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Vibratory sources as compound stimuli for the octavolateralis systems: Dissection of specific stimulation channels using multiple behavioral approaches

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Abstract

An underwater vibratory source simultaneously presents acoustic and hydrodynamic disturbances. Because vibratory dipole sources are poor sonic projectors, most researchers have assumed that such sources are of greatest relevance to the lateral line system (LL). Both hydroacoustic principles and empirical studies have shown that vibratory dipole sources are also a potent stimulus to the inner ear of fishes. Responses to vibratory sources in mottled sculpin (*Cottus bairdi*) were assessed using unconditioned orienting, differential and non-differential-classical conditioning. Orienting responses are dominated by LL inputs and eliminated by LL pharmacological inactivation. Simple conditioning depends on inputs from other systems and was not affected by LL inactivation. Differential conditioning alters behavioral control, and sculpin could be conditioned to ignore substrate borne vibrations and respond only to hydroacoustic stimulation of the ear. The lateral line and inner ear of mottled sculpin do not necessarily exhibit range fractionation, as both systems operate over a similar distance from the animal (within 1.5 body lengths) and respond to many of the same sources. Vibratory dipole sources generate compound stimuli that simultaneously activate multiple octavolateralis systems, and animals make use of the channels differentially under different behavioral tasks.

Keywords

Auditory; Lateral Line; Octavolateralis; Multisensory

The hydroacoustic world of fishes is rich with information. The density of the aquatic medium and the nature of moving sources results in spatially complex stimulus fields that can be described in terms of acoustic pressure, incompressible (hydrodynamic) flows and oscillating particle motions associated with propagated pressure waves. Hydrodynamic fields are produced by a variety of biotic and abiotic sources, including ambient currents (which include everything from convective motions to ocean tides), the respiratory and most other motor actions of other animals (including most limb movements and stridulatory acts), and traditional

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sound sources, such as percussion (or volumetric changes) of a gas bladder (Coombs & Montgomery, 1999; Denissenko, Lukaschuk, & Breithaupt, 2007; Hanke, Brucker, & Bleckmann, 2000; Kirk, 1985; Müller, Van Den Heuvel, Stamhuis, & Videler, 1997). Fishes are capable of analyzing these fields with an array of sensors that can extract at least four distinct physical parameters related to a single source. Depending on the complement of sensors present in a given species (Braun, Coombs, & Fay, 2002, Braun and Grande 2008), this could include spatial and temporal patterns of hydrodynamic motions (both acceleration and velocity), point pressure fluctuations, and whole body accelerations. The existence of multiple sensory modalities for detecting hydro-acoustic sources allows animals to detect multi-dimensional information about their environment and presents great challenges for experimental studies of sensory function.

Most existing studies of octavolateralis function have focused primarily on a single modality, yet in nearly all cases the stimulus sources used can stimulate more than one sensory channel (e.g. audition and lateral line). Studies focusing on lateral line sensory abilities have generally used vibratory sources to produce local hydrodynamic effects, even though these sources also produce acoustic effects as well. In the small arenas typically used in lateral line studies, sound waves themselves cannot propagate (Rogers & Cox, 1988), but acoustic pressure does fluctuate with source vibration. The acoustic pressure fluctuations, their underlying particle motions, and the local incompressible flow immediately surrounding the source are all relevant stimuli to the inner ear (Kalmijn 1988, 1989; Platt, Popper, & Fay, 1989). Although the spatial complexity of dipole flow fields has been mathematically modeled and is well understood, most studies using vibratory sources have neglected the implications for potential stimulation of the inner ear. Only a handful of studies have examined vibratory sources as potential inner-ear stimuli (Casper & Mann, 2006; Coombs, 1994; Coombs & Fay, 1997; Dailey & Braun, 2008; Enger, Kalmijn, & Sand, 1989; Fay, 1969).

Many lateral line studies using vibratory sources have shown that some responses to dipoles are dependent on the lateral line. Since orienting responses to vibratory sources are abolished in mottled sculpin with inactivated lateral line systems, it is clear that this behavior requires the lateral line (Coombs, Braun, & Donovan, 2001; Hoekstra & Janssen, 1986). This does not show, however that the same sources do not simultaneously stimulate other senses, or that lateral line input is sufficient for controlling other behaviors. Neurophysiological studies have shown that dipole sources are potent stimuli to inner ear (saccular) afferents in goldfish and that auditory nerve responses are driven by the pressure component of the dipole stimulus field acting on the anterior gas bladder chamber (Coombs & Fay, 1997, see also Coombs & Braun, 2003). Casper and Mann (2007) recently used dipole sources to investigate auditory brainstem responses in two species of sharks and such vibratory sources appear to be robust stimuli to the inner ear in non-pressure sensitive fishes. Dailey and Braun (2008), following up on Coombs (1994), have also shown that conditioned suppression of respiration in response to a low frequency dipole source depends on inner ear, but not lateral line inputs in goldfish.

We report on three experiments that demonstrate the compound nature of vibratory dipole stimuli. We analyzed the detection of vibratory dipole sources using both an unconditioned orienting response associated with the natural prey capture behavior of mottled sculpin and classically conditioned suppression of respiration as measures of detection. In addition, two different conditioning regimes were used to determine if subjects could be conditioned to respond to different aspects of the vibratory dipole sources (inadvertent substrate-borne vibrations and water-borne hydroacoustic effects). We demonstrate that vibratory dipoles are detected by both the inner ear and the lateral line in mottled sculpin (*Cottus bairdi*), a benthic hearing generalist. Using multiple training paradigms we also show that animals can be selectively conditioned to attend to specific individual components of the compound vibratory stimulus.

