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Measuring Sensory Memory: Magnetoencephalography Habituation and Psychophysics

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Vision and audition each have several levels of sensory memory, and constructing experiments to selectively measure one or anther of these memories has been an elusive goal. In this chapter we consider one apparently successful example: Z.-L. Lu, S. J. Williamson, and L. Kaufman (1992b), who measured the retention of the precise loudness of a tone in a very short term auditory memory. The psychophysically measured immediate memory for tonal loudness decayed in a period of a few seconds (depending on the observer) to the average loudness of recently heard tones (which was maintained in a higher level short-term auditory sensory memory). A critical component of this experiment was the establishment of a well-defined higher level sensory-memory representation so that the decay of the very short term memory trace could be observed without contamination. In their habituation paradigm, the same tonal stimulus was repeatedly presented with a fixed interval between presentations, and the magnetoencephalography (MEG) response was recorded. The longer the interval between successive presentations, the greater the response. The recovery of response amplitude from prior stimulation reflects continuing activation and therefore offers physiological access to memory duration. MEG recordings of habituation to the stimuli in the

loudness experiments revealed two sites in temporal cortex: (a) a primary A1 site that reflects the tonal memory studied psychophysically and (b) another auditory memory site in the nearby auditory association cortex. By replicating the psychophysical conditions precisely in habituation, and by separating the two N1 MEG components, for each subject both the psychophysically measured memory for loudness and the memory inferred from habituation of A1 were found to decay with an identical time constant. Between subjects, the lifetime (time constant of the decay) of memory for loudness varied from 0.8 to 3 sec. In addition, an example of the decay of very short term visual memory (iconic memory) is given in which the psychophysically measured lifetime and the electroencephalographic (EEG) lifetime determined in a habituation experiment seem to agree quite closely. MEG is preferred to EEG because of its superior ability to isolate and localize sources, and MEG is preferred to functional magnetic resonance imaging (fMRI) because of its temporal resolution. MEG is an ideal tool for studying sensory memory.

MEMORY REGISTERS

Sensory memory refers to the initial, modality-specific neural representation of sensory stimuli. Sensory memory is often contrasted with *short-term memory* and *working memory* (which are assumed to be less modality specific than sensory memory), and all of these are distinct from *long-term memory*. In functional terms, sensory memory is comparable to a register in a computer. In a human or a computer, if one wants to know what the last auditory input was, one examines the auditory sensory register. On the other hand, accessing the contents of long-term memory in a computer requires two registers: (a) a *memory access* register, for the memory address of the particular contents, and (b) a *memory contents* register for the contents themselves. In human long-term memory, the address of the contents (memory access) is computed from *retrieval cues*, which may be partial contents, context, or related items. The brain mechanism by which the contents become available and useful is not understood.

The prevailing view of short- and long-term memory systems is that there are one or more modality-specific sensory registers in each sensory modality, plus a register or registers for short-term and/or working memory, plus functionally distinct long-term memory systems (i.e., for episodic, semantic, procedural, and perhaps other forms of long-term memory).

LEVELS OF MEMORY AND PROCESSING

The conceptualization of sensory memories as registers is almost certainly too simplistic. In biological sensory processing there is a considerable amount of memory—perhaps more aptly called *retention*—that is inherent in the processing itself, and this memory may differ for different stimuli at every stage of processing. For example, visual sensory memory exists in the receptors and bipolar cells of the retina as an afterimage. These cells do not constitute a register in the usual meaning of the word, but they can retain a representation of the input image long after it has been removed. The afterimage is a negative of the original stimulus that is perceived on subsequent stimulation. The original stimulus can itself persist in the retina as *persistence of sensation*.

An *afterimage* is sensory memory that is specific to the eye of stimulation. Stimulating the other eye may make it more difficult to extract the information, but it is relatively easy to demonstrate the eye specificity. A characteristic that has often been used to define visual sensory memory is that a subsequent stimulus overwrites the memory. To the extent that subsequent stimuli in the same eye are more effective at overwriting memory contents than stimuli in the other eye, the memory is maintained in neurons prior to binocular combination. In the literature there is a clear distinction between (retinal) afterimages and perhaps non-retinal retention mechanisms, which are eye specific, on the one hand, and visual sensory memory (Sperling, 1960; called *iconic memory* by Neisser, 1967), which is not eye specific, on the other hand.

