that are found in Gymnotiformes (modified from Szamier and Wachtel (1970); Szabo (1974)) Threshold curves of electroreceptors that were recorded in the *Brachyhypopomus occidentalix* (adapted from Dunning (1973) and Shumway and Zelick (1988)) (reprinted from (Stoddard, 2002))

a more accurate stimulus image.

It is known that the frequency sensitivity of ampullary receptors range from $0Hz$ to $50Hz$ and the tuberous electroreceptors are sensitive to a high frequency range from $100Hz$ to $2,000Hz$ (MacIver, 2001). In tuberous sensory systems, it is possible to detect the change of electric field in the range of $0.1\mu V$ (Rasnow, 1996). The ampullary electroreceptors have different sensitivity in marine and fresh water species, $0.001\mu V$ and $0.1\mu V$ respectively.

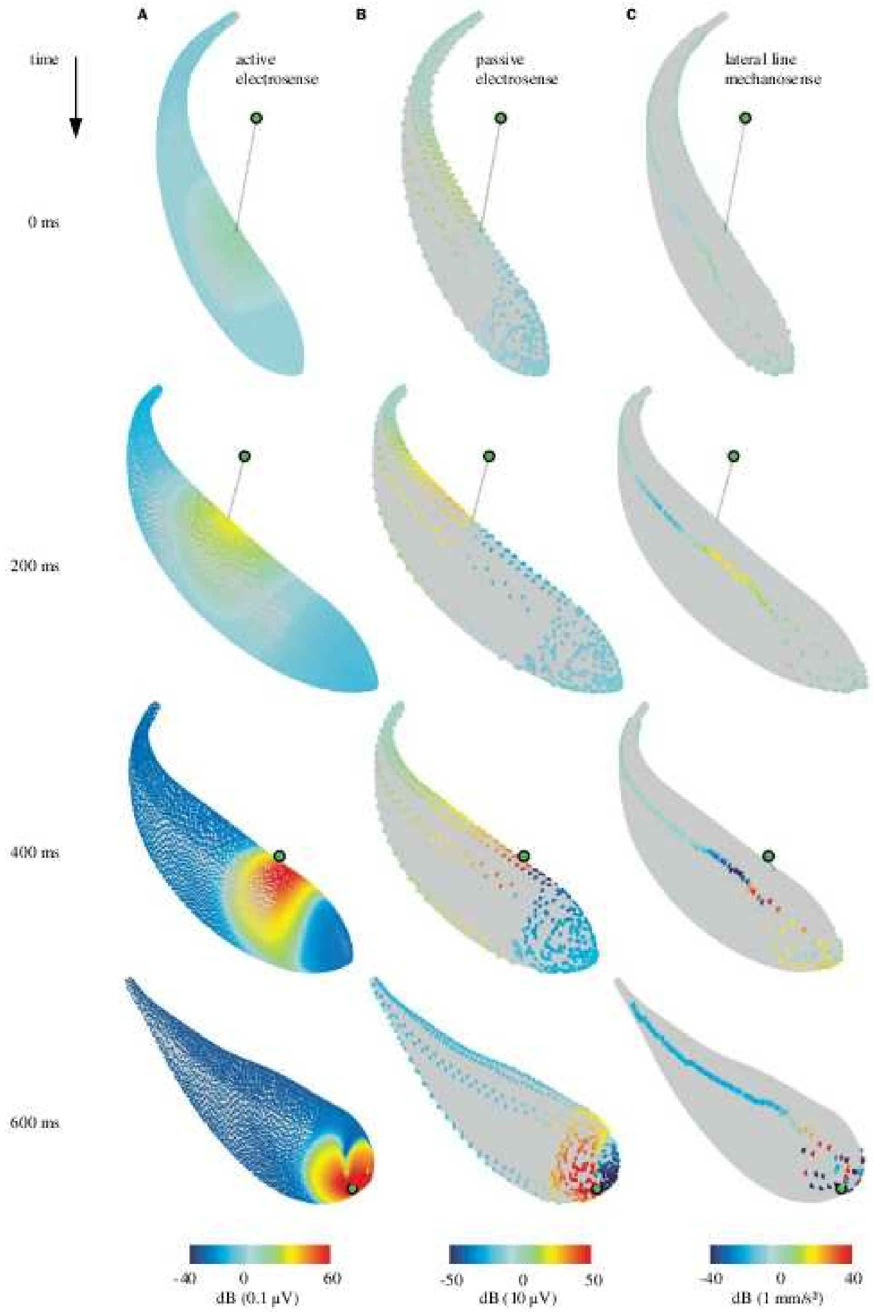
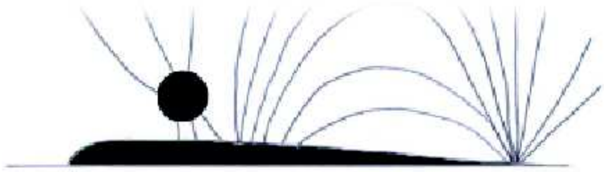


Figure 2.5: Selected ‘snapshots’ show responses of receptors respectively (a) tuberous electroreceptors, (b) ampullary electroreceptors (c) mechanosensory lateral lines of the prey capture behavior. Images are shown on a logarithmic color scale in units of decibels; the 0 dB reference is taken to be the estimated threshold sensitivity (active electrosensory : $0.1\mu V$, passive electrosensory : $10\mu V$, mechanosensory : $1mm/s^2$) (reprinted from (Nelson et al., 2000))

2.3 Electrolocation

Lissmann and Machin (1958) tried to explain the mechanism of localization of the target object and suggest the connection between the reception of self-generated electric fields and the recognition of an object's position. Lissmann (1951) was the first to find that *Gymnarchus niloticus*, which is weakly electric fish, shows special characteristics in behavior, with flexible swimming forwards and backwards and the ability to avoid the object. It is suggested that the electric signal that is generated from their EO may be involved in these characteristics. The construction is that weakly electric fish use a self-generated electric field to get information (Lissmann, 1974). The mechanism to identify the target object by detecting the distortion of the electric field generated by their own electric organ is called active electrolocation (Bastian, 1986; von der Emde et al., 1998) (Fig.2.6).

(a)



(b)

Figure 2.6: Distortion of self-generated electric field by the neighbor object; the object has low conductivity in (a) and high conductivity in (b) (modified from (Lissmann and Machin, 1958))

Nelson (2005) divided electrolocation behavior into three classes; detection, characterization, and localization. Weakly electric fish first, decide whether the target object exists in a near-field, understand characteristics such as the size and conductivity, and localize the position of the target object. The process of the electrolocation is actually not distinctly classified, but accomplished at the same time.

2.4 Modeling of the electric field

In biological experiments, measured values on the surface of fish are too small to acquire a stimulus image. Therefore, to obtain valid data the target object should be close to the fish. Heiligenberg (1975) proposes research using computer simulation to overcome the limitation of biological simulation. Fig. 2.7 shows the suggested model of the weakly electric fish; (gymnotoid) that includes the electric organ and the body surrounded by highly resistive skin surface. The electric field is derived by the laplace equation.

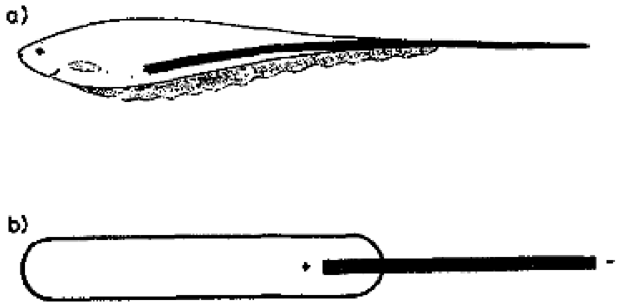


Figure 2.7: Weakly electric fish (a) and modeling schematics (b). The thick black bar indicates the electric organ. (reprinted from (Heiligenberg, 1975))

Sicardi et al. (2000) set the electric field generated by electric organ as an electric current. The current density normal to the interface J_n derived as

$$J_n(x,y) = \frac{\sigma_1\sigma_2}{2\pi\varepsilon_1(\sigma_1+\sigma_2)a^3}\frac{p(x^2/a^2+y^2/a^2-2)}{(x^2/a^2+y^2/a^2+1)^{5/2}} \tag{2.1}$$

where σ_1 is the conductivity of the first dipole when the small sphere, is represented as a dipole and σ_2 is the other one. ε means electric permitivity, a indicates the distance of the dipole from the skin of the fish and p is the dipolar moment.

Rasnow (1996) derived the electric field by modeling of the electric organ as the collection of electric poles and shows the effect of simple objects. Chen et al. (2005) reviewed the mathematical electric field modeling and advanced the effect of simple objects.

The electric organ can be modeled as a group of poles; therefore the electric potential is derived as the sum of the potential produced by each pole (Rasnow, 1996; Chen et al., 2005). When those poles are distributed uniformly along the mid-line of the weakly electric fish, *A. albifrons*, the electric potential, $V(\vec{x})$, is derived as

$$V(\vec{x}) = \sum_{i=1}^{m} \frac{q/m}{|\vec{x}-\vec{x}_p^i|} - \frac{q}{|\vec{x}-\vec{x}_n|} \tag{2.2}$$

where $\vec{x}$ determines the electric potential in space. There are $m+1$ poles to compose the electric organ, m positive poles and one negative pole. $\vec{x}_i$ is the position of the i_{th} positive pole, and $\vec{x}_n$ negative pole, and q is the normalized potential magnitude. The total sum of charges of electric poles of the weakly electric fish is zero, therefore the magnitude of one positive electric pole is q/m and the negative pole $-q$. It is known that generally the value of q has a magnitude from $8mV$ to $20mV$ (Chen et al., 2005). Since the electric field is the gradient of the electric potential and the electric field, $E(\vec{x})$, at the $\vec{x}$ is derived as

$$E(\vec{x}) = -\nabla V(\vec{x}) = \sum_{i=1}^{m} \frac{q/m}{|\vec{x}-\vec{x}_p^i|^3}(\vec{x}-\vec{x}_p^i) - \frac{q}{|\vec{x}-\vec{x}_n|^3}(\vec{x}-\vec{x}_n) \tag{2.3}$$

Chen et al. (2005) calculate the transdermal potential difference $V_{td}(\vec{x}_s)$ to consider the component that projected perpendicularly onto the electroreceptor. Actually the incidence angle of the electric field to the electroreceptor determines the shape and size of modulation (Caputi, 2004; Caputi and Budelli, 2006). The transdermal potential difference, $V_{td}(\vec{x}_s)$, at the $\vec{x}_s$ is derived as

$$V_{td}(\vec{x}_s) = E(\vec{x}_s) \cdot \hat{n}(\vec{x}_s) \frac{\rho_{skin}}{\rho_{water}} \tag{2.4}$$

where $\vec{x}_s$ is a position of electroreceptor on the skin surface of the fish. $E(\vec{x}_s)$ is the electric field and $n(\vec{x}_s)$ normal vector at the electroreceptor. ρ_{skin} is the resistivity of the skin and ρ_{water} for water. ρ_{skin}/ρ_{water} is the ratio of resistivity and the value of ρ_{skin}/ρ_{water} ranged from 0.1 to 0.5.

Chen et al. (2005) reviewed the simple sphere object perturbation in the electric field, as Rasnow (1996) also showed. When the $\vec{x}$ is the observation point, the position of one electroreceptor, the object perturbation, $\delta V(\vec{x})$, is calculated as

$$\delta V(\vec{x}) = \chi \frac{a^3 E(\vec{x}_{obj}) \cdot (\vec{x}-\vec{x}_{obj})}{|\vec{x}-\vec{x}_{obj}|^3} \tag{2.5}$$

where $\vec{x}_{obj}$ is the center of an object, a the radius of the object, and χ the electrical contrast that is ranged from 1 (a perfect conductor) to -0.5 (a perfect insulator). The transdermal potential difference due an object, $\Delta V_{td}(\vec{x}_s)$, is

$$\Delta V_{td}(\vec{x}_s) = -\nabla(\delta V(\vec{x}_s)) \cdot \hat{n}(\vec{x}_s) \frac{\rho_{skin}}{\rho_{water}} \tag{2.6}$$

Many electroreceptors distributed on the surface of weakly electric fish makes a two-dimensional electric image. The sensor reading of each electroreceptor can be modeled as above, and it makes possible to predict the connection of the electric image and the mechanism used to identify the target objects. Generally the group of electroreceptors arranged along the rostrocaudal line from head to tail is used for the generation of electric signal curves. A lot of researchers study the simple electric image acquired from the sensory line to know how weakly electric fish identify a target object with poor visual sensing. It is possible also to generate an electric image for one electroreceptor with the stream of time when a target object moves along the rostrocaudal line of weakly electric fish.

There is no direct connection between the characteristics of electric images and the properties of the target object. The electric signal creates a bell-shaped curve along the rostrocaudal axis of weakly electric fish. The width, slope, peak amplitude, and position of peak may provide information about the target object. In the next chapter, distance measures are reviewed, which is relevant to the distance of the object from the weakly electric fish and irrelevant to the size and conductivity.

2.5 Electric images

People can wonder about the role of these electroreceptors. In the case of humans, information about circumstance is acquired from vision. The vision of humans is a composite of a lot of neurons; therefore just two eyes can replace many receptors. Electroreceptors of a weakly electric fish are very simple relative to the human eye, and it can sense the amount of disturbance of self-generated electric fields. Stimuli from each electroreceptor produce an electric image and this stimulus image gives us a hint of how a weakly electric fish identifies the target object. The sensor line draws a bell-shaped curve called the ‘electric image’. The electric image feature provides information about the target object.

Caputi and Budelli (2006) readjusted the meaning of the "electric image". The image of sensory systems can be divided into three types of images; physical, stimulus, and neural images. The physical image is the energy pattern stimulated by pre-receptors. The stimulus image is transformed by the array of sensory cells. The receptors and neurons are encoded by stimulus and it generates the neural image. Von der Emde (2006) redefined the "electric image" as a stimulus image which represents the local change of electroreceptors on the skin's surface.

When the target object is located in the near-field of the weakly electric fish, the object is projected onto an electric image. The electric image is different from the visual image in the sense of the 'perspective'. There is no focusing mechanism in the electrolocation and one-to-one mapping between properties of objects and characteristics of images. Therefore the electric image is affected by size, distance from the skin of the fish, shape, and conductivity. These properties make it difficult to extract the information in an electric image to humans, but weakly electric fish show good performance for identifying objects and navigating in complex environments.

In this thesis, the electric perturbation of an electrosensory system is usually represented as an electric image. The electric image is usually represented as change of electric potential. The electric perturbation caused by a target object is small compared to the baseline transdermal potential. To understand the electrolocation mechanism of the system, it is assumed that other background components, such as the effects of a tail bending and non-conducting boundaries, can be removed and the effect of a target object represented in equation (2.6) will be shown as the electric image. It is possible to represent the electric image in the sensory and time domain. The spatial electric image will show the sensor readings along the rostrocaudal sensory line and the temporal electric image will be the temporal change at one electroreceptor when weakly electric fish move forward. It is possible to use approximated fish model such as the box model and tappered model to simplify the analysis (Babineau et al., 2006). The approximated model did not negatively change the experiment result. In this thesis, the sensory plane follows the box model (Babineau et al., 2006). In Chapter 3, the two-dimensional sensory plane will be used to show the change of the electric perturbation and most of electric image show the change of the electric field in the rostrocaudal sensory line. The sensory plane is parallel to the fish and the normal vector of each sensor is vertical to the fish. The rostrocaudal sensory is arranged in the same dorsoventral axis of the mid-line of weakly electric fish. The sensor intervals are not the same overall in experiments, but the sensor gap is usually selected as $2mm$. The sensor intervals determine the resolution of the electric image and affect the distance measurement. The relationship between resolution of the electric image and the accuracy of the relative slope will be discussed in Chapter 3. In Chapter 6, the smaller gap will be used to extract accurate distance measurement.

2.6 Reafferences

Movements of the tail cause a distortion of the self-generated electric field itself, and it is regarded as a negative effect to extract a novel signal from the electric image(Engelmann et al., 2008). Fig. 2.8 shows the effect of tail bending. Bending of the tail towards the target object increases the potential difference and decreases global contrast. The abrupt increase of the electric signal disturbs the understanding of the surroundings and identifying the target object. To compensate for the influence of the tail bending, it is known that weakly electric fishes use "reafference".

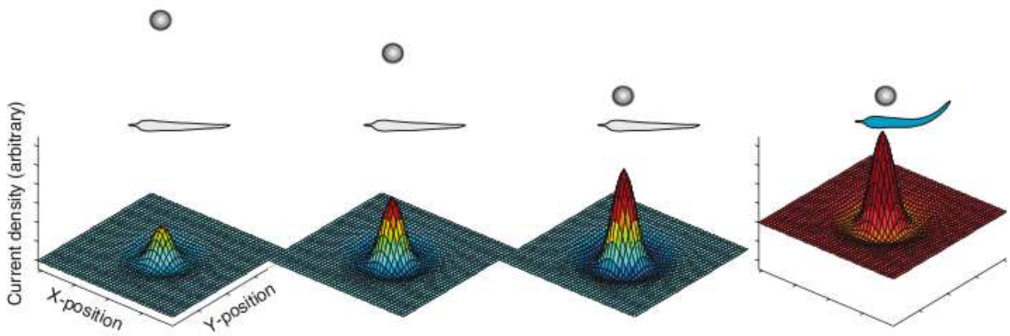


Figure 2.8: Electric image when the lateral distance of the target object decreases, and the tail bends towards the target object. Tail bending causes an increase in modulation and decrease in contrast (reprinted from Engelmann et al. (2008))

Reafference was introduced by von Holst and Mittelstaedt in 1950, and refers to the component of sensory input generated by a entity's own movements or actions (Nelson and Paulin, 1995). Nelson and Paulin (1995) study the reafference system of the electrosensory system of the elasmobranch. The neural processing for extracting novel signals is associated with DON circuitry and contains the common mode rejection and adaptive filter. Caputi (2004) reviewed reafference in the electrosensory system. The active sensory system involves strategies to acquire the desired signal from a noisy background, control of active generation of the energy source and pre-receptor mechanism.

The pyramidal cells in Gymnotiformes ELL shows the filtering mechanism (Bastian, 1995, 1996, 1999). The reafferent signals of electroreception can be removed by the pyramidal cells, and the proprioceptive electrosensory signals and descending signals also help filtering. It was also mentioned that these cells cancel the repetitive and predictable electrosensory input signals. Weakly electric fish might acquire novel electrosensory input including demanded information such as the location and characteristics of a target with cancellation of unnecessary signals. The tail bending pattern mentioned as the reafferent pattern can be removed by these pyramidal cells.

Sometimes weakly electric fish showing the tail bending movement seems to improve the searching process (Lannoo and Lannoo, 1993; MacIver, 2001). Weakly electric fish show a variety of motor control, such as back and forth swimming to scan the target, reverse swimming, tail probing. In elasmobranches, they sway the head to identify prey (Kim, 2007). The tail-bending movements might be electrolocation strategies such as a head swing of elasmobranches. It will be a challenging subject to investigate the positive effect and the information generated by their tail bending movements. Chapter 4 considers the tail-bending movement to improve the electrolocation.

2.7 Summary of Chapter 2

Weakly electric fish have a special organ called an EO and generate a weak electric field for electroreception. There are three types of sensors found in weakly electric fish; the ampullary electroreceptors, tuberous electrosensors, and mechanosensory lines. The tuberous electroreceptors are sensitive to self-generated electric fields and used for active electrolocation. The EO can be modeled as many electric poles. The transdermal potential can be calculated as the sum of electric potential caused by each electric pole. We focus on the electric field model based on Gymnotiformes. The transdermal potential values at electroreceptors are used to represent an electric image. The representation of electrosensory stimuli as an electric image and detailed electrolocation mechanism will be discussed in Chapter 3. The electric field model introduced in this chapter is used for overall experiments of the thesis.

Chapter 3

Electrolocation in electric images

Features such as maximum peak location, relative slope, and relative width in an electric image are used to localize a target object in three-dimensional spaces. It is known that weakly electric fish also recognize the characteristics of a target object, the size, shape, and electrical properties. This thesis concentrates on the localization mechanism of weakly electric fish. In this chapter, the basic concept of electrolocation will be studied. The location of maximum amplitude indicates the position of a target and there are distance measurements, the relative slope, distance between maximum peak and minimum position, and FWHM. The relative slope and FWHM is introduced in this chapter and the relative slope will be a major method to estimate the lateral distance of a target object.