General Method

Animals

Mottled sculpin, *Cottus bairdi*, ranging from 7.5 to 9.5 cm standard length, were collected from Lake Michigan using baited minnow traps. Animals were housed in 150 or 300 l aquaria and maintained at 13–17° C. All protocols used in handling animals were in accordance with humane treatment and were approved by the Loyola University Institutional Animal Care and Use Committee.

Materials

A schematic representation of the experimental arenas used in these experiments is shown in figure 1. A vibrating dipole stimulus was created by oscillating a small plastic bead (6 mm diameter) attached to a minishaker (Brüel and Kjaer, 4810) by a 16-gauge syringe needle. Bead vibrations were driven by the amplified output of a digital-to-analog converter (Experiment 1: Modular Instruments, Inc.; Experiments 2 and 3: Tucker Davis Technologies). In all cases, the stimulus consisted of a sequence of five 500 ms pulses of 50 Hz sinusoids, each separated by 500 ms of silence (for a total of five seconds). Each 500 ms pulse was gated by a cosine function resulting in a 10 ms rise-fall time. Stimulus calibration was based on a displacement sensitive photonic sensor (Mechanical Technology, Inc.) in air. Hydrophone (Brüel and Kjaer, 8103, sensitivity -211.7 dB RE: $1 \text{ v}/\mu\text{Pa}$) recordings were also made along linear transects (every 2 mm) through the test arena to verify that the stimulus has the spatial structure of a dipole field (based on modeled predictions, see Coombs et al., 1996). Stimulus amplitude was set to 50 dB SL (sensation level, or dB above an empirically determined threshold) at a distance of 1.5 cm based on threshold estimates from previous studies (Coombs & Janssen, 1990a). At this sensation level, peak-to-peak source displacement was 3 mm, corresponding to an acceleration of 300 m s^{-2} and a velocity of 1 m s^{-1} for a 50 Hz source. The velocity of water motions at the fish would of course be smaller. As will be described below, this fixed-amplitude stimulus was presented over a wide range of source-fish distances. The peak fluid accelerations created by this source would be expected to decline by 18 dB per distance doubling (Kalmijn, 1988), so theoretically, this source would fall below threshold at 12 cm (see also Coombs, Fay, & Janssen 1989).

Procedure

In all experiments the stimulus was presented at varying distances from the fish along a transect originating at the approximate center of mass (at the level of pectoral fin insertion) and extending out perpendicularly to the long axis of the fish (see figure 1). The axis of bead vibration was always parallel to the long axis of the fish. In experiment 1, the experimenter 'lured' the fish to a randomly assigned distance (within several cm). Exact distances were measured from video records post-hoc (see below). In experiments 2 and 3, the minishaker was mounted to a three-axis system of sliding plates controlled by stepper-motors. Thus the distance between the fish and the dipole source was under computer control and could be changed remotely. The primary difference between the experiments was the dependent variable, which was an unconditioned orienting response for experiment 1 and conditioned respiratory suppression in experiments 2 and 3. The specifics of each type of measurement will be described in the methods section of each experiment, but the analysis of all three experiments was identical, regardless of response measure used.

Data Analysis

All data were treated according to the principles of signal detection theory using an analysis of the receiver operating characteristics (ROC) of the subject's responses. This analysis uses graded responses by the subjects as a confidence rating, which was measured as either an

orienting error (Experiment 1) or degree of respiration suppression (Experiments 2 and 3). Complete respiratory suppression and perfect orientation (0° error) were interpreted as highly confident detection responses, while the opposite, no turn towards the source (180° error) or unchanged respiration ($SR = 0.5$, see methods for experiments 2 and 3) was interpreted as a non-detection response. Intermediate degrees of respiratory suppression/orienting errors were considered to reflect a range of detection confidences. For any given source distance, the relative probabilities of possible response magnitudes was compared for responses to the source and during the control trial periods. ROC analysis consists of comparing the cumulative probability of any given response strength to a signal with the cumulative probability of the same range of responses during a blank trial. In other words, for every possible confidence level of the subject, the cumulative probability to for any lesser response was compared during no-signal and signal conditions to estimate false alarm and correct detection probabilities. The ROC curve is the function of these probabilities for each possible response. The area underneath an ROC curve, called $p(A)$, is theoretically equal to the percent correct in a two alternative forced choice task, so a $p(A)$ above 0.76 may be used as a detection threshold (Geisheider, 1997).

In all experiments, control trials were conducted with the bead positioned at a range of distances from the subject, equal to the distances used during signal trials. For each data set, an analysis of variance could not reject the null hypothesis that responses to the control stimulus at different distances sampled distance-specific populations. Therefore all control trial 'distances' within an experiment type were combined and analyzed as a single set of control trial responses. In this and all experiments, data from all animals were pooled to create one set of response probabilities.

