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ELECTRORECEPTION IN CATFISH: PATTERNS FROM MOTION

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Abstract. An electrosensitive catfish, *Ictalurus melas*, was trained in a two-alternatives forced-choice conditioning paradigm to discriminate between the electric fields of two direct-current (dc) dipoles, spaced 12 cm apart, the dipole axes parallel to the swimming path of the subject. The dipole size could be varied between 1 and 10 cm. The dipole current was about 5 µA. When two dipoles of different sizes were presented simultaneously, the subject's electrodiscrimination performance exceeded the 85% correct choices level provided the dipole of 1 cm was tested against a dipole with a span of 1.5 cm or more. The average stimulus strength at 1 cm distance from the dipole axis ranged from 1 to 10 mV/cm. The swimming speed of the subject was 7 ± 3 cm/s. The potential swing over the skin caused by the subject passing the dipole, matched the frequency band of the ampullary electroreceptor organs. Apparently motion of the fish with respect to a stationary direct-current stimulus source, or vice versa, generates a biologically adequate form of reafferent stimulation. Without relative motion an electrical dc-source would remain unnoticed.

Key words : Conditioning, direct-current, electric flow, dipole discrimination, two-alternative forced-choice (2AFC), electrolocation, electro-orientation, sensory-motor integration, exafferent, reafferent.

INTRODUCTION

Among the electroreceptive fish there are many species that do not have electric organs. Such fish are said to have «passive» electroreception. Cartilaginous fish, sharks, rays, and bony fish such as species of Siluriformes, belong to this category (MOLLER, 1995). Electrophysiological studies in such «passive electroreceptive» fish have revealed the receptive characteristics of the various electrosensory organs (DIJKGRAAF & KALMIJ , 1966; MOLLER, 1995; MURRAY, 1962; PETERS & BUWALDA, 1972; ROTH, 1968, 1972; ROTH & SCHLEGEL, 1988) and some principles of central processing (ANDRIANOV *et al.*, 1974; KNUDSEN, 1976a,b; MCCREERY, 1977; MONTGOMERY, 1984; WEILLE DE, 1983). Ecophysical studies have shown what kind of electrical stimuli are present in the habitat (BUTSUK & BESSONOV, 1981; KALMIJN, 1972; PETERS & BRETSCHNEIDER, 1972; ROTH, 1972). In addition, behavioural experiments have revealed that «passive electroreceptive» fish are capable of prey detection (GUSEV *et al.*, 1986; KALMIJN, 1971; PETERS & MEEK, 1973; ROTH, 1972), prey localization, and spatial orientation with respect to electric fields that occur everywhere in nature (DIJKGRAAF, 1968; KALMIJN *et al.*, 1976a,b; PETERS & VAN WIJLAND, 1974, 1993; ROTH, 1972; SISNEROS *et al.*, 1998; WILKENS *et al.*, 1997). In spite of this rather complete general impression of the role of passive electroreception in everyday fish life, questions concerning feature detection of external fields remain largely unexplored. Particularly the paradoxical mismatch between the tuning curve of the electroreceptor organs (band pass filter) and the predominant direct-current (dc) nature of the natural stimuli remains enigmatic (PETERS *et al.*, 1988, 1995). Has the fish to move with respect to a dc source – or vice versa – in order to detect it?

In addition to our earlier frequency discrimination studies (PETERS & BARETTA, 1998), where two exafferent electric alternating current sources were used as exafferent stimulus sources, we present here the first results of a frequency discrimination study where motion with respect to a stationary dc source generates a reafferent electrical stimulus that does match the bandwidth of the electroreceptor organs. The results presented hereafter tell us that passive electroreceptive fish do indeed recognize patterns from motion. A fish that passes an electric dc-current source generates in this way its own reafferent electric stimulus.

MATERIAL AND METHODS

The experiments were performed on a single male specimen of *Ictalurus melas* of 22 cm total length and a weight of about 160 g. The subject was kept in a rectangular all-glass tank of 110 by 30 cm with a water depth of 10 cm, at 18 °C. The water resistivity was kept between 300 and 340 μS/cm. Between tests the subject was allowed to swim freely either in full daylight or in the dark. During the tests, which were performed at night, there was complete darkness, except for light emitted by indicator LEDs of the equipment.

Each test began with an intertrial interval period (ITI) of 30 s, marked by switching on a light above the tank. This induced the subject to hide under an opaque shelter. At the end of the ITI the light was switched off, upon which the subject started to swim in the direction of the other end of the tank, where two parallel electrical dipoles were presented simultaneously. The dipoles were of different sizes. One dipole had the electrodes spaced at a fixed distance of 1 cm. The electrode spacing of the other dipole could be varied between 1 and 10 cm. The dipoles were 12 cm apart, and parallel to the swimming direction of the subject. The subject was trained to receive food upon turning in the direction of the smaller of the two dipoles (Fig. 1). The stimulus current was about 5 μA, which produced voltage gradients of 1 to 10 mV/cm at about 1 cm from the dipole axis. Upon choosing correctly, the subject received some food delivered via a peristaltic dispenser, and an additional 60 s of darkness. Upon the subject choosing falsely, the lights were switched on immediately, which urged the subject to return to its shelter again, waiting for the next trial. In this way 4 sessions of 50 trials per night were done. The experiment began with testing the discrimination between a 1cm and a 10 cm dipole. These sessions were repeated 20 times. Then, following the same schedule, 7, 4, 3, 2, 1.5, and 1.2 cm dipoles were tested against the 1 cm reference dipole. After completion of the series, the discrimination between a 1 and 3 cm dipole was tested again, while the amplitudes of the dipole fields were randomized, and after a silk screen had been placed that kept the subject at

1 cm or more from the electrodes. A more detailed description of the general setup is given in PETERS *et al.* 1995.