The relative slope is the ratio of maximal slope to maximal amplitude. It is shown that a relative slope is a possible distance measurement in a distance discrimination experiment with pulse-type weakly electric fish, the mormyrid *Gnathonemus petersii* (von der Emde et al., 1998; von der Emde, 1999; Schwarz and von der Emde, 2001). It is assumed that the relative slope is also available for the wave-type weakly electric fish, such as Gymnotiformes. The experiments use the electric field model of the wave-type electric fish and the relative slope is used for distance measurement.

Relative slope change is affected by both rostrocaudal position and lateral distance. We use change of the relative slope when weakly electric fish swim forward. Gymnotiformes show back and forth swimming when they capture prey (Lannoo and Lannoo, 1993; Nanjappa et al., 2000; MacIver, 2001) and it is assumed that this kind of weakly electric fish have a preferred sensor zone for electroreception and use the temporal information. This experiment was based on the proceeding (Sim and Kim, 2010b). In contrast to Gymnotiformes, wave-type weakly electric fish, it seems that pulse EOD species do not use back and forth swimming for electrolocation. This study might be available for the electrosensory system of wave EOD species.

3.1 Spatial structures of electric images

An electric image can be considered a spatial and temporal structure. Since weakly electric fish have approximately 14,000 tuberous electroreceptors (MacIver, 2001), the distortion created due to the vicinity object is projected onto the surface of the fish, and a two-dimensional electric image is generated. Transdermal potential values are inversely proportionate to the lateral distance of the target object from the fish (equation 2.6).

When the distance between the electroreceptor and the object increases, the electric perturbation rapidly decreases. Consequently, when the target object is located at the mid-point of the sensory line, the electric image draws a bell-shaped curve. The peak amplitude is dependent on the size and distance of the target object. Fig. 3.1 shows the change in transdermal potential at the sensory line when the rostrocaudal position, lateral distance, and size of a target object are varied. Fig. 3.1 shows the simulation result based on the electric field model and study on an electric image (Rasnow, 1996).

Rasnow (1996) shows the effect of characteristics of a simple object, lateral distance, shape of object (sphere or ellipsoid in the weakly electric fish, *A. leptorhynchus*). From the simulation, a relationship between features of the electric image and characteristics of the object is derived. The peak position determines the rostrocaudal position of the object. The peak amplitude becomes smaller when the object moves away from the fish body. However, the amplitude is affected by not only the distance, but also the size of a target. The larger the target object, the greater the electric perturbation (Fig. 3.1 (f)). How can we determine whether there is a large-sized object distant from the body, or a small-sized object close to the body? When there are two different objects that have the same peak amplitude, it is known that relative width, relative slope, or a full-width at half-maximum (FWHM) make it possible to discriminate the two objects (Rasnow, 1996; von der Emde et al., 1998; von der Emde, 1999; Sicardi et al., 2000; Chen et al., 2005; Babineau et al., 2006; von der Emde, 2006).

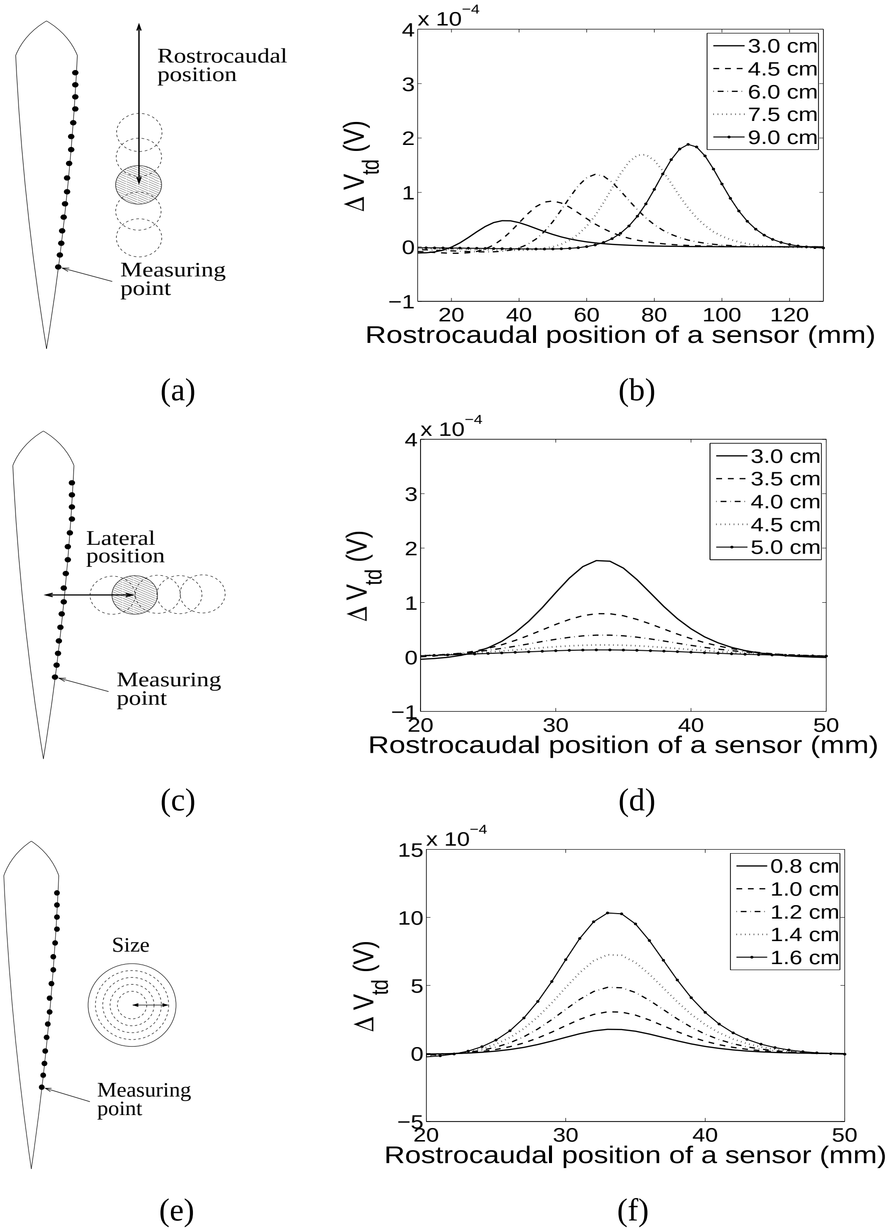


Figure 3.1: The transdermal potential. (a), (c), and (e) is a schematic to show how the object parameter changes, where the solid line represents the electric organ, and circles on the line represent the target object. (b), (d), and (f) show the change in transdermal potential due to an object. In the case of (a) and (b), the object if far away from the head and keeps a lateral distance. The rostrocaudal distance from the head changes with an interval of 20 mm. In (c) and (d), the lateral distance from the mid-line of the fish changes with an interval of 5 mm. (e) and (f) show changes when an object size varies with an interval of 4 mm. (modified from (Sim and Kim, 2010e; Rasnow, 1996))

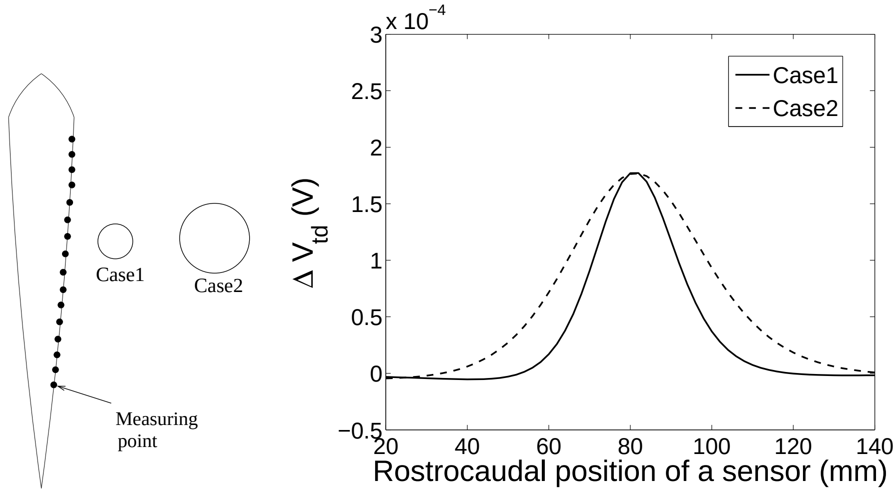


Figure 3.2: Electric images due to a target object being near weakly electric fish (two different objects have the same peak amplitude and position); an object (CASE 1) with a radius of $1cm$ and a distance of $3cm$, and an object (CASE 2) with a radius of $2cm$ and a distance of $4.5cm$

It was shown that Gymnotiformes might use the relative width of electric image to estimate the lateral distance (Rasnow, 1996). Two kinds of relative relative widths were introduced to estimate the lateral distance; the width of the electric image at half the peak amplitude and 90% amplitude. Chen et al. (2005) used the FWHM (full-width at half-maximum) for distance estimation. There was other experiment of electrolocation in wave EOD species that the difference between the rostral and caudal peak location can be used as a function of lateral distance of a target object (Babineau et al., 2006). The relative slope was usually used for electrolocation of pulse EOD species, *Mormyrids* (von der Emde et al., 1998; von der Emde, 1999; Sicardi et al., 2000; von der Emde, 2006). It was shown that the relative slope can be used to estimate the lateral distance for Gymnotiform model in simulations.

Fig. 3.2 shows an example of two object perturbation curves that have the same maximal intensity. Two different curve widths depend on the size of target object; the width increases as the object size becomes larger.

Fig. 3.2 shows two different cases that have the same maximal amplitude with a different combination of the lateral distance and size. These coupled connections indicate that there is another cue to identifying the lateral distance and size independently. The lateral distance of a target object is an important feature when weakly electric fish catch the prey. Weakly electric fish show a very precise approach to prey and capture behavior (Lannoo and Lannoo, 1993). It is possible to suppose that weakly electric fish understand and track the exact position of the prey through the electrolocation process from detection to capture.

Actual behaviors of weakly electric fish are studied (von der Emde et al., 1998; von der Emde, 1999; Schwarz and von der Emde, 2001). *G. petersii* is trained to determine a certain target between two objects with prey compensation. In experiments, it has been noticed that weakly electric fish can discriminate the distance of a target object and the ratio of the maximal slope and maximal amplitude (Fig. 3.3). This ratio is a very reasonable cue to measuring distance, since weakly electric fish show recognition behaviors that consider cubes are closer than spheres at the same distance. The ratio of the maximal slope and maximal amplitude follow this tendency also.

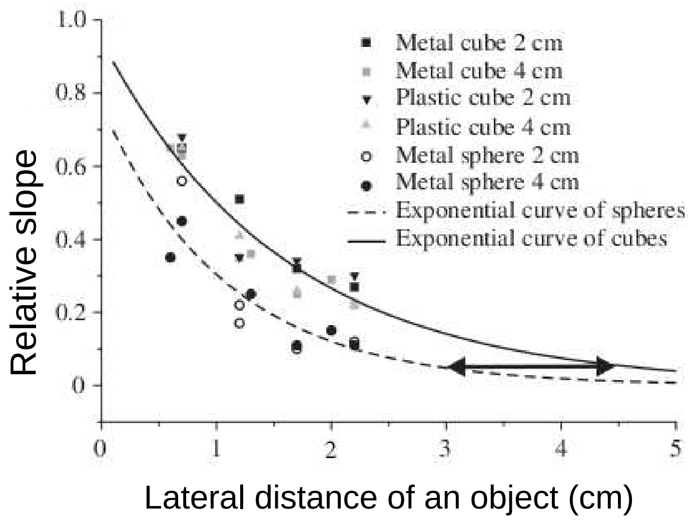


Figure 3.3: Relative slope which is maximal slope/maximal amplitude ratio of different electric images when target objects are two different-sized spheres (circles) and four different type of cube (squares and triangles) (reprinted from (von der Emde, 1999))

Sicardi et al. (2000) called the ratio of the maximal slope and maximal amplitude the relative slope, and verifies validity of the relative slope as a distance measure theoretically. We found that it might possible to use the relative slope for distance estimation of Gymnotiformes in analytical simulations based on the electric field model of wave-type weakly electric fish. In the next section, it will be shown that the relative slope can be used for wave EOD species.

In the simulation results of the paper (Sicardi et al., 2000), the width varied when the distance of the object from the fish changes. The width in electric images is also affected by the shape, size, and conductivity of the target object. However, the relative slope shows stronger independence than the width to the size and conductivity of the target object. Chen et al. (2005) adopted the full-width at half-maximum (FWHM). The FWHM is the width in electric images when the intensity becomes half of maximum. The FWHM is largely independent of the size and conductivity of a target object (Chen et al., 2005). FWHM also can be a distance measure to discriminate the lateral distance of the target object.

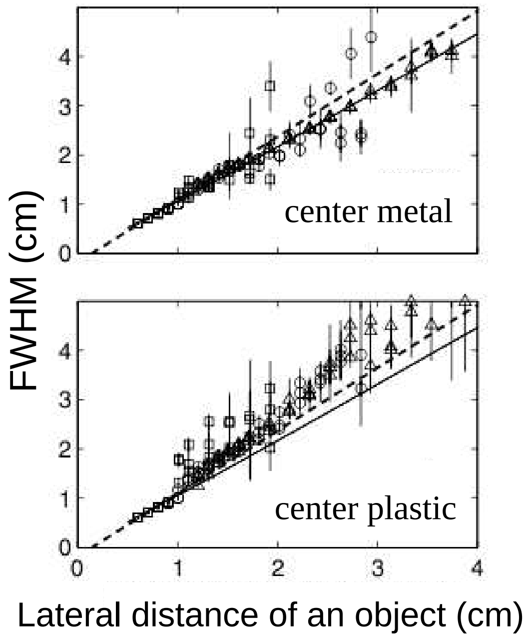


Figure 3.4: FWHM versus the lateral distance of the target object for different object sizes (different marker) (reprinted from (Chen et al., 2005))

3.2 Localization of a target object in electrosensory system

It is important issue to localize a target to all animals including weakly electric fish. Weakly electric fish use electrolocation for prey capture and navigation. In three-dimensional space, we can separate underwater space into rostrocaudal, lateral and dorsoventral space classifications with respect to weakly electric fish.

Rostrocaudal axis indicates the direction from head to tail.

Lateral axis represents the direction from the midline of weakly electric fish to the side of the fish's body.

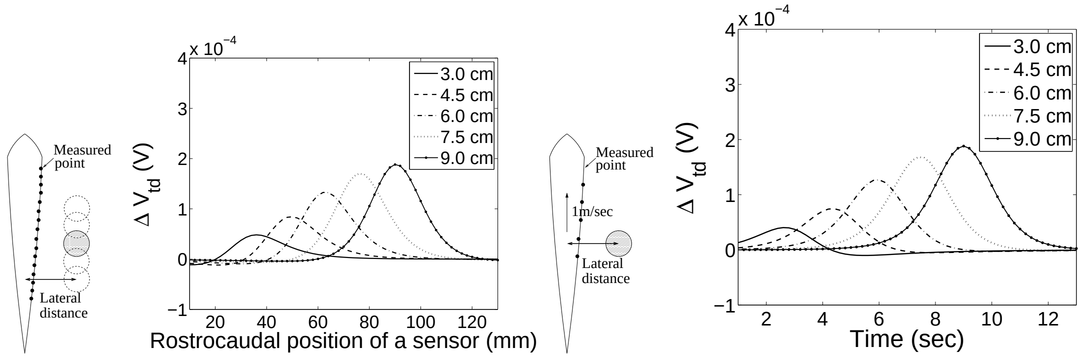
Dorsoventral axis is the line leading from the ventral to dorsal area.

We will study the localization mechanism in weakly electric fish through electric images. Object perturbation is the amount of change of electric potential when a target object is near the electric fish. It has been shown that the peak amplitude of perturbation appears at the sensor position closest to the target object (Chen et al., 2005). The result can be explained by equation (2.5), because the object perturbation is inversely proportional to the cubed value of distance between the center of the object and sensor position.

Chen et al. (2005) studied the temporal structure of *A. albifrons*' electrolocation closely, the result was similar to the spatial structure (von der Emde et al., 1998; von der Emde, 1999; Schwarz and von der Emde, 2001). When a small target object moves along the rostrocaudal line of the fish, the change is recorded and simulated theoretically(Chen et al., 2005). Fig. 3.5 shows spatial and temporal electric images when the lateral distance and size of target object is fixed. The intensity is affected by position as well as the size and conductivity of the target object. In a spatial electric image, the peak position matches the rostrocaudal position of the target from the head of the weakly electric fish as shown in Fig. 3.5 (a). The temporal sensor readings of an electroreceptor are represented in Fig. 3.5 (b). In a temporal electric image, the position of maximum intensity indicates the point of time when a target object is closest to a specific electroreceptor. In electric images, we can directly extract the rostrocaudal position of a target. To estimate the lateral distance of a target, we need another feature such as relative slope and FWHM.

We focused on the relative slope as a measurement of the lateral position of a target object unrelated to the size and electrical property of object. The independence of the relative slope and object properties has already been studied (von der Emde et al., 1998; von der Emde, 1999; Sicardi et al., 2000; von der Emde, 2006). Fig. 3.3 shows that there is no change due to object size and electrical constant. The relative slope is affected by the lateral distance of a target object and we can use this as a distance measure.

In this thesis, the lateral distance is measured from the center of the target object and it can be a problem when a target object is large. It is assumed that the lateral distance



(a) (b)

Figure 3.5: Electric images when the lateral distance and size of a target object is fixed (a) spatial sensor readings with varying rostrocaudal positions of a target object (b) temporal sensor readings with varying rostrocaudal positions of sensors (the velocity of the weakly electric fish is $0.01 m/sec$) (modified from (Sim and Kim, 2010e))

can be derived by subtracting the radius of the object from the distance to the center of the object (Engelmann et al., 2008). It is known that weakly electric fish can measure the size of the target by using the width, peak amplitude, and phase of electric images (Assad et al., 1999). Weakly electric fish might use the lateral distance to the center and the size of the target to estimate the lateral distance.

In this thesis, the relative slope is mainly used to localize a target object in most of experiments. FWHM is used as a distance measurement of an electrosensory system for the first time in Chen et al. (2005). In this research, FWHM was focused on the wave-type weakly electric fish, Gymnotiformes. As shown in Fig. 3.4, the FWHM is analytically independent on the electrical property, but there is little difference between metal and plastic in measured data. Though, the FWHM is still largely independent on the electrical property of a target, the relative slope seems more reasonable measurement for distance estimation. The relative slope of different shaped objects, a cube and sphere, show different relative slope and it worked for distance discrimination experiments with pulse EOD species (von der Emde et al., 1998; von der Emde, 1999; Schwarz and von der Emde, 2001). It is assumed that the relative slope can be applied to wave-type weakly electric fish, though the distance discrimination experiments are made for pulse-type weakly electric fish.

3.3 Spatial and temporal relative slopes

The relative slope is the ratio of maximal slope to maximal amplitude and it is possible to apply to spatial and temporal electric images. We can redefine relative slope as spatial slopes and temporal slopes. Spatial sensor readings along the rostrocaudal sensory line generate spatial electric images and we can extract the spatial slope. It is possible to represent a spatial slope as

$$Spatial\ relative\ slope = \frac{max_i\,\{I(x_{i+1},t) - I(x_i,t)\}}{max_i\,\{I(x_i,t)\}} \tag{3.1}$$

where there are n electroreceptors along the rostrocaudal sensory line $x_1, x_2, \ldots, x_n$ on the skin surface. $I(x_i,t)$ is a transdermal potential difference at a given position x_i in a given time t. When we use a temporal electric image with temporal sensor readings at one electroreceptor, a temporal slope can be defined as

$$Temporal\ relative\ slope = \frac{\max_k\,\{I(x,t_{k+1}) - I(x,t_k)\}}{\max_k\,\{I(x,t_k)\}} \tag{3.2}$$

This relative slope shows the ratio of maximal slope and maximal amplitude in different domain. In previous research, the relative slope is extracted from the electric image along the sensory line (von der Emde et al., 1998; von der Emde, 1999; Sicardi et al., 2000; von der Emde, 2006). In Fig. 3.6, it is shown that the temporal relative slope is also available for distance estimation. Both spatial and temporal relative slope are not affected by the size and conductivity of a target object.

