are: A, Ala; C, Cys; D, Asp; E, Glu; F, Phe; G, Gly; H, His; I, Ile; K, Lys; L, Leu; M, Met; N, Asn; P, Pro; Q, Gln; R, Arg; S, Ser; T, Thr; V, Val; W, Trp; and Y, Tyr.
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Behavioral Lifetime of Human Auditory Sensory Memory Predicted by Physiological Measures

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Noninvasive magnetoencephalography makes it possible to identify the cortical area in the human brain whose activity reflects the decay of passive sensory storage of information about auditory stimuli (echoic memory). The lifetime for decay of the neuronal activation trace in primary auditory cortex was found to predict the psychophysically determined duration of memory for the loudness of a tone. Although memory for the loudness of a specific tone is lost, the remembered loudness decays toward the global mean of all of the loudnesses to which a subject is exposed in a series of trials.

Stimulation of human sense organs is initially represented for a brief period by a literal, labile, and modality-specific neural copy. The term iconic memory refers to the initial representation of visual stimuli, and echoic memory is its counterpart for auditory stimulation (*1*). The latter form of memory is essential for integration of acoustic information presented sequentially over an appreciable period of time (*2*). Memory experiments suggest that the duration of echoic memory is about 2 to 5 s (*3*). We lack physiological evidence for the locus of echoic memory, although psychophysical experiments (*4*) suggest a central rather than peripheral site for memory storage.

The nature of decay of sensory memory is by no means clear. The simple decay of sensory memory could be reflected by an increase in uncertainty of the comparison of recently heard memory items with a probe item. However, even this approach might be constrained by the possibility that subjects retain general information about the context but lose information about the specific item. Early in this century, Hollingworth (*5*) discovered a central tendency: The judged magnitude of a stimulus (measured in different modalities) lies near the middle of the range of stimuli used in the experiment (*6*). The range of stimuli also affects subsequent judgments of these stimuli (*7*). Experiments using the method of partial report (*8*) suggest that the decay of sensory memory is a passive process, so that it may well be reflected in reproducible characteristics of neuronal activity.

Experiments with animals (*9*) indicate the presence of a neuronal memory trace by a decrement in the responses of single cells when a stimulus is presented repetitively. Advances in magnetoencephalography (MEG) have made it possible to determine noninvasively the strength of neuronal activity in specific sensory regions in the human brain with high sensitivity and temporal resolution (*10*). This technique revealed that the neuronal activation trace in primary auditory cortex established 100 ms after the onset of a tone stimulus (the N100 component) decays exponentially with time. This approach also showed that the lifetime in association cortex is several seconds longer than that in primary cortex (*11*). These findings confirm the idea that short-term memory traces are modality-specific (*12*). Further, the results show that the N100 component of the event-related potential or field may well play a role in echoic memory, although no evidence was found for this component that supports short-term memory scanning (working memory) (*13*).

Four right-handed adults (two males and two females) volunteered as subjects after providing informed consent (*14*). The task for each subject was a two-alternative forced choice: press one button if the probe tone appeared louder than the test tone or the other button if it appeared softer (*15*). No immediate feedback was provided, but subjects were informed of the experimental results after the end of each session. A total of 6000 trials was collected for each subject. All the analyses were based on the data after exclusion of the first 20% of the trials of every session. We discounted these results because it was during this first set of presentations that the range of the loudness in the session was established. For each delay condition, a cumulative Gaussian distribution was fit to the psychophysical data of loudness judgments. The equal loudness point was defined as the mean of the Gaussian distribution, and the uncertainty was the standard deviation of the distribution. Separate magnetic field recordings of auditory-evoked responses of similar tones were also collected for the subjects for whom there were no existing MEG data (*11*).

