pared to the no-afterimage case, afterimage vestibular response has significantly higher gain and lower phase lag over the range tested ($P < .05$). Similar effects were seen for the vestibulo-ocular frequency response when aperiodic motion was studied, with and without an afterimage (*12*). This difference between the dark and afterimage tracking cases supports the perceptual feedback hypothesis.

The observation that fast phases are virtually eliminated by a foveal afterimage supports the interpretation that the overriding information used for saccade generation is displacement of the target image from the foveal threshold (*13*). The increase in amplitude of the slow phase during afterimage tracking may imply the existence of a positive feedback loop not present during rotation in the dark. With path II in Fig. 1 open (no retinal motion), the remaining feedback (path I) is positive. Any perceived target motion generates a smooth eye movement in the same direction, presumably of the same velocity ($G = 1$ in Fig. 1). Corollary discharge, in the absence of any retinal feedback, results in a new perceived target velocity in the direction of the eye movement, and with velocity K times that of the eye and the original perception. Since the system is stable (no runaway pursuit instability is seen in afterimage tracking), the positive feedback loop must have gain less than unity ($K < 1$). On the other hand, the corollary discharge theory would require that $K = 1$ so that the stability of the perceived world is maintained during eye movements. The perfect cancellation implied by $K = 1$ would indicate that eye movements have no net effect on perceived target velocity in normal tracking, and would effectively open the feedback loop.

A possible explanation is that the corollary discharge gain is less than unity—that compensation for pursuit tracking is only partial, as may be observed by noting the apparent motion of a stationary background during fast pursuit tracking of a target. Supporting this explanation is the experiment of Dichgans *et al.* (*14*) showing that the subjective velocity of a moving visual target is about 1.6 times greater when viewed by stationary eyes (retinal motion only) than when tracked with pursuit motion. This suggests that the corollary discharge accounts for only about 63 percent ($K = 1/1.6$) of the retinal image motion associated with smooth eye movement, and that the slow phase amplitude in our foveal afterimage experiment should increase to as high as 2.5 times the value for vestibular nystagmus in the dark. Under normal tracking, the system remains effectively under negative feedback control while retaining the essential function of corollary discharge for perception (*15*). Partial cancellation might also account for the oculogyral illusion, the apparent motion of a real, head-fixed target during vestibular stimulation. Despite attempts at visual fixation, some vestibular nystagmus persists. The motion illusion is in the direction opposite to the slow phase component (in contrast to the case in afterimage tracking), which indicates incomplete compensation for the slow eye movement.

Finally, there are two alternative explanations for the current results which cannot yet be dismissed. (i) The removal of the fast phase of nystagmus may have eliminated a mechanical interaction between the phases (*16*). (ii) The presence of a visual stimulus (afterimage) in itself may have raised the level of subjective attention and increased the gain in the vestibulo-ocular reflex arc. In this regard, it should be recalled that increase in attention by other means and attempts to stare straight ahead increase the vestibulo-ocular gain.

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15. The gain for semicircular canal output to smooth eye velocity, from Fig. 1, is G for vestibular nystagmus in the dark, $G/[1 + (1 - K)G]$ for normal tracking, and $G/(1 - KG)$ for afterimage tracking. Assuming that $G = 1$ and $K = 0.6$, the slow phase velocity amplitude ratio should be $1/(1 - 0.6) = 2.5$, or 8 db higher with afterimage tracking than with no vision, which is somewhat greater than the observed shift. Normal eye tracking remains under negative feedback. Caution must be exercised in assigning quantitative loop gains, however, as these gains show adaptive changes when the external visual feedback is changed to open loop tracking [G. Vossius, *Prog. Cybern.* **2**, 111 (1965)].
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Spout of the Gray Whale: Its Physical Characteristics

Abstract. *In a calm lagoon of Baja California the spout or blow of adult and young gray whales,* Eschrichtius robustus, *was observed. Of three calves the maximum flow rate was 200 liters per second, and the duration of both expiration and inspiration was slightly less than 1 second. Gas passes through the external nares at 44 meters per second during inspiration and four to five times this rate during expiration. At this latitude the whale's spout consists mainly of seawater blown up during expiration.*

Every year from December through March a remarkable biological phenomenon attracts much attention in Southern California. It is the nearshore migration of the gray whale, *Eschrichtius robustus*, on its way to calve and breed in or near the lagoons of Baja California, Mexico. Little is actually seen of the whale, but all observers, amateur or professional, can easily see the product of its unique mode of breathing, the spout.

