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Automatic Gain Control in Harbor Porpoises (*Phocoena phocoena*)? Central Versus Peripheral Mechanisms

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Abstract

A previous study indicated no automatic gain control (AGC) in the auditory system of a harbor porpoise (*Phocoena phocoena*) as revealed by recording auditory evoked potentials to simulated echoes (Beedholm et al., 2006). The same harbor porpoise did change the rate and amplitude of its echolocation clicks during stationary echolocation when presented with an artificial target at a fixed delay. The animal spontaneously changed its click rate in such a way that the emitted level (in dB, arbitrary reference) of a click decreased as the inter-click interval (ICI) decreased (click emission rate increases), according to a 14.5 log (ICI) function. This same relationship was found when the animal swam toward a target (a fish). It reduced the amplitude of its clicks as it approached the target with a -14 to -17 log R (best-fit), which is close to the expected -20 log R found in other studies. The combined results indicate an incomplete AGC working on the transmitter side and might be explained by constraints in the sound production apparatus that couple the sound amplitude to the click rate.

Key Words: automatic gain control, AGC, echolocation, prey capture, target simulator, harbor porpoise, *Phocoena phocoena*

Introduction

In sonar and radar, the concept of automatic gain control (AGC) is a process of adjusting the transmitter output level and/or receiver sensitivity to keep the received level of the target more or less constant over a range of distances. In some cases, the amplitude of the sound source is varied with the range (R) to the target as spherical spreading (-20 log R function). This means that the incident sound level at the target will decrease by 6 dB when the distance to the target doubles due to spherical spreading loss, neglecting frequency-specific attenuation. In a sonar context without AGC, the relationship between target distance, R, and received echo in dB (relative to the emitted level) becomes 40 log R. That is, the echo reflected off a small target also suffers spreading loss, so the received echo level is decreased by an additional 6 dB. So, for each doubling of distance to the target, the echo is reduced by 12 dB for a constant emitted click level.

Within the field of biosonar, the concept of AGC was first introduced by Kick & Simmons (1984) who found that the hearing sensitivity of the big brown bat (*Eptesicus fuscus*) decreased by 11 dB per halving of target distance, a value very close to compensating for the two-way spreading loss when the amplitude of emitted echolocation signal is not regulated. Hartley (1992b) later sparked a debate over this issue as he found that the peak emission level depended on the distance to the target proportionally to a 20 log R function. In other words, the bat reduced its output level by 6 dB for each halving of distance to the target. Coupled with Kick & Simmons' (1984) value for decreasing sensitivity during approach, Hartley's result of decreasing output level implies a surprising overcompensation that would render perceived echo levels as decreasing during approach. Hartley (1992a), in an accompanying paper, suggested a solution to this apparent conundrum. He reported that hearing sensitivity depended on target range as well, namely by 20 log R. When this result is considered together with his 20 dB log R relationship between emitted levels and range, the result is perfect AGC. The supposed advantage of a complete AGC (40 log R) is that the perception of the target in the auditory system remains constant and independent of target range.

The first report of toothed whale click levels and distance to target showed that the amplitudes of clicks reduce roughly by 20 log R as free-ranging white-beaked dolphins (*Lagenorhynchus albirostris*) approached the recording hydrophone array (Rasmussen et al., 2002). This discovery led Au & Benoit-Bird (2003) to propose an AGC mechanism for toothed whales following the 20 log R curve and working on the transmitter side of the sonar system. This is only a partial AGC that keeps the level of the sound impinging on the target constant, but it also allows the received echo levels to increase by 6 dB per halving of the distance while approaching a target.