Cobalt Chloride inactivation of the lateral line system

Cobalt Chloride (CoCl_2) has been widely used to pharmacologically inactivate lateral line receptors (Karlsen & Sand, 1987). We treated animals in a 2.5 l aquarium containing Ca^{++} free water with 0.1mM CoCl_2 for 24 hours. At this dose and duration, CoCl_2 reversibly blocks the lateral line for more than one week, with full recovery after around ~ 2 weeks (Karlsen & Sand, 1987; Coombs et al, 2001). Animals were tested on the following day, and, if needed, twice more, with one day rest between sessions (within six days of treatment). If necessary, animals were treated again, two weeks after the initial treatment. These animals could then be tested in as many as three sessions following each CoCl_2 treatment (i.e. within five days after treatment). This treatment was used in experiments 1 and 3.

Experiment One: Unconditioned Orienting Response

Animals

The subjects of this experiment were a group of 7 mottled sculpin, *Cottus bairdi*, ranging from 7.5 to 9.5 cm standard length. These individuals had previously been blinded by enucleation at least two weeks prior to all testing.

Procedure

The detection of the vibratory source was measured using the unconditioned orienting response of mottled sculpin, which consists of a rapid turn of the head and body in the direction of the source shortly after signal onset. The initial orienting response is typically followed by a varying number of hops towards the source, eventually culminating in a feeding strike at the bead (Coombs, 1995). Although this natural prey capture sequence does not require conditioning and is readily evoked in food-deprived sculpin (Coombs & Janssen 1990), food reward is necessary to prevent extinction of the behavior over time. Individual subjects were placed in $50 \times 50 \times 36$ cm Plexiglas tank on a vibration-isolated surface (TMC). To start each

trial, the subject was enticed into position (randomly determined) with a small piece of squid held by long-nosed forceps (the forceps were gently removed from the water before beginning the stimulus trial). Subjects were lured to starting positions in one of four distance ranges (3–6, 6–9, 9–15, or 15–18 cm) and the experimenter initiated the trial. Trials consisted of a five second period that either contained the vibratory stimulus (signal trials-70% of all trials) or an equal time of silence (blank trials-30% of all trials) to assess false alarm probability. All trials were videotaped from below, and exact initial distances and source angles were measured from digitized video frames. Coombs (1999) presented an analysis of the frequency of orienting responses from the same dataset. In the present report, we provide a new analysis using only the orienting error as a graded response that may be used in a Receiver Operating Characteristic (ROC) analysis. The orienting error is the angular separation between the fish and source after the initial orienting response (figure 2), (or after 5 seconds in the case of non-responses). The orienting error thus ranges from 90° (weakest response: no change from initial position) to 0 ± 15° (strongest response: orienting turn that brings the animal to within 15° of the bead). This analysis includes 521 signal trials and 235 non-signal trials from seven subjects.

Results

The probability densities for the range of orienting responses are given for all stimuli in figure 3. At distances of 4, 6 or 8 cm, animals exhibit a wide range of response magnitudes, and accurate turns towards the source (= small orienting errors) occur with high probability. At distances of 10 cm or more, animals make very few turns of more than a few degrees (resulting in large orienting errors), and only infrequently turn dramatically towards the source. Receiver operating characteristic curves for all distances are shown in figure 4. Detectability estimates were extracted from these ROC curves using the area beneath each curve ($p(A)$), and these values are shown as a function of distance in figure 5. As shown, stimuli of 10 cm or farther were not consistently detectable.

Cobalt chloride treatment effectively abolished the orienting response in all animals and subjects never responded to vibratory sources with orienting behaviors. As measured by this behavioral paradigm then, these stimuli were not detectable by fish without functional lateral line systems.

Discussion

The dataset presented above is the same dataset presented in Coombs (1999), but reanalyzed for comparison with experiments 2 and 3. Coombs (1999) presented an extensive analysis of orienting responses to dipole sources in multiple positions and presented both reaction time and response rate data. Coombs (1999) showed that responses probabilities declined and reaction times increased dramatically when source distance exceeded 10 cm. The present analysis provided similar conclusions. In Coombs (1999), a move towards the source was judged as a 'hit' if the distance to the source was decreased by a minimum of 5 mm and/or the angular separation was decreased by 5 deg within 2 sec of stimulus onset. The probability of hits and false alarms (during blank or control trials) was then used to determine a d' or detectability function of distance. Typical signal detection analyses use a criterion of $d'=1$ as a minimum level of detectability. In Coombs (1999), $d'=1$ occurred when the dipole source was 11.6 cm from the fish. In the present analysis based on the error of the first orienting turn, $p(A) = 0.76$ at 8 cm from the fish. It would seem that the present analysis is more conservative, which is not surprising, given that definition of a hit in Coombs (1999) included both large and small orienting errors, while the present analysis uses the degree of orienting error as a confidence measure. As can be seen in figure 3, large turning angles (and thus, small orienting errors) become increasingly unlikely for source distances of 10 cm or more. Further discussion of the results of experiment 1 will be presented in the general discussion section.

Experiment 2: Conditioned Responses to Vibratory Dipoles

Animals and Materials

The subjects of this experiment were 2 Mottled sculpin, *Cottus bairdi*, 7.5 and 9.5 cm in standard length. These animals had functional vision but these experiments were conducted in darkness following 45 minutes of dark adaptation.

The arena (71 × 76 × 25 cm, water depth 7 cm) rested on a vibration isolation system (Kinetic Systems), enclosed within a sound-attenuating chamber (IAC).

