for other volatile and moderately volatile metals. If this is the case, estimates of their fluxes to seawater based only on data from mid-ocean ridge hydrothermal systems would be lower limits. But the degassing process may affect only the surfaces of flows, because Po in the single mesocrystalline sample we analysed was <20% degassed on eruption. Future studies should evaluate the fine-scale variations in Po and other volatiles, such as CO_2 and volatile metals, with depth in submarine flows.

The importance of the ^{210}Po–^{210}Pb dating discussed here is that it not only confirmed the suspicions[4] of observers in the submersible *Alvin* that mid-ocean ridge eruptions had taken place shortly before their April 1991 visit to 9° 50′ N on the EPR, but that it provided the only information about the number and timing of eruptions as well. When the same area was revisited after a 9-month hiatus, much of the physical evidence for recent volcanic activity had disappeared, although other nearby regions appeared to be active[5]. Along such portions of the mid-ocean ridge system, the ^{210}Po-^{210}Pb chronometer has the potential to provide information about the temporal variability of submarine eruptions with unprecedented time resolution, particularly when used together with detailed direct and remote observations. This chronometer, when combined with other recently developed radioactive tracers of MORB eruptions (for example, refs 22–24), will undoubtedly allow for even greater understanding of the temporal variability of submarine eruptions and their effect on the geology and biology of the ridge ecosystem. ☐

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New whale from the Eocene of Pakistan and the origin of cetacean swimming

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MODERN whales (order Cetacea) are marine mammals that evolved from a land-mammal ancestor, probably a cursorial Palaeocene–Eocene mesonychid[1–3]. Living whales are streamlined, lack external hind limbs, and all swim by dorsoventral oscillation of a heavily muscled tail[4,5]. A steamlined rigid body minimizes resistance, while thrust is provided by a lunate horizontal fluke attached to the tail at a narrow base or pedicle[6]. We describe here a new 46–47-million-year-old archaeocete intermediate between land mammals and later whales. It has short cervical vertebrae, a reduced femur, and the flexible sacrum, robust tail and high neural spines on lumbars and caudals required for dorsoventral oscillation of a heavily muscled tail. This is the oldest fossil whale described from deep-neritic shelf deposits, and it shows that tail swimming evolved early in the history of cetaceans.

The early evolution of whales is illustrated by partial skulls and skeletons of five archaeocetes of Ypresian (early Eocene) and Lutetian (early Middle Eocene) age (Table 1), all found in sediments deposited near or in the ancient Tethys Sea. *Pakicetus*[7–10] is the oldest fossil whale known, and it is also the smallest early archaeocete, with a skull and auditory bullae about half the size of those of the other four genera. All have dense auditory bullae, showing that they were at least partially aquatic, but *Pakicetus* lacks anatomical features required for directional and efficient hearing in water[8,10]. *Ambulocetus*[11], the earliest marine archaeocete known to date, has a long femur and long foot and is interpreted to have been an otter- or seal-like foot-propelled swimmer[11]. *Indocetus*[12] resembles *Ambulocetus* in having long hind limbs, but it also has a robust sacrum with four solidly fused centra and large proximal tail vertebrae, suggesting that it was a caudally propelled swimmer[13]. *Protocetus*[14–16] is more advanced in having a reduced single-centrum sacrum, meaning that its lumbocaudal trunk was flexible like that of modern whales. *Protocetus* has a sacrum that did not articulate directly with the pelvis[14], and it must have been fully aquatic because it could not support its weight on land. *Rodhocetus* described here is the first early archaeocete with a complete thoracic, lumbar and sacral vertebral column. It retains primitive features seen in land mammals, but also exhibits derived characteristics found only in later cetaceans.

Order Cetacea
Suborder Archaeoceti
Family Protocetidae
Rodhocetus kasrani, new genus and species

Etymology. *Rodho*, geological anticline where the type was found, and *cetus*, Latin, whale (masc.); *kasrani*, Baluch tribe inhabiting the type area.

Holotype. Geological Survey of Pakistan/University of Michigan [GSP-UM] 3012, cranium and lower jaws found with a partially articulated postcranial skeleton including cervical vertebrae C2–C7, thoracics T1–T13, lumbars L1–L6, sacrals S1–S4, caudals Ca1–Ca4, most ribs, sternal manubrium and xiphisternum, left and right os coxae, and left femur (Fig. 1). Tooth wear and fusion of vertebral epiphyses show specimen to be fully adult. Type found by X. Zhou in 1992 is conserved at the Geological Survey of Pakistan, Islamabad.