Fig. 3.6 shows the relative slope when the lateral distance of a target changes from 2*cm* to 5*cm* in spatial and temporal electric images. The two phase relative slopes can be obtained from equation 3.1 and 3.2. In Fig. 3.6 (a), the relative slope curves are different with different rostrocaudal positions. The sensor readings of electroreceptors are affected by the distribution of electric poles. When we read the intensity of electroreceptors with time intervals, a temporal relative slope is less affected by the measuring sensor position compared to a spatial relative slope. As shown in Fig. 3.6, a temporal relative slope is less affected by the relative rostrocaudal position of a target than a spatial relative slope. We will compare two relative slopes, the spatial relative slope and temporal relative slope in Chapter 5.

In Fig. 3.6 (a), the relative slope depends on not only the lateral distance but also the rostrocaudal position of a target object. The change of relative slope in the rostrocaudal line is smaller than in the lateral line (see Fig. 3.7). The degree of decrease is larger

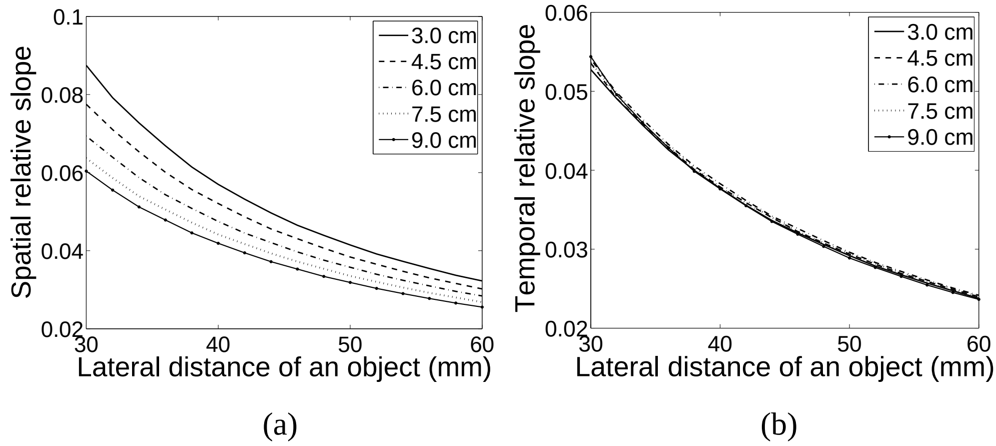


Figure 3.6: Relative slopes when the lateral distance of the target object changes from $2cm$ to $5cm$ (a) spatial relative slope with varying rostrocaudal positions of a target object (b) temporal relative slope with varying rostrocaudal positions of sensors (the velocity of the weakly electric fish is $0.01m/sec$) (modified from (Sim and Kim, 2010e))

when the lateral distance of a target object changes. Fig. 3.7 shows the change of relative slope when the rostrocaudal position and lateral distance of a target changes with the same change interval of $0.5cm$. On the x axis, the change step of a target object is represented. The lateral distance of a target changes from $3cm$ to $9.5cm$ and the rostrocaudal position from the head changes from $2cm$ to $8.5cm$.

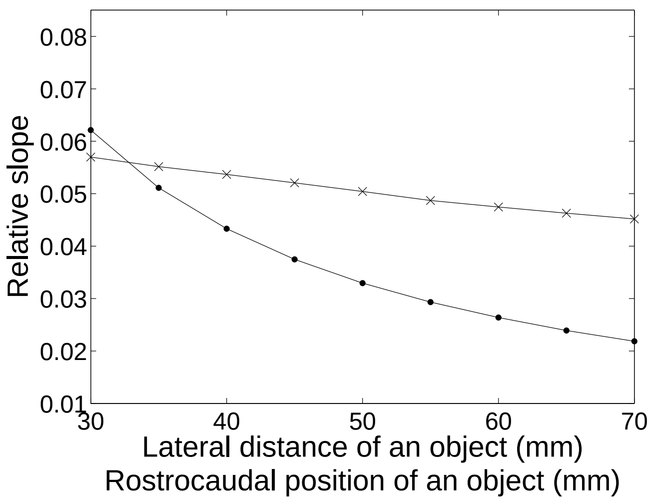


Figure 3.7: Difference of effects due to a lateral and rostrocaudal changes. The relative slope changes more rapidly when lateral distance changes (the change of a lateral distance marked by '.' and the change of a rostrocaudal position marked by 'x')

Since a lot of electroreceptors are distributed over the whole skin surface, the multiple spatial readings can detect the change of a relative slope in both rostrocaudal and dorsoventral line. The dorsoventral distribution of electroreceptor has same work with a rostrocaudal sensory line. Sensor readings from this distribution determine the height of a target object. Consequently, multi-electroreception of weakly electric fish provides two-dimensional electric images and the location of target object can be extracted in both rostrocaudal and dorsoventral axis.

In Fig. 3.8 show relative slope acquired from rostrocaudal and dorsoventral electric image when a target object moves along three-dimensional axis. We can see the relative slope change in a rostrocaudal sensory line from Fig. 3.8 (a) to (c). When a target object moves from fish to side or from head to tail, relative slope decreases. The relative slope is largest when a target object is located in the same dorsoventral line with measured rostrocaudal sensory line. In Fig. 3.8 from (d) to (f), the relative slope obtained from dorsoventral sensory line is presented. The relative slope in a dorsoventral sensory line shows similar pattern with the relative slope in a rostrocaudal axis. Fig. 3.8 (b) and (f) is similar because the object moves along the series of sensors, respectively. Fig. 3.8 (c) and (e) has alike curvature also because the object far away from the midpoint of a sensor array vertically. When we read a dorsoventral sensory line, the relative slope is larger with an object in a same rostrocaudal position with sensory line. The relative slope decreases when a target object far away from the weakly electric fish.

To study the relative slope with position changes of a target object in three-dimensional space, we study the relative slope change acquired from the sensory plane (Fig. 3.9). In two-dimensional electric images, we can detect how relative slope affected by the movements of a target object. As shown in Fig. 3.9, the relative slope is affected by every change of an object location in the rostrocaudal, lateral, and dorsoventral. Thus, the relative slope cannot be a function to localize the exact position of a target object in three-dimensional space. For example, in Fig. 3.9 (c), the relative slope acquired from the spatial readings of a rostrocaudal sensory line when object moves around the given two-dimensional plane. Each single line indicates same relative slope value. There are a lot of object location which has same relative slope. This can be a reason why weakly electric fish has many electroreceptors on the surface. From the spatial readings of sensory plane, the rostrocaudal position and height of a target object can be acquired directly. Then the relative slope variation can be decided uniquely for the lateral distance and we can use a relative slope to estimate the lateral distance.

To estimate the lateral distance of a target object, we need whole distance map. We

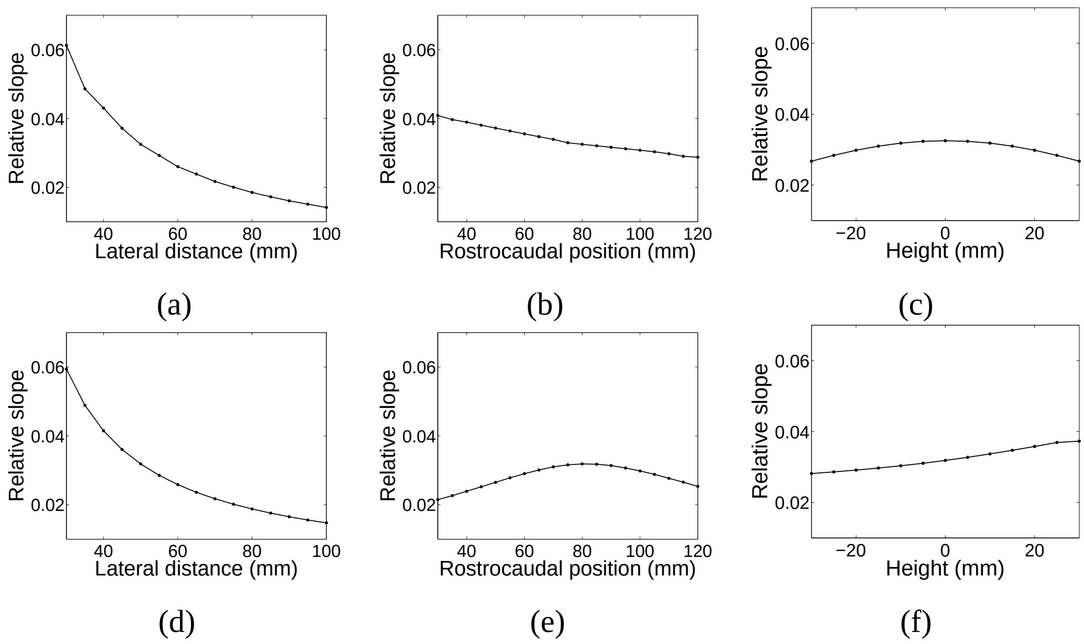


Figure 3.8: The relative slope when the location of a target object changes in three-dimensional space (a), (b), and (c) change of relative slope in the rostrocaudal sensory line when the lateral, rostrocaudal, and dorsoventral position of a target varies respectively (d), (e), and (f) change of relative slope in the dorsoventral sensory line when the lateral, rostrocaudal, and dorsoventral position of a target varies respectively

have to decide a rostrocaudal position of a target object for localization of a lateral distance. When a rostrocaudal position of a target is decided, a lateral distance of a target can be obtained by relative slope. The rostrocaudal position of a target can be easily decided by peak position in electric image, but weakly electric fish should memorize whole relative slopes at each rostrocaudal position of a target. We will study change of relative slope when weakly electric fish swim forward to reduce a load for memory of whole distance map.

The spatial and temporal slope uses the ratio of maximum difference to maximum amplitude. In the neural network to compare the difference and electric perturbation, neurons might be stimulated by the electric perturbation in a row along the rostrocaudal sensory line or in time sequences. We can assume there might be an array arranged spatially and temporally to realize the distance estimation mechanism neuronally. In another layers, neurons can calculate the slope and maximum value with the neurons in the first layer. To obtain the ratio of maximal difference and amplitude, we need multiplicative neuron system. It is difficult to represent the multiplication neuronally,

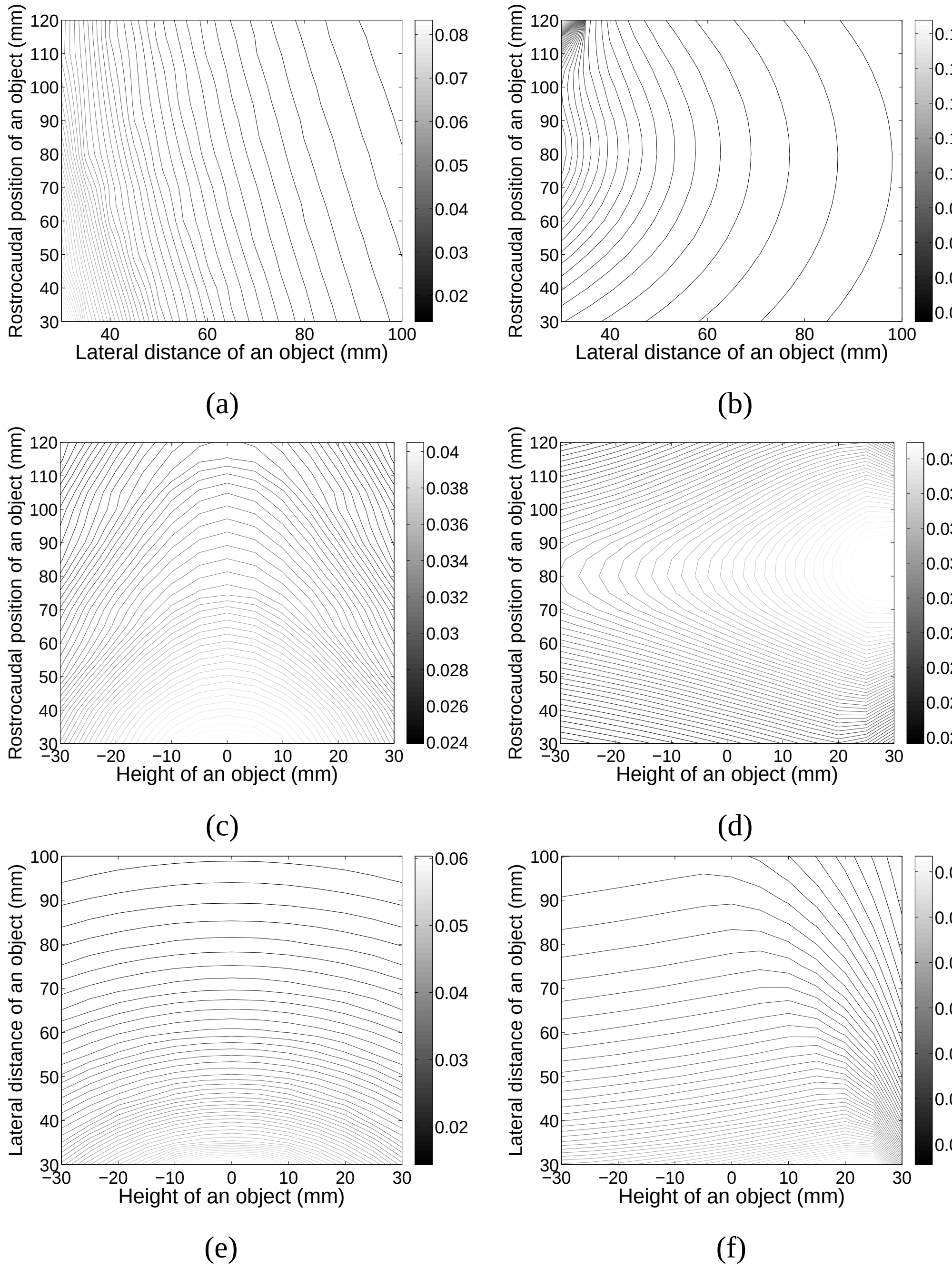
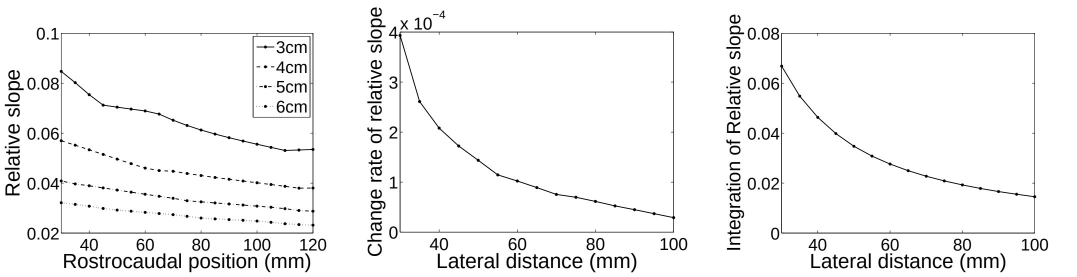


Figure 3.9: The contour of a relative slope when a position of a target changes in three-dimensional space (a), (c), and (e) obtained from the series of sensors in the rostrocaudal axis, (b), (d), and (f) in the dorsoventral axis; (a), (b) the lateral distance and rostrocaudal distance changes, (c), (d) the rostrocaudal distance and height changes, and (e), (f) the lateral distance, and a height changes

however, it might be possible with a combination of activations and weights as as Gabbiani et al. have shown (Gabbiani et al., 2002).

3.4 Change of relative slope

When weakly electric fish capture their prey, they almost always show back and forth swimming. As mentioned in previous section, the relative slope is affected by object positions in rostrocaudal, lateral and dorsoventral axis. We focus on the relative slope obtained from a rostrocaudal sensory line. We can draw relative slope curves when weakly electric fish swim forward and the relative rostrocaudal position of a target changes from head to tail with respect to weakly electric fish. Fig. 3.10 (a) shows change of relative slope when the relative rostrocaudal position increases from head at each lateral distance of a target. We use change of relative slopes as shown in Fig. 3.10 (a). It is assumed that weakly electric fish have a preferred sensor zone for electrolocation. When they swim back and forth, it seems that weakly electric fish put the target on the specific sensory region of trunk. Fig. 3.10 (b) and (c) show the change of the relative slope when a target object located in this sensory region. The change of relative slope decreases at two points near head and beginning of tail when the lateral distance of a target increases. Fig. 3.10 (b) shows the change rate and Fig. 3.10 (c) represents the integration of relative slope at each rostrocaudal position of a target from head to tail (Sim and Kim, 2010b,a).



(a) (b) (c)

Figure 3.10: Change of relative slope (a) relative slope change when rostrocaudal position of a target changes with different lateral distance (b) change rate of relative slope (c) integration of relative slope (modified from (Sim and Kim, 2010b,a))

It is possible to represent the change and integration of relative slope as difference and sum of relative slopes. When weakly electric fish put the target at the sensory region from x_n near the head to x_m close to the beginning of tail, the change of relative slope can be represented as

$$Change\ of\ relative\ slope = \frac{R(x_n) - R(x_m)}{x_m - x_n} \tag{3.3}$$

where $R(x)$ indicates the relative slope at x and the integration of relative slope is derived as

$$Integration\,of\ relative\,slope = \sum_{i=m}^{n} R(x_i) \tag{3.4}$$

It is shown that change rate and integration of relative slopes draw similar curves with an original relative slope graph. Fig. 3.10 (c) shows a smooth curve. The integration of relative slope seems to have low pass filtering effect when the fish swim forward. To utilize change rate and integration of relative slope, we need both spatial and temporal electrosensory information, but the lateral distance of a target can be decided by single change pattern. It is possible to use change of relative slope because of their behavior pattern, back and forth swimming for prey capture. Actually, weakly electric fish might use crude localization for prey capture and do not use a fine-tuned memorized map of the relative slope. The change of relative slope might be useful for realization of the electrosensory system in the electric machine.

3.5 Summary of Chapter 3

This chapter introduces distance measurements, relative slope and FWHM, and the relative slope is mainly used to estimate the lateral distance of a target object in the thesis. In three-dimensional spaces, weakly electric fish have to estimate the rostrocaudal, dorsoventral, and lateral position. When the two-dimensional sensory image is used for localization, the rostrocaudal and dorsoventral position can be measured by a location of maximum amplitude. The relative slope is the ratio of maximal slope to maximal amplitude and indicates the lateral distance of a target object. It is possible to measure the lateral distance regardless of the size and electrical property in the electrosensory system.

The relative slope can be divided as spatial relative slope and temporal relative slope. When the electric image is drawn along the rostrocaudal sensory plane, the spatial relative slope is extracted from the spatial electric image. The temporal relative slope can be acquired from the temporal electric image caused by temporal changes at an electroreceptor when weakly electric fish swim forward. Two types of relative slopes are independent of the size and conductivity of a target object. The relative slope was introduced as a distance measure for pulse EOD species (von der Emde et al., 1998;

von der Emde, 1999; Schwarz and von der Emde, 2001). It is possible to apply this method to wave EOD species, which is the basic electrolocation model of this thesis.

When the rostrocaudal position of a target object changes, the relative slope is affected (see Fig. 3.6). The temporal relative slope seems largely independent of the rostrocaudal position of a measured electrosensor and a target object. The spatial information acquired from the sensory plane is useful information and the relative slope change was shown on the sensory plane in this chapter. The spatial relative slope changes when a rostrocaudal, dorsoventral, and lateral position changes and weakly electric fish might consider the change of relative slope to identify the exact position of a target. The rostrocaudal and dorsoventral position of a target is directly indicated by the location of maximum intensity. Then, weakly electric fish can estimate the lateral distance by relative slope. Weakly electric fish show back-and-forth swimming when they capture prey and it can be used for electrolocation. When weakly electric fish swim back and forth, the relative slope changes, and both the change rate and integration of relative slope provide another distance measurement. The change and integration of relative slope are similar to the original relative slope. These measures use temporal changes and do not have to consider the rostrocaudal position of a target. In addition, the integration of relative slope can be useful to identify the accurate position of a target in a noisy environment.

Chapter 4

Electrolocation with active-body movements

The pulse EOD species, *Gymnotus carpo, Rhamphichthys rostratus, and Brachyhypopomus cf. brevirostris* tend to swim forward when they capture prey (Nanjappa et al., 2000). It was reported that Mormyrids show lateral and radial motor actions (Toerring and Belbenoit, 1979; von der Emde, 1990), but it seems that their backward swimming or side searching are not foraging behaviors for electrolocation (Nanjappa et al., 2000). In contrast to the pulse EOD species, *Apteronotus albifrons* show strong back-and-forth swimming and tail-bending movements (Lannoo and Lannoo, 1993). Other wave-type weakly electric fish show similar foraging pattern and it was suggested that the active body movements such as a back-and-forth swimming and tail-bending movements might help to enhance the quality of an electric image (Nanjappa et al., 2000; Bacher, 1983; MacIver, 2001). The body movements of weakly electric fish affect electrosensory signals. In this thesis, the temporal change of electrosensory system will be discussed in two chapters, Chapter 4 and Chapter 5. In this chapter, the temporal change with tail-bending movements will be studied and is based on previous studies (Sim and Kim, 2009b, 2010a,c).

