Cortical Control of Sound Localization in the Cat: Unilateral Cooling Deactivation of 19 Cerebral Areas

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Malhotra, Shveta, Aimee J. Hall, and Stephen G. Lomber. Cortical control of sound localization in the cat: unilateral cooling deactivation of 19 cerebral areas. J Neurophysiol 92: 1625–1643, 2004; 10.1152/jn.01205.2003. We examined the ability of mature cats to accurately orient to, and approach, an acoustic stimulus during unilateral reversible cooling deactivation of primary auditory cortex (AI) or 1 of 18 other cerebral loci. After attending to a central visual stimulus, the cats learned to orient to a 100-ms broad-band, white-noise stimulus emitted from a central speaker or 1 of 12 peripheral sites (at 15° intervals) positioned along the horizontal plane. Twenty-eight cats had two to six cryoloops implanted over multiple cerebral loci. Within auditory cortex, unilateral deactivation of AI, the posterior auditory field (PAF) or the anterior ectosylvian sulcus (AES) resulted in orienting deficits throughout the contralateral field. However, unilateral deactivation of the anterior auditory field, the second auditory cortex, or the ventroposterior auditory field resulted in no deficits on the orienting task. In multisensory cortex, unilateral deactivation of neither ventral or dorsal posterior ectosylvian cortices nor anterior or posterior area 7 resulted in any deficits. No deficits were identified during unilateral cooling of the five visual regions flanking auditory or multisensory cortices: posterior or anterior ii suprasylvian sulcus, posterior suprasylvian sulcus or dorsal or ventral posterior suprasylvian gyrus. In motor cortex, we identified contralateral orienting deficits during unilateral cooling of lateral area 5 (SL) or medial area 6 (6m) but not medial area 5 or lateral area 6. In a control visual-orienting task, areas 5L and 6m also yielded deficits to visual stimuli presented in the contralateral field. Thus the sound-localization deficits identified during unilateral deactivation of area 5L or 6m were not unimodal and are most likely the result of motor rather than perceptual impairments. Overall, three regions in auditory cortex (AI, PAF, AES) are critical for accurate sound localization as assessed by orienting.

INTRODUCTION

Identifying the location of a sound source may determine whether an animal survives predation or starves. A current challenge in auditory neuroscience is the investigation of how the brain “creates” and processes auditory space to determine the location of a sound source (Middlebrooks 2002; Middlebrooks et al. 2002). In auditory cortex, previous studies have determined that primary auditory cortex (AI) is critical for accurate sound localization (Jenkins and Masterton 1982; Jenkins and Merzenich 1984). However, little is known about the functional organization of the higher auditory pathways (Rauschecker 1998a).

Previous behavioral studies in monkeys and cats have identified that unilateral ablations of the entire auditory cortex produce profound sound localization deficits (Beitel and Kaas 1993; Casseday and Diamond 1977; Heffner 1997; Whitfield et al. 1972). More restricted unilateral lesions, limited to AI, impair a cat’s ability to localize brief sounds in the contralateral field (Jenkins and Masterton 1982; Jenkins and Merzenich 1984). Unfortunately, on a behavioral level, no previous studies have examined the contribution of specific regions in non-AI cortex to sound-localization behavior (Middlebrooks 2002). Anatomical studies have implicated the auditory field in the anterior ectosylvian sulcus (AES) (Meredith and Clemo 1989) in auditory spatial processing due to its dense projection to the intermediate and deep layers of the superior colliculus (Meredith and Clemo 1989). Electrophysiological studies of AES find neurons with spatial selectivity (Korte and Rauschecker 1993; Middlebrooks et al. 1994; Nelken et al. 1997). The neurons in AES are very sensitive to features of sounds that are spatially informative and are less sensitive to sound features that are independent of spatial direction (Nelken et al. 1997). In addition, recent electrophysiological studies have identified neurons in the posterior auditory field (PAF) that show specificity for auditory stimulus location (Stecker et al. 2003b). Therefore both electrophysiological and anatomical investigations suggest that regions outside of AI, such as AES and PAF, may play a role in sound-localization behavior.

Based on these findings, we sought to test the hypothesis that, in addition to AI, specific regions of non-AI cortex may be involved in accurate sound-localization behavior. The goal of the present study was to examine the contributions that AI cortex and 18 other cortical loci make to sound localization behavior in the cat. We used orienting to an acoustic stimulus as a behavioral index for accurate sound localization and examined performance before, during, and after unilateral reversible cooling deactivation of each cortical locus (Lomber 1999). Overall, we identified that unilateral deactivation of areas AI, AES, or PAF in auditory cortex all produce unimodal orienting deficits to acoustic targets in the contralateral field.

METHODS

Overview

Twenty-eight adult domestic cats were obtained from a U.S. Department of Agriculture-licensed commercial laboratory animal-breeding facility (Liberty Labs, Waverly, NY) and housed in an “enriched” colony environment with water provided ad libitum. Caloric intake was restricted to the testing sessions and to 1 h at the conclusion of each day when the animals had free access to dry cat food (Purina cat chow). All procedures were conducted in agreement with the costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

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with the National Research Council’s Guidelines for the Care and Use of Mammals in Neuroscience and Behavioral Research (2003) and with the approval of the Animal Care and Use Committee of The University of Texas at Dallas.

After training on the orienting task, cooling loops were uni- or bilaterally implanted over multiple cortical loci. After cryoloop implantation, performance on the task was tested while all cortical loci were warm and active and while each region was unilaterally cooled and deactivated. Each of the 19 loci (Fig. 1) was examined in at least three different hemispheres in at least two cats (Table 1).