A study by Supin et al. (2004) on a false killer whale (*Pseudorca crassidens*) pointed to an AGC mechanism operating on receiver sensitivity with a full 40 log R relationship as indicated in the average auditory brainstem response (ABR). The ABR to the echo from a real target remained constant for increasing target distances (decreasing received echo levels), even though the animal used the same click amplitude at all times. Thus, the sensitivity of auditory processing increased with distance, suggesting a central AGC mechanism in this false killer whale presumably based on forward-masking (Supin et al. 2007). On the other hand, studies on a harbor porpoise showed constant ABR responses to simulated echoes of constant high amplitudes as the delays increased, suggesting no AGC mechanism in this porpoise (Beedholm et al., 2006).

Odontocetes generally process the echo from the preceding click before emitting the next click and shorten the interval between clicks when approaching a target (Au, 1993). This pattern holds for harbor porpoises as well (Teilmann et al., 2002; Verfuss et al., 2005). FM bats have a similar behavior in that they avoid overlap between the outgoing signal and the returning echo, except at high signal rates (Schnitzler & Henson, 1980; Kalko, 1995). In almost all insectivorous bats, the amplitude of the echolocation signal falls as the signal rate increases when the bat approaches a target (Simmons et al., 1979) or when the target approaches a trained bat (Hartley, 1992b).

Like in bats, we observed a fixed relationship between click amplitude and click rate in a harbor porpoise (*Phocoena phocoena*) trained to capture fish and, in another experiment, to echolocate while stationary; as the click rate rises, the amplitude falls. Here, we test the hypothesis that the coupling between click rate and click amplitude exists regardless of target range (echo delay). We discuss the consequences in relation to AGC.

Materials and Methods

A captive male harbor porpoise, "Eigil," was trained to capture dead fish (herring) in front of an array consisting of four Reson TC4034 (Reson, Slangerup, Denmark) hydrophones in a "Y"-shaped array (see Schotten et al., 2004). The length of each arm was 54.5 cm from the center hydrophone. A small underwater video camera was mounted about 10 cm above the center hydrophone to visualize fish captures. The amplification (70 dB) was set so echolocation clicks did not overload the system. The clicks were recorded to hard disk at a rate of 800 ksamples/s/channel using an A/D converter (ADLink, NuDAQ, PCI-9812/10, Adlink Technology, Taiwan). The porpoise was sent to the capture site by a trainer located about 30 m away. Clicks that were most intense at the center hydrophone (assumed to be close to on-axis) were used to calculate distances to the approaching animal, using time-of-arrival differences, and from these the corresponding source levels (Rasmussen et al., 2004; Schotten et al., 2004).

The same harbor porpoise was trained to station in front of a small, sound transparent, vertically oriented PVC plate (10 x 10 x 1 cm) 1.5 m below the water surface (Figure 1). The porpoise was participating in a study to evaluate the ABR to an artificial target (Beedholm et al., 2006). Methods for artificial click (echo) generation are described in Beedholm et al. (2006). The porpoise routinely produced copious amounts of echolocation clicks during the experiments. Even if artificial clicks were not presented, the animal produced echolocation signals of varying rates, a habit he might have learned during previous experimentation. For the present investigation, the animal's clicks were picked up by a Reson TC4013 hydrophone 0.5 m in front of the melon, amplified (ETEC preamplifier, custom built, 1-MHz bandwidth, high pass at 10 kHz) by 56 dB and digitized with 12-bit accuracy at 800 ksamples/s. A video camera was placed a few centimeters under the surface directly above the porpoise's melon. While video recordings were being made, the output of a click detector was recorded on one of the audio channels. Sometimes Eigil turned his head slightly to the right during trials, but using the synchronized video and click detector recordings, the high rate audio recordings were trimmed to smaller segments of several seconds containing only clicks produced when he faced straight ahead towards the hydrophones. The trigger level for artificial clicks was set at 132 dB re 1 µPa (peak equivalent [pe] rms), and the artificial click delay was about 4.5 ms. The received level of the artificial click at the animal was kept constant at 120 dB re 1 µPa (pe rms). A visual check was made by browsing the time series in *Cool Edit* (Syntrillium Software Corporation) to identify and clean up a few instances of non-porpoise click-like disturbances above the threshold level. The artificial clicks were manually silenced from the recordings so as not to interfere with ICI calculations and amplitudes of clicks emitted by the porpoise. An automated routine picked out the signals (512 points) and calculated the peak amplitude and the click rate. The first click in each of the 19 click sequences was discarded since the instantaneous click rate was then undefined. A total of