Referred specimen. GSP-UM 1852, left and right dentaries with much of the lower dentition, collected in 1981 by W. Ryan 1.6 km north of Rakhi Nala and 3 km west of Rakhi Munh rest house, 90 km southwest of the type locality (29°58′06″ N, 70°06′43″ E, 39 K/1 15′ quadrangle).

Type locality. Middle of valley drained by Bozmar Nadi, Rodho anticline of Zinda Pir anticlinorium, Sulaiman Range, near the

TABLE 1 Skull and femur measurements of *Rodhocetus kasrani* compared with those of other early archaeocetes

	Pakicetus inachus[7–10] Lower Kuldana Fm. Pakistan Late Ypresian Riverine TA3.1 low-stand* ~49.5–49.0 Myr* (~52.5–52.0 Myr)†	*Ambulocetus natans*[11] Upper Kuldana Fm. Pakistan Ypresian–Lutetian Shallow marine TA3.1–TA3.2 ~49.0–48.5 Myr (~52.0–51.5 Myr)	*Rodhocetus kasrani* Lower Domanda Fm. Pakistan Early Lutetian Deep neritic TA3.2–TA3.3 ~46.5 Myr (~49.5 Myr)	*Indocetus ramani*[12,13] Upper Domanda Fm. Pakistan Early Lutetian Shallow marine TA3.3 shelf-margin ~46.5–46.0 Myr (~49.5–49.0 Myr)	*Protocetus atavus*[14–16] Lower Mokattam Fm. Egypt Middle Lutetian Deep neritic TA3.3 high-stand ~46.0–45.0 Myr (~49.0–48.0 Myr)
Cranium					
Condylobasal length (cm)	30.0 – 32.0‡	—	61.5	62.0‡	58.0
Width across supraorbital processes (cm)	—	—	19.5	20.0–21.0	16.7
Width across zygomatic arches (cm)	14.5	—	26.0	26.0‡	24.0
Width across exoccipitals (cm)	9.1	—	22.0	22.0	—
Auditory bulla length (mm)	25.5	63.0‡	60.0	62.0–70.0	54.0–55.0
Auditory bulla width (mm)	22.5	45.0	46.0	45.0	40.0
M^1 crown length (mm)	17.3	25.0	24.3	21.5‡	22.0
Mandible					
Mandibular fossa height (mm)	Small	—	65.0 (large)	—	—
Mandibular symphysis length (cm)	—	—	22.0§	—	—
M_3 crown length (mm)	17.8	—	24.5	—	—
M_3 crown width (mm)	8.9	—	13.8	—	—
M_3 crown height (mm)	12.0	—	28.7	—	—
Femur					
Head diameter (acetabulum; cm)	—	—	3.1 (3.2)	(4.0)	—
Total length (cm)	—	28.0	17.8	25.0‡	—

* Correlations and ages in million years based on planktonic foraminiferans[18,19], nannofossils[20] and sea-level sequence stratigraphy with radiometric calibration of Haq *et al.*[17]. † Alternative ages in parentheses reflect timescale of Berggren *et al.*[23]. ‡ Estimate. § Mandibular symphysis extends to point just posterior to P_2.

