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Automatic gain control in the echolocation system of dolphins

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In bats[1] and technological sonars[2], the gain of the receiver is progressively increased with time after the transmission of a signal to compensate for acoustic propagation loss. The current understanding of dolphin echolocation indicates that automatic gain control is not a part of their sonar system[3]. In order to test this understanding, we have performed field measurements of free-ranging echolocating dolphins. Here we show that dolphins do possess an automatic gain control mechanism, but that it is implemented in the transmission phase rather than the receiving phase of a sonar cycle. We find that the amplitude of the dolphins' echolocation signals are highly range dependent; this amplitude increases with increasing target range, R, in a 20 log(R) fashion to compensate for propagation loss. If the echolocation target is a fish school with many sound scatterers, the echoes from the school will remain nearly constant[4] with range as the dolphin closes in on it. This characteristic has the same effect as time-varying gain in bats and technological sonar when considered from a sonar system perspective.

A well-established method to increase the dynamic range of sonar is to vary the gain of the receiver as a function of time from the transmission of a sonar pulse—a technique referred to as time-varying gain, or TVG[2]. The gain of the receiver is programmed to increase with time to compensate for a one-way spherical spreading loss of 20 log(R), or for a two-way loss of 40 log(R). The gain is usually increased in a 20 log($c\Delta t$) or a 40 log($c\Delta t$) fashion (where c is the speed of sound and Δt is the time elapsed from the time of transmission, so that $c\Delta t$ is equivalent to R), until a specific maximum gain level is reached.

The auditory system of the bat *Eptesicus fuscus* performs a process that is analogous to TVG. The bat's hearing sensitivity decreases at the moment of a sonar signal emission and then begins to increase at a rate of 12 dB per doubling of the elapsed time, which is equivalent to a 40 log($c\Delta t$) response. This process continues until an elapsed time of approximately 6.4 ms, corresponding to a target range of 1.4 m, after which the bat regains its normal hearing sensitivity[1]. Therefore as the bat closes within 1.4 m of its prey, the amplitude of the echoes remains constant if the transmission level remains constant. The reduced sensitivity is the result of the bat's middle-ear muscles contracting in synchrony with a vocalization to protect the auditory system from the emitted sound. The muscle contraction actually begins before the onset of vocalization[5,6]. Such an automatic gain control phenomenon has not been observed with dolphins[7]. However, recent echolocation signal measurements of free-ranging dolphins suggest that their echolocation system also possesses a gain control capability.

Accurate measurements of echolocation signals used by free-ranging dolphins in the wild can be difficult to obtain, because the echolocation beam pattern is relatively narrow[7]. If echolocation signals are not measured close to the axis of the animal's beam, the signals will be distorted[7]. It is also extremely difficult to determine the distance of a moving dolphin from the recording hydrophone in order to determine the source level (sound pressure level 1 m from the dolphin) of the signals. We have successfully overcome these problems by using a short-base-line array of four hydrophones arranged as a symmetrical star, shown schematically in Fig. 1[3,8,9]. The array structure resembles the letter "Y", with each 45.7-cm-long arm separated by an angle of 120°. A spherical hydrophone is connected to the end of each arm, with a fourth hydrophone connected at the geometric centre of the "Y." Each hydrophone output is connected to a simultaneous sampling four channel analog-to-digital converter controlled by a transportable PC aboard a boat. Calibration measurements obtained with the array and a simulated dolphin signal indicated only a 12% error in the range estimation at 25 m, which translated to a propagation loss error of only 1.1 dB (ref. 3).