**Apparatus**

Training was conducted in an orienting arena very similar to that described by Stein et al. (1989), which allowed for the presentation of either acoustic or visual stimuli. The apparatus (Fig. 2) was a semi-circular arena (90 cm diam) that consisted of 13 pairs of miniature speakers and red, 2-V (DC) light-emitting diodes (LEDs). The speakers (No. 25RF006, Mouser Electronics, Mansfield, TX) were 2.5 cm in diameter with a frequency response of 500 Hz to 5 kHz. The speaker/LED combinations were mounted 15° apart along 180° of the azimuthal plane. The pairs were located 45 cm from the animal’s start position and positioned at cat’s eye level. A food-reward tray was located under each speaker/LED pair. The speakers emitted broad-band white-noise bursts (100 ms in duration) and were calibrated at 78 dB SPL using a prerecorded 1 kHz taped tone using the 1 kHz 1/3 band white-noise bursts (100 ms in duration) and were calibrated at 78 dB SPL using an Extech (Tampa, FL) datalogging light meter (No. 401036). Two individuals were required to conduct the experiments: the experimenter and the animal handler. The experimenter conducted the experiment, recorded the responses, and controlled the stimuli. In addition, the experimenter viewed a video monitor that displayed images from an overhead video camera that looked down on the apparatus and was used to determine the accuracy of the orienting response. Cooling deactivation sessions were videotaped. The videotaped responses were reviewed when the experimenter was unable to determine orienting position during testing. The animal handler was responsible for monitoring the animal and positioning it in the center of the apparatus and was blind to the stimulus presentation sequence.

**Behavioral training and task**

After acclimation to the testing apparatus, each cat was pretrained to stand in the center of the arena and orient and approach, theillumination of the red LED at the 0° position. A piece of low-incentive food was then presented from the reward tray below the stimulus. During training, the animal’s attention was attracted to the central LED, the LED was extinguished, and the sound was presented at 1 of the 12 peripheral speakers or the central speaker. After the animal approached the stimulus, it received the moist food reward from the food tray below the speakers. Any response other than a prompt direct approach to the appropriate stimulus was scored as incorrect. The cat was conditioned to approach the 0° position when an acoustic stimulus could not be localized and receive the low-incentive food. Premature responses were not scored and were unrewarded. Twenty-eight trials formed a block with each of the 12 peripheral positions tested twice and the central position tested four times. Five blocks of data were collected in each session for a total of 140 trials. Catch trials, where no secondary stimulus was presented, were randomly conducted. As a control, the animals were also trained to orient to a visual stimulus. The only difference in this procedure was that the secondary stimulus consisted of a flashed red 2-V (DC) LED. During the later stages of training and during testing, behavioral procedures remained the same although the cats wore a loose-fitting harness and a lightweight tether that supported the cooling tubes and microthermocouple wires. The tether, tubes, and wires were connected to a loop directly above the animal. Training was complete when a criterion performance level of 80% correct was reached on two consecutive days.

**Surgical procedures**

Cooling loops were implanted after training was complete. Cryoloops were fabricated by shaping loops of 23-gauge (0.635 mm
TABLE 1. Cerebral areas examined in 28 cats

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Cortical loci examined in both the left (L) and right (R) hemispheres indicated. AAF, anterior auditory field; AES, anterior ectosylvian sulcus; aMS and pMS, anterior and posterior middle suprasylvian sulcus; dPE and vPE, dorsal and ventral posterior ectosylvian gyrus; dPS and vPS, dorsal and ventral posterior suprasylvian gyrus; PAF, posterior auditory field; PS, posterior suprasylvian sulcus; AI and AII, primary and second auditory cortex; VPAF, ventral-PAF; 5L, 5m, 6L, 6m, lateral and medial areas 5 and 6, respectively; 7a and 7p, anterior and posterior area 7.

J Neurophysiol • VOL 92 • SEPTEMBER 2004 • www.jn.org
OD) stainless steel hypodermic tubing to conform to 1 of the 19 areas examined (Lomber et al. 1999). Prior to surgery, all loops were sterilized with ethylene oxide gas.

During the 24-h period before cooling-loop implantation, all cats were fasted and given an anti-inflammatory medication (dexamethasone, 1.0 mg/kg im). Eighteen hours prior to surgery each cat was sedated with ketamine (20 mg/kg im) and an indwelling feline catheter was inserted into a cephalic vein. To reduce respiratory and alimentary secretions, all animals were given additional dexamethasone and atropine (0.03 mg/kg sc) on the day of surgery. Cannulation of the cephalic vein permitted the administration of anesthetic and the infusion of fluids (2.5% dextrose and half-strength lactated Ringer solution). Pentobarbital sodium (~25 mg/kg to effect) was infused (intravenously) to induce general anesthesia. The animal was then installed in a stereotaxic apparatus and prepared for surgery using antiseptic procedures. Body temperature, respiration, and heart rates were continuously monitored. A midline incision was made in the scalp, and the temporalis muscles were detached medially and reflected laterally. Craniotomies were made over the desired regions, and the dura was incised and reflected to expose the cerebrum. Cryoloops were secured to the skull by using stainless steel skull screws and dental acrylic.

**Postoperative procedures and implant care**

At the conclusion of each major procedure, the dura was replaced or artificial dura, Gelfilm (The Upjohn, Kalamazoo, MI), was placed over the cerebrum. With the exception of where the tubes exited the skull, the previously removed skull piece was replaced. Additional acrylic was applied to secure the cooling loop and bone pieces. Dermal incisions were closed with 3-0 silk sutures that were removed 1 wk later. Buprenorphine analgesic (0.01 mg/kg im) was administered during the initial period after awakening. Decreasing doses of dexamethasone were administered over the next several days, and fluids (2.5% dextrose and half-strength lactated Ringer solution, 20 ml/kg sc) were infused as needed. The cats also received Ambi-pen systemic antibiotic (300,000 U im) for 1 wk to guard against any possible infection. The skin surrounding the implant was inspected daily for deterioration and any discoloration and Panalog (Squibb, Princeton, NJ) antibiotic ointment was applied prophylactically as needed.

**Behavioral testing and cooling deactivation**

After cooling-loop implantation and prior to any deactivations, baseline performance levels were reestablished. This was done to ensure that neither the surgical procedure nor the cryoloop itself interfered with performance. A three-step testing paradigm was used: collection of baseline data with all sites active (1 block), testing begins with the cooling of a cryoloop (3 blocks), and after completion of all cooling, baseline levels are reestablished (1 block). A typical daily testing session was ~1 h in duration. In total, for each cerebral area examined in every hemisphere, ≥24 trials were collected at each target locus both before and after cooling deactivation and ≥48 trials/locus were collected during cooling deactivation. During the testing procedure, the cats wore a harness and a tether that supported the thermocouple wire and the cooling tubes. Deactivation of individual cerebral areas was accomplished by pumping cold methanol through the lumen of the cryoloop tubing. Cryoloop temperature was also monitored through a microthermocouple attached to the union of the loop. Thermal measures were also used to obtain reasonable estimates of the extent of deactivated cortex. Each animal had two to six cryoloops (Table 1). As ~3 wk was necessary to assess each cryoloop, the animal’s were generally tested over a period of 2–5 mo.