Figure 1 illustrates the neuromagnetic data with which the psychophysical data were compared. The strength of the N100 component of the response of primary auditory cortex increased with the interstimulus interval (ISI) and approached a maximum value for ISIs exceeding a few seconds. In all cases, such curves could be fit by the mathematical expression $A(1 - e^{-(t-t_0)/\tau})$, with fitting parameters of amplitude A, lifetime τ, and time of decay onset t_0 (*16*). We emphasize that the shape of the curve in each case is determined by a single

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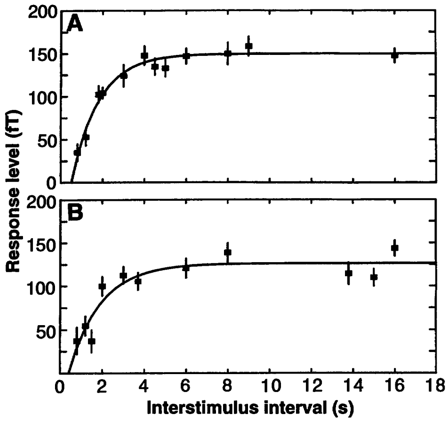

Fig. 1. Peak magnetic field strength near the scalp, ~100 ms after the onset of a tone-burst stimulus (the N100 component), increases with interstimulus interval, as shown for (**A**) the left hemisphere (τ = 1.3 s) and (**B**) the right hemisphere (τ = 1.5 s) of subject SW. The field sensor was placed over each hemisphere at a location where it monitors activity in the primary auditory cortex.

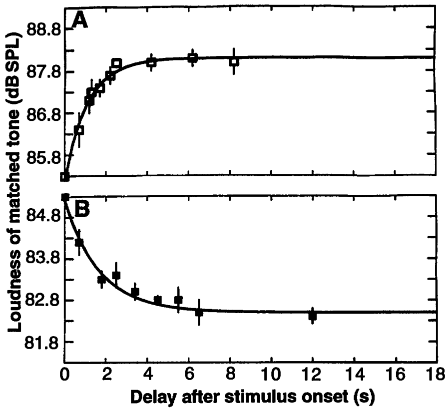

Fig. 2. Remembered loudness of a tone for subject SW determined by a forced-choice match with probe tones presented at different delays after the test tone; SPL, sound pressure level. Data represented by the open symbols (**A**) were obtained when the mean loudness of the test and probe tones was 2.5 dB greater than that of the test tone; τ = 1.1 s. Data represented by the closed symbols (**B**) were obtained with the mean loudness 2.9 dB lower than that of the test tone; τ = 1.5 s. Error bars denote the standard deviation for each delay.

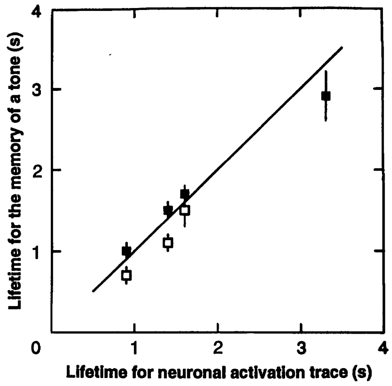

Fig. 3. Agreement across four subjects between behavioral lifetimes for the decay of the loudness of a tone after its presentation and physiological lifetimes for the decay of the neuronal activation trace in primary auditory cortex. Open symbols denote behavioral lifetimes when the mean loudness of the probe tones is higher that of the test tones, and closed symbols denote the results when the mean loudness is lower than that of the test tones.

parameter, τ. The difference between the response strength for long ISIs and that for shorter ISIs provides a measure of the diminishing activation trace. According to the relation just given, the activation trace decays exponentially with time: $Ae^{-(t-t_0)/\tau}$. For each subject, the left and right hemispheres have essentially the same lifetimes for the N100 activation trace (*11*). Moreover, the lifetime of the activation trace for the subsequent component with 180-ms latency (P180) was the same as that for the N100 component (*17*) for each subject. This result suggests that the lifetime may well be characteristic of the cortical area because sources for both N100 and P180 lie in the primary auditory cortex (*18*). By contrast, lifetimes for responses that arise in the association auditory cortex are significantly longer than those of the primary cortex (*11*).