Procedure

Conditioned suppression of respiration has been widely used to study auditory sensitivities in fishes (Fay, 1995). We used mild electrical shock as the unconditioned stimulus (UCS) which causes a brief cessation of respiration (UCR). The UCS (2–10V at the source, 60 Hz AC, 100 msec) was delivered through two wire mesh electrodes (36 cm² surface area) 55 cm apart. Respiration was recorded differentially through two carbon rod electrodes (~1 cm long, 2 mm diameter), amplified (10,000x), low-pass filtered (cutoff frequency: 10 Hz), and digitized at a sample rate of 1 kHz using Tucker-Davis Technologies System II signal processing system. One electrode was mounted directly under the fish's head underneath the cage and a second electrode was placed along the tank wall 6–10 cm from the fish. A ground-reference electrode was placed in the far corner of the tank.

The amount of respiration during a trial was quantified using the Pythagorean theorem to approximate the “length of line” measure (Fay, 1995) such that:

$$R = \sum_{i=1}^x \sqrt{(v_{i+1} - v_i)^2 + 1^2} - x$$

where R = respiration, v_i = instantaneous voltage, and x = number of samples (subtracted to set complete suppression to a value of zero). This measure is equivalent to envisioning the respiratory waveform as a folded string, which when unfolded and laid out in a straight line can be measured for its length. Such a measure is sensitive to both respiration rate and amplitude. A trial consisted of a 10 second sample of respiration, broken into two five-second blocks. Changes in respiration were measured in the form of a ratio:

$$SR = \frac{R_2}{R_1 + R_2}$$

where R_1 = respiration during the first five seconds and R_2 = respiration during the second five seconds. The resulting suppression ratio ranges from 0 to 1.0, with unchanged respiration resulting in an SR of 0.5 (see figure 6). Acceleration of respiration was sometimes seen (SR of 0.6 and above) and generally taken as an indicator of stress. If respiratory acceleration was seen repeatedly, the session was ended and the fish returned to its home aquarium.

In previous reports, and in the current study, random samples of respiration had a mean suppression ratio of 0.5 with a standard deviation of approximately 0.1. Although it was not used in the present analysis, an SR of 0.39 or less can be used operationally as a threshold criterion for a positive response and was used during training as an arbiter of stimulus control. In the analysis presented below, however, the ROC analysis accounts for the full range of responses and SR is treated as a graded response.

Animals were restrained in a tent-shaped cage constructed of balsa wood and an open mesh (aperture diameter of 4 mm). The cages were size-specific and allowed the animal to maintain a natural resting posture without restricting fin movements. Animals could move forward and back or right-left approximately 1–2 cm, but could not turn around. The dipole source was mounted to a computer-controlled motorized positioning system and stimuli were presented according to the method of constant stimuli, with each distance category (every 2 cm from 4–30 cm from the fish) presented in random sequence over a session of 40 trials.

Conditioning Regime

Subjects were first acclimated to restraint in the experimental cage and the dark arena for a period of approximately four hours. On the second following day (48 hours later), they were conditioned to suppress respiration by repeated pairing of the vibratory stimulus (CS) at a distance of 4 cm and the UCS. Subjects began to exhibit conditioned suppression of respiration within 10–20 trials. The training phase consisted of 40 deliveries of the CS-UCS pairings. Subjects were subsequently tested every second day (every 48 hours).

Testing Procedure

Prior to all testing sessions, animals were pre-tested with the 4 cm training stimulus. Subjects were only tested after they displayed three consecutive correct responses ($SR < 0.4$ in response to the vibratory stimulus) within 10 preliminary trials. Animals that did not fulfill these requirements were returned to their home tanks and retested two days later. Reinforcement of the CS was given with every presentation during pre- and test periods, regardless of the animal's response.

Test sessions consisted of 40 trials, with inter-trial intervals of random duration about a mean of 180 seconds. Stimuli (bead distances of 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30 cm from the fish) were presented in random order. The bead and vibrator assembly was raised and moved to the next position 10 seconds after each trial. A total of 248 trials from two subjects were used in this analysis. No-signal (blank) trials consisted of 10 seconds of silence (with the bead in the water but not vibrating) and were presented on approximately 30% of all trials. The blank trial dataset included 116 trials from these subjects.

Results

The probability densities for the range of responses to dipole stimuli are shown in figure 7. This group of animals was conditioned using a non-differential training regime and responded vigorously to bead vibrations at all distances presented. The animals generally responded with low suppression ratios (high detection confidence), particularly at distances of less than 12 cm. There was a tendency for a bimodal distribution of response probabilities (e.g. 16, 18, and 22 cm), but this was not a reflection of individual differences between the two animals tested. Both individuals showed similar bimodal distributions of responses, with decreased response strengths at intermediate distances. The receiver operating characteristics of this group are summarized in figure 8. The resulting detectability function is shown in figure 5.

Discussion

The extended detection range contrasted sharply with the results of experiments using unconditioned orienting responses and with expectations based on previous studies. This discrepancy was easily resolved by observing that positive detection responses continued even if the vibrating bead was elevated above the water level (data not shown). This led us to believe that fish may have been detecting some other cue – most likely substrate vibrations transmitted from the minishaker through the walls of the experimental booth. To test this hypothesis, we

undertook a more complicated training regime to selectively condition fish to water-borne rather than substrate-borne vibrations, the results of which follow.