For both orienting tasks, we calculated percent correct responses. Performance was assessed with a mixed ANOVA with one within hemisphere variable (warm vs. cold; locus of cooling loop). Orienting responses were assessed with multi-factor mixed ANOVA variables (warm vs. cold, azimuth, locus of cooling loop). The order of sessions was counter-balanced among areas (loops), functional states (active vs. deactivated), and hemispheres.
Radiolabeled 2-deoxyglucose administration and tissue processing

After completion of all behavioral studies, each cat received a systemic intravenous injection of \(^{14}\text{C}\)-2 deoxyglucose (2DG; 100 \(\mu\text{Ci/kg iv}\)) as described previously (Payne and Lomber 1999). One day prior to administration, a venous catheter was inserted into a cephalic vein. During 2DG administration, the animals were fully conscious to maximize uptake. The cats were comfortably restrained in a veterinary cat sack, and the inlet and outlet tubes of the cryoloop(s) were connected to the cooling circuit. In each cat, a single loop was deactivated or two loops (1 in each hemisphere) over heterotopic loci were cooled. After temperature stabilization (~5 min), the first of four boluses of 100 \(\mu\text{Ci/kg}\) of 2-deoxy-\(d\)-[\(\text{U-14C}\)] glucose was administered. The remaining boluses were injected at 5-min intervals. Ten minutes after the final injection, heparin (2,000 U/kg iv) and sodium nitrite (1 ml of 0.1% solution, intravenously) were administered, and the cat was deeply anesthetized with pentobarbital sodium (40 mg/kg iv) and perfused with fixatives in accordance with the recommendations of the American Veterinary Medical Association Panel on Euthanasia (Beaver et al. 2001). The brain was quickly exposed, (~4 min), removed from the skull, blocked, and photographed. The brain was coated with egg albumin and placed in methylbutane (~35°C). After 30 min, the brain was transferred to a −80°C freezer for subsequent tissue processing.

The brains were sectioned in a cryostat (~20°C) at 35 \(\mu\text{m}\), and every fifth section was collected on coverslips. Hemispheres that contained PAF, ventral-PAF (VPAF), or dorsal (dPE) or ventral (vPE) posterior ectosylvian gyrus cooling loops were cut in the horizontal plane (Fig. 3), while all other hemispheres were cut in the coronal plane. Dried sections were applied to X-ray film and processed using routine procedures (Payne and Lomber 1999). The extent of the

**FIG. 3.** Representative cooling deactivation reconstructions for 8 loci examined. A, B, D, F, and H: each reconstruction shows a lateral (left is anterior) and dorsal (top is anterior) view of the left hemisphere with 3 coronal sections in the vicinity of the deactivation locus. C and E: deactivation reconstructions showing a lateral (left is anterior) view of the left hemisphere with 3 horizontal sections in the vicinity of the locus. G: deactivation reconstruction showing a medial (right is anterior) and dorsal (top is anterior) view of the left hemisphere with 3 coronal sections in the vicinity of the deactivation locus. Blackened region, the extent of the cooling-induced deactivation, as assessed by severely reduced \(^{14}\text{C}\)-2 deoxyglucose (2DG) uptake (~25% reduction). These standardized drawings are adaptations from Reinoso-Suárez (1961). Cr, cruciate sulcus; ss, suprasylvian sulcus; aes, anterior ectosylvian sulcus; pes, posterior ectosylvian sulcus.
deactivated area was then determined by delineating the region of decreased 2DG uptake. Cooling-induced decreases in 2DG uptake are obvious (Payne and Lomber 1999) and only require imaging equipment to assay the gradients on the fringes of the deactivation. For these purposes, we used an MCID Elite imaging-analysis system (Imaging Research, St. Catharines, Ontario, Canada). The borders of the region of decreased 2DG uptake (>25% reduction) were determined by standardizing the brains with 1°C standards (Amersham, Arlington Heights, IL) and calibration curves (Gonzalez-Lima 1992) and correlating the region with the similar site from a population of normal, nondeactivated brains that were not part of this study. The results from these analyses are provided in Fig. 3.

Every fifth section was processed histochemically for the presence of cytochrome oxidase by exposing the sections to 200 mg of 3,3′-diaminobenzidine and 100 mg of horse heart cytochrome-C in 300 ml of a phosphate-buffered solution (pH = 7.4) for 7–8 h at 21°C as we have done in the past (Payne and Lomber 1996). Adjacent sections were stained using conventional methods for the presence of Nissl bodies.

Cerebral areas investigated

We used reversible cooling deactivation (Lomber et al. 1999) to examine the contributions that the 19 individual regions of cortex made to acoustically mediated orienting. The positions of the different loci are described in the following text.

AUDITORY REGIONS. We examined six regions within the auditory cortex: the AI, the PAF, the anterior auditory field (AAF), the second auditory cortex (AII), the VPAF, and the AES. The AI loops were 6 mm long and extended lengthwise across the middle ectosylvian gyrus, from the dorsal tip of the AES to just posterior of the posterior ectosylvian sulcus (about A4–A10) (Reale and Imig 1980) (Fig. 1). Cryoloops were also placed on PAF, located caudal and ventral to AI. Loops were ~6 mm long and extended from the anterior one-third of the dPE to the fundus of the dorsal half of the posterior ectosylvian (PE) sulcus. At this location, the PE sulcus is ~2.5 mm deep. The AAF cryoloops were ~6.5 mm long and were located on the crown of the anterior suprasylvian gyrus between A11 and A17.5. Loops ~6 × 3 mm were placed on AII, which lies ventral to AI and extends between the AES and posterior ectosylvian sulcus (Reale and Imig 1980). Loops ~8 mm long were also placed on VPAF. These loops extended from the anterior one-third of the PE and extended to the fundus of the PE. A heat-shielding compound was also applied to the anterior side of the PAF and VPAF loops to keep the cooling deactivations localized to the posterior bank of the posterior ectosylvian sulcus. Finally, the auditory field contained in AES occupies a region at the posterior end of the AES with the largest portion of the field located on the dorsal bank and fundus (Clarey and Irvine 1986; Meredith and Clemo 1989; Mucke et al. 1982). Loops ~6 × 3 mm were placed in the posterior two-thirds of the AES where both the auditory and visual representations are located (Rauschecker et al. 1997). Therefore placement of the AES cooling loops was similar to loops implanted by others (Jiang et al. 2001, 2002).