In Chapter 4, it is assumed that weakly electric fish use the temporal change when they bend their tails and this study can be available for wave-type weakly electric fish. This chapter will study relative slope change with tail bending movements and how it help to extract accurate distance information. The temporal pattern of tail bending movements could be a cue for distance estimation in itself. The normalized tail bending pattern is not affected by the size and electrical properties of a target object. It is also a possible strategy using the relative slope when the tail is bent to ascertain sure the accuracy of the distance.

4.1 Temporal structures of electric images

So far, research about electrolocation has concentrated on the spatial information acquired from distribution by numerous electroreceptors. Of course, there have been studies using temporal structures when weakly electric fish swim forward. When weakly electric fish capture their prey, they exhibit a variety of movements such as back-and-forth swimming and tail-bending movements. It is suggested that tail-bending movements can be a behavior pattern of weakly electric fish to enhance the information acquired from the electrosensory system (MacIver, 2001). Generally, however, the effect of tail bending movements have not been not considered because tail bending generates abrupt changes in the electric field. In this chapter, we consider the tail bending movements as a factor in localizing a target object in active electrosensory systems. When a target object is near a weakly electric fish, the perturbation of a target is considered as having high-frequency characteristics in a spatial electric image. In contrast, the temporal pattern of tail bending movements causes slower changes and has low-frequency characteristics.

When the weakly electric fish shows active movements such as tail bending, the temporal structure is markedly distinct from the spatial structure. The effect of the movements of weakly electric fish will be discussed in next chapter. We will cover in this chapter what additional information we can obtain from temporal tail bending patterns.

4.2 Body modeling and tail bending movements

For simulation, we set the body length to $21cm$ and the length of electric organ to $15.47cm$, and fixed the density of the electric poles at $10 poles/cm$, following the body model from other works (Chen et al., 2005; Babineau et al., 2006). The number of electric poles is approximately 150, and these poles are located along the midline of weakly electric fish. All poles are positive except the last negative pole at the end of the tail. For simulation, we put many electrosensors on the body surface. The electrosensors are symmetrically distributed on both left and right sides of the weakly electric fish.

When the electric fish bends its tail, approximately 65% of the body length is allowed to bend. The rostral portion of the body maintains itself in a straight line. The bending angle is defined by the angle between the body axis and the line from a certain pivot point to the end of tail. The tail-bending angle ranges from $-45°$ to $45°$. We assume that the caudal portion of the tail draws a circular arc around the pivot. A radius R of this curvature can be calculated as $R = L/2\theta$, where θ is a bending angle and L is a bended proportion of body length. The center point or rotational axis of the curvature is at a distance R from the pivot point of the body.

Fig. 4.1 shows the temporal sequence of transdermal potential acquired from tail-bending movements when a lateral distance of a target object changes. Each potential curve shows temporal variation depending on the tail-bending phase. The tail-bending angle starts from $-45°$ to $45°$ and again returns from $-45°$ to $45°$. When the tail is bent close to the target object, the potential increases. We can see the peak of potential amplitude when the tail is closest to the target object because the small distance of a target object from the body axis increases the electric field potential.

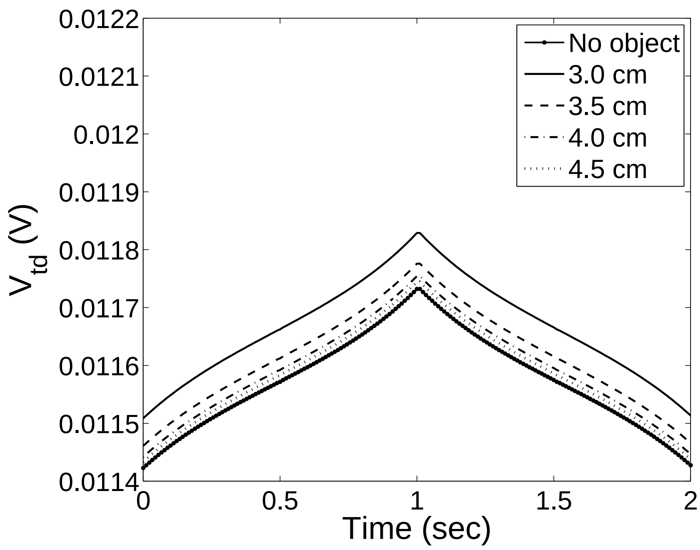
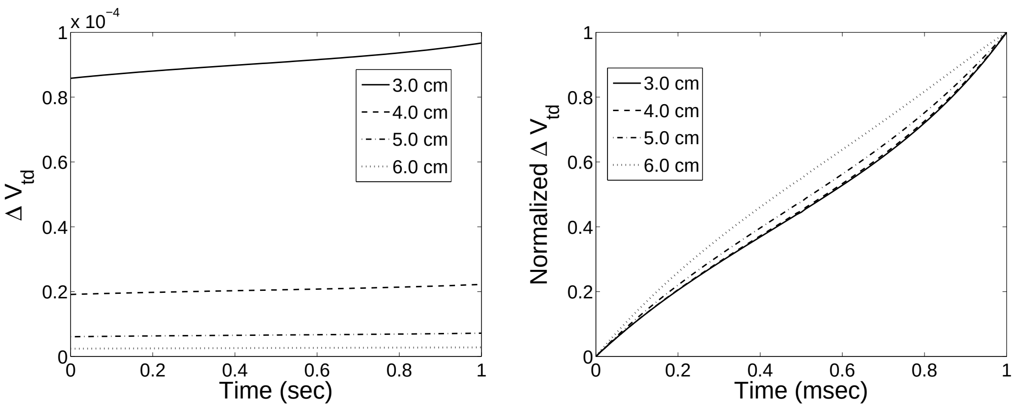


Figure 4.1: Transdermal potential measured at $8cm$ from the head when a tail bends from left to right and right to left; the lateral distance of a target object changes (the bottom curve represents the transdermal potential without an object) (modified from (Sim and Kim, 2010c))

The temporal change of a transdermal potential when the tail is bending from side to side is affected by the position, size, and conductivity of a target object. Fig. 4.1 deals with transdermal potential at electroreceptors. It is difficult to extract distance information from a transdermal potential because of the effects of object characteristics and low frequency characteristics of temporal patterns. When we consider the distortion of transdermal potential caused by a target object, we can obtain more interesting results.

4.3 Pattern of tail bending

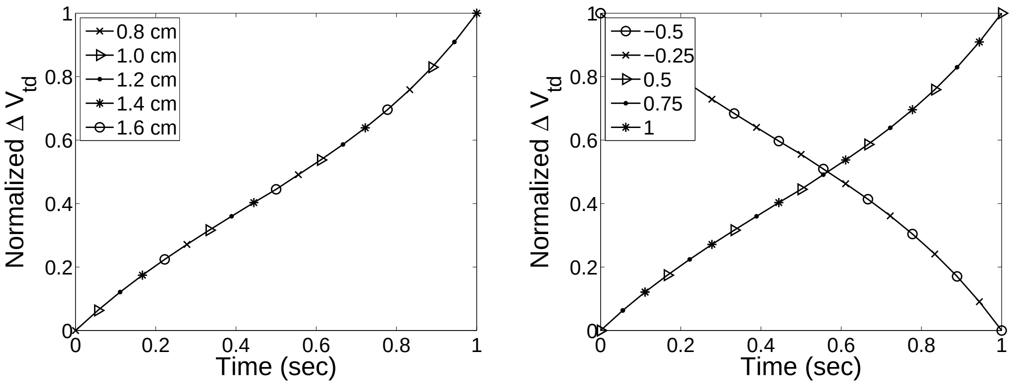
Fig. 4.2 (a) shows the temporal change of transdermal potentials when weakly electric fish bend their tails from side to side. The temporal tail bending pattern depends on the position, size, and conductivity of a target and it is not easy to extract novel information from this tail-bending pattern. In contrast to a spatial reading of a sensory array, there seems to be no distinct pattern of curves, peak or slope. When we normalize this temporal tail-bending pattern, we can find distinctive characteristics.



(a) (b)

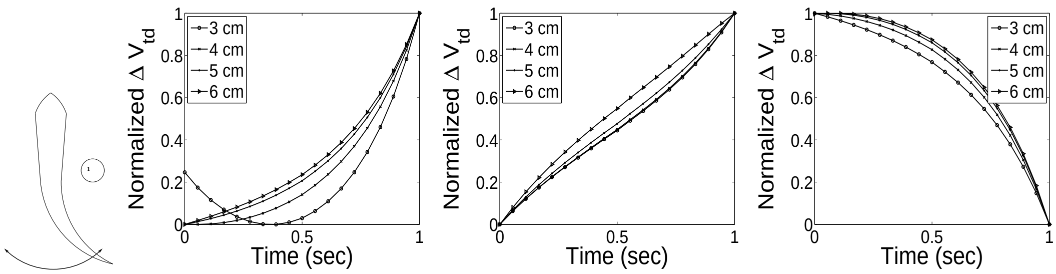
Figure 4.2: Tail-bending patterns when a lateral distance of a target object changed as $2.5cm$, $4cm$, $5.5cm$, $7cm$, and $8.5cm$ (a) Unnormalized tail-bending pattern and (b) normalized tail-bending pattern (modified from (Sim and Kim, 2010c))

A temporal reading of one electroreceptor also gives us a hint on how measure the distance of a target object. Fig. 4.3 (a) shows that object size has no effect on a normalized tail bending curve. The conductivity of an object is also not a factor in varying a temporal electric image. In Fig. 4.3, line (b) with the 'o' and 'x' markers have negative conductivity and the other positive. These two patterns match exactly when the negative conductivity line is reversed.



(a) (b)

Figure 4.3: Normalized tail bending pattern (a) the object size changes with an interval of 4 mm (0.8, 1.2, 1.6, 2.0 and $2.4mm$) (b) the electrical constant changes, 1, 0.5, 0.25, -0.25, -0.5 (the marker 'o' and 'x' have negative electrical constants and the others negative electrical constants) (modified from (Sim and Kim, 2009a,b, 2010c))



(a) (b) (c)

Figure 4.4: Normalized tail-bending patterns when the lateral position of the target object varies as marked in legend; readings of stimuli were recorded at (a) $2cm$, (b) $3.5cm$, and (c) $5cm$ (modified from (Sim and Kim, 2009a,b, 2010c))

As shown in Fig. 4.3, the normalized pattern of tail-bending movements are dependent on only the relative position of a target object and therefore is independent from the size and conductivity of the target object Sim and Kim (2009a, 2010a). Fig. 4.4 shows pattern changes of tail-bending curves at each sensor position.

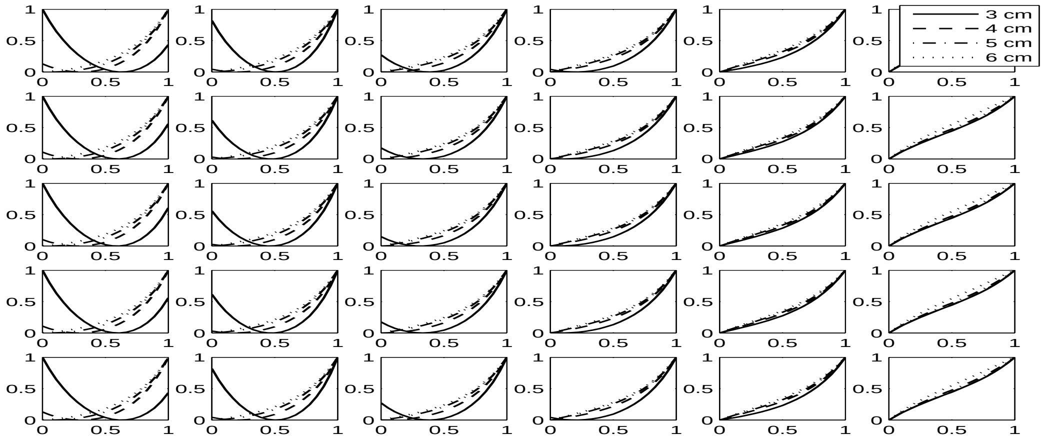
The normalized temporal bending pattern can be used as a distance measurement, such as the relative slope. Strictly speaking, the normalized bending pattern is changed by the lateral and rostrocaudal position of a target simultaneously. The difference in temporal patterns in Fig. 4.4 is due to the difference of measured points. We can also notice that temporal patterns change with different measured positions. When we measure temporal potential change at the sensor located in front of a target, a temporal pattern shows a consistently increasing pattern. In contrast to these increasing patterns, Fig. 4.4 (c) consistently decreases at a sensor near the tail.

Fig. 4.5 shows change of temporal tail-bending patterns when the target object moves respectively along the lateral, rostrocaudal, and dorsoventral axis. We can use this temporal pattern to localize a target object without consideration of other properties of objects such as size and electrical constant. There seems to be no direct cue to estimate the location of a target object in temporal tail-bending patterns. When the target object moves in three-dimensional space, we can detect the abrupt change of a temporal pattern at the fixed sensor. In Fig. 4.5, sometimes temporal change has a consistent increase or decrease and sometimes creates a bow-shaped curve when weakly electric fish bend their tails. Each column represents a rostrocaudal position of a sensor from head to tail and each row represents the position of a sensor in a dorsoventral axis. A sensor from the first column is $4cm$ away from the mouth, and then it moves at an interval of $2cm$. The sensors (depicted in rows) are distributed at $-2cm$, $-1cm$, $0cm$, $1cm$, and $2cm$ respectively with respect to the center of a weakly electric fish. This indicates that the location of an object changes the temporal pattern. If we observe the temporal variation of tail-bending at a fixed electroreceptor, we can find the cue to localizing the location of an object.

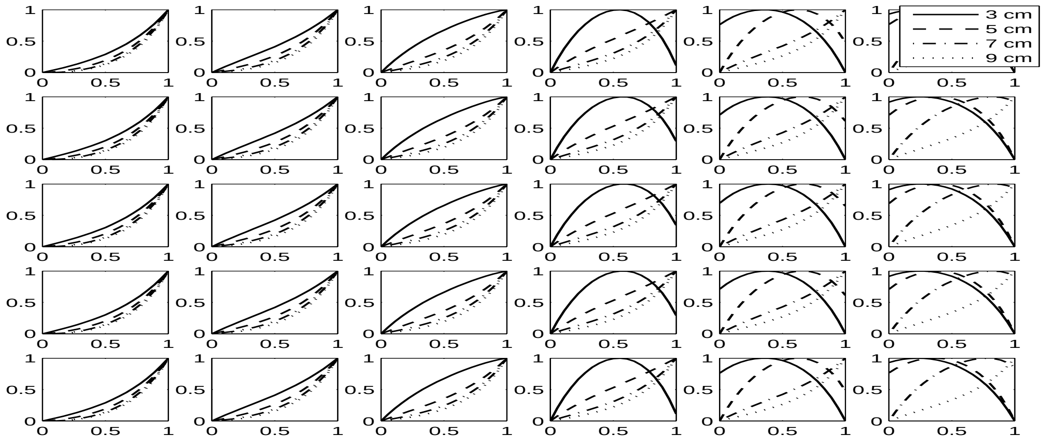
The temporal sequence of an electric signal can be found with a only few electroreceptors. If multiple electroreceptors are not available, then this temporal pattern for a time interval can give us distance information. This measurement is independent of the object size and conductivity; however, temporal patterns are affected by the rostrocaudal and lateral position of a target object. The rostrocaudal position is identified directly from the peak location in the electric image. Consequently, when the rostrocaudal position of a target object is determined, we can estimate the lateral distance with a tail-bending curve.

4.4 Integration pattern of tail bending

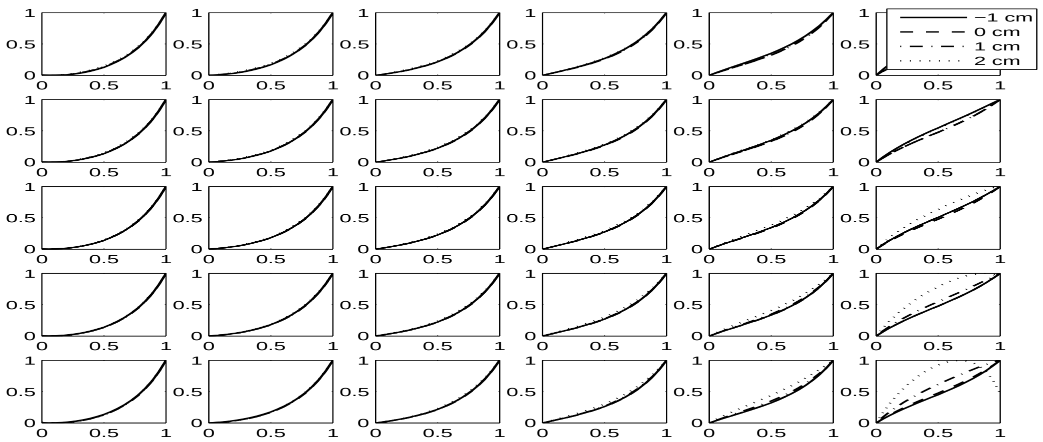
To find a direct cue to localize a lateral position of a target object, we study the integration of a tail-bending curve extracted from temporal sensor readings at one electrosensor. When we use the relative slope of a tail-bending curve, there are irregular leaps



(a)



(b)



(c)

Figure 4.5: Normalized tail-bending pattern; one figure shows normalized temporal changes when a target object moves near one electroreceptor in the sensory plane (each column indicates a rostrocaudal position of a sensor and each row represents a dorsoventral location); the object initially located at $8cm$ from the head in the rostrocaudal axis, $5cm$ from the fish's skin in the lateral axis, and the same dorsoventral position with respect to a fish; (a) a target object moves along the lateral line (b) a rostrocaudal line (c) a dorsoventral line (modified from (Sim and Kim, 2010c))

at certain points, because a temporal tail-bending pattern sometimes only decreases or increases consistently and sometimes show a change in a change of direction. The relative slope is not a good characteristic to measure the distance of tail bending curves because the temporal curve has no regular increase or decrease.

In other word, the integration curve shows stable changes for a moving target object. Fig. 4.6 (a) and (b) shows the integration of tail bending curves at a fixed sensor position when a target object moves. The rostrocaudal position changes in Fig. 4.6 (a) and the dorsoventral position changes in Fig. 4.6 (b). In Fig. 4.6, integration of temporal change decreases when a target object move far away from the electrosensor. Fig. 4.6 (e) and (f) shows the consistent decreasing pattern when the target object is far away from the midline of fish at the lateral axis. Consequently, we can estimate the lateral distance of a target object by the integration of temporal change of a tail bending pattern.

Actually, the integration of tail-bending patterns is affected by the size of a target object. When the integration of tail-bending pattern is normalized by the integration of tail-bending at the fixed position, the normalized integration of a tail-bending pattern can be used as distance measure regardless of the size of a target.

From these results we can conclude that tail bending movements help weakly electric fish acquire sensory information to localize a target object. Of course, when we calculate the relative slope of the integration curve when there is tail bending movement, we need both a spatial and temporal sequence.

4.5 Relative slope change with tail bending movements

In Fig. 4.7, we can see that a change in electric images with different tail bending angles, $-45°$, $0°$, and $45°$. There is a difference in transdermal potential with a fixed target object when weakly electric fish bend their tails. It seems that the effect of tail bending movements is not an ignorable factor because the difference due to tail bending is not small compared to the difference caused by different lateral distances of a target in the dorsoventral sensory line. When weakly electric fish bend their tails, both width and maximum intensity changes.