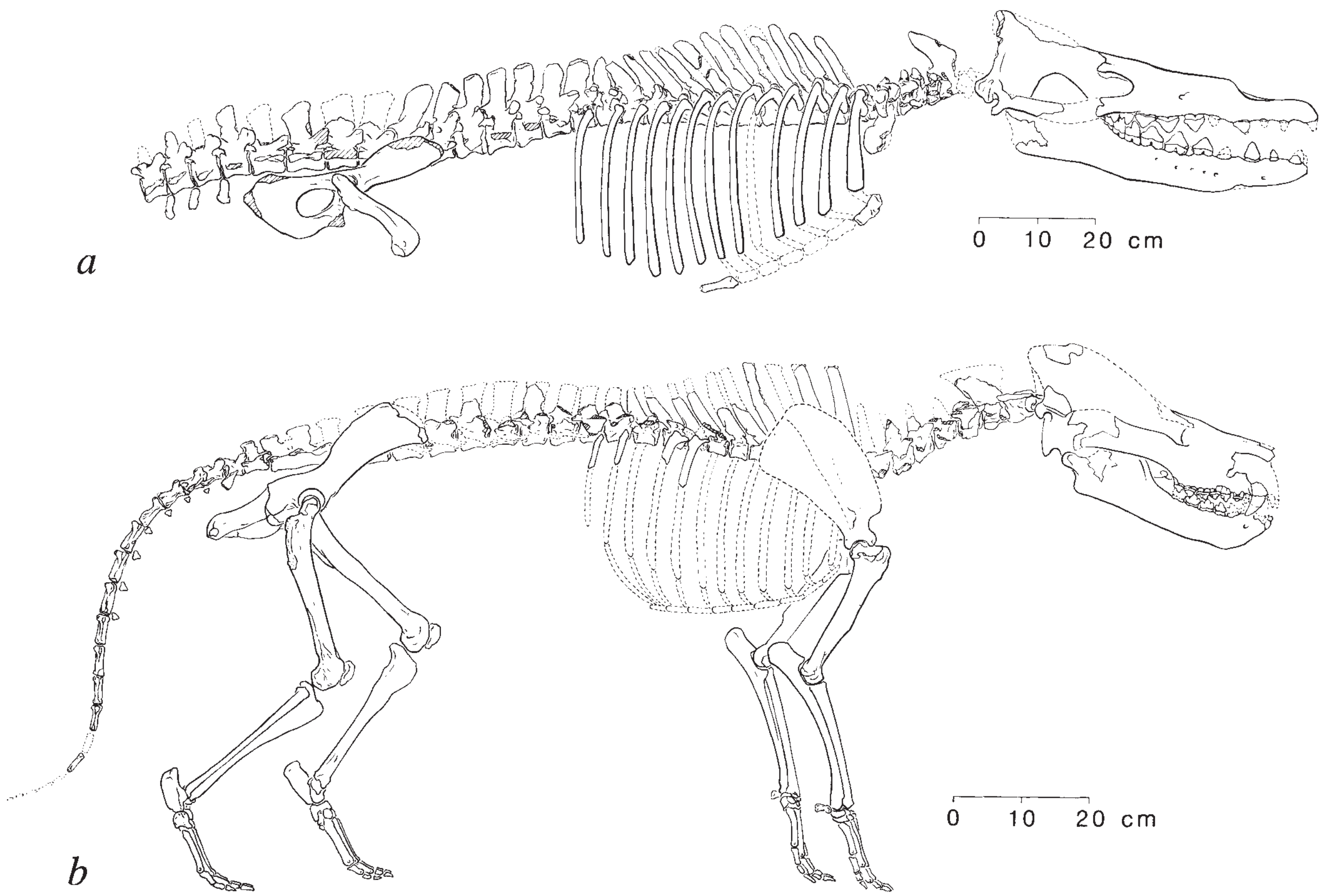
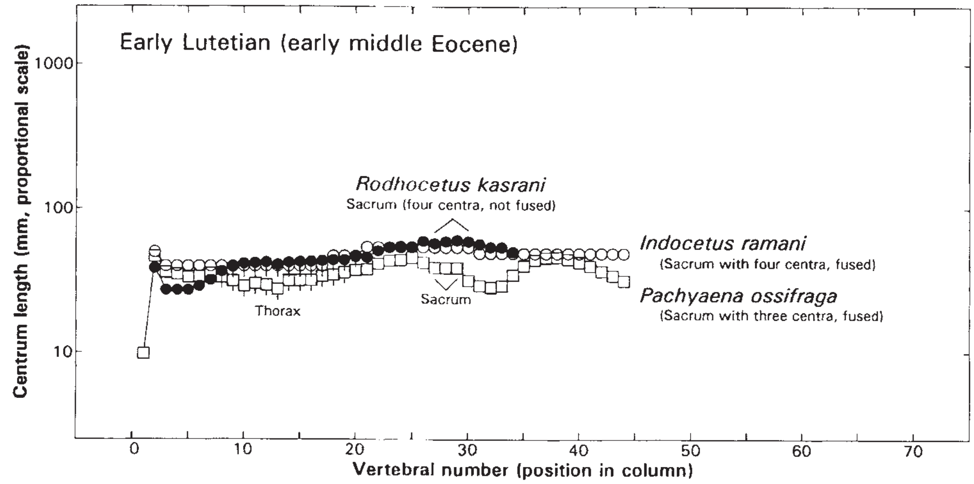