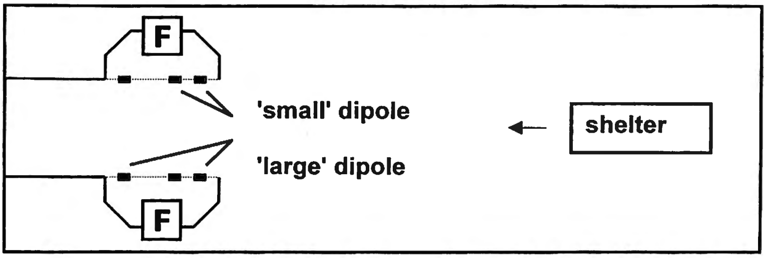

Fig. 1. – Overview of the tank with stimulus electrodes and feeding compartment. During the intertrial interval the fish hides at right under an opaque shelter. At « lights out », it starts to swim into the feeding compartment (direction of arrow), passing the two direct current sources of unequal size. Turning towards the dipoles at right or at left causes the lights to be switched on again, or food to be delivered, depending on the position of the positive discriminant, i.c. the 1cm dipole. The dotted line represents an infrared beam that monitors the subject's position. The silk screen, not shown here, was put horizontally one cm above the dipole electrodes, between the two feeding compartments. F : food dispenser in compartment with electrodes. Black blocks on dotted line are electrodes delivering the stimulus.

RESULTS

The outcome of this experiment was that the subject could recognize the different stimulus situations. The subject mastered discrimination between a 1 cm and a 10 cm

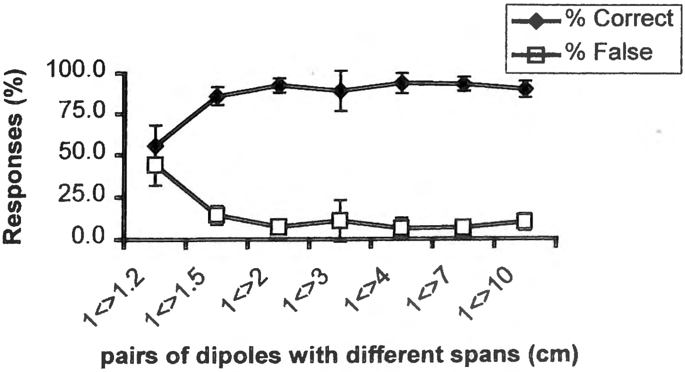

Fig. 2. – Direct-current dipole discrimination performance of *Ictalurus melas*. The « rewarded dipole » had always a span of 1 cm. The non-rewarded dipole size was varied between the experiments from 10 cm to 1.2 cm. Error bars are standard deviations of the different sessions (n=20). Each point in the graph represents the average score of 20 sessions of 50 trials each.

dipole within 30 sessions, without specific shaping. Dipoles of smaller sizes could be discriminated equally well from the reference dipole. At dipoles of 3 cm the number of mistakes began to increase (Fig. 2). Dipoles of 1 cm length and 1.2 cm could not be discriminated. Placing an electrically transparent silk screen (polyamide) 1 cm above the stimulus electrodes, in order to control the distance of the subject to the stimulus, did not affect discrimination between dipoles of 1 and 3 cm. When the stimulus amplitudes were randomized, the discrimination performance remained equally good.

The average swimming speed, calculated from the reaction times, was 7 ± 3 cm/s.

DISCUSSION

The relative ease with which the subject could be conditioned to the dipole-size discrimination task betrays its familiarity with such a kind of stimulus presentation. Indeed, electrical stimulus situations as presented above occur in nature abundantly. Also earlier laboratory observations revealed that *I. melas* turns toward an electrically simulated dc-prey when it has already passed it by several cm, and that it is very well able to follow a trail of small dc-dipoles.

The two simultaneously presented electrical fields are detected as a single field, being the sum of both dipole fields. This field is sampled by the ampullary electroreceptor organs dispersed over the skin. Apparently the catfish is able to transpose the stimulation patterns to «food at right» or «food at left». The present experiment does not reveal which specific feature of the electric field is used for making the decision to turn right or left, but even a very simple neural mechanism, like a bisensor network (*cf.* HOPKINS *et al.*, 1997; SCHÖNE, 1984), could achieve this. Any imbalance between the two halves of such a neural network could steer the subject in either of the two directions. It is not clear from this first experiment how we should describe the internal representation of the electric field. What is clear is that the subject is capable of responding in a biologically adequate way to the simultaneous presentation of two dc-dipoles of different sizes, and that it is able to associate these stimulus situations, which occur in nature, with the position of a potential prey.

From the swimming velocity and the distance to the dipole we conclude that the potential swing over the skin caused by the subject passing the dipole, matches the frequency band of the ampullary electroreceptor organs. The results presented here demonstrate that passive electroreceptive fish do indeed recognize patterns from motion. An electrosensitive catfish passing an electric direct-current source apparently generates its own reafferent electric stimulus.

The experiments are being continued.

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