sisted so long in some of our animals that had recovered from lateral hypothalamic lesions. There are at least two possible explanations. (i) Perhaps recovery from spreading depression is sometimes not as complete as is generally assumed. With our method, we often found some cortical damage, though relatively slight, in the area of application of KCl. Our animals, having a reduced amount of functional tissue in the lateral hypothalamus, revealed the deficit, whereas unoperated animals were not so sensitive. Perhaps this reduction in the amount of serviceable tissue is also why the regulation of food and water intake is easily disturbed in animals recovered from lateral hypothalamic lesions (*2*). Other methods, such as surgical removal of neocortex, should therefore be used to study this problem. (ii) Even if complete cortical recovery is assumed, it is possible that recovery of normal lateral hypothalamic activity, after removal of cortical facilitation, depends on the amount of serviceable tissue present. With a reduction in such tissue, recovery of normal activity is much slower. One might then expect spreading depression to reinstate other subcortical syndromes in which recovery occurs. Our more recent work supports this view: after recovery, the hyper-emotionality of septal lesions is clearly reinstated for about 2 weeks by one administration of spreading depression. However, in contrast to lateral hypothalamic animals, rats with septal lesions show no exaggerated impairment of feeding or drinking after spreading depression. This is a control for a possible enhanced effect of spreading depression on feeding and drinking in animals with dura puncture and lesions in other parts of the brain. Our findings, therefore, when taken together with the evidence that spreading depression decreases the activity of cells in the lateral hypothalamus, suggest that cortical activity may facilitate and maintain recovery from lateral hypothalamic lesions by enhancing the activity of depressed but intact tissue adjacent to those lesions.

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Lateralization of Sounds at the Unstimulated Ear Opposite a Noise-Adapted Ear

Abstract. *We have discovered conditions of monaural stimulation under which a sound image can be located toward the contralateral, unstimulated ear; the phenomenon helps to clarify divergent experimental results. A tentative model is presented, together with some testable psychophysiological consequences.*

Auditory fatigue (we shall call it adaptation) is a temporary change in the functional state of the ear. Various psychophysical measures may be used to assess this change (*1*); a common procedure is shown in Fig. 1. The observer is seated in an anechoic chamber. Noise stimuli are presented dichotically (that is, separately to each ear) for a brief period. By means of an attenuator the subject adjusts the intensity of the noise in one ear so that, for a fixed intensity in the other ear, the two intensities appear equal.

Instead of this so-called simultaneous dichotic loudness balance, the subject's task may be to adjust the variable noise so that a fused sound image is centered between the two ears; this median-plane lateralization balance is the method we used. A fixed period is allowed for the balance to be made, and a brief rest period separates successive balances. After an initial series of balances, the adapting stimulus remains on in one ear (the adapting ear). At the end of the adapting period, the stimulus is momentarily introduced to the unadapted (control) ear as in the preadaptation balances; the adapted ear continues to be stimulated. As adaptation proceeds, the subject adjusts the intensity of the comparison (probe) stimulus to progressively lower levels. Subtracting the mean difference of the adaptation balances from the mean difference of the preadaptation balances gives a measure of adaptation in decibels (db). In making simultaneous dichotic balances it is assumed that the control ear is adapted very little by the comparison stimulus and that judgments of lateralization or loudness yield the same results (*2*).

Various experimenters have determined auditory adaptation for pure tones and noises (*3–5*); all agree that adaptation increases with the intensity of the adapting stimulus, reaching asymptote for any intensity somewhere between 3 and 10 minutes, taking longer for higher intensities, and longer for noises than for tones. The simultaneous method, used by all but one worker, required from 15 to 30 seconds for a balance. Von Békésy (*4*) found 18 db of adaptation after 2-minute stimulation with an 800-cy/sec tone at about 90 db SPL (sound pressure level), by measuring with a 200-msec probe immediately after cessation of the adapting tone. Yet adaptation was only 3 db and 1 db after 2 and 5 seconds of recovery, respectively. The rapid, exponential recovery suggested that an allowance of 15 seconds for making a simultaneous balance would lead to underestimation of the amount of adaptation.