We can see the change of relative slope with tail bending movements in Fig. 4.8. Fig. 4.8 (a) shows the relative slope change extracted from the rostrocaudal sensory

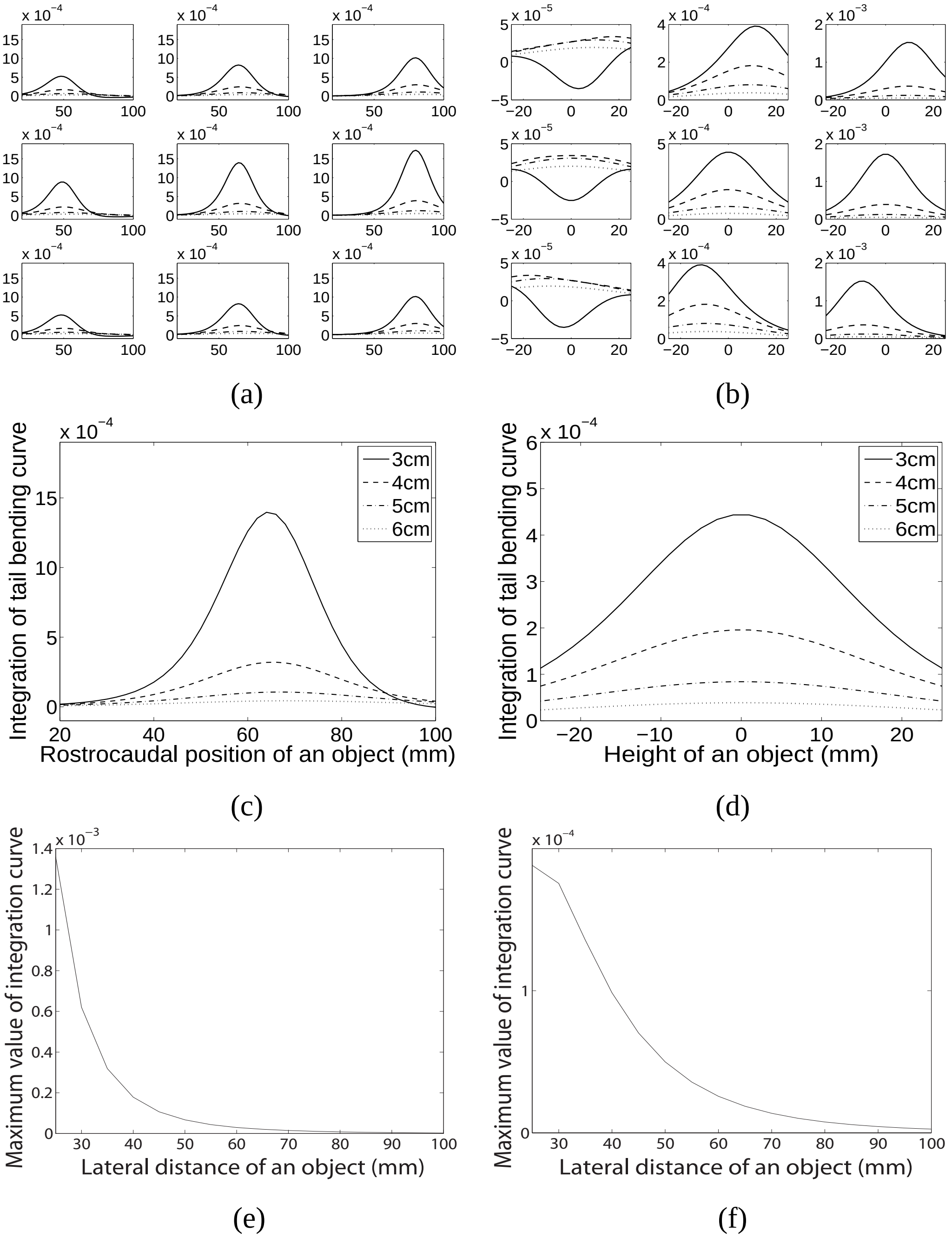
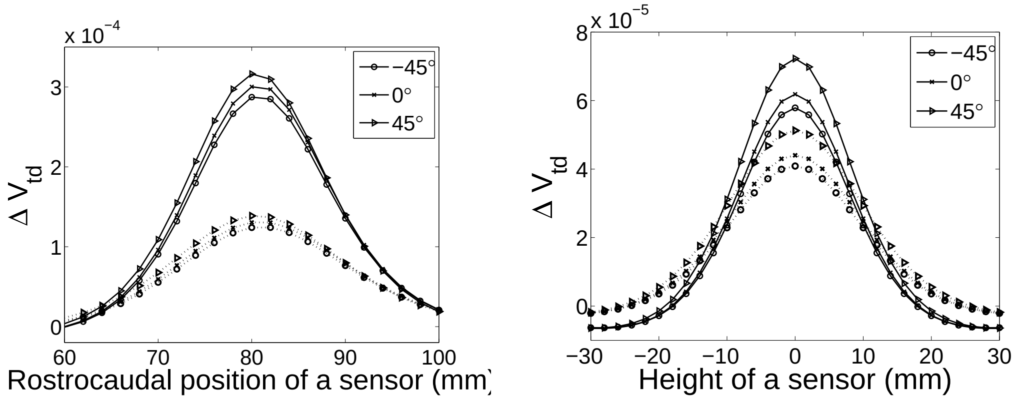


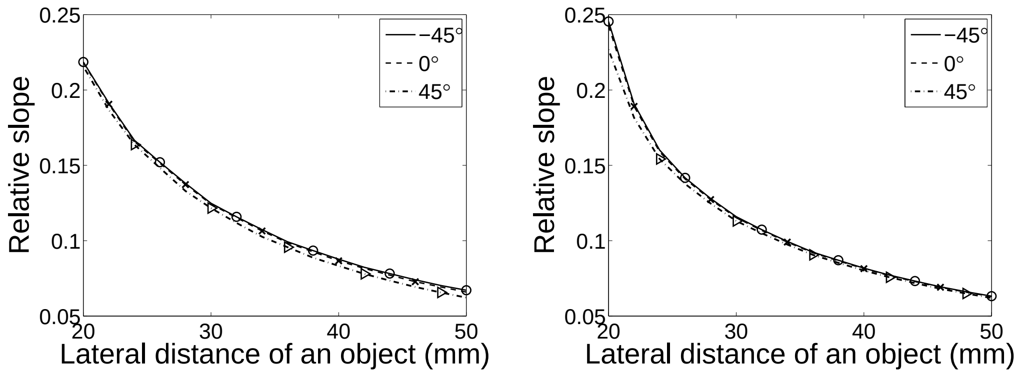
Figure 4.6: The integration of tail-bending patterns when the lateral distance of a target object changes, $3cm$, $4cm$, $5cm$, and $6cm$ (a) the rostrocaudal position of a target object changes as marked in x axis and (b) the dorsoventral position of a target object changes. (c) and (d) show integration curves at the center point of the sensory plane of (a) and (b). (e) and (f) show the maximum value at each integration curve when the lateral distance of a target object changes.



(a) (b)

Figure 4.7: Electric images when weakly electric fish bends their tails from right to left with different lateral distances of a target, using a 'solid line' for $3cm$ and 'dashed line' for $4cm$ (a) electric image along the rostrocaudal sensory line (b) along the dorsoventral sensory line

line and Fig. 4.8 (b) for the dorsoventral sensory line. The effect of tail bending movements is not small in transdermal potential. However, we can claim that the change of relative slope caused by tail bending movements is neglectable. The range of tail bending movements from side to side is wider than the forwarding movement (about $1cm$), but the change in relative slope is very small.

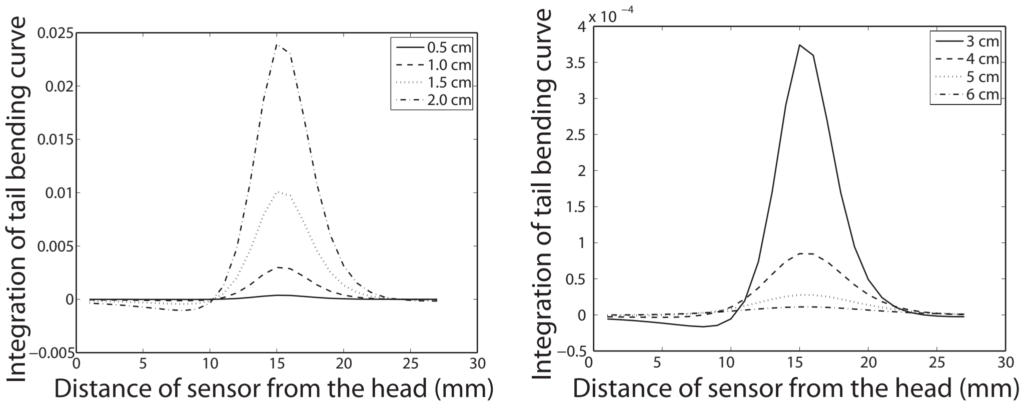


(a) (b)

Figure 4.8: Relative slope when weakly electric fish bend their tails (a) along the rostrocaudal sensory line (b) along the dorsoventral sensory line

We can use relative slope change to extract more accurate distance information. When distance information obtained from temporal sensor readings does not confirm object position, other static spatial information from tail bending can be helpful. We can accumulate static spatial sensory readings at each point in time when a weakly electric fish bends its tail from side to side. Relative slopes at each point in time can be compared to determine the exact distance of a target. When we use an average relative slope with tail bending, we can identify an object position more accurately in a noisy environment.

It is also possible to localize a fixed target object through integrated temporal tail-bending patterns acquired from the rostrocaudal sensory line. When the size and lateral distance of a target object changes, the integration value also varies at each electroreceptor. We can detect a different integration pattern for the position of a measured electrosensor. The integration of temporal tail-bending patterns creates a bell-shaped curve. Fig. 4.9 (a) shows that the integration of temporal changes with tail-bending movements when the size of a target object becomes larger. When lateral distance of a target changes, electric images change as shown in Fig. 4.9. The integration curve shows a similar pattern with a static spatial electric image with a fixed tail. The peak position of the integration curve indicates the rostrocaudal position of a target object and we can extract the relative slope in this integration of temporal tail-bending patterns.



(a) (b)

Figure 4.9: The integration of tail bending curves when (a) the size and (b) the lateral distance of a target object changes along the rostrocaudal sensory line

The relative slope of the integration curve considers all integration values at the rostrocaudal line. As shown in Fig. 4.10, there is little difference between the relative slope of the integration curve and the relative slope acquired from the sensory line when there is no movement from the weakly electric fish.

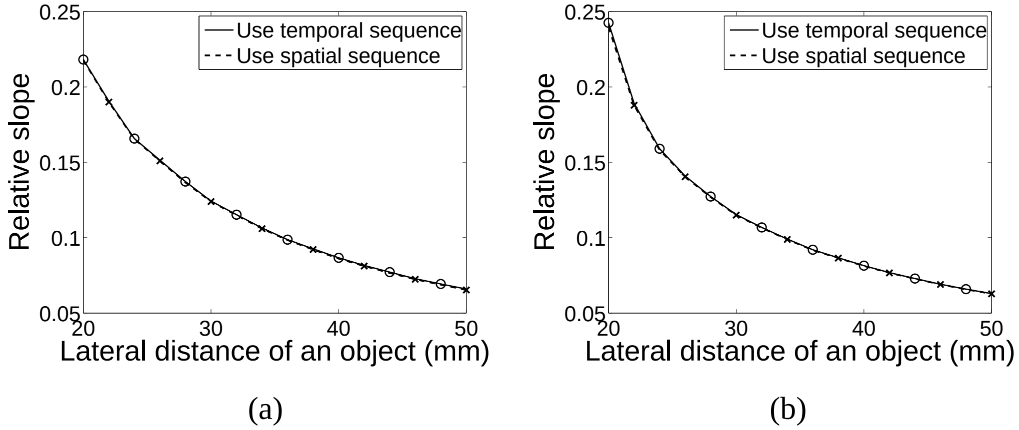


Figure 4.10: Relative slope through static spatial electric image when tail is fixed straight (‘dashed line’) and through integrated electric image when the tail is bent side to side (‘solid line’) (a) electric image along the rostrocaudal sensory line (b) along the dorsoventral sensory line

We can use temporal sensor readings of a single electroreceptor to obtain the relative slope in integrated electric images. When we use the relative slope of the integration curve using spatiotemporal information, we can take advantage of multiple electroreceptions. In a noisy environment, the integration of tail-bending movements is expected to compensate for the noisy signal. If we use the spatiotemporal information, which is the combination of temporal and spatial structures of an electric image, we can identify a target object more effectively. The de-noising method will be discussed in Chapter 6.

Weakly electric fish do not show the tail-bending movements frequently as the back-and-forth swimming. It is not sure whether weakly electric fish use the tail-bending movements to identify a target object, however, the tail-bending movements can help to find accurate distance measurement in noisy environment as shown in this chapter.

In this thesis, it is assumed that the tail bending pattern can be utilized as the additional source for electrolocation or canceled to exploit spatiotemporal information. In section 2.6, reafference was introduced. It is known that weakly electric fish can cancel the effect of tail-bending movements (Bastian, 1995, 1996, 1999). In Chapter 4, the tail bending pattern is considered as meaningful sensory signals for electrolocation. This temporal change can provide additional information to localize a target in noisy environment as shown in this chapter.

4.6 Summary of Chapter 4

It was mentioned that the reafferent electrosensory signal can be removed by reafference of prymidal cells and proprioceptive electrosensory input in Chapter 2. In this chapter, the temporal tail-bending patter is considered a meaningful source for electrolocation. First, it was shown that the tail-bending pattern can be a distance measure itself. The normalized tail-bending pattern is not affected by a size and conductivity of a target object. When we use temporal potential change, it is possible to measure distance with only a single electroreceptor. Weakly electric fish have approximately $14,000$ tuberous electroreceptors (Nelson et al., 2000; MacIver, 2001). To realize the electrosensory system, it is difficult to use sensors as much as weakly electric fish. The tail-bending pattern can be useful for electroreception with small sensors.

When the electrosensory signals are affected by noise, weakly electric fish might use electrosensory image with tail bending movements. The relative slope extracted from the spatial electric image with a bent tail is similar to the relative slope with a straight body. If the relative slope does not seem correct, weakly electric fish can compare the relative slope with tail-bending movements. The integration of tail-bending patterns provide the integrated electric image. It was shown that the relative slope from the integrated electric image have little difference from the original relative slope. In a noisy electric image, it is difficult to extract a correct relative slope. The integrated electric image can provide a noise filtering effect and more accurate distance measurements. The noise reduction method of electrosensory system will be studied in Chapter 6. We will consider the effect of another type of movement, back-and-forth swimming, in the next chapter.

Chapter 5

Electrolocation using spatiotemporal structures in complex scenes

In the previous chapter, the distance measurement is used for one target object. When a target object is near weakly electric fish, the electric perturbation draws a bell-shaped curve. Multiple objects generate superimposed electric image with multiple peaks, and a maximal amplitude, slope, and width of electric perturbation of one target object is distorted by neighbor objects. In this chapter, we expand the concept of relative slope to the spatiotemporal domain. The relative slope introduced in Chapter 2 can be interpreted as the spatial and temporal relative slope. The spatial relative slope extracts the maximal difference of sensor readings at the sensory domain and the temporal relative slope observes that change in the time domain. The concept of the relative slope will be expanded to the spatiotemporal domain in this chapter.

When there are multiple objects in the near-field of weakly electric fish, the electric perturbation is not equal to the sum of electric perturbations caused by each target object (Babineau et al., 2007; Engelmann et al., 2008). In this chapter, it is assumed that the difference between the original electric perturbation of multiple objects and the sum of electric perturbation of each target is small to simplify the problem. The content of this chapter is based on proceeding research (Sim and Kim, 2010e).

Weakly electric fish shows different foraging behaviors according to species, pulse EOD and wave EOD species (Nanjappa et al., 2000). It was reported that Gymnotiform fish (wave-type EOD species) swim back and forth when they capture prey (Lannoo and Lannoo, 1993; Nanjappa et al., 2000).

It is also noted how weakly electric fish identify a target object when there are background objects, and this study is based on the paper by (Sim and Kim, 2010d). There is a research about the spatial acuity (Babineau et al., 2007). When background objects exist behind the target object, it is not easy to localize a target object. The electric image of a target object is distorted by background objects. The closer inter-distance between background objects, the more difficult identification of a target object. The background objects change the maximal slope and maximal amplitude, and it is difficult to extract the distance information. However, it is possible to estimate the rostrocaudal position of a target object in electric images by the maximal spatial difference of the electric image generated by sensor readings. This will be shown in this chapter.

5.1 Spatiotemporal electric images

In this chapter, we use spatiotemporal information to localize a target object. The temporal structure caused by tail-bending movements provides us with other distance measurements. Spatiotemporal electric images can be a measure for multiple objects (Sim and Kim, 2010e).

This chapter will handle the spatiotemporal electric images obtained when weakly electric fish swim forward. The distribution of a large number of electroreceptors on the skin surface makes a spatial domain structure and temporal sensor readings of each electroreceptor produce a time domain structure. When weakly electric fish remain stationary, we use the relative slope to estimate the distance of a target object. The concept of relative slope can be expanded in the spatiotemporal electric image.

When there is more than one object, there is a superposition of electric image for each object. The superposition changes the intensity and shape of an electric image and makes it difficult to use the relative slope for distance measure any longer. To measure distances of multiple objects, other distance measurements are needed that is less affected by superposition.

5.2 Relative slope in spatiotemporal electric images

Spatial sensor readings along the rostrocaudal sensory line generate spatial electric images and these measurements are introduced in Chapter 3. The spatial relative slope can be represented as

$$Spatial\ relative\ slope = \frac{max_i\left\{I(x_{i+1},t) - I(x_i,t)\right\}}{max_i\left\{I(x_i,t)\right\}} \tag{5.1}$$

where there are n electroreceptors along the rostrocaudal sensory line $x_1, x_2, \ldots, x_n$ on the skin surface. $I(x_i,t)$ is a transdermal potential difference at a given position x_i in a given time t. In the temporal electric image with temporal sensor readings at one electroreceptor, the temporal relative slope can be defined as

$$Temporal\ relative\ slope = \frac{\max_k\left\{I(x,t_{k+1}) - I(x,t_k)\right\}}{\max_k\left\{I(x,t_k)\right\}} \tag{5.2}$$

Both spatial and temporal relative slope consider the maximal slope and amplitude. In this chapter, four different types of slopes will be studied including a spatial relative slope and a temporal relative slope in spatiotemporal electric images. These four types of slope with respect to different domains (space and time domain) can be represented as (Sim and Kim, 2010e)

Case1 : a slope as a space-to-spatial slope,

$$Space\text{–}to\text{–}spatial\ slope = \frac{\max_i\left\{I(x_{i+1},t_k) - I(x_i,t_k)\right\}}{\max_i\left\{I(x_i,t_k)\right\}} \tag{5.3}$$

Case2 : a slope as a time-to-spatial slope,

$$Time\text{–}to\text{–}spatial\ slope = \frac{\max_k\left\{I(x_{i+1},t_k) - I(x_i,t_k)\right\}}{\max_k\left\{I(x_i,t_k)\right\}} \tag{5.4}$$

Case3 : a slope as a space-to-temporal slope,

$$Space\text{–}to\text{–}temporal\ slope = \frac{\max_i\left\{I(x_i,t_{k+1}) - I(x_i,t_k)\right\}}{\max_i\left\{I(x_i,t_k)\right\}} \tag{5.5}$$

Case4 : a slope as a time-to-temporal slope,

$$Time\text{–}to\text{–}temporal\ slope = \frac{\max_k\left\{I(x_i,t_{k+1}) - I(x_i,t_k)\right\}}{\max_k\left\{I(x_i,t_k)\right\}} \tag{5.6}$$

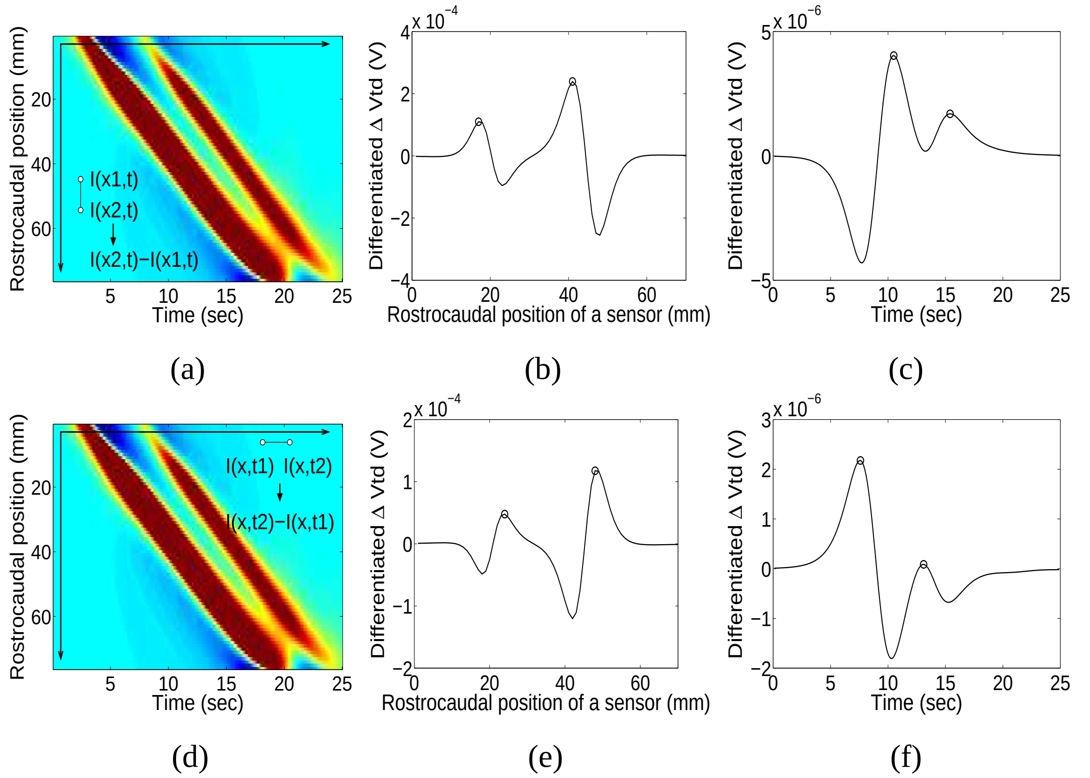
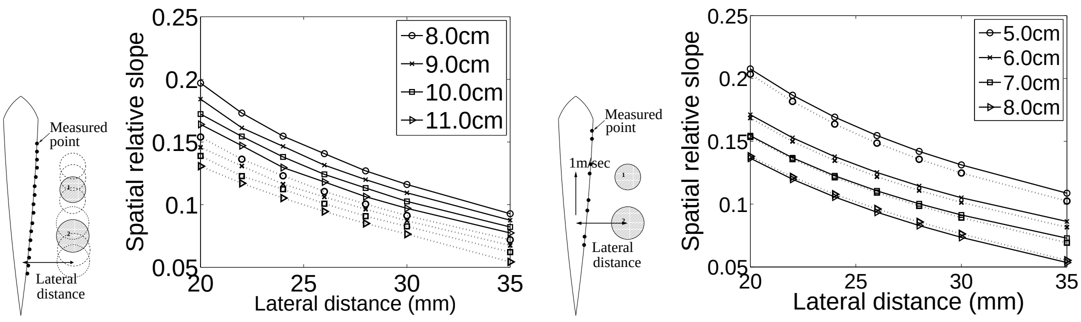


Figure 5.1: Differentiated electric image with two target objects in a spatiotemporal domain (a) spatial slope diagram (b) spatial difference in a space domain (c) in a time domain (d) temporal slope diagram (e) temporal difference in a space domain (f) in a time domain (two target objects are located at $7cm$, $12cm$ from the mouth with radius $0.8cm$, $1.2cm$, respectively) (reprinted from (Sim and Kim, 2010e))

where $I(x,t)$ is the intensity value of electric images, x is the position of an electroreceptor, and t is the measured time.