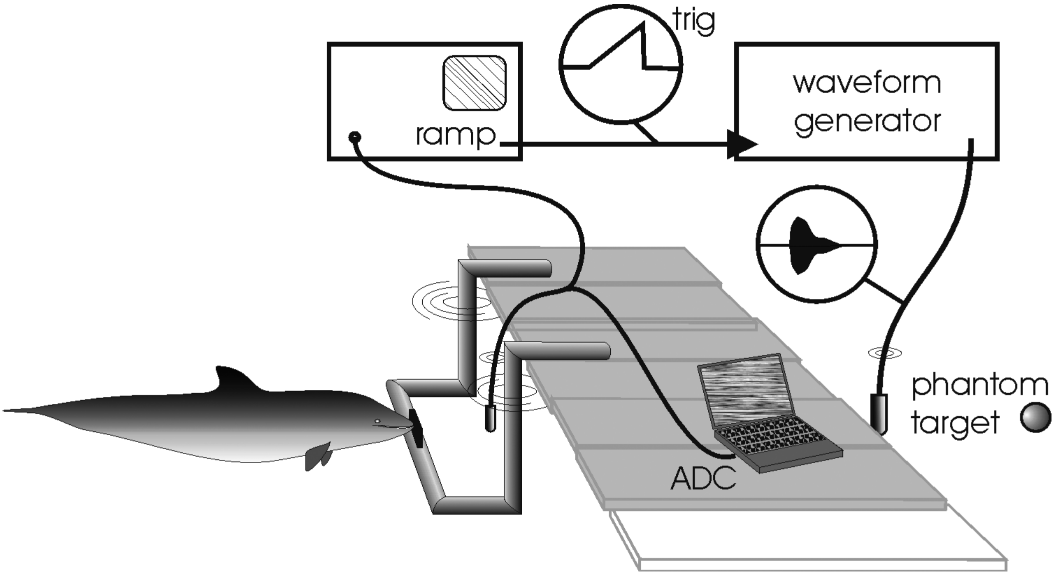

Figure 1. Drawing of the setup (not to scale); the click emitted by the harbor porpoise was captured by a hydrophone and triggered an artificial click that was transmitted back to the animal from a second transmitting hydrophone with a constant delay. The artificial click delay was constant (4.5 ms) as was the received level of the artificial click (120 dB re 1 µPa [pe rms]). See the "Materials and Methods" section for more information.

5,518 clicks from three trials were analyzed. A diagram of the setup is shown in Figure 1.

Results

Figure 2 depicts the emission levels of the harbor porpoise while stationed at the plastic square and with an artificial target at a constant echo delay. The upper panel (A) shows the raw data while the middle (B) and lower (C) panels show the mean (*n* = 10) amplitude of the emitted signal (above the chosen threshold level of 132 dB re 1 µPa pe rms) as a function of the mean click rate and mean ICI. The logarithmic function that best describes the relationship between the mean (*n* = 10) amplitude and the mean ICI is shown as the red curve in the lower panel (C) while the blue curve shows the 20 log ICI. The 14.5 log ICI fit is significantly better than the 20 log ICI fit (F-test of variances, F-value = 1.36, df = 550, 551, $p < 0.001$). In a free-ranging animal, the change in ICI represents the change in distance to the target, but in this experiment, the delay to the artificial target remains constant at about 4.5 ms.