In late January and early February we took advantage of the whales being in the calm water of the lagoons to observe and make a refined examination of the timing and structure of the spout. During this period we had the opportunity to capture and hold calves in shallow water for periods of

about 20 minutes (*1*). Three animals were studied; their body lengths were 4.77, 5.21, and 5.78 m. The purpose of this report is to describe some characteristics of expiration and inspiration of these individuals and comment on some observations of adult animals.

Duration of expiration and inspiration, flow rates, and tidal volumes were obtained by placing a flowmeter over the blowhole. The unit was coupled to the whale by means of a small inner tube, which functioned as a gasket. A pipe 25 cm in diameter and 82 cm long conducted air to the flowmeter element. The element is a 25 cm by 2.5 cm complex of capillary tubes which act as a resistor. It creates a small pressure drop across the element, in which flow is laminar and linear with the pressure change. The pressure change is preserved on a high-speed recorder. The pressure difference is never more than 2 cm of water, which does not bother the whale. The flow trace is integrated to give volume. The entire system is calibrated with a flowmeter having an orifice 7.6 cm in diameter, which itself had been previously calibrated with standard spirometric equipment.

Characteristics of the breath of free-swimming whales were obtained by taking fast sequential pictures of adults and calves in the lagoons with a 35-mm, motor-driven camera and telephoto lens. The frame rate of the camera was calibrated by photographing a running stopwatch.

Statistics of the blow are summarized in Table 1. The 5.21-m whale had expirations which averaged larger than his inspirations by a substantial amount. He seemed somewhat disturbed at times by the flowmeter over his blowhole. This may have caused him to expire more forcefully and to inspire more tentatively.

During inspiration the two nares open to their maximum diameter. From photographs we have estimated the area of the nares of the 4.77-m whale during inspiration. The maximum area is 26.35 cm^2. At the measured peak inspiratory flow rate of 116 liter/sec the air velocity would be 44 m/sec. Serial pictures of the nares show that they are narrow slits during expiration. Therefore, velocities at this time would be four to five times faster than when the nares are fully open. Such high velocities would generate an explosive thrust against anything over the blowholes.

Some cetologists speculate that the whale's spout is vapor caused by condensation of heated and compressed gas rapidly expanding as it escapes from the lungs; therefore it condenses in the tropics as well as the polar regions. Doubtless some vapor is present in the spout of polar whales that expel saturated tidal air near

Table 1. Statistics of the blow; length of neonates averages 4.5 m. Abbreviations: *E*, expiration; *I*, inspiration; BTPS, body temperature, pressure, saturated; ATPS, ambient temperature, pressure, saturated; $\bar{x}$, mean; S.D., standard deviation; and N = number of samples.

Body length (m)	Tidal volume (liters, BTPS)				Duration (sec)			Flow rate (liter/sec, ATPS)			
	Maximum	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	Maximum	$\bar{x}$	S.D.	N
4.77											
E	38	24	7.5	26	0.54	0.13	25	101	72	16.3	36
I	40	26	7.0	31	0.40	0.11	30	116	97	11.9	36
5.78											
E	62	38	14.1	17	0.49	0.19	18	202	124	39.6	18
I	53	29	11.5	14	0.38	0.10	12	176	109	28.6	13
5.21											
E	56	32	12.2	6	0.41	0.09	5	150	118	20.7	7
I	25	18	6.7	3	0.38	0.12	4	126	88	25.9	4