To avoid this difficulty we used a 500-msec pulse of noise in the control ear. Preadaptation balances were made by turning on the 500-msec probe in both ears at the same time, the probe being set at a random intensity in the control ear and at a fixed intensity in the ear to be adapted. The listener judged whether the fused intracranial sound image was left or right of the median plane. Fifteen seconds separated each trial. [Recovery from the probe is complete in about 100 msec (*6*).] After 10 minutes of noise in one ear, during

which time the control ear was never stimulated, adaptation was measured by a second series of centering balances.

The adapting and probe noises were produced by a single random noise generator (*7*) whose amplified output was passed through three independent attenuator sets (*8*). One attenuator controlled the probe stimulus in the control ear, one controlled the adapting stimulus, and the third controlled the intensity of the probe noise in the adapted ear. Electronic switches (*9*) set for rise and fall times of 25 msec turned on the probe and comparison noises in the separate earphones for 500 msec. Subjects wore headsets with doughnut cushions holding Permoflux PDR-600 matched earphones; in another phase of the experiments, the cushions covered Beyer DT-507 200-ohm insert receivers. All electrical measurements were made with a Ballantine model 320 True RMS Voltmeter. Absolute pressure calibrations were made in 6- or 2-cm^3 cavities by means of a Bruël and Kjaër type 4134 condenser microphone, type 4151 Artificial Ear, and type 4220 Pistonphone.

One male listener (WL) and one female (JP), with normal hearing, were run in the complete series; a third (male) was run in a partial series with similar results. Data given here are based on means of two separate series of determinations each for WL and JP.

The structure of the main experiment is given in Table 1. Adapting series were carried out with the adapting noise at 30, 60, 80, 90, or 100 db SPL; for each of these levels the intensity of the probe noise (in separate sessions) was at 60, 80, 90, or 100 db. A condition in which both adapting and probe noises were at 30 db was also run. With the adapting noise at 60, 80, 90, or 100 db SPL and probe noise lowered to 30 db in the adapted ear, it was not possible to center the sound image. Even when the probe noise in the control ear was below the threshold for that ear, or not delivered, or even when that earphone was disconnected from the circuit, the sound image was lateralized away from the median plane toward the unadapted, control ear.

In simple language, it appeared that after 10 minutes of adaptation at 60 db or higher, momentary reduction of the noise in the adapted ear caused the sound image to be heard at or toward the unstimulated ear. The smaller the reduction, the nearer to the midline the sound image moved, and when the

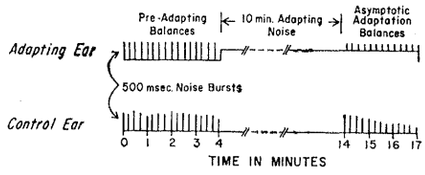

Fig. 1. Scheme of the method used. Here the probe noise is of higher intensity than the fatiguing noise.

decrement was sufficiently small (about 2 db) it was located at the adapted ear. In short, we had discovered one of the conditions of monotic stimulation under which a sound image could be located anywhere in auditory space, including at or near the contralateral ear.

When adapting and probe noises are equal, adaptation increases with intensity of the adapting noise, as expected (see the upper-left to lower-right diagonal of Table 1). Furthermore, for a given adapting intensity, adaptation tends to be maximum when probe and adapting noises are equal in SPL. Whenever the probe noise is more intense than the adapting noise, there is less adaptation, which is almost zero with the probe noise at 100 db and the adapting noise at 30 db. This new result was expected on the assumption of a statistical distribution of receptor thresholds.