MULTISENSORY REGIONS. We examined four regions that we classified as multisensory: the vPE, dPE, and anterior and posterior area 7 (7a and 7p). On the ectosylvian gyrus, Bowman and Olson (1988a,b) described adjacent auditory and visual “belts” extending along the central and posterior thirds of the posterior ectosylvian (PE) gyrus, respectively. To test if these belts have any role in orienting, we subdivided the region into a ventral and a dorsal half and placed more vertically oriented, 3 × 8 mm cooling loops over each region (Fig. 1). The crown of the middle suprasylvian gyrus, between areas 21a and 5 corresponds to area 7 (Hassler and Muhs-Clement 1964; Olson and Lawler 1987). We further subdivided area 7 into posterior (7p) and anterior (7a) portions. Cooling loops were placed between P1–A6 and A6–A13 to cool areas 7p and 7a, respectively.

VISUAL REGIONS. We examined five regions that were located within the suprasylvian sulcus and gyrus: the posterior (pMS) and anterior (aMS) regions of the middle suprasylvian sulcus, the posterior suprasylvian sulcus (PS), and the dorsal (dPS) and ventral (vPS) posterior suprasylvian gyrus. The pMS sulcal loops were ~9 mm long and extended in the middle suprasylvian sulcus from P2 to A7. The aMS sulcal loops were ~9 mm long and placed in the middle suprasylvian sulcus from A6 to A15. Loops were also placed in the PS to deactivate both the anterior and posterior banks. The dorsal and ventral halves of the PS gyrus were also examined. The vPS includes the majority of areas 20a and 20b (Tusa and Palmer 1980), and the dPS includes the entire posterior bend of the suprasylvian gyrus. Both vPS and dPS cryoloops had unusual shapes; a “T” and an “L,” respectively.

MOTOR REGIONS. We also examined four motor areas: lateral and medial divisions of area 5 and lateral and medial divisions of area 6. Area 5 extends from the anterior splenial sulcus, across the lateral sulcus, to the anterior suprasylvian sulcus (Avendaño et al. 1985; Ghosh 1997b). We subdivided area 5 into lateral and medial portions using the lateral sulcus. The medial portion includes area 5 (5m) of the anterior marginal gyrus and the lateral portion includes area 5 (5L) of the anterior suprasylvian gyrus. We also examined the lateral and medial portions of area 6. Cooling loops were placed anteriorly along the ventral bank of the cruciate sulcus for the lateral portion of area 6 (5L) and placed on the midline for medial area 6 (6m).

RESULTS

Cortical structure

For each of the deactivated cortical sites, the cytoarchitecture of Nissl-stained sections was characteristic of healthy cortex (Ghosh 1997a; Sanides and Hoffman 1969). We could find no evidence of physical damage, gliosis or necrosis. Moreover, there was no alteration in cytochrome oxidase histochemistry. Therefore neither the presence of the cryoloops nor their repeated deactivation over several months altered the structure or long-term function of the 19 cortical sites assayed. The only evidence of the presence of the cryoloops was that some sulci were slightly wider than normal and in some cases, small indentations in sulcal walls or gyral surfaces that conformed to the curvature of the loop tubing could be identified. These depressions were shallow and have been illustrated elsewhere (Lomber and Payne 1996, 2000).

Cooling deactivations

Examples of the deactivations of eight of the loci examined are illustrated in Fig. 3. The extent of the deactivation was determined from 2DG radiograms, and regions showing greatly reduced 2DG uptake, compared with surrounding structures, are indicated in black on diagrams of the whole brain and in coronal or horizontal sections. All regions of deactivation were highly circumscribed and extended beyond the perimeter of the loops by 1–1.5 mm. Loops inserted into the AES (e.g., Fig. 3F) deactivated both banks, whereas PAF and VPAF loops (Fig. 3, C and E) only deactivated the posterior bank of the AES. Gyral loops deactivated exposed surfaces, although they could include cortex bounding the entrances to sulci (e.g., Fig. 3, A and D). Representative reconstructions from the 11 other loci examined are provided in other publications (Lomber and Payne 2000, 2001, 2004).
Behavioral controls: pre/post warm versus rewarm

Prior to cooling-loop implantation, all cats were highly proficient at orienting to the acoustic stimulus at all positions (Fig. 4A). After cryoloop implantation, orienting performance levels were virtually identical to preimplantation response levels (Fig. 4B). The absence of any discernible differences between pre- and postimplantation performance levels shows that neither the cryoloop-implantation surgery nor the chronic presence of the cooling loops had any impact on orienting behavior (compare Fig. 4, A with B). Similarly, after the cessation of cooling, orienting responses to every position throughout the acoustic field returned to prior levels (Fig. 4C). This result indicates that the repeated daily deactivation of any of the cortical loci, over a period of several months, had no impact on the ability to orient to acoustic stimuli presented at new loci. Furthermore this result permitted us to combine the data collected prior to and after cooling deactivation and consider it normative (control) data.

![Diagram of orienting responses](Image)

**FIG. 4.** Orienting responses to an acoustic stimulus by cat 27. A: prior to bilateral cooling-loop implantation. B: after cryoloop implantation during the precooling (warm) portion of daily testing. C: during the postcooling (rewarm) portion of daily testing. Two concentric semicircles represent 50 and 100% response levels, and the length of each bold line corresponds to the percentage of correct responses at each location tested. Note that neither the presence of cooling loops (B), nor the repeated daily deactivations (C), altered performance.