Fig. 5.1 (a) and (d) show spatiotemporal electric images with two different-sized objects when weakly electric fish swim forward. A spatiotemporal electric image is differentiated in a spatial domain, ‘y’ axis and a temporal domain, ‘x’ axis. In Fig. 5.1 (a), (b), and (c), we consider the electric potential difference in a spatial domain, $I(x_{i+1},t) - I(x_i,t)$. Fig. 5.1 (b) and (c) show spatial differences along the spatial and temporal line when the electric image is differentiated in a spatial domain. The ratio of maximum spatial difference in the spatial domain to maximum value in the spatial electric image is a spatial relative slope. We redefine the spatial relative slope as a ‘space-to-spatial slope’ to discriminate from a ‘time-to-spatial slope’. A time-to-spatial slope is the ratio of maximum spatial difference of two neighboring sensors in the temporal domain to maximum value in a temporal electric image.

The spatiotemporal electric image is differentiated with respect to time, ‘x’ axis in Fig. 5.1 (d). Two different temporal slopes is considered; ‘space-to-temporal slope’ and ‘time-to-temporal slope’. In a temporally differentiated electric image, we extract the maximal temporal difference, $\max(I(x_i,t+1)-I(x_i,t))$, in a space domain and time domain as marked in Fig. 5.1 (e) and (f). The ratio of maximal temporal difference to maximal electric potentials is ‘space-to-temporal slope’ and ‘time-to-temporal slope’ with respect to two different domain, time and space.

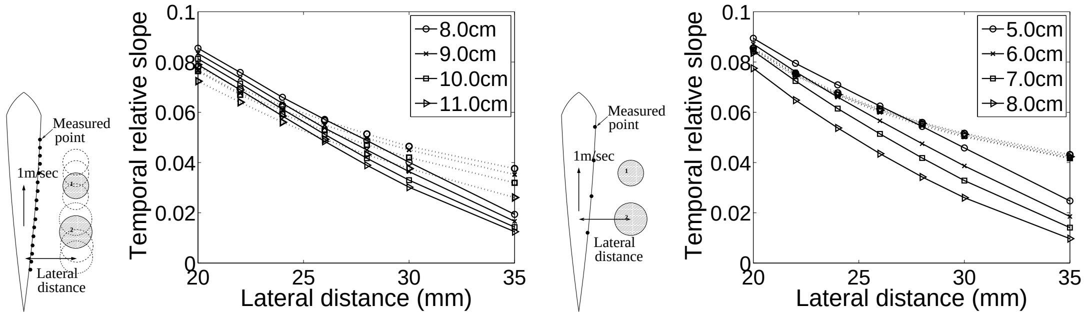


(a) (b)

Figure 5.2: Spatial relative slope when the lateral distance of the target object changes from $2cm$ to $5cm$ (a) space-to-spatial slope when the rostrocaudal position of a first target object changes (b) time-to-spatial slope when the measured position changes from the mouth with a static object (the velocity of the weakly electric fish is $0.01m/sec$) ; the ’solid line’ symbolizes the first small object, and the ’dotted line’ a large object (reprinted from (Sim and Kim, 2010e))

Fig. 5.2 shows two types of spatial relative slopes; space-to-spatial slope (equation 5.3) and time-to-spatial slope (equation 5.4), when the spatiotemporal electric image is spatially differentiated. Two types of temporal slopes are represented in Fig. 5.3 (a) for a space-to-temporal slope (equation 5.5) and Fig. 5.3 (b) for a time-to-temporal slope (equation 5.6).

When we consider two relative slopes, the spatial and temporal relative slope introduced in Chapter 3, it seems that a temporal relative slope (a time-to-temporal slope) is less affected by the rostrocaudal position of a target with respect to weakly electric fish than spatial relative slope as shown in Fig. 5.4 (also see Fig. 3.6). When there are two target objects, however, the temporal relative slope (that is a time-to-temporal slope) is also affected by the superposition of signals for each object (Sim and Kim, 2010e).



(a) (b)

Figure 5.3: Temporal relative slope when the lateral distance of the target object changes from $2cm$ to $5cm$ (a) space-to-temporal slope when the rostrocaudal position of a first target object changes (b) time-to-temporal slope when the measured position changes from the mouth with a static object (the velocity of the weakly electric fish is $0.01m/sec$) ; the 'solid line' represents the first small object, the 'dotted line' the large object (reprinted from (Sim and Kim, 2010e))

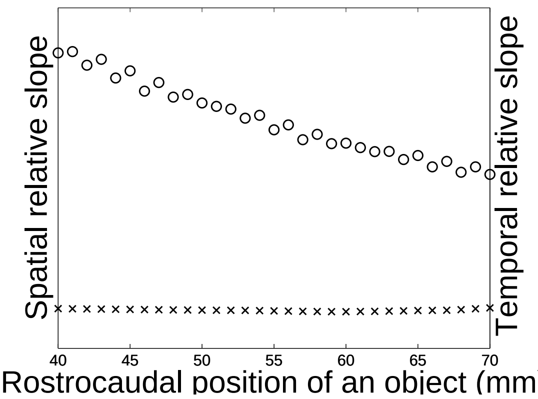


Figure 5.4: Comparison of spatial slope marked by 'o' and temporal slope marked by 'x' (reprinted from (Sim and Kim, 2010e))

When there are different-sized objects near weakly electric fish, we need distance measure independent of size and position. The time-to-spatial slope provides us with a useful distance measurement that is less affected by superposition as shown in Fig. 5.2 (b). When measured points are fixed, time-to-spatial slopes for two different objects show consistent curves without interference. The meaning of time-to-spatial slope is the ratio of maximal difference of two neighboring sensors to maximal electric potential. It is possible to measure distances of each target object regardless of size and rostrocaudal position. This study can provide a hypothesis that weakly electric fish might use the spatiotemporal information, such as the time-to-spatial slope, to localize multiple target objects.

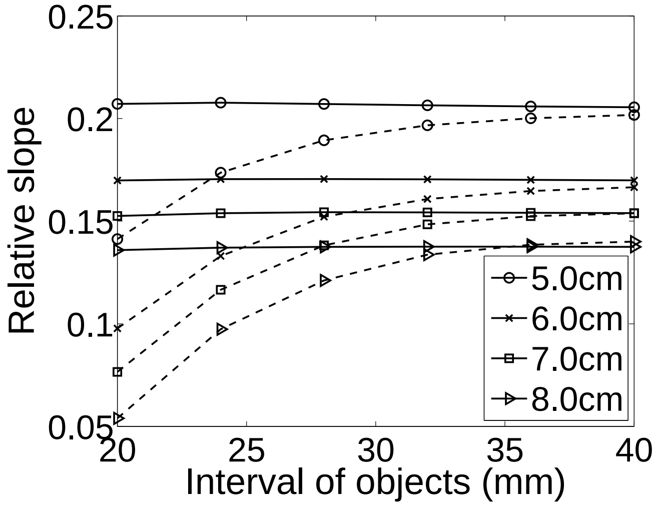


Figure 5.5: Time-to-spatial slope when the interval of two objects changes with a fixed lateral distance when the measured position changes from the head with a static object (the velocity of the weakly electric fish is $0.01 m/sec$) ; a 'solid line' represents the first object, a 'dotted line' represents a second object

Fig. 5.5 shows the superposition effect with different distance intervals of two objects. When the interval between two objects is larger than $3.5cm$, the superposition effect is negligible with respect to changes caused by lateral distance.

In the next section, the object identification in complex scenes with background objects will be discussed. In real-world environments, electric images are distorted by surroundings such as rocks, water plants, con-specifics, or other potential prey (Budelli et al., 2002). Therefore, the electric image is the result of superposition of electric potentials generated by each single object. When these background objects are far away from the weakly electric fish, the distortion effect of electric potentials decreases as mentioned above. When multiple objects are located behind a target, how to estimate the position of a target object will be studied.

5.3 Object identification with background objects

Electric images are different from visual images and there is no focusing process for identifying a target object. When there are many background objects in a sensing range, the electric image is distorted. In this study, we suggest a possible localization method when there is a closer target object with background objects.

Babineau et al. (2007) suggest the concept of “spatial acuity” similar to visual acuity. Spatial acuity is the ability of weakly electric fish to distinguish a target object from background images when a target object and object plant (background objects) are near weakly electric fish at the same time. With electric imaging, the bell-shaped curve of sensor readings is blurred when the lateral distance of a target object moves farther away from the fish (Heiligenberg, 1975). However, in a sensing range, we cannot neglect the effect of background objects.

The distance between a pair of objects in the object plant significantly influences the shape of the electric image. A smaller interval of background objects makes blurred background images because of the superposition of the sensor reading curves from each object. Therefore, when the object plant is far away from the fish and the interval between the objects of the object plant becomes smaller, the background image produced by the object plant becomes smoother and more blurred, and thus the target object becomes noticeable. In experiments, the size of a target object is fixed with 5*mm* and background objects with 9*mm*.

When background objects are near-field, it is needed to extract novel information of a target object from the distorted electric image. Fig. 5.6 shows the effect of background objects with different intervals. When the intervals of background objects increase, electric images have higher frequency characteristics. There are more distinctive peaks in Fig. 5.6 (c).

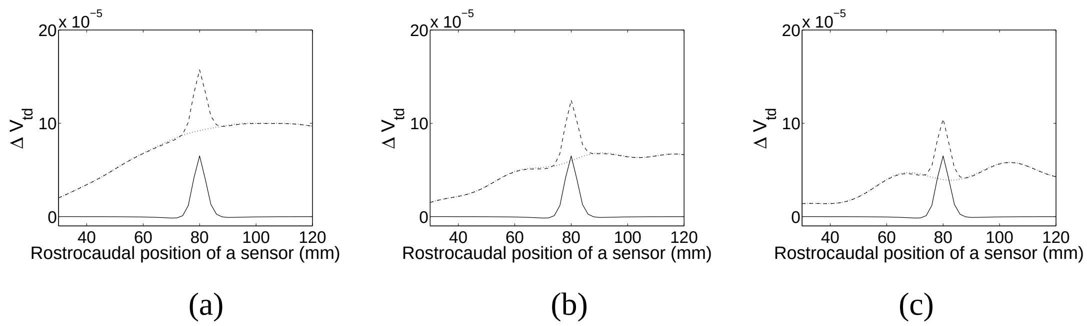


Figure 5.6: Effect of background objects with intervals of (a) 2*cm* (b) 3*cm* (c) 4*cm* (the ‘solid line’ represents a target object only, a ‘dotted line’ for background objects, a ‘dashed line’ for both target object and background objects reprinted from (Sim and Kim, 2010d))

When intervals of background objects are small, it is possible to find notable peak of a target object in the electric image as shown in Fig. 5.7. In this study, it is assumed that a target object is smaller than background objects and close to the weakly electric fish. If the size of background objects increase or background objects approach weakly electric fish, distortion of the electric image increases. Furthermore, it becomes more difficult to identify a target object when intervals of background objects are large enough to show each distinctive peak.

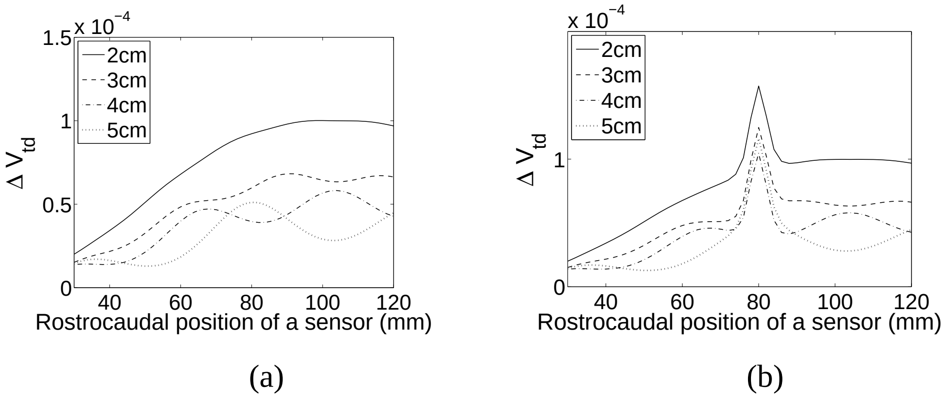
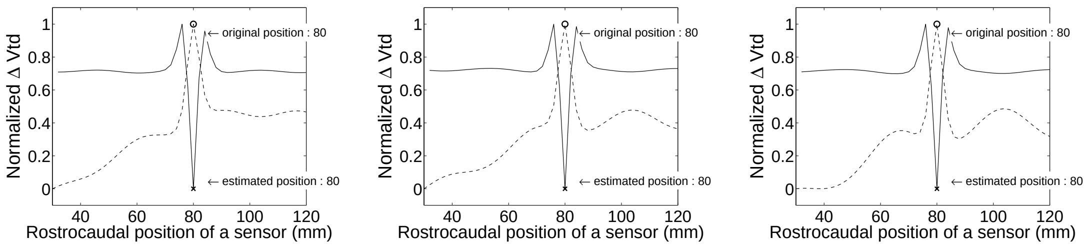


Figure 5.7: Electric image of (a) background objects and (b) a target object and background objects exist when the intervals of background objects change (reprinted from (Sim and Kim, 2010d))

The electric image caused by a target object has high frequency characteristics with a narrower width and steeper slope than background objects. In a differentiated electric image, we find that the location of the largest change is near the position of a target object. Fig. 5.8 shows a second, derivative electric image to identify the rostrocaudal position of a target object. The minimum value of second derivative electric image indicates the greatest change of electric potentials. Consequently, the minimum value of second derivative electric image shows the position of a target object which has higher frequency characteristics than background objects.

In this study, we discovered that the rostrocaudal position of a target can be identified by a difference in electric potentials because of high frequency characteristics in complex scenes. However, it is still difficult to estimate the distance of a target in complex electric images. To estimate the object distance, it is needed to extract the original slope and maximal intensity without background objects. It is impossible to extract distance measurement such as relative slope in complex electric images distorted by background objects. More studies are needed to estimate the distance of an object in



(a) (b) (c)

Figure 5.8: Electric image and differentiated electric image for both a target object and background objects with intervals of (a) $3cm$ (b) $4cm$ (c) $5cm$ (‘o’ marks original rostro-caudal position, ‘x’ is the estimated position of a target, the ‘dotted line’ a normalized electric image, the ‘solid line’ a second derivative electric image) (reprinted from (Sim and Kim, 2010d))

complex background scenes.

Weakly electric fish can use active body movements to acquire more accurate sensory stimulation. When weakly electric fish are very close to a target object, the effect of a target object will be dominant in an electric field and the effect of the background object relatively decreases. It may be helpful to study the modulation of electric image depending on active movements of weakly electric fish to understand the mechanism for object identification in complex scenes.

5.4 Summary of Chapter 5

In Chapter 5, the way weakly electric fish can identify a target object in complex scenes with multiple target objects or background objects are studied. Gymnotiformes, wave-type weakly electric fish, almost always show back and forth swimming and the temporal change might provide additional information. In previous studies, the relative slope was introduced as the ratio of maximal slope to maximal amplitude. Chapter 3 shows that the spatial and temporal relative slope is independent on the size and conductivity of a target and can be used to estimate the lateral distance. The concept of the relative slope can be expanded to the spatiotemporal electric image. We introduce four different relative slopes; a space-to-spatial slope, time-to-spatial slope, space-to-temporal slope, and time-to-temporal slope. A space-to-spatial slope is the spatial relative slope and a time-to-temporal slope matches the temporal relative slope in Chapter 3.

The spatial and temporal slope only uses one-dimensional domain and; space and time domain respectively. However, a time-to-spatial slope and space-to-temporal slope use both space and time domain. When there are multiple target objects near weakly electric fish, the time-to-spatial slope is useful in identifying each target object. Other relative slopes are affected by superposition, and it is difficult to apply those measurements to each target object. Contrary to this, there is little difference in the time-to-spatial slope between multiple target objects, and can be used to localize multiple target objects. It was assumed that multiple target objects keep reasonable interval distances. This study shows the possibility that weakly electric fish might use the time-to-spatial slope for localization of multiple target objects.

The localization of a target with background objects was also studied in this chapter. When background objects exist behind the target object, the electric image is distorted by electric perturbation of background objects and it is difficult to extract characteristics of a target object. In the differentiated electric image, the rostrocaudal position of a target object has maximum difference. The rostrocaudal position of a target object can be identified by maximal slope change. Also, it is possible to estimate the rostrocaudal position of a target in complex scenes regardless of the intervals of background objects.

Chapter 6

Electrolocation using EOD waveforms in a noisy environment

This chapter shows the noise reduction method in the electrosensory system of weakly electric fish. Most of this chapter was based on the proceedings (Sim and Kim, 2010f). In the sensory system, noise filtering is an important issue and pre-processing is positively needed to restore the original sensor signal. To estimate the lateral distance of a target object in an electrosensory system, distance measurements such as relative slope, relative width, and FWHM are used. These distance measurements use electric images, width, maximum amplitude, and peak location. It is important to gain clean electric images for accurate localization.

The spatiotemporal electrosensory signal is considered to enhance the noise filtering effect. Weakly electric fish generate an electric organ discharge (EOD) and the electric field changes periodically in the time domain. The periodic EOD pattern will be used to reduce noise with cross-correlation. So far, the EOD has not been considered in the electrosensory image. In the time domain, the temporal change of sensor signals caused by active body movements (tail-bending and back-and-forth swimming) were handled in Chapter 4 and Chapter 5. In this chapter, the EOD in the time domain will be used as a meaningful source of noise reduction.

Low pass filtering and cross-correlation will be applied to the spatiotemporal electric image to reduce noise. When a target object becomes farther away from weakly electric fish, the electric image is severely affected by noise, and the low pass filtering is not enough to preserve original information. The cross-correlation will improve the de-nosing methods by using additional temporal information. The noise reduction method using cross-correlation is based on studies (Reichardt, 1961; Poggio and Reichardt, 1973; Reichardt, 1986, 1987; O'Carroll et al., 1991; Shajahan et al., 1997). This study will provide a hypothesis that weakly electric fish might use the EOD for noise reduction. Chapter 6 concentrates on the technical part of the electrosensory system instead of mechanisms of the electrolocation of weakly electric fish. It will be shown how noise reduction methods in the spatiotemporal domain can improve accuracy.