Repetition detection (or simply *recognition memory*) is a paradigm that reveals memory that survives being overwritten. Repetition detection probes short-term visual or auditory memories that store successive events concurrently. The modality specificity of visual sensory memory can be demonstrated in a variety of psychophysical tasks, such as memory for successively presented nonverbalizable nonsense shapes. Beyond visual sensory (iconic) and visual short-term memory, deriving the taxonomy of visual memory systems has not been possible by means of psychophysical tasks. The taxonomy of auditory sensory memory systems is probably even more complicated than that of visual sensory memory systems, because auditory signals are subjected to much more complicated processing prior to reaching auditory temporal cortex area A1 than are visual signals before reaching occipital cortex area V1.

HABITUATION

In trying to sort through the complexities of sensory memory systems, it would be ideal if there were a method whereby each sensory and short-term memory system could be identified by (a) its brain location, (b) the time constant for which it retains information, and (c) the format (or encoding) of the information it retains. This is where Sam Williamson had a great insight. Habituation is an extremely powerful tool that offers a means of quickly providing the first two components of a sensory memory (location and time constant) and perhaps the third (encoding) as well.

Magnetoencephalography (MEG) is an ideal method for studying habituation, because it permits better spatial localization than electroencephalography (EEG) and because response amplitude in MEG is more directly related to neural activity than in functional magnetic resonance imagery (fMRI). The principle is as follows (Fig. 13.1). Presenting a stimulus repeatedly causes the MEG response to the stimulus to weaken. Presenting it at a slower rate gives the response more time to recover than in rapid presentations. The reference point is a stimulus sequence presented with an extremely long interval between successive presentations (stimulus onset asynchrony) that permits full recovery of the MEG response. At some critical, faster presentation rate the MEG response is reduced to only $1 - (1/e) = 0.63$ of its response to an extremely slow stimulus. The time between successive stimuli at this rate defines the *time constant* of recovery. In fact, the situation may be slightly more complicated in that recovery may not begin immediately after termination of a stimulus; there may be a *refractory period* before recovery begins. In general, therefore, there are two parameters to describe the temporal properties of habituation: (a) time constant and (b) refractory period. It is remarkable that in the examples offered by Williamson and in the other instances described in this chapter the recovery from habituation is of a simple form, exponentially limited growth, so that these two parameters are sufficient to describe the temporal dynamics.

Using flickering checkerboard stimuli and MEG recording, Uusitalo, Williamson, and Seppa (1996) were able to detect 10 brain locations with different recovery time constants. Each one of these brain locations represents a process with an inherent retention time, a process that could become a component of the overall retention time observed in a psychophysical memory experiment.

The observed retention time and resistance to interference in a psychophysical experiment will depend on whether a stimulus is re-
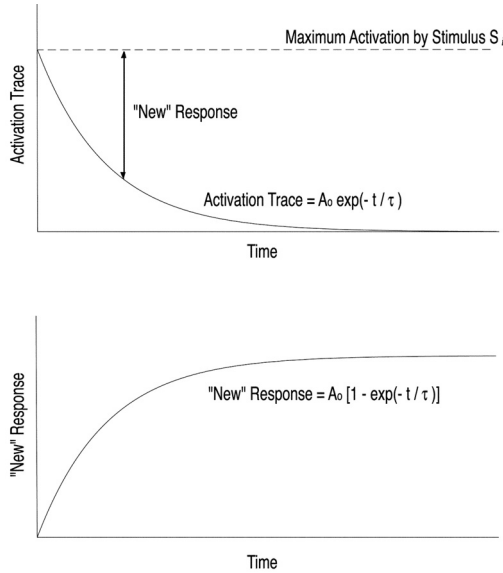
FIG. 13.1. The logic of the habituation paradigm: model relationship between activation trace and measured neuronal response from magnetoencephalography. When a stimulus S_i is presented for the first time at time $t = 0$ it produces an activation trace, $A_o \exp(-t/\tau)$ for $t \geq 0$. When the stimulus is presented again after a time t_1, it again produces an internal activation of A_o. The new response A_1 observed externally is only the difference between the residual response $A_o \exp(-t/\tau)$ and A_o, that is, $A_1 = A_o (1 - \exp(-t/\tau))[(-\exp((t-t_1)/\tau)], t \geq t_1$.

peated exactly or whether it is changed somewhat between "repetitions." Psychophysical tasks that use early sensory memories have shorter retention times than tasks in which more abstract comparisons suffice. So, a task that requires an observer to decide if two tones have exactly the same loudness will suffer when the interval between tones exceeds several seconds. A task that requires listeners to decide whether two tonal *sequences* (melodies) are identical can tolerate much longer delays between the two successive presentations, because it uses a higher level memory system. There are similar examples from visual tasks.