During actual fish captures over a distance of many meters (Figure 3), our animal reduces the source level of its click emissions as the ICI decreases (repetition rate increases) in a way that closely resembles the logarithmic fits to the ICI intervals when he is stationary (Figure 2). In the example in Figure 3A, the best-fit (17 log R) is not significantly different from 20 log R. In Figure 3B, the best-fit, 14.7 log R, is significantly different from the 20 log R fit (ratio of residual variance in an F-test: F-value = 3.09, df = 13, 14, $p < 0.05$), the same findings as in Figure 2 for the ICI values. Thus, the two examples of acoustical approach behavior seen in Figure 3 are at two different levels, one of which matches that obtained from ICI values when the same animal is stationary and presented with an artificial target at a constant distance (delay).

Discussion

Our results suggest a simple mechanical explanation for the reduction of output level with increasing rate of click production. The current understanding of click production in odontocetes is that air pressure builds up ventral to the phonic lips, which are located a few centimeters below the blow hole in the harbor porpoise (Amundin, 1991; Cranford et al., 1995). Dubrovsky et al. (2004) elaborated on an earlier model of click production that incorporates an expandable ring (sphincter) displaced by excessive air pressure when a click is produced. They presented convincing evidence that the model can be applied to click production in odontocetes. If so, maximum pressure can build up in the lower air passages and allow maximum displacement of the phonic lips, giving maximum click amplitudes when click rates are low (long ICI). As the animal decreases the ICI during a click train, there comes a point where driving pressure begins to fall, thus causing a decrease in click amplitude. In other words, it becomes physically impossible for the animal to produce intense clicks at short click intervals.

We show here that the reduction in click amplitude with decreasing click interval follows an approximate 15 log (ICI) function for the stationary animal with a stationary artificial target, a constant artificial echo delay (Figure 2). The same harbor porpoise shows a reduction in click amplitude that follows a function between 15 log R and 17 log R, when capturing a fish over a long approach (Figure 3). Thus, our animal behaves acoustically as if he is approaching a target even though he and the artificial target are stationary.

The results shown in Figure 2 may be relevant for passive acoustic monitoring of wild harbor porpoises. Note that click amplitudes in this study above 147 always occurred when the emitted click rate was below 120 clicks/s, whereas it cannot be ruled out that a low click source level (e.g., 130 dB) was produced at a low rate (< 100 clicks/s). From a signal generation viewpoint, this makes sense since it is perfectly possible to reduce the rate of click production without increasing the amplitude, but it is hard to produce intense sounds in rapid succession.

What implications do our results have on audition during prey capture? First, our previous results (Beedholm et al., 2006) showed no obvious AGC when investigated by recording the ABR on the same animal. Based on this and the present results, the incident sound level on the target remains nearly constant during approach, whereas the received echo level at the animal's ear increases by a little more than 6 dB per distance halved. This situation may just be a consequence of limitations in the sound production system; the animal might simply not be able to produce intense clicks with short click intervals. Odontocetes wait for reception of an echo before emitting the next click, and thus, as the click repetition rate increases, the amplitude decreases as the animal approaches the target. The limited echo level would represent a disadvantage if high signal-to-noise ratios improve chances for prey capture. Another explanation would lie in the clutter-limited echolocation situation of coastal porpoises. The further away a porpoise is from the target, the more irrelevant objects will be within the animal's sonar beam. Maintaining a constant click level would keep the number of irrelevant echoes constant during approach, but by reducing the click level during approach, the number of clutter echoes is reduced accordingly. This last idea would mean that the coupling between click rate and amplitude was an advantage during the hunt. Both of these situations would explain why the relationship between click level and range is different from the 40 log R, which is apparent in Figures 2 and 3.

Strategies may be different for larger odontocetes hunting larger prey in pelagic waters where clutter-free ranges are greater. Given a good signal-to-noise ratio, maintaining a constant echo level at the receiver would stabilize the target and perhaps make for easier prey tracking. Supin et al. (2004) presented data suggesting that the false killer whale has AGC at the receiver that compensates by 40 log R while it keeps the outgoing click amplitude constant at the click rates investigated. In the wild, false killer whales produce clicks at least 20 dB more powerful than the harbour porpoises (false killer whales: 201-225 dB re 1 μPa pp [Madsen et al., 2005]; porpoises: 178-205 dB re 1 μPa pp [Villadsgaard et al., 2007]); therefore, it seems more likely that a large odontocete like the false killer whale might face sensory overload at the relatively short ranges considered in these studies. The 40 log R could be compensation to keep perception constant during approach. Or it could be an effect of a gradual recovery from the inhibition caused by the powerful event of click production known as forward-masking (Supin et al., 2007).