The newly discovered monotic lateralization may be a way of measuring adaptation without the contralateral ear being used as a control; it may even be a way of assessing the interaction of the

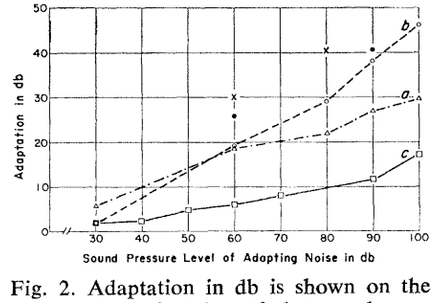

Fig. 2. Adaptation in db is shown on the ordinate as a function of the sound pressure level (SPL) above 0 db = 1 microbar (SPL) of the wide-band Gaussian adapting noise. Curves *a* and *b* give results from the present study. For *b*, adapting noise and probe noise were delivered to the right ear only; the left ear never received stimulation. Curve *c*, shown for comparison, is the mean of adaptation obtained earlier in three separate experiments (*5*) in which a probe noise lasting 15 seconds was used. The two points ● show the adaptation (means of two observers) measured monotically when an ear-insert receiver was used.

two ears. Some findings with this method appear in Fig. 2*b*; the "adaptation" data are for the same subjects as those of Fig. 2*a* and differ from those of Fig. 2, *a* and *c*, in that both adapting and probe noises were in the same ear and the other ear was never directly stimulated. The amount of monotic "adaptation" was defined as the decrement in db between the SPL's of adapting and probe noises at which the sound image was heard in the median plane. For monotic lateralization it increases linearly with SPL (Fig. 2*b*) and is about the same as that for dichotic lateralization at lower adapting intensities, but increases at a more rapid rate above 60 db.

Possible reasons for the marked differences at higher SPL are as follows: (i) that the monotic and dichotic methods measure different phenomena; (ii) that, in the dichotic method, stimulation at one ear inhibits the other centrally, either at or above the level of the accessory nucleus of the superior olivary body; or (iii) that, in the dichotic method, stimulation at one ear inhibits the other directly by cross-masking due to bone conduction. There is evidence for (ii) and (iii)—that is, for both central and direct effects (*10*). If it is assumed that (i) is false, a reasonable interpretation of the divergence of curves *a* and *b* (Fig. 2) is that stimulation of one ear leads to inhibition of the other. Otherwise the dichotic method should lead to greater measured adaptation, since the addition of noise in the control ear should cause the sound image to migrate even further toward the control ear.

The possibility of cross-hearing must be examined (*11*). Zwislocki (*12*) showed that interaural attenuation varies inversely with the contact area of the receiver. An ear-insert receiver's interaural attenuation is about 40 db greater than that of standard earphones and cushions. Accordingly, an insert receiver was substituted in the right ear, a dummy insert receiver in the left, and both were covered by doughnut cushions. At the two points measured, 60 and 90 db, 6.5 and 2.5 adaptation increases were found, respectively (Fig. 2). The smaller difference at 90 db suggests that the interaural bone-conduction attenuation buffer may not suffice for isolation when dynamic earphones with doughnut cushions are used, as in obtaining the data of Fig. 2, *a–c*. The SPL per cycle [given by SPL overall minus 10 $\log_{10}$ times bandwidth (about 5000 cy/sec)] was about 63, 53,

Table 1. Adaptation in decibels (db) for various combinations of adapting noise (rows) and the 500-msec probe noise in the adapted ear (columns). The intensity of the noises is given in sound pressure level (SPL) relative to 0 db = 1 microbar. Degree of adaptation was determined by finding the SPL of a 500-msec probe noise in the rested ear required to center the sound image in the median plane—for example, after an adapting noise of 30 db, a 60 db probe noise in the adapted ear can be balanced by a probe noise of only 2.6 db in the rested ear.