FIG. 1 Skeleton of early Middle Eocene cetacean *Rodhocetus kasrani* (*a*, holotype GSP-UM 3012) compared with early Eocene mesonychid *Pachyaena ossifraga* (*b*, ref. 3) representing the land-mammal group thought to be ancestral to whales[1,2]. Both are drawn to the same thorax + lumbus length in right lateral view (some elements are reversed from left side). Dashed lines and cross-hatching show reconstructed parts. *Rodhocetus* forelimbs, distal hind limbs and distal tail are not yet known (these were removed from the type before burial, possibly by scavenging sharks). The skeleton of *Rodhocetus* is 2 m long, as preserved, and in life, with a full tail, it may have been as long as 3 m. Note large typically protocetid skull, short neck, vertebral count of 7 cervicals, 13 thoracics, 6 lumbars, 4 sacrals, and 4 + caudals and long chevrons ventral to caudals. Thoracics T11 and T12 have overlapping neural spines, T12 is anticlinal, and T13 is diaphragmatic. The thorax anterior to T13 was relatively rigid, whereas the skeleton posterior to T13 was more flexible (enhanced by loss of fusion of sacral vertebrae).

FIG. 2 Length-of-vertebrae profile of *Rodhocetus kasrani* (solid circles) superimposed on that of land mammal *Pachyaena ossifraga* (squares; ref. 3) and archaeocete *Indocetus ramani* (empty circles; ref. 13). *Rodhocetus* profile is typically cetacean[22] in having short cervical vertebrae (here vertebral numbers 2–7, note difference from *Indocetus*) and long posterior lumbars, sacrals and anterior caudals (here vertebral numbers 25–34, note difference from *Pachyaena*).



southwestern corner of Punjab Province, Pakistan (30°46′06″ N, 70°26′37″ E, 39 J/5 Dhodak 15′ quadrangle).

Age and distribution. Both specimens are from green shales in the lower part of the Domanda Formation deposited in the transition from a high-stand to a shelf-margin sediment wedge interpreted as the transition from Tejas sea-level cycle TA3.2 to TA3.3 (ref. 17) on the basis of planktonic foraminiferans[18,19] and nannofossils[20]. The top of TA3.2 and base of TA3.3 are early Lutetian in age, early Middle Eocene, and the interval yielding *Rodhocetus* is calibrated at about 46.5 Myr[17]. Both specimens come from marine sediments in the Sulaiman Range of Pakistan but *R. kasrani* was probably widely distributed along the southern margin of ancient Tethys.

Diagnosis. *Rodhocetus* differs from *Pakicetus* and other Ypresian archaeocete species in having higher-crowned cheek teeth, larger auditory bullae, and larger mandibular foramina and mandibular canals. It differs from *Ambulocetus* in having higher neural spines on lumbar vertebrae and a much shorter femur, and it differs from *Indocetus ramani* in having a convex posterior surface of the exoccipital, shorter cervical vertebrae, unfused sacral vertebrae and a shorter femur. *Rodhocetus* differs from *Protocetus atavus* and all later whales in having external nares open above the canines and in retaining four vertebrae in the sacrum, with a larger pelvis joined to the sacrum by a normal land-mammal synarthrosis.

The skull of *Rodhocetus* is large relative to the rest of the skeleton (Fig. 1), and it has the elongated premaxillae and dentaries, broad frontal shield, high nuchal crest, and other proportions typical of archaeocete cetaceans[15] (comparative measurements in Table 1). External nares open above the upper canine. Infraorbital foramina are small. The posterior surface of the exoccipital is convex like that of *Protocetus*. Auditory bullae are large and dense, but there are no pterygoid fossae or accessory air sinuses associated with these. There is a well-developed mandibular foramen or fossa on the medial side of each dentary, with an 'acoustic window' measuring about 90 mm long by 65 mm high (bone lateral to this is 4.0 mm thick) interpreted as a wave guide to aid hearing in water[21]. Teeth are robust; lower molars have crowns higher than they are long (Table 1).