The corresponding habituation experiments seek to determine the relative effectiveness for habituation of an exact repetition compared with an altered repetition. We expect that habituation of higher brain centers that process visual stimuli would not be affected when successive stimuli alternate between a lowercase *a* and an uppercase *A* or when the spatial location of the letter *A* is jittered from presentation to presentation. Early brain processes would regard such semantically equivalent stimuli as being visually quite different and would adapt less in an alternating se-

quence than in a homogeneous sequence. Such alternating-feature sequences have been used in repetition-detection experiments to determine the level of processing of human visual repetition detection (e.g., Sperling, Wurst, & Lu, 1993). The possibility of using the same or very similar sequences to study habituation in MEG and in psychophysical performance in a detection or memory experiment offers an opportunity to correlate brain and behavior in the study of sensory processing and sensory memory.

As noted earlier, of all the paradigms used to study sensory memory, habituation paradigms are especially well adapted to MEG because of MEG's temporal resolution; the relatively direct relation of magnetic signal intensity to neural output; and because of the accuracy of brain localization relative to EEG. Another advantage of habituation paradigms is that there are psychophysical paradigms that can be related to habituation. Here we consider two instances in which habituation measured at brain locations was correlated with behavior to define the location and time constant of a sensory memory: (a) an auditory study to determine the brain location and time course of echoic memory for subtle differences in loudness and (b) a visual study of iconic memory (mostly under 1 sec) for arrays of sine-wave patches.

The auditory study of echoic memory is complete, and the main part has been published (Lu, Williamson, & Kaufman, 1992b); the visual study is still incomplete and unpublished (Yang, 1999). Although repetition detection in psychophysical visual studies and habituation in MEG might have been the ideal setting in which to correlate psychophysically derived sensory memory systems with sensory memory systems derived from MEG habituation, in fact one of the first successful correlation of a psychophysically determined sensory memory system with an MEG-determined system occurred in the auditory system.

AUDITORY SENSORY MEMORY

Very Short Term Memory for Tonal Loudness

Auditory sensory memory, also called *echoic memory* (Neisser, 1967), lasts about 2–5 sec (Glanzer & Cunitz, 1966; Treisman, 1964; Wickelgren, 1969) and is essential for integrating acoustic information presented sequentially over an appreciable period of time (Crowder, 1976). Prior to 1992, there was no physiological evidence regarding the locus of human auditory sensory memory, although psychophysical experiments

(Massaro, 1975) suggested a central rather than a peripheral site. Electrophysiological investigations (Weinberger, et al, 1990) of auditory memory functions in animals provide evidence that similar short-term memory functions are served by sensory areas of the cerebral cortex.

Lu, Williamson, and Kaufman (1992a, 1992b) exploited advantages of MEG to investigate retention of stimulus-related information within areas of the primary and association auditory cortices. They found that the lifetime of a cortical activation trace in the primary auditory cortex predicts the lifetime of behaviorally determined auditory sensory memory.

The lifetime of a cortical activation trace was obtained from measurements of the magnetic field pattern across the side of the head when the subject was presented with repeating tone stimuli. In responding to a tone, cortical areas set up activation patterns of synaptic activity that result in a weaker cortical response to a subsequent tone. In this way, sensory areas "remember" information just presented. When identical tones are presented at a fixed time interval, the response strengthens with longer intervals, in a way that permits a lifetime to be determined for the activation trace. The primary cortex has a relatively short lifetime—just a couple of seconds—but the activation trace in the association cortex persists for several seconds longer. Remarkably, by extrapolating back to an interstimulus interval of zero, it is possible to identify the time when the trace just begins to decay. For the association cortex it is the onset feature of the tone that counts. By contrast, for the primary cortex both the onset and the offset reset the trace. By extending such studies it should be possible to determine what aspects of sounds are preferentially processed by primary and association areas.