Laterization of function

Each of the 19 loci studied was examined in at least three hemispheres (Table 1). Of these three hemispheres, two were located in the right hemisphere and one was located in the left hemisphere. This experimental configuration permitted us to test for any possible hemispheric asymmetries in cooling impact and determine if there was any evidence for lateralization of function for this behavior in the cat (Fig. 5). For each of the 19 cortical loci examined, we were unable to find any evidence of functional lateralization on the acoustically mediated orienting task. For example, cooling of left AI resulted in a reduction in accurate orienting responses in the contralateral field from $94.6 \pm 1.9$ to $13.6 \pm 3.5\%$ (compare Fig. 5, A with B). Similarly, deactivation of right AI resulted in a reduction in accurate orienting responses in the contralateral field from $92.1 \pm 2.4$ to $12.4 \pm 4.3\%$ (compare Fig. 5, A with C). This null result permitted us to combine blocks of trials obtained during cooling of the paired loci in the right or left hemispheres. Therefore for convenience of presentation and comparison, we combined data from the left and right deactivations and present them using the convention of left hemisphere deactivation.

Auditory regions

**EXTENT OF DEACTIVATIONS.** Cooling of the AI cryoloops deactivated a large region of the middle ectosylvian gyrus from A3 to A10 (Fig. 3A). This region included nearly all of the classically defined area A1 (Reale and Imig 1980), the dorsal zone of AI (Middlebrooks and Zook 1983), and portions of the suprasylvian fringe (Beneyto et al. 1998; Paula-Barbosa et al. 1975; Woolsey 1960). Cooling of the AII cryoloops deactivated a swath of cortex across the middle ectosylvian gyrus, ventral to AI, between the AES and posterior ectosylvian sulcus (Fig. 3B). This region was 8 mm long and 5 mm wide. Cooling of the PAF cryoloops deactivated a region of the anterior-dPE, just posterior to the posterior ectosylvian sulcus (Fig. 3C). The deactivation extended down the posterior bank of the posterior ectosylvian sulcus to the fundus (Fig. 3C). The deactivation did not include the anterior bank of the sulcus. Therefore this region deactivated all of area PAF or area P, as defined by Imig et al. (1982). Cooling of the AAF cryoloops deactivated much of the anterior ectosylvian gyrus between A12 and A19 (Fig. 3D). The deactivation included the dorsal half of the lateral bank of the anterior suprasylvian sulcus and the dorsal half of the medial bank of the AES. Therefore this region deactivated all of area AAF or area A, as defined by Knight (1977) and Reale and Imig (1980). Finally, cooling of the VPAF cryoloops deactivated a region of the anterior-vPE, just posterior to the posterior ectosylvian gyrus (Fig. 3E). The deactivation extended down the posterior bank of the posterior ectosylvian sulcus to the fundus (Fig. 3E). The deactivation did not include the anterior bank of the sulcus. Therefore this region deactivated all of area VP, as defined by Imig et al. (1982). Cooling of the AES loops deactivated the fundus and both the ventral and dorsal banks of the posterior two-thirds of the AES (Fig. 3F). The anterior end of the sulcus was not directly affected by the cooling. Therefore cooling of this region silenced the acoustically responsive field of the AES (Clarey and Irvine 1986; Meredith and Clemo 1989; Mucke et
al. 1982) and portions of SIV, dorsally (Mori et al. 1996), and the orbito-insular area, ventrally (Clasca et al. 2000).

**BEHAVIOR.** Unilateral deactivation of A1 virtually abolished accurate orienting to sound presented in the contracooled hemifield (16.7 ± 4.1% correct responses; Fig. 6A, i; 5 cats, 9 hemispheres). This compared with control levels of 88.3 ± 2.9% correct (Fig. 6A, ii) for the same hemifield prior to and after cooling. Orienting into the ipsilateral hemifield was uniformly high (control: 86.5 ± 3.3% correct; deactivation: 85.9 ± 2.1% correct; Fig. 6A). Unilateral deactivation of the PAF resulted in the same type of contralateral deficit (14.4 ± 4.9% correct responses; Fig. 6B, ii; 3 cats, 6 hemispheres). This compared with control levels of 84.3 ± 2.1% correct (Fig. 6B, i) for the same hemifield prior to and after cooling. Orienting into the ipsilateral hemifield was also uniformly high (control: 85.2 ± 3.5% correct; deactivation: 82.7 ± 4.3% correct; Fig. 6B). Orienting responses to acoustic stimuli were unimpaired by cooling deactivation of the AAF (Fig. 6C; 2 cats, 4 hemispheres), AII (Fig. 6D; 3 cats, 5 hemispheres), and VPAF (Fig. 6E; 2 cats, 3 hemispheres). Unilateral deactivation of the AES virtually abolished accurate orienting to acoustic stimuli presented in the contracooled hemifield (24.5 ± 5.6% correct responses; Fig. 6F, ii; 5 cats, 9 hemispheres). This compared with control levels of 90.1 ± 3.5% correct (Fig. 6F, i) for the same hemifield prior to and after cooling. However, during unilateral cooling deactivation of AES, orienting into the ipsilateral hemifield was uniformly high (control: 87.8 ± 2.3% correct; deactivation: 88.1 ± 1.9% correct; Fig. 6F).

**Multisensory regions**

**EXTENT OF DEACTIVATIONS.** Cooling of the vPE loop deactivated a 5 × 10-mm region on the posterior half of the vPE. Cooling of the dPE cooling loop deactivated a 5 × 12-mm region at the posterior bend of the ectosylvian gyrus. Neither deactivation spread into the PS sulcus. Cooling of the area 7a cryoloop deactivated the anterior-central region of the MS gyrus between A5 and A14. This deactivated region was also slightly asymmetric in the medial direction. Unilateral cooling of the area 7p loop deactivated the posterior-central region of the crown of MS gyrus between P2 and A7. The deactivation did not spread to the medial bank of the MS sulcus but did spread medially, ~1.5 mm down the lateral bank of the lateral sulcus.