GSP-UM 3012 is the only early archaeocete showing the number of cervical (7), thoracic (13), lumbar (6) and sacral (4) vertebrae in the skeleton. Four caudals are preserved, but the total number is unknown. Cervical centra are shorter than those of anterior thoracics; C3–C5 each measure about 27 mm in centrum length. Anterior thoracics average about 42 mm in centrum length, posterior thoracics average 45 mm, lumbars average 54 mm, sacrals average 59 mm, and proximal caudals average 54 mm. The vertebral length profile for *R. kasrani* is compared with profiles for the land mammal *Pachyaena ossifraga*[3] and archaeocete *I. ramani*[13] in Fig. 2, which shows *R. kasrani* to have had shorter cervicals and longer sacrals than expected from either comparison. *Rodhocetus* differs from *Pachyaena* and *Indocetus* in having unfused sacral vertebrae (Fig. 3).

No forelimb elements of *Rodhocetus* have been found to date. High neural spines on anterior thoracics and long ribs give *Rodhocetus* a deep narrow thorax (measuring about 45 × 35 cm at T9). High neural spines on anterior thoracics are found in mammals such as *Pachyaena* that cantilever a heavy head and thorax above ground with the forelimbs acting as piers.

The pelvis is well preserved in GSP-UM 3012. Os coxae measure 336 mm in length and 128 mm dorsoventrally, and the

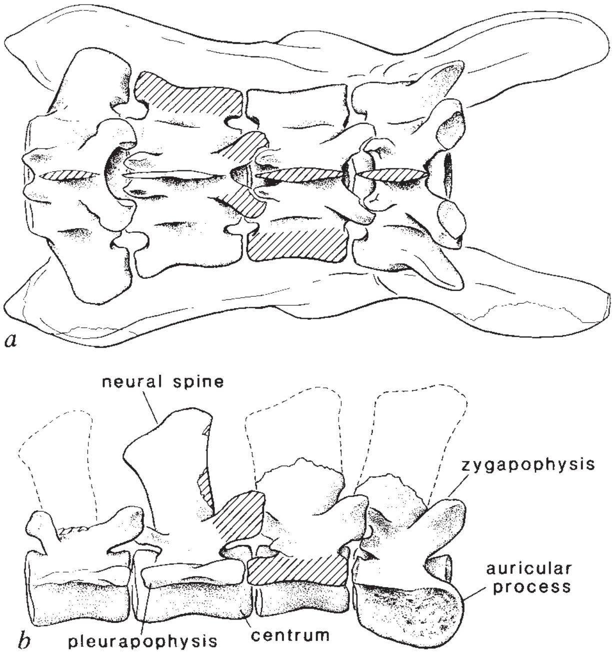


FIG. 3 Sacrum of *Rodhocetus kasrani*, GSP-UM 3012 (holotype), in *a*, dorsal view, superimposed on outline of pelvis, and *b*, right lateral view. Note well-developed pleurapophyses surrounding sacral foramina, but asynostosis of centra, neural spines, zygapophyses and pleurapophyses that are usually solidly fused in a mammalian sacrum. Tooth wear and fusion of vertebral epiphyses show specimen to be adult, so absence of fusion is not due to an early stage of ontogenetic development.

large central acetabulum is 13 mm deep. The ilium is conspicuously short compared with that of *Pachyaena*, indicating less powerful hip extension. The obturator foramen is large, measuring 67 mm in greatest diameter and 47 mm in least diameter. Pubes join at a short narrow symphysis. The pelvis of *Rodhocetus* articulates with the vertebral column by normal mammalian sacral synarthroses, meaning that *Rodhocetus* could support its body weight on land.

The femur of *R. kasrani* is only 60–70% as long as that in the similar-sized land mammal *P. ossifraga*[3] and early archaeocetes *Ambulocetus natans* and *I. ramani* (Table 1). The femoral head is large and spherical, with a deep fovea capitis femoris for the round ligament (lost in later whales[22]). The greater trochanter is slightly higher than the head. The lesser trochanter is large and medially directed. The intertrochanteric crest is well developed and encloses a deep trochanteric fossa. There is no third trochanter. The patellar groove is well developed. The lateral condyle is larger than the medial condyle, but both are large and project substantially from the body of the femur. Both condyles are directed posteriorly. Nothing is known of the rest of the hind limb.