It would seem that the beaked whale (*Mesoplodon densirostris*) also couples the emitted click level to the click rate. But, this whale has an output level that remains high and constant during low constant rate click production and then suddenly falls to a low click source level as it goes into the final high click rate "buzz" during presumed prey capture (Madsen et al., 2005). Our very loose estimates of the coupling between mean click source level and mean ICI based on the data in Figure 3 of Madsen et al. (2005) suggests a coupling close to 11 log ICI for this species.

Bats (Microchiropteran) are the only other mammals that possess a well-developed echolocation system. One important study showed that trained big brown bats (*Eptesicus fuscus*) reduced the output level of their echolocation signal as a function of distance to a moving target by a factor of 20 log R (Hartley, 1992b). The signal rate increased as distance to the target decreased, so the reduction in signal level seems correlated to increased repetition rate. It might well be that the same mechanical constraints at high signal repetition rates hold for bat sound production as proposed above for odontocetes. The middle ear reflex increases the auditory threshold transiently (Henson, 1965; Suga & Schlegel, 1972) and is probably the basis for AGC in bats. This can be 40 log R or 20 log R depending on echo delay, or shortness of target range (Hartley, 1992a,

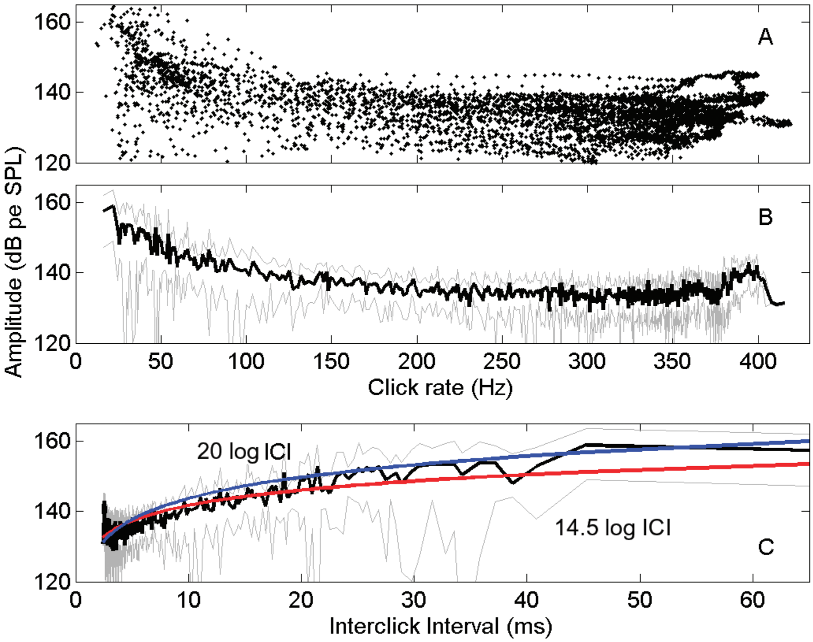

Figure 2. Amplitude of click emissions as a function of click rate and inter-click interval (ICI) from a stationary harbor porpoise, Eigil; A. Raw data points, amplitude vs click rate, B. mean amplitude (thick black line) + SD (thin gray lines) vs click rate, and C. mean amplitude (thick black line) + SD (thin gray lines) vs ICI. The best logarithmic fit is shown by the red (lower) curve, 14.5 log (ICI). The 20 log (ICI) curve is shown by the blue curve.