The symmetrical star array has been used to measure the echolocation signals of the Hawaiian spinner dolphin (*Stenella longirostris*), pan-tropical spotted dolphins (*Stenella attenuata*), Atlantic spotted dolphins (*Stenella frontalis*), white-beaked dolphins (*Lagenorhynchus albirostris*), and killer whales (*Orcinus orca*). With the exception of the killer whale, echolocating dolphins in the wild typically emit broadband, short-duration click signals (<80 μs) with a bimodal spectrum; a low-frequency peak occurs between 30 and 50 kHz, and a high-frequency peak between 80 and 120 kHz. Approximately 70–80% of the signals measured in the field have been bimodal. Killer whales emit echolocation signals that are

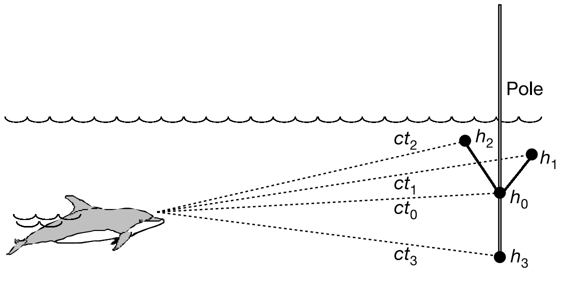

Figure 1 A schematic diagram of the symmetrical star array, with a hydrophone attached to the end of each arm and one at the centre of the array. The range of the dolphin to each hydrophone is denoted as ct_i, where c is the speed of sound in water and ti is the signal propagation time from the dolphin to the ith hydrophone. Range was determined by measuring the difference in the time of arrival of a signal at each hydrophone.

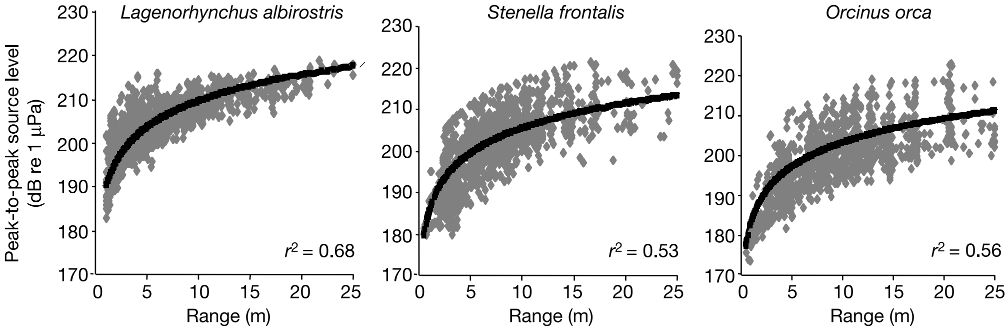

Figure 2 Source levels of three odontocete species measured in the wild as a function of the range of the animals from the symmetrical star array. The solid curve in each graph represents the function $K + [20\log(R)]$, where K is a constant that results in the best fit of the function to the measured data.

twice as long in duration and with frequency content approximately half that of the other dolphins studied.

During field measurements, dolphins often milled about 30–50 m from our boat and made 'runs' towards the array, continuously echolocating as they approached. The range of an echolocating dolphin was determined by measuring the time of arrival differences between the signal at the centre and the three other hydrophones (Fig. 1). Only signals in which the centre hydrophone detected the largest amplitude, or in which the central hydrophone detected signals that were within 3 dB of the largest amplitude, were analysed. This ensured that the dolphin's echolocation beam was directed towards the array.

In Fig. 2 we show the peak-to-peak source level of the echolocation signals of *L. albirostris*, *S. frontalis* and *O. orca* as a function of range. The data points are fitted with a function $K + [20\log(R)]$, where K is a constant that provides the best fit between the function and the measured data. The $20\log(R)$ term represents the one-way transmission loss of the echolocation signal for a given R. The echolocation signals of all the dolphin species measured with our array displayed a variation with range that can be fitted well with a $20\log(R)$ curve. The results indicate that as dolphins close in on a target, the source level of the echolocation signal decreases continuously by 6 dB for every halving of the range. This reduction in source level with decreasing range to the array is a form of dynamic time-varying gain control for the dolphin's echolocation system. Instead of the receiving gain being manipulated, the output level of the system is manipulated. In conventional sonar systems, the amplitude of the emitted signal is held constant while TVG is applied to the receiver. For the bat, the emitted signal also tends to be relatively constant close to the terminal phase of prey capture, and the hearing sensitivity is manipulated via a middle-ear muscle contraction[1]. The middle ear of dolphins is extremely complex, and its role in hearing and how it functions is unclear[10]. The ossicular chain is stiffened and tightly bound together with sheaths and annular ligaments, and the ossicles are denser and more massive than for terrestrial mammals of similar size [10]. These adaptations work against any effective middle-ear reflex, so that another means of gain control would be needed.