Rodhocetus is important for three reasons. First, it is an early archaeocete that retains high neural spines on anterior thoracics and a pelvis articulating directly with the sacrum. These are primitive characteristics of mammals that support their weight on land, and both suggest that *Rodhocetus* or an immediate predecessor was still partly terrestrial. At the same time, cervicals are short, enhancing rigidity of the anterior body, sacrals are large but unfused, enhancing power and flexibility, and the femur is reduced, streamlining the lumbocaudal trunk. These are derived characteristics of later archaeocetes and modern whales associated with aquatic locomotion. Thus the morphology of *Rodhocetus* is intermediate, as might be expected of a transitional form evolving from land to sea.

Second, *Rodhocetus* is the oldest fossil whale described from deep-neritic shelf deposits. Contemporary and slightly younger whales such as *Indocetus*, which inhabited shallower water, retained long hind limbs and fused sacral vertebrae, indicating that there was significant morphological and locomotor diversity in early archaeocete evolution. Fossils found in shallow marine environments may not represent the full range of this diversity.

Finally, most modern whales have robust lumbar and proximal caudal centra, and all lack fusion of sacral vertebrae, making the lumbocaudal column seamlessly flexible. High dorsal neural spines and long ventral chevrons limit vertebral excursion but provide leverage for powerful axial and abdominal muscles[4–6]. *Rodhocetus* has all of these functional features. This indicates that the characteristic cetacean mode of swimming by dorsoventral oscillation of a heavily muscled tail evolved within the first three million years or so of the appearance of archaeocetes. Terminal caudals are lacking in the type specimen of *Rodhocetus* and we cannot assess the possible presence of a caudal fluke, but it is reasonable to expect development of a fluke to coincide with shortening of the neck, flexibility of the sacrum and reduction of hind limbs first observed in *Rodhocetus*. This idea can be tested when a more complete tail of *Rodhocetus* is found. □

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Interocular control of neuronal responsiveness in cat visual cortex

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NEURONS in the cat primary visual cortex are selective for particular contour orientations[1] but their responsiveness can vary under certain conditions. After prolonged stimulation (adaptation), the contrast sensitivity of cortical cells is reduced[2–5] and the 'gain' (the strength of response as a function of contrast) falls[5,6]. The response to an optimal contour is also reduced when a different stimulus is superimposed on the receptive field in the same eye[7–9]. Here we report that the sudden appearance of an inappropriate stimulus in one eye can interocularly suppress the activity of cortical neurons if they are already responding to an optimally oriented stimulus in the other eye. In strabismic cats, whose cortical neurons lack binocular facilitation, even contours of similar orientation shown to the two eyes trigger such suppression. This interocular control of cortical responsiveness could serve to veto signals from one eye under conditions that would otherwise cause double vision and perceptual confusion.

If both eyes are stimulated with contours of similar orientation, most neurons in the visual cortex of normal cats exhibit binocular summation or facilitation, as long as the relative location of the images on the two retinae (retinal disparity) is optimized: such interocular interactions are thought to play a part in binocular fusion and stereoscopic vision[10–12]. When human observers view conflicting stimuli in the two eyes they usually experience alternating perceptual suppression (binocular rivalry). However, for cortical neurons the response to an optimal stimulus in one eye is hardly affected when a stimulus of orthogonal orientation is presented simultaneously in the other eye[9,13].

We studied the orientation-dependence of binocular interaction in cat striate cortex with a new procedure in which a series of grating stimuli of different orientations were presented to one eye while the recorded neuron was continuously responding to an optimally oriented drifting grating presented to the other eye. For 42 of the 45 binocular neurons studied in five normal cats (see legend to Fig. 1), responses to the continuous 'conditioning' stimulus were significantly augmented, as expected, when the other eye was shown a stimulus matched in orientation to the optimal, as long as the spatial phase relationship between the two was appropriate (Fig. 1*a*), and such binocular facilitation decreased with increasing difference in orientation between the two eyes[14]. However, for most neurons (25 out of 45), the sudden introduction of a stimulus of orthogonal orientation significantly depressed the response to the optimal conditioning stimulus (Fig. 1*a*). We wondered whether the