The psychometric functions of this experiment enable us to test the hypothesis that echoic memory directly reflects the decay of the physiological activation trace in primary auditory cortex. As shown in Fig. 2, the subjective equal loudness match displays a strong dependence on time after the test tone. In all cases it decays toward the mean of all stimuli. Thus, although memory for specific features of acoustic stimuli is lost shortly after exposure, subjects draw on longer term global experience of the stimulus pattern. They can do so if the mean loudness is either greater or less than the loudness of the test tone. The observed shift is significantly greater than the uncertainties in the measurements. These results are consistent with the "central tendency" effects (*6, 19*) and provide a neural modality-specific basis for sensory memory. As echoic memory decays, judgment is more heavily biased toward patterns of recent experience and, as described by Berliner and colleagues (*20*), tends toward the middle of the range of presented stimuli. As illustrated in Fig. 2, an exponential decay adequately describes this trend: $C + De^{-t/\tau}$, where the amplitudes C and D and the lifetime τ are fitting parameters. In this way, a unique lifetime can be defined for a subject's memory of the loudness of the sound (*21*). Similar behavior was observed in four subjects whose individual memory lifetimes range from 0.8 to 3 s. The loss of sensory memory and the growing dominance of a longer term memory are not accompanied by a marked increase in the uncertainty for the loudness of the probe that best matches the test for a given delay.

The correspondence between the physiological lifetimes of the neuronal activation trace and the behavioral lifetimes for remembered loudness is quite accurate across subjects (Fig. 3). However, a comparatively slight systematic bias appears in the values for behavioral lifetimes that depends on whether the mean loudness of probe tones is greater or less than the loudness of the standard tones. This bias may well arise from differences in the precise sequence of probe tones and how they influence the mean loudness toward which the subject's judgment decays. In any event, the close quantitative agreement for all subjects suggests that the evolution of perception is associated with the decay of the cortical memory trace.

These results suggest that noninvasive measurements of cortical activation lifetimes may provide an objective and meaningful characterization of sensory memory lifetimes for individual subjects. We achieved this end by exploiting an advantage in MEG whereby the precise location and orientation of the neuronal source current are established (*10, 11*) so that its field pattern can be predicted. This information helped to identify locations over the scalp where the magnetic field of only that particular source was appreciable. Another feature of this technique is its rapid time response, which permits changes over fractions of a second to be well characterized. The present study suggests that extensions of these procedures may be used to characterize a variety of memory functions that are supported by cortical areas of other sensory modalities.

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14. All studies were carried out in a quiet, magnetically shielded room. Subjects sat comfortably with left and right index fingers resting on separate keys of a computer keyboard. Tone bursts of 200-ms duration, including 12-ms ramps at onset and offset, were generated by an Amiga 1000 computer and presented monoaurally by Etymotic Research type ER-3A earphones. Each experimental session consisted of 100 trials with a 5-s interval between the end of one trial and the beginning of the next. Each trial consisted of a test tone presented to one ear followed by a delay and a probe tone delivered to the other ear (delay randomly chosen with equal probabilities from 1, 2, 4, 6, and 8 s in one block and 0.8, 1.5, 2.5, 3.5, and 5.3 s in another block). The intensity of the test tone was fixed at 85.3 dB with its frequency randomly selected with equal probabilities from 800, 900, and 1100 Hz. The frequency was always the same for the probe tone and its corresponding test tone, and the ear of presentation for the test stimuli was fixed in each session but alternated across sessions.
15. In each session, the intensity of the probe stimulus was randomly chosen with equal probabilities from one of two lists: (71.0, 74.5, 77.0, 78.9, 80.5, 81.8, 83.0, 84.0, 84.9, 85.8, 86.5, 87.2, 87.9, 88.5, 89.0, 89.5 dB) or (83.0, 84.0, 84.9, 85.8, 86.5, 87.2, 87.9, 88.5, 89.0, 89.5, 90.0, 90.5, 91.0, 91.4, 91.8, 92.2, 92.5 dB) (sound pressure level). The first list has a mean loudness that, together with the test stimulus, is 2.9 dB lower than the loudness of the test tone, and the second list has a mean that is 2.5 dB greater than the loudness of the test tone. The difference between the mean and test was sufficiently small that the subject could not judge which list was presented.
16. The onset of decay, specified by the value of t_o, begins at the offset of the preceding tone. As explained in (*11*), the N100 response to the offset of a tone is habituated to the onset of the same tone, which implies that the two activation traces have appreciable commonality. Thus an activation trace is established in primary auditory cortex by a tone-burst stimulus expressing information contained in the early or late portions of the tone.
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21. Because the overall change in loudness was kept relatively small, an exponential decay would have the same exponent whether loudness is expressed in terms of the power amplitude, pressure amplitude, or logarithm of the power amplitude (in decibels).
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