In order to maintain a constant echo level for a single prey item as a dolphin closes in, the gain of the sonar system should vary as $40\log(R)$ rather than $20\log(R)$. However, many dolphin species forage on fish schools[11]. Sonar echoes from a fish school would be similar to volume reverberation, consisting of the sum of many individual echoes reflecting from individual fish. The amplitude of echoes from volume reverberation increases with decreasing range as a function of $20\log(R)$ (ref. 1). Therefore, as a dolphin closes in on a fish school, the amplitude of the echoes will remain constant as the animal dynamically and progressively reduces the amplitude of the outgoing signal at a rate of $20\log(R)$. When a dolphin closes in on a single prey, the echo level will increase as the distance between dolphin and prey decreases, but not as rapidly as in a situation where there is no gain control.

The dynamic control of the echolocation source level is probably not the result of a cognitive process, but rather a natural consequence of how echolocation clicks are produced. Dolphins typically emit echolocation clicks at a rate that allow the echoes to return to the animal before the next click is emitted[7]. Consequently, the repetition rate increases as an animal closes on a target[12,13]. The clicks are produced within the nasal system of the dolphins by manipulating the air flow through the phonic lips, previously referred to as the dorsal bursae/monkey lips complex[14,15]. Dolphins initially pressurize their nasal system[16] and then emit a click train, with the clicks occurring at relatively low repetition rate and the animal continually adjusting the rate as targets are located[17]. If the dolphin chooses to keep the amount of acoustic energy emitted relatively constant or within certain limits for each pressurization cycle, then the amplitude of the signal can be high when the repetition rate is low but must continually decreases as the repetition rate increases. The data in Fig. 2 are consistent with the notion that there is a coupling between repetition rate and source level.

An advantage of having a coupling between source level and target range, and subsequently click repetition rate, is that the relative size of a target can be inferred from the reception of a few echoes. The source level of echolocation signals is coupled to target range, so that for a given range, the source level is predictable within some small variation, making relatively simple the comparison of the level of a specific echo with levels of echoes from previous experience. The range of a target does not need to be accounted for, but is automatically factored in by the coupling of source level and repetition rate of the signals. At long ranges, scanning of the beam by the dolphin, an effective method at short ranges, will not be useful in determining the size of a target because the area a sonar beam covers can be much larger than the target. However, a dolphin can still determine the relative size of a target by the levels of the echoes. From a conventional sonar design perspective, the notion of time-varying gain is always associated with the receiver. However, if the receiver gain cannot be controlled, then an alternative is to control the level of the transmitted signal, as in the case of a dolphin. Working within a dolphin's physiological constraints to maximize the efficiency of echolocation, the dolphin sonar system has arrived at a gain control system that is different from those of bats and technological sonars, but which is just as effective. ☐

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Involvement of *Notch* and *Delta* genes in spider segmentation

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It is currently debated whether segmentation in different animal phyla has a common origin and shares a common genetic mechanism[1,2]. The apparent use of different genetic networks in arthropods and vertebrates has become a strong argument against a common origin of segmentation. Our knowledge of arthropod segmentation is based mainly on the insect *Drosophila*, in which a hierarchical cascade of transcription factors controls segmentation[3,4]. The function of some of these genes seems to be conserved among arthropods, including spiders[5,6], but not vertebrates[1,6–8]. The *Notch* pathway has a key role in vertebrate segmentation (somitogenesis) but is not involved in *Drosophila* body segmentation[1,7,9]. Here we show that *Notch* and *Delta* genes are involved in segmentation of another arthropod, the spider *Cupiennius salei*. Expression patterns of *Notch* and *Delta*, coupled with RNA interference experiments, identify many similarities between spider segmentation and vertebrate somitogenesis. Our data indicate that formation of the segments in arthropods and vertebrates may have shared a genetic programme in a common ancestor and that parts of this programme have been lost in particular descendant lineages.