Adapting noise	Probe noise				
	30	60	80	90	100
30	6.0	2.6	2.2	1.9	1.4
60	*	18.8	8.6	6.2	5.4
80	*	24.0	22.0	15.0	12.0
90	*	25.4	27.0	26.9	16.1
100	*	25.3	25.8	29.2	29.6

* At these levels of the adapting noise, centering was not possible; even when the probe noise in the rested ear was below threshold (or not delivered) the sound image was lateralized away from the median plane toward the rested ear.

43, and 23 db for overall SPL's of 100, 90, 80, and 60 db, respectively. Adaptation measured at 90 db or higher is thus an underestimation due in part to interaural leakage, while that measured at 80 db or below is an accurate estimate, if interaction is purely mechanical.

Some further observations bear on the interdependence of the two ears. The development of monotic adaptation is easy to observe by simply decreasing the noise instantaneously for 500 msec every 15 seconds after it is turned on. At first a brief loudness decrement is heard, localized at the stimulated ear. After about a minute the sound image moves a little inward toward the median plane and then moves through the median plane, stopping its migration at or near the contralateral ear. The phenomenon may be observed for pure tones and clicks as well as noise, but with pure tones the sound image has little tonal quality. If the adapting noise is turned off completely, the sound image is heard near the contralateral ear but moves quickly through the midline, its loudness dying below threshold as it moves toward the recovering ear. It is important to relate our experimental results and these observations to other work on binaural hearing.

Rosenzweig has made a substantial experimental and theoretical case for the cortical correlates of auditory localization (*13*). In his model, the magnitude of the ratio of the activities of the two auditory cortices determines where a click will be localized (at the cortex of the cat, in the head of man). Hall (*14*) has recently recorded the electrical activity of single nerve cells in the accessory nucleus of the superior olivary nucleus of the cat. Some cells fired only in response to ipsilateral stimulation, some only to contralateral, some to bilateral stimulation. Patterns of excitation and mutual inhibition, induced by averaging over many cells, were similar to cortical patterns. Hall's model is essentially identical with an earlier one of van Bergeijk (*15*). It is supposed that time and intensity are mapped independently of each other in the accessory nuclei of the superior olive. Excitatory and inhibitory neural signals interact at the accessory nucleus neurons, giving rise to the well-known time-intensity trade. Van Bergeijk claims that his model is a "variation on a theme of von Békésy," but it is really a considerable advance beyond Békésy's because it takes account of recent anatomical and neurological findings. One of us (*16*) has generalized van Bergeijk's model to embrace adaptation phenomena.

We give now a few consequences of these models in the light of monotic adaptation. (i) If the electrical response of the auditory cortex is measured at asymptotic adaptation of one or both ears it should be possible to obtain ipsilateral responses to a sufficiently large decrement in the adapting stimulus at one ear. (ii) Penfield *et al.* (*17*) found that when various points of one hemisphere of the exposed auditory cortex of a conscious man are stimulated, the man reports hearing "localized" sounds. Most sounds appear to be from the contralateral side, some appear to come from both sides, but none are reported to come from the side ipsilateral to stimulation. However, after asymptotic adaptation of one or both ears, the "bilateral" points and perhaps even the "contralateral" points should be heard at the ipsilateral side. (iii) The cortex of one hemisphere may suffice for normal, albeit impaired, lateralization. In fact, a case has been reported of a hemispherectomized patient who could localize dichotically presented clicks separated in time by about 200 μsec, about twice the value for normal subjects (*18*).

Adaptation is a pervasive psychophysiological process (*19*). It should be useful in studying interactions of paired sensory systems above the receptor level. Cortical responses evoked by monoptic and dichoptic lights are similar to those reported for the auditory system (*20*). Even the axiomatic belief of visual psychophysicists in the absolute independence of the two eyes has been impugned by Fiorentini and Radici's demonstration (*21*) of interaction between noncorresponding areas of the two retinas. The role of bilaterality and adaptation in localization and quality of sensation in touch and taste has been detailed recently by von Békésy (*22*).

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