Experiment 3: Differential Conditioning

Animals and Materials

The subjects of this experiment were a group of 5 Mottled sculpin, *Cottus bairdi*, ranging from 7.5 to 9.5 cm standard length. These animals had functional vision but these experiments were conducted in darkness following 45 minutes of dark adaptation.

The experimental arena used in these experiments was the same as in experiment 2.

Conditioning procedures—Experiment 3 used a more complex differential conditioning procedure that aimed to eliminate potential responses to stimulus parameters other than water motions (e.g. substrate vibrations). These subjects underwent a three-stage conditioning procedure designed to extinguish responses to airborne sounds or substrate vibrations before testing. As in experiment 2, animals were first acclimated to restraint in the experimental cage and the dark arena for a period of approximately four hours.

Forty-eight hours later, the subject was returned to the arena and acclimated to the noises made during minishaker translocations and substrate vibrations. While the animal was confined to the holding cage, the bead-vibrator assembly was raised out of the water (7 cm travel, taking approximately 1 second), held silent for 6–10 seconds, followed by vibrations identical to the CS, but with the bead suspended in air above the water acting as an aerial loudspeaker above the tank. It can be assumed that this source creates both air-borne sound fields as well as substrate vibrations through the wall of the test chamber. In the present context however, we assume that the most salient aspect of this source for the subjects was the accompanying substrate vibration (see discussion). One to three seconds following the pulse train in air, the bead was lowered back into the water and held silent for 10 seconds. The cycle then repeated, with 10 s periods of the bead silent underwater alternating with 10 s periods of the bead suspended above water (five seconds of silence followed by five seconds of 500 ms 50 Hz pulses). No reinforcement was given. Within 30 minutes, animals resumed a normal breathing pattern and appeared to ignore the sounds of the motors and the vibrations of the minishaker raised in the air above the tank. This acclimation period, which extinguished responses to the minishaker-in-air source was continued for three to four hours and the animal was returned to its home aquarium.

Forty-eight hours later, the subject was returned to the experimental arena and a third training session was given to condition responses to the bead-vibrations in water and to continue the acclimation process begun in the last training session. In this session, the subject was presented with 40 pairings of the bead vibration underwater at 4 cm and the UCS. Between each stimulus presentation, the inter-trial period consisted of a series of minishaker translocations and vibrations identical to those presented during the previous acclimation period. During the inter-trial, the minishaker assembly was raised out of the water and moved to a new random distance location where it remained silent for five seconds followed by five seconds of 500 msec 50 Hz pulses (in air), with no reinforcement (as during the previous session). After a 1–3 second pause, the bead was returned to a distance of 4 cm and lowered back into the water. The bead was then held silent for 10 seconds and then the cycle repeated. This cycle of movements is represented graphically in figure 9A. The inter-trial intervals were thus composed of this repeated cycle of source movements (linear translations in and out of the water and to new distance points) and aerial vibrations, with a randomly chosen length of two, three, or four repetitions (giving inter-trial intervals of 90–240 seconds). The repeated presentations to aerial

vibrations (without reinforcement) were used to assess residual responding during testing (see below) and to maintain the previous conditioning session's control.

Testing procedures—As in experiment 2, subjects were only tested after they displayed three consecutive correct responses ($SR < 0.4$ in response to the vibratory stimulus) within 10 preliminary trials. Additionally, experiment 3 subjects were also required to display unmodified respiration in response to the translocations and aerial vibrations of the bead during the inter-trial periods. Animals that did not fulfill these requirements were returned to their home tanks and retested two days later. Subjects that failed to be under adequate stimulus control in three consecutive pre-testing sessions were removed from the experiment. Reinforcement of the CS was given with every presentation during pre- and test periods, regardless of the animal's response.

Experiment 3 test sessions consisted of 40 trials, with repeated cycles of motions and vibrations presented during the inter-trial period. In addition to signal trials at each of the stimulus distances (bead vibration in the water at 4, 6, 8, 10, 12, 14, 16, 18, 20 cm), two types of control trials were also presented (figure 9A) to collect non-signal responses for use in the signal detection analysis. Ten percent of all trials were completely blank, with the bead lowered into position in the water, but not vibrated. Thus these **bead-in** control trials consisted of 10 seconds of silence and can be used to measure responses in the absence of any vibratory stimulus. Thirty percent of all trials were **bead-out** control trials that consisted of 5 seconds of silence, followed by 5 seconds of 50 Hz pulses, but with the bead elevated out of the water (hence delivering substrate vibrations only). These bead-out controls were used to monitor the effectiveness of the differential training procedure. If training extinguished responses to this stimulus, there should be no difference between responses to silence (bead-in control) and responses to bead vibrations above the water surface (bead-out control). Since the differential conditioning was indeed successful (see below), we used the bead-out control trials as “blank” trials in the receiver operating characteristic (ROC) analysis. The remaining 60% of trials were signal trials, consisting of five seconds of silence, followed by five seconds of 50 Hz vibrations with the bead in the water. A total of 642 signal trials, 186 bead-out control trials and 138 silent bead-in control trials were used in this analysis.