6.1 EOD waveforms and object perturbation

It is difficult to extract a clear electric image in a noisy environment. In this chapter, it is suggested that the cross-correlation method be used to reduce the effect of noise in the underwater environment (Sim and Kim, 2010f). Weakly electric fish have an electric organ (EO) that is composed of modified nerve and muscle cells, and the EO generates a waveform characteristic electric organ discharge (EOD) (Bennett, 1971; Zimmermann, 1985; Bass, 1986; Zakon, 1986, 1988; Kramer, 1990, 1999). Waveforms of a lot of Gymnotiformes and most Mormyriforms are pulse waveforms with large intervals. Another waveform characteristic of EOD is periodic waves. The electrolytes of EO generate simultaneous firing, and the electric signal has a waveform in the time domain. The temporal electrosensory signals are used in the time domain to extract accurate distance measurement.

There are two types of EOD waveform; pulse and periodic wave. There are six types of EOD waveforms composed of mathematical and realistic models (Stoddard and Markham, 2008). Fig. 6.1 shows these six types of waveform in the time domain. Each waveform has a different sampling rate and period. The period of pulse waveforms is $4ms$ as shown in Fig. 6.1 (a) - (c). Two types of waveform, Fig. 6.1 (e) and (f), have a period of $1ms$ and realistic model of waveform, Fig. 6.1, has a period of $2ms$.

The tuberous electroreceptors are sensitive to a high frequency range from $100Hz$ to $2,000Hz$ (MacIver, 2001) as mentioned in section 2.2. The six EOD models were based on the paper (Stoddard and Markham, 2008). Three EOD models have a frequency of $250Hz$ in Fig. 6.1 (a)-(c) and the others have a frequency of $1KHz$ or $500Hz$. Notably, two EOD models were based on the realistic waveform of *Brachyhypopomus*

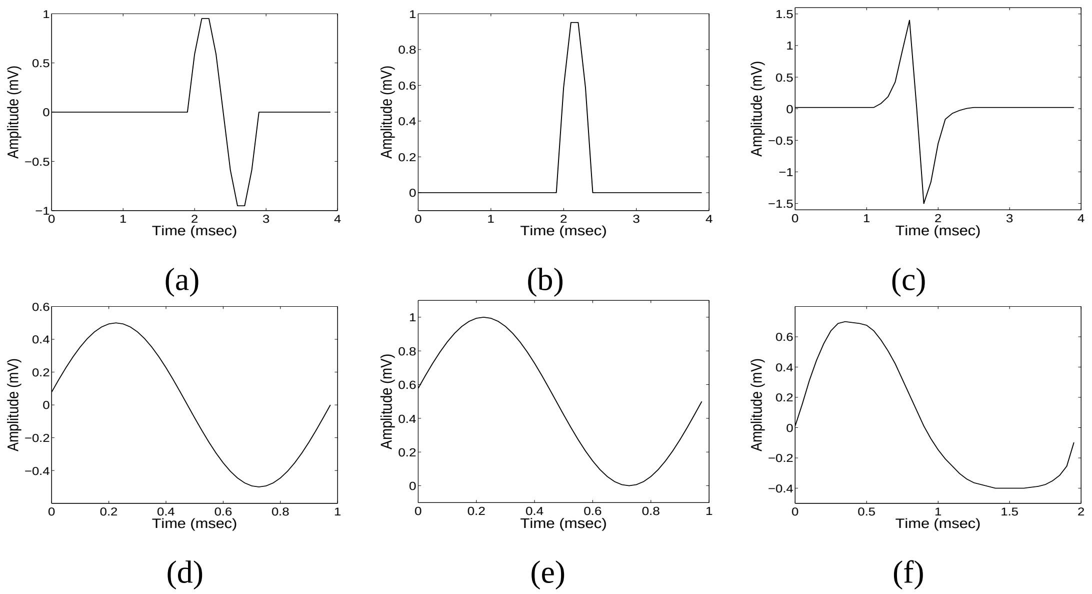


Figure 6.1: EOD waveform (a) sine pulse (b) cosine pulse (c) pulse of *Brachyhypopomus pinnicaudatus* (d) sine wave (e) sine wave with DC offset (f) waveform of *Eigenmannia virescens* (modified from (Stoddard and Markham, 2008))

pinnicaudatus and *Eigenmannia virescens*. The frequencies of EOD models can be measured at electroreceptors.

Fig. 6.2 shows the electric image when there is uniformly distributed random noise with a variance of 10% of a maximum object perturbation when the rostrocaudal position of a target object is $8cm$ from the head and the lateral distance is $3cm$ from the fish in the time domain with six types of waveforms (Fig. 6.1). All types of waveforms are affected by noise.

In this chapter, the low pass filtering and cross-correlation in the spatiotemporal domain are used for noise reduction. Two steps of the noise reduction process in a time domain and space domain provides a remarkable effect (Sim and Kim, 2010f). The noise reduction strategies are established in both space and time domain. In a spatial domain, a low pass filter will be used as a simple and common method for reduction of noise. This electric image acquired from sensor readings of the rostrocaudal sensory line can be smoothed by low pass filtering, because noise usually has high frequency characteristics. The noise reduction in the time domain before the low pass filtering enhances the effect of noise filtering. It is already verified that the composition of two methods, low pass filtering in the space domain and cross-correlation in the time domain give us a more effective noise reduction process (Sim and Kim, 2010f).

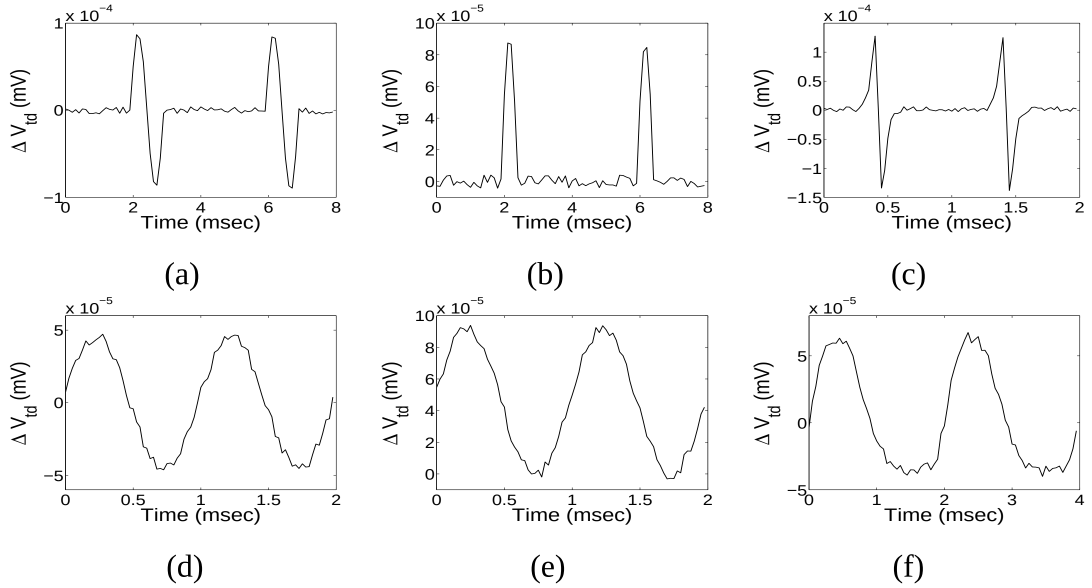


Figure 6.2: EOD waveform when there is uniform random noise with a variance of 5×10^{-8} for two cycles (a) sine pulse (b) cosine pulse (c) pulse of *Brachyhypopomus pinnicaudatus* (d) sine wave (e) sine wave with DC offset (f) waveform of *Eigenmannia virescens*

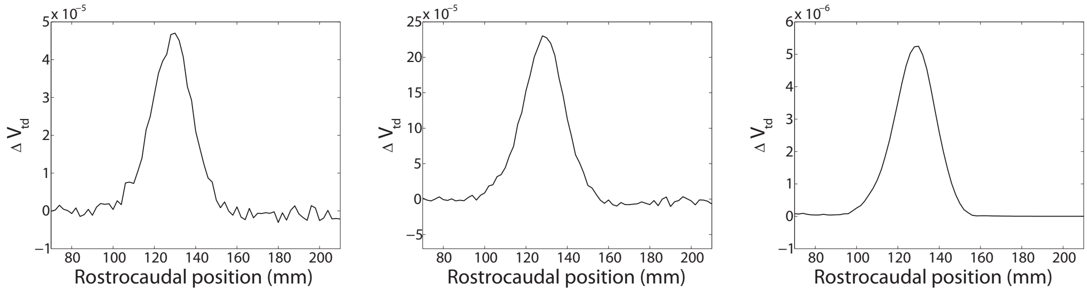
6.2 Noise reduction in a temporal structure

It is suggested that pulse wavelengths of weakly electric fish take advantage of the communication with a low duty cycle, and they share the time for efficiency of communication (Kramer, 1999). In contrast, weakly electric fish that use wave waveforms cannot use this time-sharing manner for communication. However, it is possible that wave-type waveforms are more effective for electrolocation. In this section, first, the temporal domain de-noising method is concentrated. The noise reduction methods will be applied to six EOD models shown in Fig. 6.1.

In this section, we show two types of noise reduction strategies in a time domain. EOD waveforms have periodic characteristics. We used five periods of EOD waveforms in simulation experiments. The averages of amplitudes at a specific phase or cross-correlation in a temporal sequence can be used. Fig. 6.3 shows the restored electric image along the rostrocaudal sensory line with two noise reduction strategies :

Method 1 : Take the average of intensities at a regular point for one period at each electroreceptor

Method 2 : Use the cross-correlation for one period at each electroreceptor



(a) (b) (c)

Figure 6.3: Noisy electric image and noise-reduced electric image (a) the noisy image (b) the restored electric image with method 1 (c) with method 2 (uniform random noise is distributed with a variance of 15% of maximum object perturbation when a rostrocaudal position of a target object is $8cm$ from the head, a lateral distance $3cm$; SNR is approximately $55.89dB$ in the time domain)

The periodicity of waveform gives us useful information in the time domain. In Fig. 6.1, *Brachyhypopomus pinnicaudatus* can generate 250 pulses for $1sec$ and *Eigenmannia virescens* can produce wave EOD waveforms with $1kHz$ cycles. Method 1 uses the periodicity of waveforms. The electric potential values at regular points at each cycle are taken and the average of values provides de-noised electric image. In this simulation, five cycles are used and the process is repeated ten times. Fig. 6.3 (a) shows the de-noised electric image when we use method 1. Method 1 is not an effective method compared to another methods using cross-correlation as shown in Fig. 6.3. The signal-to-noise ratio is defined as

$$SNR = 10 \times log_{10} \frac{P_{signal}}{P_{noise}} \tag{6.1}$$

where P is average power and we use SNR to represent the amount of noise in figures.

The cross-correlation was introduced to reduce the noise in a temporal signal (Reichardt, 1961; Poggio and Reichardt, 1973; Reichardt, 1986, 1987; O'Carroll et al., 1991; Shajahan et al., 1997). The cross-correlation can be calculated at each electroreceptor as the maximum of cross-correlation signals of the self-generated EOD waveform and the signal distorted by a target object and noise. Fig. 6.4 shows the schematic of the cross-correlation to remove noise. The cross-correlation along the rostrocaudal sensory line of two waveforms, its own EOD waveform and the distorted waveform, generate a de-noised electric image.

As shown in Fig. 6.5, the relative slope is distorted in noisy environment. When a target

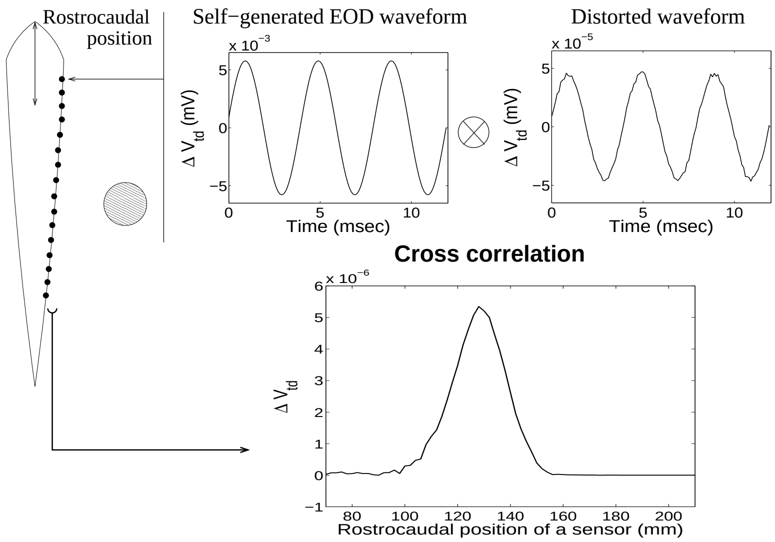


Figure 6.4: Process of de-noising electric image using cross-correlation (modified from (Sim and Kim, 2010f))

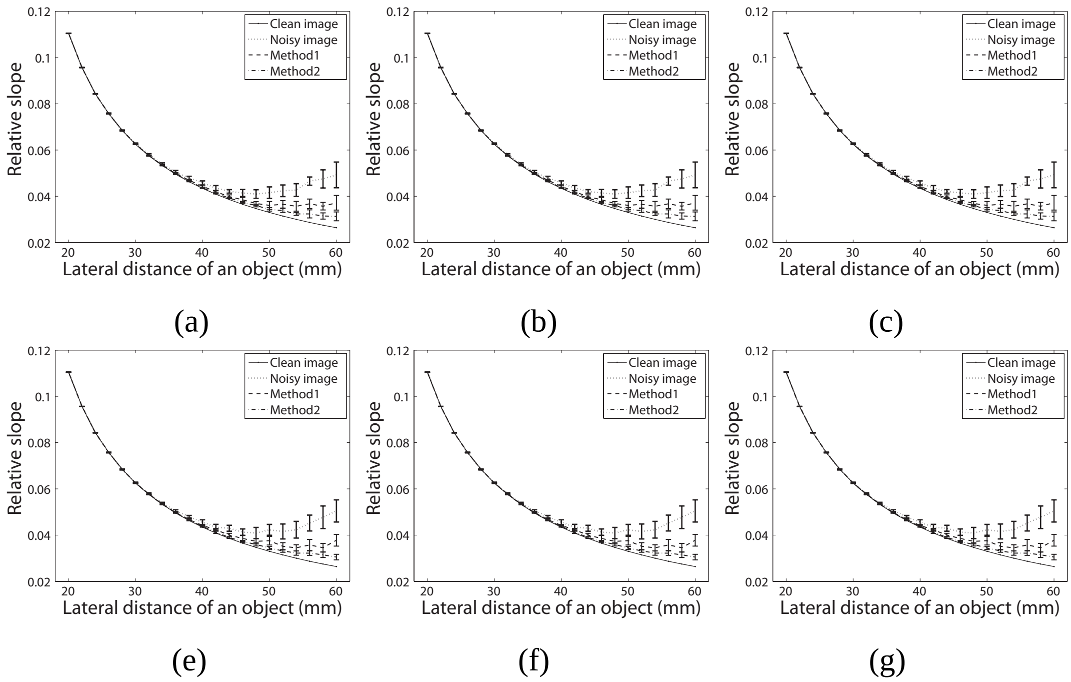


Figure 6.5: Relative slope with two types of noise reduction methods (method 2 and method 3) in a temporal domain with six EOD waveform model (a) sine pulse (b) cosine pulse (c) pulse of *Brachyhypopomus pinnicaudatus* (d) sine wave (e) sine wave with DC offset (f) waveform of *Eigenmannia virescens* when there is uniform random noise with a variance of 10% of a maximum object perturbation when a rostrocaudal position of a target object is $8cm$ from the head and a lateral distance $4cm$; SNR is approximately $94.03dB$ in the time domain at a lateral distance of $3cm$

object is farther than 3*cm* from a fish, it is difficult to estimate the lateral distance of a target in a noisy electric image. Two noise reduction methods, method 1 and method 2, help to find a more accurate relative slope. Fig. 6.5 shows relative slope when two noise reduction methods are applied to six types of EOD waveform models. Method 1 uses only five points at temporal sequence for five cycles of EOD and method 2 needs the whole sensor readings for one period of EOD. The relative slope using method 2 for noise reduction is more similar to that at clean electric image. In the next section, the cross-correlation will be used as noise reduction method in a temporal domain.

6.3 Noise reduction in a spatiotemporal structure

In the previous section, the temporal noise reduction was tested. The low pass filter is known as a simple and common noise filter. This filter will be used as the spatial denoising method and the noise reduction process is applied in both the time and space domain. The low pass filter and cross-correlation is used to create a spatiotemporal electric image in a noisy environment. Three different noise reduction methods in spatiotemporal domain are described (Sim and Kim, 2010f).

Method 1 : low pass filter in a spatial domain

Method 2 : cross-correlation in a temporal domain

Method 3 : cross-correlation in a temporal domain and then low pass filter in a spatial domain.

A fifth order Butterworth filter is applied as a low pass filter along the rostrocaudal sensory line. The low pass filter reduces high frequency components, which are characteristics of noise. Fig. 6.6 and Fig. 6.7 show the results of the low pass filter in a spatial domain. The cut-off frequency determines the frequency range of filtered electric signal.

Fig. 6.6 and Fig. 6.7 show the noisy electric image with two types of noise and denoised electric image by low pass filter in a space domain. The lateral distance of a target object is 2.0*cm* for (a) and (c), and 4.8*cm* for (b) and (d) in Fig. 6.6 and Fig. 6.7. The cut-off frequency is set to 0.1 and 0.2 and it seems that the cut-off frequency of 0.1 is more desirable in maintaining the original slope information. When a target object moves away from weakly electric fish, the intensity of the electric image decreases.