**BEHAVIOR.** Orienting in response to acoustic stimuli was unimpaired by cooling deactivation of ventral (Fig. 7A; 2 cats, 4 hemispheres) and dorsal PE gyrus (Fig. 7B; 4 cats, 6 hemispheres) and both areas 7a (Fig. 7C; 4 cats, 8 hemispheres) and 7p (Fig. 7D; 2 cats, 4 hemispheres).

**Visual regions**

**EXTENT OF DEACTIVATIONS.** Cooling of the pMS loops deactivated a region that extended from approximately coronal level P3 to A8 and included both banks of the sulcus. Therefore this region included areas posteromedial (PMLS) and -lateral (PLLS) lateral suprasylvian, dorsal-most dorsolateral suprasylvian visual area (DLS), the posterior portion of areas anteromedial (AMLS) and -lateral (ALLS) lateral suprasylvian (Palmer et al. 1978), and all of lateral suprasylvian visual area.
FIG. 6. Orienting responses to a sound before and after (i) and during (ii) unilateral cooling deactivation of 6 areas of auditory cortex: AI (A), PAF (B), AAF (C), AII (D), VPAF (E), and AES (F). Bottom: icons of medial and lateral views of cat brain. ■, site and extent of deactivation. Data summarized for the following numbers of sites and animals: A, 9 hemispheres in 5 cats; B, 6 hemispheres in 3 cats; C, 4 hemispheres in 2 cats; D, 5 hemispheres in 3 cats; E, 3 hemispheres in 2 cats; F, 9 hemispheres in 5 cats. Note that deactivation of AI, PAF, or AES resulted in a contralateral, but not ipsilateral, orienting deficit. Conventions apply to similar subsequent figures.
(LS) and posterior ectosylvian visual area (PEV) [from the nomenclature of Grant and Shipp (1991) for the same region]. Cooling the aMS cryoloops included the anterior middle suprasylvian and middle ectosylvian cortices that contribute to the medial and lateral banks of the middle suprasylvian sulcus from approximately A5 to A16. This region corresponds to areas AMLS and ALLS and the anterior portion of areas PMLS and PLLS (Palmer et al. 1978). Cooling of the PS cryoloops deactivated both the anterior and posterior banks of the posterior suprasylvian sulcus, which include areas DLS and VLS of Palmer et al. (1978). The deactivation did not extend to the ventral end of the sulcus, resulting in only a small region of area PS (Updyke 1986) being deactivated. Cooling of the dPS loops deactivated the dorsal portion of the posterior suprasyl-
vian gyrus and the posterior bend of the suprasylvian gyrus. This region included area 21a (Tusa and Palmer 1980) and the central-vision representation of area 19 (Tusa et al. 1979). Cooling of the vPS cryoloops deactivated the ventral portion of the PS gyrus including most of areas 20a and 20b (Tusa and Palmer 1980) and portions of area PS (Updyke 1986).

Behavior. For the sound-localization task, no deficits were identified during unilateral deactivation of any of the five visual cortical regions examined (Fig. 8, A–E).

**Motor regions**

Extent of Deactivations. Cooling of the area 5L loop deactivated a 5 × 9-mm region on the crown of the anterior marginal gyrus (Fig. 3H). This region included the dorsal-most aspect of the suprasylvian sulcus and the lip of the lateral sulcus. Therefore the area 5L loops deactivated all of area 5L (Avendano et al. 1985; Ghosh 1997b) and portions of SHR (Garraghty et al. 1987) and the gyral portion of SV (Mori et al. 1991-1996). Cooling of the area 5m loop deactivated a 5 × 12-mm swath of cortex of the dorsal surface of the cerebrum extending medially from the lateral sulcus, over the marginal gyrus, and descended down the medial aspect of the hemisphere ending 2 mm superior to the cruciate sulcus. Cooling of the area 6L cryoloop deactivated an anteromedial region of the cerebrum (5 × 8 mm) running anteriorly along the ventral bank of the cruciate sulcus. Cooling of the 6m cooling loops deactivated a 4 × 8-mm region of deactivation on the medial surface of the hemisphere along the ventral bank of the cruciate sulcus (Fig. 3G).

Behavior. Unilateral deactivation of 5L virtually abolished accurate orienting to sounds in the contracooled hemifield (17.3 ± 4.8% correct responses; Fig. 9A, ii; 3 cats, 5 hemispheres). This compared with control levels of 88.1 ± 3.3% correct (Fig. 9A, i) for the same hemifield prior to and after cooling. Once again, however, during unilateral cooling deactivation of 5L, orienting into the ipsilateral hemifield was uniformly high (control: 90.6 ± 2.5% correct; deactivation: 86.6 ± 3.9% correct; Fig. 9A). Orienting responses to acoustic stimuli were also impaired during deactivation of 6m (16.7 ± 3.9% correct responses; Fig. 9D, ii; 5 cats, 8 hemispheres). This compared with control levels of 84.6 ± 4.3% correct (Fig. 9D, i) for the same hemifield prior to and after cooling. Orienting into the ipsilateral hemifield was uniformly high (control: 82.4 ± 3.1% correct; deactivation: 84.2 ± 2.8% correct; Fig. 9D, ii). Orienting responses to sounds were unimpaired during deactivation of 5m (Fig. 9B; 3 cats, 6 hemispheres) and 6L (Fig. 9C; 3 cats, 6 hemispheres).

Orienting accuracy

During unilateral deactivation of areas AI, PAF, AES, 5L, and 6m, there was a profound reduction in orienting accuracy to an acoustic stimulus when it was presented in the contralateral hemifield. Prior to cooling deactivation, the animals had previously been trained to report to the central (0°) position when they were unable to detect and localize the sound source. However, in actuality, when the animals did not respond to the correct sound localization, they seldom went to the central position. Instead, we found that the animals made responses to incorrect speaker locations. Plots of the animals’ accuracy before and during cooling deactivation of these five loci are provided in Fig. 10. In general, responses to the target location were highly accurate before and after cooling deactivation (Fig. 10, top). For both hemifields, these responses ranged between 82 and 90% accurate. However, during unilateral cooling deactivation (Fig. 10, bottom), accuracy dropped to between 14 and 24% accurate throughout the contralateral hemifield. For areas AI, PAF, and AES, inaccurate responses were both undershoots and overshoots of the target position (Fig. 10, A–C, bottom, contralateral field). For the two regions of motor cortex that produced orienting deficits to sounds, all inaccurate responses were undershoots (Fig. 10, D and E, bottom, contralateral field). Therefore these results seem to suggest that the impairment revealed during cooling of the two motor regions (areas 5L and 6m) is fundamentally different from the deficits revealed during deactivation of the three auditory regions (AI, PAF, AES).