In this study, we used a repeated measures, within subjects design wherein conditioned animals would be trained and tested intact, subsequently treated with CoCl_2 to pharmacologically inactivate the lateral line system and retested for an equal number of trials. Because all conditioned animals eventually stopped responding, only two animals provided a full set of data in both untreated and CoCl_2 treated conditions. A total of 356 signal trials and 90 blank trials from these subjects following CoCl_2 treatment were included in this analysis.

Results

After undergoing the complete course of training and extinction of responses to substrate vibrations, the animals in this group were tested only if their responses to minishaker vibrations with the bead out of the water had been extinguished (i.e. $SRs > 0.4$). During testing, this stimulus (vibrations in air) was used as a control trial for comparison with signal (water vibrations) trials. To assess the true measure of responses to vibrations conducted through the substrate, responses to the vibrating bead above water (bead-out) were also treated as signal trials and compared to responses to a motionless bead in the water near the fish (bead-in). The response probability densities in both conditions are shown in figure 9B and C. ROC analysis suggests that the bead out condition is not ‘detectable,’ in this case because detection responses have been driven to extinction during training. Since this analysis indicated that responses to the bead out condition are essentially unchanged from non-vibratory (bead-in) conditions, the

response probabilities in bead-out conditions can be effectively used as control trials compared to the responses evoked by a bead vibrating in the water nearby.

This comparison is shown for each stimulus distance in figure 10, with the resulting ROC curves shown in figure 11. The general pattern of results is similar to those shown in figure 3, but not figure 7. With increasing source distances, the probability of robust responses (low SR) decreases dramatically around 8–10 cm. The likelihood of a positive response to the stimulus falls below chance at approximately 11 cm (Figure 5).

Cobalt Chloride Inactivation of the Lateral Line—Following testing, these animals were retested following pharmacological inactivation of the lateral line. Using a within subjects design required large numbers of test sessions to complete the detection testing under intact and inactivated conditions. With repeated testing, all subjects eventually stopped responding (no suppression to either the CS or the UCS), making this experiment difficult to complete. Only two subjects completed enough tests to be included, but their results were quite consistent. Behavioral responses during this phase of testing can only be mediated by another octavolateralis sense, or with sufficient stimulus intensity, perhaps by the somatosensory system as well. The distribution of responses in CoCl_2 treated animals is shown in figure 12. The resulting psychometric detection function (figure 5) shows a striking similarity between the responses of lateral-line ablated animals and intact animals in the group II condition (also compare figures 10 and 12). Note that positive detection responses to the bead out control condition were equally unlikely for both pre and post CoCl_2 differential conditioning groups, indicating that the extinction conditioning was still effective after manipulation of the sensory periphery.

Discussion

The results of experiment three demonstrate that differential conditioning leads animals to use a subset of available information when stimulated with compound dipole sources. The results following lateral line inactivation show that behavior is guided by only a subset of available information, as the behavior was unchanged with or without lateral line inputs. Further discussion of these results follows below, with comparisons to the first two experiments as well.

General Discussion

The present results indicate that different sensory channels are utilized in different behavioral contexts and that the experimental paradigm used in a psychophysical study may dictate which channel will be probed. The orienting response is readily evoked and has been extensively characterized (Hoekstra & Janssen, 1986; Coombs, 1995; Coombs et al., 2001; Coombs & Janssen, 1990a, 1990b). It is the initial component of a sequence of horizontal motions preceding a feeding strike at a vibratory source. Multiple studies have shown that this unconditioned response depends on intact lateral line function (Hoekstra & Janssen, 1986; Abboud & Coombs, 2000; Coombs et al., 2001). The present study, however also demonstrates that the very same stimulus that fails to evoke orienting responses in lateral line-inactivated fishes is still quite detectable to them via other channels (figure 5). That is, after conditioning, animals respond to the vibratory source with or without intact lateral line systems. The lack of an orienting response in inactivated sculpin suggests that lateral line information has primacy in foraging contexts, and that other channels may not be sufficient to trigger feeding. The role of other sensory channels in the orienting response (or foraging) can not be directly judged and it is not experimentally feasible to study behavioral responses in animals with inner ear ablations. It can be said, however that the inner ear alone is *not sufficient* to trigger an orienting/feeding response.

Animals that underwent a non-differential conditioning regime (experiment 2) responded robustly to vibratory stimuli at distances that may be unrealistic for a hearing generalist that presumably detects the particle motion rather than pressure component of the acoustic nearfield. Trial and error testing quickly demonstrated that animals would respond identically whether the vibrating source was in the water or not. We presumed that these responses were dependent on either the subject's ability to detect vibrations transmitted to the substrate of the experimental arena from minishaker mounted on the adjacent wall or by inner ear detection of the airborne sound source transmitted through the water surface.

Although the present experiments cannot distinguish between these possibilities, we suggest that substrate vibrations are the more likely stimulation channel. An aerial dipole source is a poor sound projector (relative to loudspeakers with cone projectors) and produces relatively low amplitude sound fields. Much of this energy (as much as 99%) will be lost at the air-water interface and the resulting sound field in the water near the sculpin should be quite weak indeed. Finally, unlike some groups of fish, which have auditory specializations (compressible air cavities that are in close proximity to or mechanically linked to the ear) for transducing the pressure component of sound, mottled sculpin have no compressible gas cavity (no gas bladder) for transducing sound pressure. Hawkins and Johnstone (1978) demonstrated that low-frequency sources just above the water surface must produce pressures 40–50 dB higher than those produced by underwater sources in order to be detected by Atlantic salmon, a species that possesses a swimbladder without coupling specializations. It is thus unlikely that sculpin without any swimbladder are able to detect the underwater sound pressure component of a weak aerial dipole source.