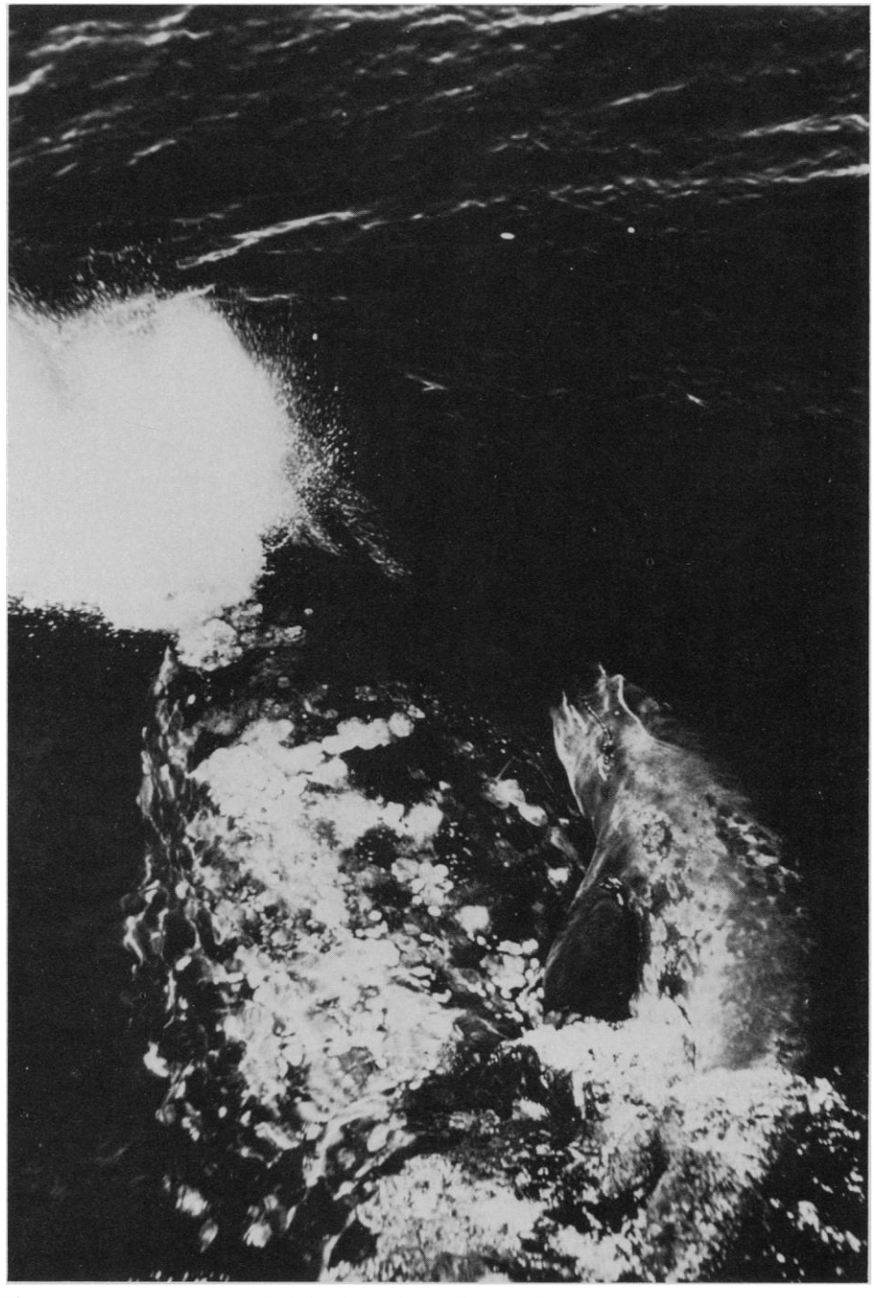

Fig. 1. An adult mother gray whale has begun her expiration while the nares are still submerged. The calf sliding off her back is about 5 m in length, and gives some idea of the amount of water being forced upward in the blow.

37°C into subzero air. But in warmer climates vapor is probably not an important part of the spout. Our observations of whales in Baja California calving lagoons, where the air temperature was usually between 10° and 20°C, show the following.

1) A spout does not appear every time they breathe. When animals float quietly and do not submerge between breaths a spout is not produced, or is weakly evident.

2) Small spouts are sometimes seen from slowly swimming animals whose nostrils are apparently wholly above the sea. The water source here may be a result of the mechanism of the nostrils closing. For example, the bottlenose porpoise, *Tursiops truncatus*, often submerges while the blowhole is still open, and water leaks down into a wedge-shaped cavity that is closed by nasal plugs at the superior bony nares (*2*). If the gray whale is similarly lax in closure of its blowholes (nostrils), sufficient water could be trapped to produce the smaller spouts.

3) Serial photographs of gray whales show that the blow often begins before the nostrils break the surface. Fully developed spouts then occur and they are dense at the nostrils, containing large drops or even ragged sheets of water (Fig. 1). Upward in the spout the water is atomized to a mist. Theoretically, if the spout were condensation due to rapid expansion and cooling of expired gases, the major effect should occur high in the spout and not at the nostrils.

In sum, the gray whale's spout is composed mainly of seawater, and its magnitude is controlled by the way in which the whale begins and ends its respiratory cycle.