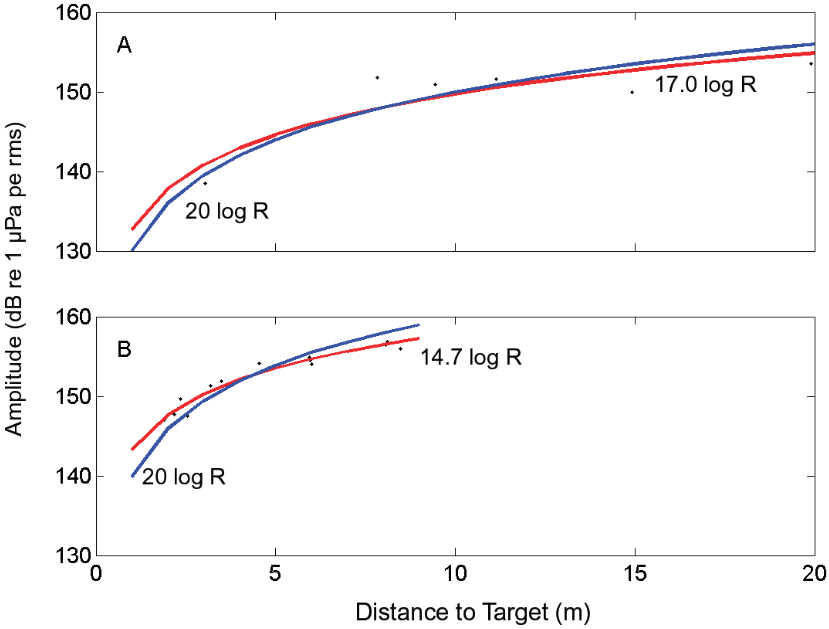

Figure 3. Relationship between apparent source level (dB) and distance to a hydrophone array during prey capture; the apparent source level was calculated from the arrival times of clicks at a 4-hydrophone array. The fish prey was less than a half meter in front of the array. A and B represent two trials from the same harbor porpoise, Eigil.

1992b; Simmons et al., 1992). The results of the Beedholm et al. (2006) experiment ruled-out the existence of a middle ear reflex in the harbor porpoise investigated even though the anatomical requirements (*m. stapedius*, *stapes*) are present.

Finding a 20 log R relationship between range and source level (Au & Benoit-Bird, 2003) should be handled with caution. Apparent source levels (ASL) (Møhl et al., 2000; Rasmussen et al., 2002) are found by back-calculating the received levels, taking into account the expected spherical spreading and absorption losses. Imagine for the sake of argument that the recorded amplitude is constant. In this case, the 20 log R is always a perfect match, regardless of the distance since the ASL (in dB) is found by adding the value 20 log R to the received level data, so plotting a constant received level against R always gives a 20 log R relationship. A constant received level would also occur if the noise level were so high that it dominated the recording in an rms measure of amplitude. Or, more seriously, a constant received level would occur if the recording were clipped due to a mismatched dynamic range in peak-to-peak measures of the click amplitude. Consequently, finding a 20 log R relationship should initially cause concern.

Another methodology that leads to finding a 20 log R relationship is using a predefined signal amplitude as the threshold for including signals in the data set. The further away the signal source, the more powerful the signal must be to meet the amplitude criterion at the measuring hydrophone due to spreading losses. Once again, the result is a 20 log R relationship, however, without any AGC.

Obviously, target distance is not related to click amplitude in our studies with the animal stationary and with a fixed artificial target delay. Instead, we have shown that the relationship between ICI and click amplitude is related by a formula close to 15 log ICI (Figure 2). This leads to speculation that the 20 log R relationship found in other odontocete studies also may reflect constraints in the click production rate. This does not mean that the animals suffer from the perceptual instability of echoes due to the ICI and amplitude relationship. The results do suggest, however, a simple mechanism that might explain this relationship in a rather straightforward and mechanical way and that the 20 log R observation does not necessarily imply an evolutionary pressure to stabilize the sound level on the target.

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