Orienting to visual stimuli

Orienting to visual stimuli was also examined during deactivation of the five regions that resulted in deficits in orienting to acoustic stimuli. Unilateral deactivation of none of the sites in auditory (AI, AES, or PAF) cortex resulted in any significant changes in orienting to visual targets in either the contralateral or ipsilateral visual fields (Fig. 11, A–C). In contrast, deactivation of both sites in motor cortex resulted in profound orienting deficits to visual targets presented in the contralateral hemifield (Fig. 11, D and E, ii). During unilateral deactivation of area 5L, orienting accuracy in the contralateral hemifield fell from 89.8 ± 3.6% correct (Fig. 11D, i) to 0.0% correct (Fig. 11D, ii). Similarly, during unilateral deactivation of area 6m, orienting accuracy in the contralateral hemifield dropped from 81.1 ± 3.6% correct (Fig. 11E, i) to 0.0% correct (Fig. 11E, ii). Additionally, and in contrast to the effects in the ipsilateral field during cooling of areas 5L and 6m on the aural orienting task (Fig. 9, A and D), accuracy in orienting to visual targets actually improved in the ipsilateral field during unilateral cooling deactivation. During unilateral deactivation of area 5L, orienting accuracy to visual targets in the ipsilateral hemifield rose from 85.3 ± 1.7% correct (Fig. 11D, i) to 99.3 ± 0.7% correct (Fig. 11D, ii). Similarly, during unilateral deactivation of area 6m, orienting accuracy to visual targets in the ipsilateral hemifield increased from 86.6 ± 1.8% correct (Fig. 11E, i) to 98.7 ± 1.3% correct (Fig. 11E, ii). In conclusion, unilateral deactivation of either areas 5L or 6m results in orienting deficits in the contralateral field to either acoustic or visual targets.

Discussion

In this study, we systematically examined the contributions of 19 regions of the cat cerebrum to accurate orienting to an acoustic stimulus. Overall, we identified five regions that contribute to acoustically-mediated orienting. These regions include AI, PAF, AES, 5L, and 6m (Fig. 12). However, our control task, which examined orienting to visual stimuli, re-
revealed that not all of these areas are specialized for mediating orienting to only acoustic targets. In the visual-target task, deactivation of either area 5L or 6m yielded profound orienting deficits to static visual targets presented in the contralateral field. These deficits are in accord with our other orienting studies using moving visual targets (Lomber and Payne 2004). In contrast, deactivation of AI, PAF, or AES did not result in any deficits on the visual target task. Taken together, the...
deficits identified during area 5L or 6m deactivation are likely to be motor deficits, due to the nonmodal specific impairments (both acoustic and visual deficits), whereas the deficits identified during AI, PAF, and AES deactivation were unique to acoustic stimuli. Based on these findings, we will focus the discussion of these results on areas AI, PAF, and AES.
AI

Virtually all previous behavioral work on sound localization in the cat has focused on AI (Beitel and Kaas 1993; Casseday and Diamond 1977; Jenkins and Masterton 1982; Jenkins and Merzenich 1984; Whitfield et al. 1972). In these studies, unilateral destruction of AI resulted in profound sound localization deficits to targets presented in the contralateral field. Therefore the present findings of our study, using reversible cooling deactivation of AI, are in agreement with previous work. In addition to the cat, severe localization deficits to acoustic stimuli presented in the contralateral field after destruction of AI have also been identified in ferrets and monkeys (Heffner 1997; Kavanagh and Kelly 1987). Jenkins and Merzenich (1984) further defined spatial location functions within AI by making small unilateral cortical lesions limited to particular frequency bands. After the ablations, cats could not localize brief tones presented at frequencies destroyed by the lesion within the contralateral hemifield (a frequency-dependent contralateral deficit). However, sound localization remained normal within the ipsilateral hemifield and in the contralateral field to frequencies unaffected by the lesion (Jenkins and Merzenich 1984).

Although deficits can be localized to individual frequency bands within AI, another subdivision of AI that needs to be behaviorally investigated for a possible role in sound localization is the dorsal zone (DZ) of AI. DZ extends from the dorsal margin of AI into the ventral bank of the suprasylvian sulcus (Middlebrooks and Zook 1983). This region contains neurons with a high degree of spatial tuning and a strong modulation of latencies by source location (Stecker et al. 2003a). In total, DZ neurons seem to possess the qualities necessary for spatial localization. In our present study, deactivations of AI included both AI proper and DZ. Therefore it was not possible for us to determine whether the contralateral spatial localization deficits were specifically due to deactivation of AI, DZ, the adjacent suprasylvian fringe, or combinations of all.

PAF

Within non-AI, unilateral cooling deactivation of PAF yielded contralateral orienting deficits. PAF contains a tonotopic map (Reale and Imig 1980) and receives the majority of its thalamic input from the ventral division of the medial genulate nucleus (MGN), with lesser projections from the medial and dorsal divisions of MGN (Huang and Winer 2000; Morel and Imig 1987). Neurons in PAF seem to be uniquely suited to perform spatial localization functions as they are capable of complex tuning characteristics (Heil and Irvine 1998; Loftus and Sutter 2001), they respond at significantly longer latencies than other fields (Phillips and Orman 1984; Phillips et al. 1995; Stecker et al. 2003b), and their latencies vary strongly with stimulus location (Stecker et al. 2003b). Given these neuron attributes, it was not surprising that unilateral deactivation of PAF results in profound spatial localization deficits at a behavioral level.