On the other hand, substrate vibrations can be detected at extremely low amplitudes in this (Hoekstra & Janssen, 1986; Janssen, 1990; Whang & Janssen, 1994) and other species (Lema & Kelly, 2002). Although our behavioral arena was isolated by a compressed-air table and these vibrations were not detectable with the accelerometers available to us, it is possible that they were within the range of sculpin's sensitivity. These responses to non-water borne stimuli could be readily abolished by extinction conditioning (figure 9). This demonstrates that animals are capable of using two modes of stimulation independently (substrate and water-borne vibration channels). The artificial nature of this training distinction (conditioning responses to anything versus only to specifically hydroacoustic stimuli) makes it difficult to extrapolate to natural behaviors, but the present results clearly show that sculpin can detect low frequency vibratory sources without their lateral line systems. Further, despite their ability to detect vibratory sources with their inner ears, sculpin will not respond to such stimuli with feeding behaviors unless they can detect lateral line input. Inner ear systems respond to the same stimuli and guide conditioned behaviors equally well with or without lateral line input. More importantly, individual stimulation modes can control behavior independently in a conditioned task. *In three different behavioral experiments, three different combinations of sensory channels were used to guide behavioral responses to the same stimulus source.*

We have argued (Braun et al. 2002), following Platt et al. (1989) that the octavolateralis system is best conceived as a multi-dimensional array of sensors that detect low-frequency acoustic and hydrodynamic stimuli. A single organ, such as the otolithic inner ear, may be stimulated by more than one type of stimulus energy, and a single stimulus source may stimulate multiple sensory channels. Vibratory objects generate local incompressible (net) flow that stimulates both the lateral line and inertial inner ear. Vibratory objects can also produce propagated pressure changes that can stimulate the inner ear in two ways. Some species possess specialized transduction mechanisms that translate pressure fluctuations to mechanical stimulation of the inner ear (Braun & Grande, 2008). In non-specialized species, the oscillatory particle motions underlying the pressure fluctuations may stimulate the inertial inner ear directly (Lu, Popper, & Fay, 1996). How are these diverse forms of environmental information and sensory

stimulation used, and why is there a multiplicity of sensory channels? Recently (Braun et al. 2002) suggested that there are five basic ways in which multiple octavolateralis channels might relate to one another (figure 14). (1) Each channel may be completely independent, with no cross-channel modulation or higher level integration of information. That is, in situations where multiple channels are stimulated, the multiplicity is *redundant*. (2) On the other hand, channels may interact *synergistically*, with information from multiple channels combined within the nervous system, resulting in improved performance relative to individual channels, even if any single channel may be sufficient for the behavioral task in question. (3) A similar mode of interaction has been termed *accessory* integration (Warren & Welch 1986), referring to situations where stimulation of an accessory sensory channel modulates another sensory channel, but the primary channel alone is sufficient to guide behavior and the accessory channel alone is not. (4) It is also possible that a behavioral task requires more than one sensory system, perhaps in a *complementary* fashion. Information from any single channel may be insufficient for appropriate responses, but multiple channels are required. (5) Finally, animals may partition the information requirements of a behavioral task among multiple sensory channels: a phenomenon termed *fractionation*. Many behavioral tasks rely on information from multiple channels, but not necessarily simultaneously or otherwise in combination. Rather the task may be subdivided into modules or phases where particular channels are needed. For instance, prey acquisition in many fishes is typically reliant on vision at long distances, but can utilize either vision or lateral line at close range, without any evidence for synergistic interactions at close range (New, 2002). As another example of multimodal fractionation of information during a behavioral sequence, mottled sculpin apparently use the ear to detect substrate vibrations of buried prey. After the initial detection, however, sculpin rely on the lateral line for localizing the prey just before and during the final strike phase of the prey capture sequence (Janssen 1990).

The results of this study demonstrate that vibratory stimuli are detected by multiple octavolateralis sensory systems, but behavior may sometimes be controlled by distinct subsets of sensory modalities. The behavioral approach and training regime had substantial effects on the relevance of octavolateralis subsystems and stimulus transmission channels for each behavioral task. Although these behavioral ‘tasks’ (orienting or suppressing respiration according to a conditioned rule) may be considered poor stand-ins for the diversity of natural behavioral contexts, it is apparent from the present results that animals can make distinctions between different sensory systems or transmission channels within a given sensory system and that behaviors can be guided by individual channels alone. Following the logic of figure 14, it is clear that none of the behavioral tasks in this study required both lateral line and inner ear inputs. Elimination of the lateral line either eliminated behavior (experiment 1: orienting responses) or had no influence (experiment 3: differential conditioning). Thus the lateral line is clearly not needed for detecting vibratory sources, but animals will not or cannot make feeding responses based on inner ear detection of those sources alone. This result allows us to conclude that inner ear and lateral line information is not combined synergistically (as defined above) under the conditions of this study. These systems are also not redundant for the natural, unconditioned behavior, as inner ear information alone will not guide feeding strikes (Janssen, 1990). It is likely that feeding on epibenthic prey by mottled sculpin relies heavily on lateral line inputs with inner ear information acting in a complementary or accessory manner, if such information is used at all. For buried prey that create substrate vibrations, sequential fractionation of information by different modalities may take place, with the inner ear contributing to the initial detection and the lateral line contributing to final localization and capture of the prey. Elimination of inner ear function is necessary before any firm conclusions can be reached about the nature of multimodal interactions during unconditioned and natural prey capture behaviors.