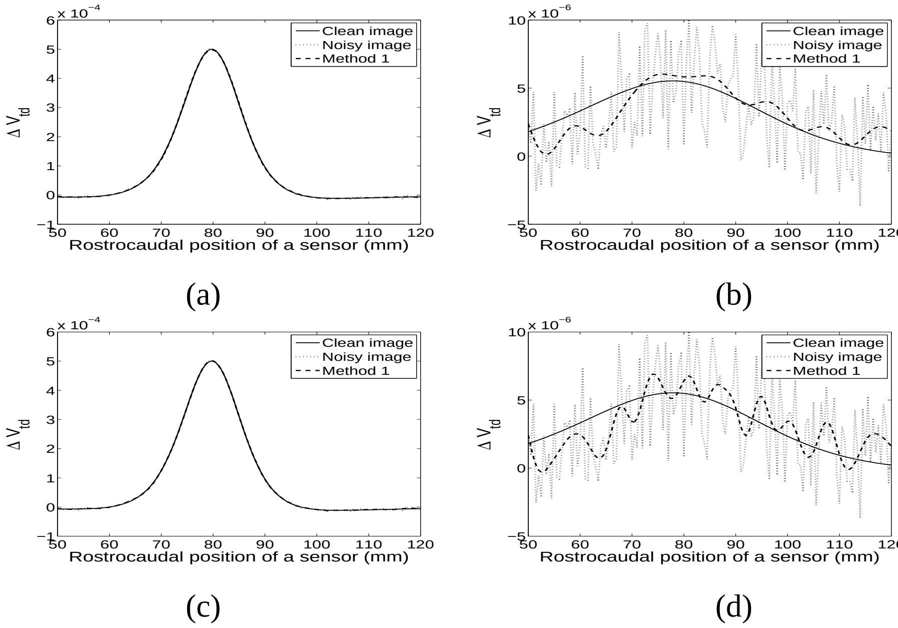


Figure 6.6: De-noised electric image with method 1 when random noise is distributed uniformly with a distribution range of $10 \times 10^{(-6)}$ (a) and (c) lateral distance of a target object is $2cm$ (b) and (d) $4.8cm$ (the ‘solid line’ is the electric image without noise, the ‘dotted line’ the distorted electric image, the ‘dashed line’ the filtered image and cut-off frequency is 0.1 for (a) and (b), 0.2 for (c) and (d)) (reprinted from (Sim and Kim, 2010f))

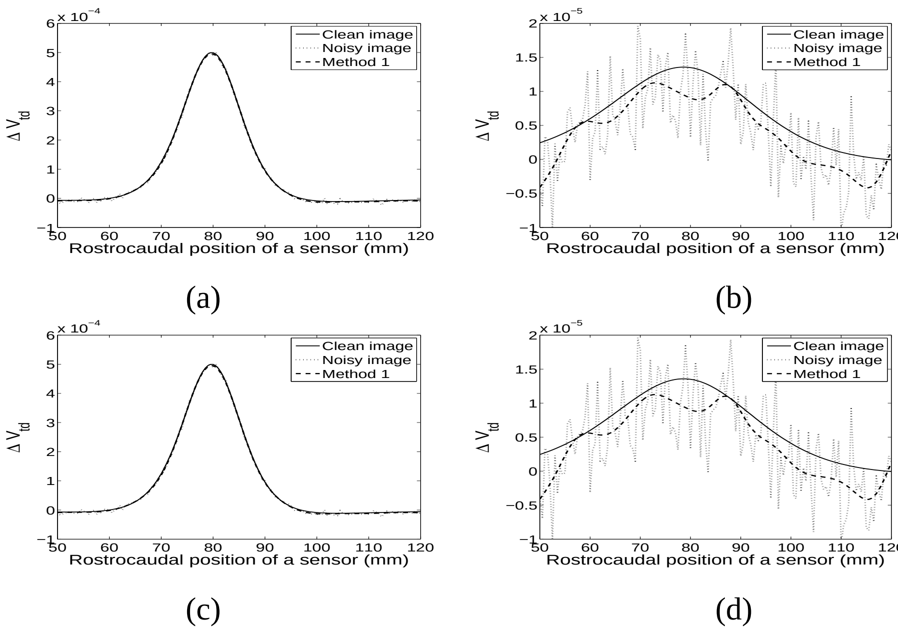


Figure 6.7: De-noised electric image with method 1 when Gaussian noise is distributed with a variance of $5 \times 10^{(-6)}$ (a) and (c) lateral distance of a target object is $2cm$ (b) and (d) $4.8cm$ (reprinted from (Sim and Kim, 2010f))

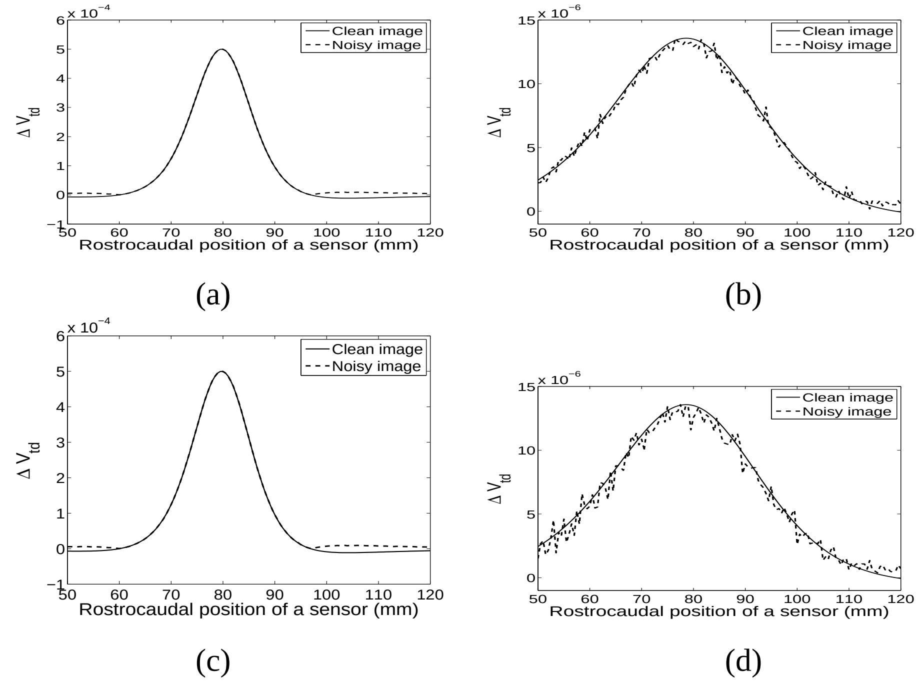
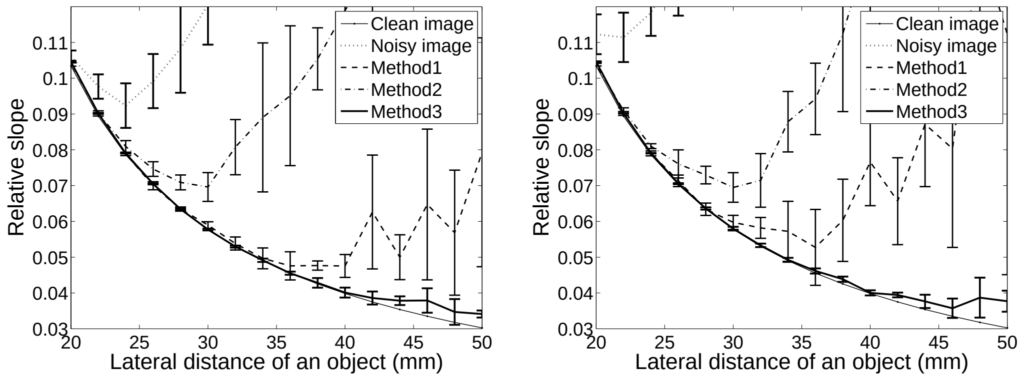


Figure 6.8: De-noised electric image with method 2 where noise exists (a) and (b) uniform noise with a distribution range of $10 \times 10^{(-7)}$ (c) and (d) Gaussian noise with a variance of $5 \times 10^{(-6)}$ (a) and (c) lateral distance of a target object is $2cm$ (b) and (d) $4.8cm$ (the 'solid line' represents an electric image without noise, the 'dotted line' the distorted electric image, the 'dashed line' the filtered image) (reprinted from (Sim and Kim, 2010f))

The original electric signal can barely be restored. Fig. 6.8 shows the result of the de-noised electric signal when method 2 is used. In method 2 and method 3, five cycles are used for the cross-correlation.

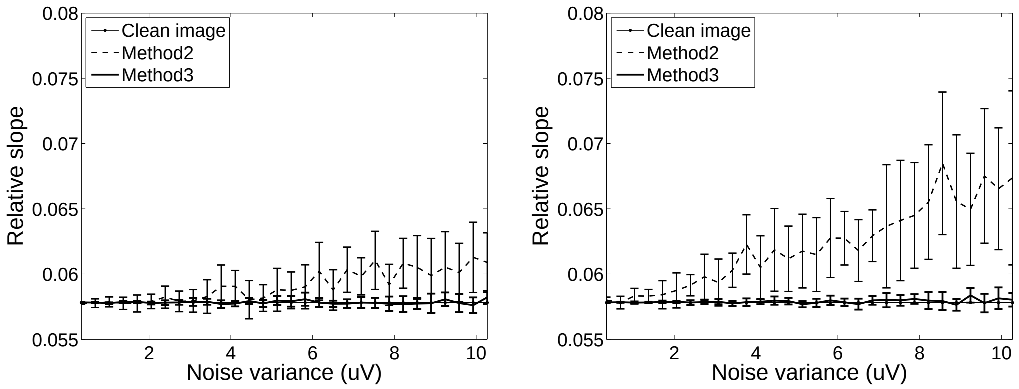
When a target object moves away from the weakly electric fish, it is difficult to restore the original electric image from noisy signals. The distortion of an electric image seems to be small compared to using method 1 with a cut-off frequency of 0.1.

When we use method 2, we can acquire a restored electric image. Fig. 6.8 shows an electric image without noise and a restored electric image through by method 2. As shown in Fig. 6.8, the distortion of electric images remain in the restored electric image. The combination of two methods, method 1 and method 2, in the spatiotemporal domain provide an effective noise filter. When a low pass filter is used for a restored electric image with cross-correlation, remaining distortion (see - Fig. 6.8) will be smoothed. In method 3, it is possible to extract a more accurate distance measurement.



(a) (b)

Figure 6.9: Relative slope with noise reduction methods 2 and 3 in a temporal domain with six EOD waveform model (a) sine pulse (b) cosine pulse (c) pulse of *Brachyhypopomus pinnicaudatus* (d) sine wave (e) sine wave with DC offset (f) waveform of *Eigenmannia virescens* when there is uniform random noise with a variance of 30% of a maximum object perturbation when a rostrocaudal position of a target object is $8cm$ from the head and a lateral distance $4cm$; SNR is approximately $72.87dB$ in the time domain at a lateral distance of $3cm$



(a) (b)

Figure 6.10: Relative slope when method2 and method 3 are used for six EOD waveform models (a) pulse of *Brachyhypopomus pinnicaudatus* (b) waveform of *Eigenmannia virescens*

Fig. 6.9 shows relative slope when three types of noise reduction methods are applied. The relative slope is very close to the original relative slope without noise when method 3 is used. This method is also effective when a target object moves far away from weakly electric fish and the effect of noise increases.

Method 1 considers a static spatial electric image when the electric potential is maximized in the time domain. When the EOD decreases in a time domain, noise severely distorts the electric image and it is difficult to extract accurate distance information. In method 2, whole temporal sequences are handled and the SNR increases compared to method 1. The capacitance of a target object affects the phase of the electric image in the time domain (von der Emde, 1993, 1998, 1999). It can be possible to extract the phase by shift depending on capacitance cross-correlation.

Fig. 6.10 shows the relative slope in restored electric images, when added noise is proportional to maximal intensities. The noise level indicates the ratio of distribution range to maximum intensity of electric image. Even though the noise level increases, relative slope using method 3 remains in an acceptable range for electrolocation. This study shows that weakly electric fish might improve the accuracy of the electrolocation by using the spatiotemporal information with their EODs, composition of the cross-correlation and low pass filtering.

The electrosensory system is not a common and commercialized sensor system. The electrosensor can be useful in the dark sea to identify the location of a target and its characteristics. To develop the electrosensory system as realized mechanical system, more research is needed for stabilization, electrosensor, structures of the system, and so forth. The noise reduction process will be an important issue to handle the original sensory image. Actually, the sensory range of weakly electric fish is not large enough to be used in the biomimetic robot system.

The thresholds in afferents were shown in the study (Engelmann et al., 2008). Weakly electric fish might not be sensitive to noise. Although the amount of noise used in experiments is large compared to noise detected by weakly electric fish, this experiment can be helpful for application of biomimetic robotic fish when the system is severely affected by noise.

6.4 Summary of Chapter 6

Actually, it is impossible to record sensor readings without noise. When a target object moves far away, the effect of noise becomes severe. Therefore, pre-processing for noise reduction is very important in identifying a target object in an electrosensory system. The noise reduction method is introduced for both the space and time domain. In this chapter, the noise reduction methods are discussed. First, a low pass filter, the fifth order Butterworth filter, is applied to the spatial electric image along the rostrocaudal sensory line. Second, the cross-correlation using EODs is used in the time domain. This method might need additional memory to save temporal sequences and higher complexity to compute, but it helps to extract cleaner object features from a restored electric image.

In previous chapters, it was shown that spatiotemporal information provides additional information for identifying target objects. The spatiotemporal information is also useful in removing noise. It is assumed that active body movements of weakly electric fish help to extract more accurate information from noisy and complex electric images. The study of spatiotemporal structures due to active body movements of weakly electric fish will provide us with useful leads in understanding active electrosensory mechanisms.

Chapter 7

Conclusion

Weakly electric fish use active electrolocation with their own electric field. They detect changes in electric signals distorted by prey, rocks, and noise. Weakly electric fish can extract novel information from corrupted electric images. They use this information to identify the target object, explore surroundings, and communicate with their conspecifics.

There have been many studied on the electroreception process of electric fish. In this thesis, it was investigated how the electric fish localize target objects using multi-electroreception or temporal sensor readings with active tail bending movement. The sensor readings from multiple electroreceptors covering the surface of weakly electric fish and create a bell-shaped curve when the target object is near the trunk. The distortion of the electric field is largest when the distance of an electroreceptor and a target object becomes smaller. When the target moves farther from weakly electric fish, the maximal peak decreases and intensity is affected by the size and conductivity of a target object. The methods are needed to measure the distance of a target that is not affected by size and conductivity.

When both an electric fish and a target object are fixed in a certain position, the tail bending movement of a fish gives temporal information and this pattern can measure a target object distance. Of course, it is reasonable to believe that the presence of many electroreceptors and active movements of an electric fish such as a tail bending and a forward motion gives accurate information about objects. But even a few sensor readings with the tail-bending movement of fish or spatial information acquired from many electroreceptors at once is enough to measure the distance of a target object. Many studies are concentrated on spatial sensor readings acquired from multi-electroreceptor or temporal readings at a fixed electroreceptor when a target object goes forward along the rostrocaudal axis of a weakly electric fish. The position of maximum amplitude indicates the rostrocaudal position of a target object, and the relative slope gives us the measurement to identify the lateral distance of a target object (von der Emde, 1999; Schwarz and von der Emde, 2001; Sicardi et al., 2000). The FWHM also decides the lateral distance (Rasnow, 1996; Chen et al., 2005). The relative slope and FWHM are useful parameters in discriminate the object distance without consideration of other characteristics such as conductivity and size.

However, there is no study to identify the height of a target object with electroreceptors distributed on a dorsoventral axis from a ventral to a dorsal area of weakly electric fish. In addition, there is no experiment that connects the problem of localization of a target and tail-bending movements. In this research, we show the role of electroreceptors spread on the sensory plane, on both the rostrocaudal and dorsoventral axes. In addition, another distance measurement is studied - the temporal sensor readings when weakly electric fish bend their tails.

7.1 Pattern of tail bending

The temporal readings can be interpreted by two points of view. First is the temporal pattern due to movement of a target object, and another is the sequence of readings with active movements of weakly electric fish, such as tail bending, that distort the electric field itself. In Chapter 4, it was shown how can temporal pattern caused by tail bending movements help weakly electric fish localize a target object. This tail bending movements might be restricted to wave EOD species. When the tail of a fish bends from -45° to 45°, the bilateral symmetry varies rhythmically with bending of the EO. This distortion of the electric field produces a temporal pattern and the temporal information gives us the distance measurement of a target object without being concerned with other properties of the object; for example, size and an electrical constant. It can be very useful when there is not enough sensor information to use as spatial information.

The temporal tail-bending pattern is affected by position, size, and electrical property of a target, but the normalized tail-bending pattern is independent of characteristics of a target such as size and conductivity. It is possible to use the integration of temporal tail-bending patterns to estimate the distance of a target such as relative slope and FWHM in a spatial structure. The temporal tail-bending pattern makes it possible to use an electrosensory system with only a few sensors. When electric potentials are integrated at each electroreceptor with tail bending movements, the relative slope obtained from the integrated electric image provide a distance information with a low pass filtering effect.

7.2 Distance estimation for multiple objects

In Chapter 5, the electrolocation in complex environment was dealt with. There was no research on electrolocation of multiple target objects. When there are more than two objects near a weakly electric fish, the electric image is affected by superposition. It is not easy to determine the whole electric image. In this thesis, a spatiotemporal electric image is introduced to measure distances of multiple objects. The concept of a relative slope can be expanded to an spatiotemporal electric image. In previous studies, a relative slope extracts the maximum spatial difference at the sensory domain. It was shown that a time-to-spatial slope takes the spatial difference at the time domain when weakly electric fish swim forward and has a role of distance measurement. When two objects are not far enough apart to extract two different electric images, it is hard to estimate the distances of multiple objects. A time-to-spatial slope is less affected by the superposition of multiple objects. It is possible to estimate distances of multiple objects at the same time when interval of objects is large enough to avoid superposition.

Secondly, when there are one target object and background objects near weakly electric fish, how can weakly electric fish identify a target object? In complex scenes with background objects, the localization of a target object is difficult without another additional process. In this study, it was assumed that a target object is closer to weakly electric fish than background objects. It is possible to identify the rostrocaudal position of a target object from complex electric images. Even if a target object is small and doesn't show a distinctive peak in electric image, the electric signal due to a target object has high frequency characteristics. In a differentiated electric image, the position which has maximal difference indicates the rostrocaudal position of a target. However, there is al problem to estimate the lateral distance of a target. The distance measurements such as relative slope and FWHM are not available in superposed electric image. Weakly electric fish might use active body movements to identify a target object in complex scenes. When weakly electric fish are close to a target object, the effect of background objects decreases and weakly electric fish can use the electric image with background cancellation.

7.3 Noise reduction in spatiotemporal electric image

It is studied that the periodic characteristics of EODs in temporal structures can make the electrosensory system more resistant to noise in Chapter 6. Weakly electric fish generate periodic electric discharge. There are two types of EOD, wave and pulse. In this study, a low pass filter and cross-correlation was introduced in the spatiotemporal domain to reduce noise. Low pass filtering is a common method for noise reduction. When the noise increases, de-noised electric image show a distorted curve and relative slope is affected by distorted maximal slope and amplitude. The temporal information which have periodical characteristic can be used to reduce noise effectively. When we apply a low pass filter in a spatial domain and cross-correlation in a temporal domain, the relative slope in a de-noised electric image is very close to the relative slope in a noisy electric image.

7.4 Future work

In this thesis, the electric field model of wave EOD species, Gymnotiformes, is basically applied to overall experiments. The pulse and wave EOD electric fish have different EO organization and foraging strategies. The comparative study of two species will help to understand the electrolocation mechanism of weakly electric fish. There are several possible topics to understand and realize the electrolocation system.

7.4.1 Other distance measurements

The relative slope is a major method in estimating the lateral distance of a target object in this thesis. The tail bending movement was suggested as a distance measurement in Chapter 4; however, the temporal tail-bending pattern should be integrated and normalized in order to be used as a measurement. There can be other distance measurements for electrolocation. On the other side of the fish, electric perturbation is generated. In this thesis, the electric perturbation of the other side of a target is not studied. It can provide information for identification of a target object and help to enhance the electrosensory signal.

The comparative study of distance measurements can help to understand the electrosensory system of pulse and wave EOD species. Usually, the relative slope is used for pulse-type electric fish and the relative width and FWHM is applied to wave-type species. The relative slope was available for the electric field model based on wave EOD species. There isn't an explanation for the reason why the relative slope was used only for the pulse-type fish.

Actually, weakly electric fishes show different decision in accordance with the shape of an object, and we can accept the difference of the relative slope due to the shape of a target object to measure the distance. In this thesis, the experiment was conducted without consideration of shape and capacitance. To the suggested method, the shape and capacitance should be considered.

7.4.2 Distance measurement in complex scenes

Chapter 5 considers two different complex environments. First, when there are multiple target objects, what is the distance measurement available? A time-to-spatial slope was suggested. However, the inter-distance should remain within a certain range. Weakly electric fish can't detect multiple targets when the interval is not large enough. Comparing the biological experiments and simulation results to validate the time-to-spatial slope is needed. In this experiment, the temporal change due to the EOD and other movements are not considered. The other movements can be removed by the reafference; however, it is not sure that the EOD can be cancelled. The complex temporal change can be a problem for electrolocation.

Secondly, when background objects distort the electric image, it is still possible to localize the rostrocaudal position of a target. It was assumed that a target object is closer to the fish and smaller than background objects. But the lateral distance of a target object cannot be easily identified. To extract the lateral distance of a target with background objects, other methods are needed. Maybe pattern matching will help the restoration of electric image of a target object. It is not easy to restore the electric image of a target because the size, electrical property, location, and shape affects the shape of the electric image. If we can extract the electric image in complex electrosensory images, the extracted electric image will provide information for identification of a target object.

7.4.3 Comparative study on biological experiments

In computer simulations, it is difficult to validate the suggested electrolocation mechanism and model. The observation of movements and change of electric potential on the surface of weakly electric fish will help to find the electrolocation mechanism and validate the suggested model.

7.4.4 Realization of the electrosensory system

Additional studies are needed in order to apply electrosensory systems to underwater vehicles and fish-like robots. To realize an electrosensory system, the characteristics of developed electrosensory systems and arrangement of electrosensors should be studied. The ultrasonic sensor is common underwater sensory system. The comparative research of characteristics of ultrasonic waves and electric fields can help to develop the underwater sensory system. It is possible to apply the electrolocation mechanism to the ultrasonic sensor system.

7.4.5 Identification of other characteristics of an object

In this study, we concentrated on the localization problem. It is known that weakly electric fish can identify not only a position, but also other characteristics of a target such as size, shape, and electrical property. There is no confirmed measure for identification of these characteristics of a target. When the electrosensory system can be used to identify characteristics of an object, it will be useful for the realization of an electrosensory system for underwater vehicles.

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