AES

With respect to behavioral investigations, following AI, AES is probably the most extensively examined region of acoustically-responsive cortex. AES contains adjacent sensory fields, with some overlap, that are responsive to visual ( Olson and Graybiel 1987), auditory (Clarey and Irvine 1986) or somatosensory (Clemo and Stein 1982) stimuli (Rauschecker 1995). Previous studies have extensively examined the role that AES plays in multisensory integration and its contribution to processing in the superior colliculus (Jiang et al. 2001; Wallace et al. 1993). AES would be expected to have a significant influence over the superior colliculus (SC) due to the dense projections arising from AES that terminate in the SC (Harting et al. 1992; Meredith and Clemo 1989; Tortello et al. 1980). Previous behavioral studies have shown that deactivation of AES produces orienting deficits to visual and acoustic stimuli simultaneously presented at positions in the contralateral field (Jiang et al. 2002; Wilkinson et al. 1996). However, neither study identified deficits to unimodal visual nor acoustic stimuli presented in the contralateral field. Therefore our present findings appear discordant with earlier studies (Jiang et al. 2002; Wilkinson et al. 1996). The studies of Wilkinson et al. (1996) used stimuli that operationally reduced auditory stimulus intensity to near threshold levels (45-55dB SPL) for the testing room. Subsequent deactivation of AES cortex disrupted multisensory and behavior responses to combined visual and auditory stimuli but did not appear to render the unimodal auditory stimuli any more ambiguous than they already were (Jiang et al. 2002). Furthermore, Meredith and Clemo (1989) showed that cooling deactivation of the auditory field of AES resulted in only a minor increase in threshold for acoustically responsive neurons in the SC but did not eliminate auditory responses. Thus there appears to be a conflict between our present findings and the earlier published observations that does not appear to be resolvable at the present time. However, in agreement with our findings, earlier studies have failed to identify visually mediated orienting deficits during AES deactivation (Jiang et al. 2002; Lomber and Payne 2004; Wilkinson et al. 1996).

Corticoretectal influences

The SC plays a key role in orienting of the head and eyes to visual or acoustic stimuli (Apter 1946; Hess et al. 1946; Lomber et al. 2001; Sprague and Meikle 1965). Internally, the SC can be divided into superficial and deeper layers (Kanaseki and Sprague 1974) with the superficial layers connected almost exclusively to visual structures (Graybiel 1975; Harting and Guillery 1976; Harting et al. 1992), whereas deeper layers receive afferents from visual, auditory, and somatosensory cortices (Clemo and Stein 1984; Harting et al. 1992; Meredith and Clemo 1989; Tortello et al. 1980) as well as brain stem sources (King et al. 1998). Accordingly, superficial layer neurons are exclusively visual, whereas deeper neurons respond to visual, acoustic, and somatosensory stimuli, and many respond

FIG. 10. Spatial localization accuracy to the acoustic target from the 5 sites that yielded orienting deficits during unilateral deactivation. Target position is indicated on the x axis (negative values indicate left hemifield). Orienting response is indicated by the y axis. Area of the circle at each position indicates the percentage of correct responses. Top: accuracy in both hemifields before and after unilateral (left) cooling deactivation. Note the excellent performance, with nearly all responses to the correct position. Bottom: accuracy in the left (negative target loci) and right (positive target loci) hemifields during left cooling deactivation. Note excellent performance in the left (ipsilateral) field and inaccurate performance in the right (contralateral) hemifield.
to more than one modality (Meredith and Stein 1986; Peck 1990; Stein et al. 1976; Wallace et al. 1993). Furthermore, visual space has been identified to be mapped in both the superficial (Feldon et al. 1970) and deep (Meredith and Stein 1990) layers of the SC, whereas auditory space is only mapped in the deeper layers (Middlebrooks and Knudsen 1984; Palmer
and King 1982). Therefore it is often presumed that a cerebral region involved with the spatial localization of acoustic stimuli should have strong projections to the SC. Indeed, this is true of AES but does not seem to be the case for either AI or PAF (Meredith and Clemo 1989). Therefore the present findings seem to suggest two alternative explanations of how AI and PAF may be involved in spatial localization. First, output from AI and PAF may require the involvement of at least one other cerebral area prior to the passing of their signals to the SC. Presumably, areas AI and PAF would have to output to a region that has strong projections to the SC, like AES. A second possibility is that areas AI and PAF do not involve the SC in the accurate guidance of the head and eyes to an acoustic target. In this scenario, areas AI and PAF may bypass the SC and project directly to the brain stem (Chiba 1980). However, we expect that it is most likely that signals emanating from AI or PAF gain access to brain stem motor centers by means of projections to AES then onto the SC and the brain stem in turn.

"Where" processing system?

Similar to the visual system, the auditory system must deal with the perceptual problem of determining the spatial location of a stimulus. Visual information in extrastriate visual cortex has been proposed to be processed by two “parallel” cortical streams originating from primary visual cortex (Mishkin et al. 1983; Ungerleider and Mishkin 1982). A dorsal (“where”) stream has been implicated in spatial and motion processing, whereas a ventral (“what”) stream has been identified to process object and pattern discrimination functions. A similar segregation of sensory processing has also been proposed in non-AI of the monkey with a where stream for processing sound-source localization and a what stream for identifying auditory patterns based on the spectral and temporal characteristics of sound (Rauschecker 1998b; Rauschecker and Tian 2000; Rauschecker et al. 1997).

In the cat, we have demonstrated that what and where processing in non-AI can be doubly dissociated between the AAF and PAF, respectively (Lomber and Malhotra 2003). In light of the present study, the cerebral regions involved in spatial localization clearly involve more than one region of auditory cortex. Therefore while it is possible to dissociate what and where processing regions in auditory cortex of the cat (Lomber and Malhotra 2003), it is likely that spatial localization involves a network of cerebral regions working in concert as proposed by others (Hall 2003; Middlebrooks 2002; Middlebrooks et al. 2002; Zatorre et al. 2002).

FIG. 12. Summary of cortical loci that produce a contralateral orienting deficit during unilateral cooling deactivation (12). Medial (left) and lateral (right) views of the left hemisphere originally displayed in Fig. 1. During independent unilateral deactivation, 3 regions of auditory cortex (A1, PAF, or AES) and 2 regions of motor cortex (5L or 6m) resulted in a contralateral orienting deficit. Histograms show percent change from control levels of orienting performance in both the ipsilateral (I) and contralateral (C) hemifields during unilateral deactivation of each locus. Percent change <1% is not shown.
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