On the other hand, in conditioned tasks that recruit inner ear function, the lateral line can be blocked without effect. It remains to be seen how lateral line inputs (while not involved in this conditioned response) might combine with inner ear function in other tasks or the lateral line can support conditioned behaviors in the absence of inner ear stimulation. It does seem likely that lateral line information will combine with inner ear stimulation in some contexts, especially when stimulus sources are very close – e.g. short-range communication (Satou, Takeuchi, Takei, Hasegawa, Matsushima, & Okumoto. 1994a, Satou, Takeuchi, Takei, Hasegawa, Matsushima, & Okumoto. 1994b, Weeg & Bass, 2002).

In conclusion, we have shown that vibratory dipole stimuli are compound stimuli that simultaneously stimulate at least two octavolateralis channels: the otolithic endorgans of the inner ear and the lateral line. Further, we have shown that conditioning can be used to selectively isolate individual sensory and/or stimulus transmission channels. It is likely that sensory inputs from each octavolateralis channel are used independently in distinct behavioral contexts (fractionation) or that if information is combined; it is in an accessory or complementary manner in specific behavioral situations.

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Figure 1.

Schematic representation of the behavioral arenas used in these experiments. The subject (Fish) was either lured to the position indicated (experiment 1) or confined there in a tent-shaped cage (experiments two and three) and the stimulus was positioned along a transect perpendicular to the long axis of the fish. Source vibrations were parallel to the fish's long axis. The position of recording and stimulating electrodes (experiments 2 and 3) are also shown as connected to the differential amplifier and the variable transformer respectively.

Starting Position = 90°

Figure 2.

Schematic diagram of the behavioral measure used in experiment 1. The vertically oriented fish outline shows the initial starting position of the subject relative to the source (black circle, with vibration axis indicated by arrows). The second fish outline shows the position of the fish after the initial orienting turn to the vibrating bead. The new angle to the source (θ) is the orienting error.

Figure 3.

Probability densities of all response possibilities in experiment 1. The probability of responses to blank trials is shown under the dashed line and the probability of any given response to a signal trial is shown under the solid lines. Each panel represents all responses to stimuli at a given distance, as indicated in the upper left corner of each graph. Note that the x-axis is plotted in descending values, to position higher confidence ratings (less orienting error after the first turn) to the right.

Figure 4. Receiver operating characteristic curves for each stimulus distance in experiment 1.

Figure 5. Detectability curves based on the ROC analyses for all three experiments. The horizontal dashed line represents a minimal level of detectability ($p(A) = 0.76$).

Figure 6.

Measures of respiratory suppression from three trials during a training session. The first five seconds of respiration is shown under the heading prestimulus. The CS is delivered during the second five seconds of the trial and is immediately followed by the UCS (arrows). The relative amplitude of respiration during the second five seconds is represented as a suppression ratio (SR) of the respiration during the stimulus (stim) to the five seconds prior to the CS (pre) plus the respiration during the stimulus.

Figure 7.

Probability densities of all response possibilities for all subjects in Experiment 2 (trained without differential conditioning). The probability of responses to blank trials is shown under the dashed line and the probability of any given response to a signal trial is shown under the solid lines. Each panel represents all responses to stimuli at a given distance, as indicated in the upper left corner of each graph.

Figure 8.
ROC curves for response probabilities for each stimulus distance (symbols) in experiment 2.

Figure 9.

(A) Schematic representation of the presentation schedule in experiment 3. A train of source vibrations (Pulse Train) is shown as a grey box. The bead travel is shown schematically reading from left to right. The bead begins in the water and is raised and lowered several times between trials. The two types of control experiments (Bead Out Control and Bead In Control) are also shown. (B) Response probabilities during these conditions is compared, using the Bead Out Control as a “signal” and the Bead In control as a non-signal condition to generate the ROC curve shown in C.

Figure 10.

Probability densities of the responses of all subjects in experiment 3. The probability of responses to control trials (bead vibrating out of the water) is shown under the dashed line and the probability of any given response to a signal trial is shown under the solid lines. Each panel represents all responses to stimuli at a given distance, as indicated in the upper left corner of each graph.

Figure 11.

ROC curves of all responses in experiment 3. Each stimulus distance is shown by different symbols.

Figure 12.

Probability densities the responses of two subjects in experiment 3 following CoCl_2 inactivation of the lateral line system. The probability of responses to blank trials is shown under the dashed line and the probability of any given response to a signal trial is shown under the solid lines. Each panel represents all responses to stimuli at a given distance, as indicated in the upper left corner of each graph.

Figure 13.
ROC curves for CoCl₂ inactivated animals in experiment 3.

Figure 14. Schematic decision tree for evaluating multisensory interaction type. After Braun et al. 2002.