Segmented body plans are found in different animal groups, such as arthropods, vertebrates and annelids, that are not closely related in current phylogenies[10]. The complexity of generating a segmented body plan might argue for a common origin of segmentation and a common genetic programme[1,2]. In the past two decades, however, genetic analyses in the fruitfly *Drosophila*[3,4] and in various vertebrates such as mouse, chick and zebrafish[7–9,11–14] suggest that fundamentally different mechanisms and gene networks are involved in arthropod and vertebrate segmentation. *Drosophila* segments are generated by a successive spatial refinement along the anterior–posterior axis under the control of a hierarchical cascade of transcription factors[3,4]. By contrast, the formation of vertebrate somites involves a molecular oscillator, known as the segmentation clock, that drives the periodic expression of genes in the presomitic mesoderm[7,8,13,14]. Each wave of oscillatory gene expression results in the formation of one somite. *Notch* and *Delta* genes are crucial components of this vertebrate segmentation clock[8,15].

One *Notch* gene and two *Delta* genes (*Delta-1* and *Delta-2*) have been identified in the spider *C. salei*[16]. Here we have analysed their role in segmentation. In the spider, segments are sequentially generated from a posterior growth zone[17]. The *Notch* gene is expressed in this growth zone and resolves into segmental expression just before the segments form (Fig. 1a, e). There is a stronger accumulation of *Notch* transcripts at the posterior border of the newly formed stripes. *Notch* is expressed in the newly formed segments in the same register as the *engrailed* gene, which defines the parasegment boundary (ref. 6 and data not shown). The segmental expression of *Notch* fades in more anterior segments.

The spider *Delta-1* gene is expressed in a dynamic pattern in the growth zone (Fig. 1c, d). Initially *Delta-1* is expressed in a posterior

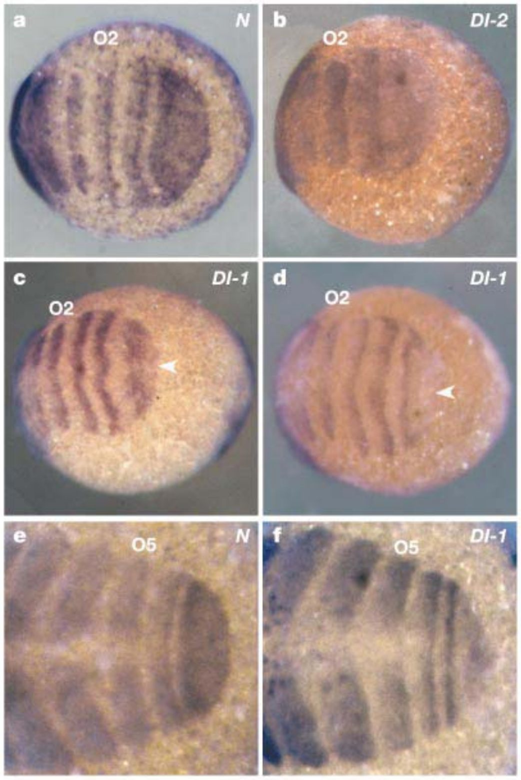

Figure 1 Expression of *Notch*, *Delta-1* and *Delta-2* genes during segmentation in the spider *C. salei*. **a**–**d**, *In situ* hybridization shows the expression of *Notch* (**a**), *Delta-2* (**b**) and *Delta-1* (**c**, **d**) in the posterior growth zone of embryos. The stripe corresponding to the just forming second opisthosomal segment is labelled O2. Arrowheads in **c** and **d** point to the posterior end of the embryo proper. **e**, **f**, Posterior end of slightly older embryos stained for *Notch* (**e**) or *Delta-1* (**f**). The most recently formed segment, the fifth opisthosomal, is labelled O5. In all embryos anterior is to the left.