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Biogenesis of Erythropoietin: Evidence for Pro-Erythropoietin in a Subcellular Fraction of Kidney

Abstract. *The light mitochondrial fraction of hypoxic rodent kidneys, called the renal erythropoietic factor, contains erythropoietin in a pro, or inactive form. Erythropoietin is released from this inactive form when the renal erythropoietic factor is incubated with normal serum. The biogenesis of erythropoietin possibly involves a system in kidney reminiscent of the proinsulin-insulin system in pancreas.*

The biogenesis of erythropoietin (Ep), although extensively investigated, has not yet been elucidated. Gordon *et al.* (*1*) presented extensive evidence indicating that under both normal and hypoxic conditions, the biogenesis involves interaction between a renal erythropoietic factor (REF), also called erythrogenin, and a normal serum component. The REF is found mainly in the light mitochondrial fraction of kidney homogenates, which is largely composed of lysosomes. These findings suggest alternative mechanisms for the biogenesis of Ep (*2*). Thus, it may be postulated that the REF is a renal enzyme that activates a serum substrate, possibly derived from the liver (*1*); only suggestive, rather than conclusive, evidence favoring this hypothesis was presented (*3*). In addition, in accordance with the original concept of Kuratowska (*4*), the possibility should be considered that the REF contains a pro-Ep factor which is activated by normal serum. This hypothesis, however, is unsubstantiated by experimental evidence. Finally, the possibility cannot be excluded that the REF contains both Ep and an inhibitor of Ep that is not chemically linked to Ep and would be rendered inactive by a serum factor, thus unmasking the Ep activity.

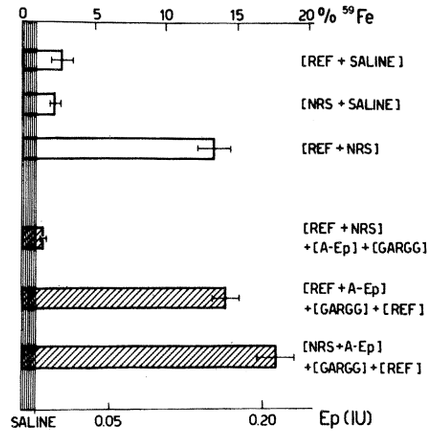

Fig. 1. REF plus NRS: incubation with A-Ep and GARGG. Percent of ^{59}Fe incorporated into red blood cells (means ± S.E.M.) and corresponding international units of Ep in assay mice receiving (first three bars from the top) rat REF plus saline, normal rat serum (NRS) plus saline, or REF plus NRS, respectively. The other three vessels (REF plus NRS; REF; NRS) were incubated with antiserum to Ep (A-Ep) and then GARGG; REF and NRS vessels were subsequently incubated with NRS or REF, respectively. All mixtures were finally injected in assay mice.

Our results indicate that a pro-Ep molecule in the REF is rendered active by incubation with normal serum. We therefore suggest that the biogenesis of Ep is mediated by a system consisting of pro-Ep and Ep that is reminiscent of the proinsulin-insulin complex in pancreas (*5*).

Female CF 1 mice (20 to 25 g), male Wistar rats (150 to 200 g), and young, albino male rabbits were maintained with standard laboratory diets and given free access to tap water. The REF was prepared (*6*) from kidneys of hypoxia-exposed rats or rabbits (0.42 atm of air for 18 hours). Serum from normal rats or rabbits was dialyzed against 100 volumes of the disodium salt of EDTA (0.005*M*) for 24 hours at 4°C. The material was redialyzed against deionized water (100 volumes) for 24 hours and the dialyzate, called rat or rabbit normal serum, was frozen at −20°C until needed. In the incubation procedures, equal volumes of REF and normal serum were incubated for 45 minutes at 37°C in a water bath incubator with constant shaking. In control vessels, REF or normal serum was incubated with equal volumes of physiological saline under the same conditions. In experiments with rabbit antiserum to Ep and goat antiserum to rabbit γ-globulin (GARGG), (Antibodies Inc.) (*7, 8*), the vessels (REF, normal serum, or REF and normal serum, or both) were then incubated with an appropriate amount of antiserum to Ep for 20 minutes under the above conditions. Thereafter, in order to eliminate a possible excess of antiserum to Ep, GARGG was added to the vessels for 15 minutes under the same conditions. The mixture was finally centrifuged at 2000 rev/min for 15 minutes and the sediment was discarded. Our antiserum to Ep was obtained by a modification (*7*) of the procedure of Schooley and Garcia (*9*). One milliliter of the antiserum neutralizes up to 125 international units (I.U.) of human Ep (*10*). The appropriate amount of GARGG had been ascertained by testing against known quantities of antiserum to Ep. This control procedure was always re-