To establish psychological correlates of the lifetime of the activation traces in the auditory cortex, Lu et al. (1992b) set up a psychoacoustic experiment to study decay of loudness memory following the presentation of a pure sine wave tone. It is known from human behavioral studies carried out early in the twentieth century that a person's remembrance of the loudness of a tone decays exponentially with time to the mean loudness of recently heard tones; that is, a listener's memory of a particular tone is lost with time, and the listener is forced to rely on his or her memory of the mean loudness of all the tones recently heard (an effect known as the *central tendency;* Helson, 1964; Hollingworth, 1909, 1910; Ipsen, 1926; Lauenstein, 1933; Needham, 1935; Woodrow, 1933).

Lu et al. (1992b) showed that, for individual subjects, physiological lifetimes determined magnetically, and behavioral lifetimes determined from tone-matching studies, agree within an accuracy of better than 20%.

Memory lifetimes ranged from 0.8 to 3 sec for individuals who participated in this study. These results provide strong evidence that the primary auditory cortex serves auditory sensory memory, and the lifetime of that memory can be gauged by studies of neuronal activity in that area of the brain. We review this study later.

Measuring Neural Activity in the Primary and Association Auditory Cortices

The N100 Component

Technical advances in low-temperature physics have provided the essential instrumentation (MEG) for recording the magnetic field of the human brain. The N100 component, a major peak in the magnetic waveform of the evoked neuromagnetic response, normally occurs about 100 msec after the onset of a tone burst. Many aspects of the N100 component have been studied in both EEG and MEG over the past few decades. For example, from MEG research (Pantev et al., 1988) we know that neural sources of N100 in response to tone bursts of different frequencies lie in different locations within the primary auditory cortex (the so-called *tonotopic map*).

Separating Primary and Association Cortex Contributions to N100.   Before 1992, it had been speculated that activities from several brain regions contributed to the auditory N100, although there was no definitive evidence. Lu et al. (1992a) postulated that contributions to the N100 from other brain regions were obscured because the usual rates of tone burst presentation (about 1 per second) in previous studies were too fast to permit recovery of slower brain regions. Using a 6.0-sec interstimulus interval (ISI), they discovered a magnetic field pattern near the scalp (Fig. 13.2B) that is significantly different from the pattern using fast (ISI = 1.2 sec) presentation rates (Fig. 13.2A). Although it is possible to account for the observed field pattern at short ISIs with one neural source (in the primary auditory cortex), the field pattern at long ISIs indicates an additional neural source in association auditory cortex (see Fig. 13.3). These data showed that in addition to the neural contribution from the primary auditory cortex a neural source from auditory association cortex also contributed to the N100.

To distinguish the two sources that contribute to the early MEG response to a tonal burst, Lu et al. (1992a) designated the contribution from
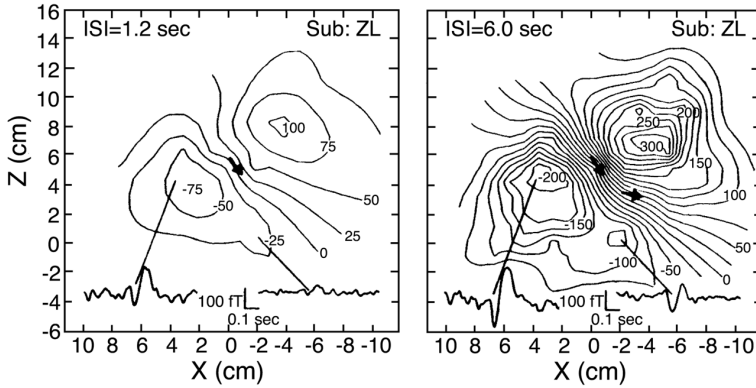
FIG. 13.2. Isofield contours for subject ZL characterizing the measured field pattern over the left hemisphere 100 msec following the onset of a tone burst stimulus. Arrows denote the direction of current dipole sources that account for each pattern, with their bases placed at the dipole's surface location. In the right panels, the upper arrow is the N100m source and the lower arrow is the L100m source. Insets illustrate response waveforms obtained at the indicated positions. Both waveforms also exhibit a 200-msec component. ISI = interstimulus interval. Reprinted from *Brain Research, 527,* Z.-L. Lu, S. J. Williamson, & L. Kaufman, Human auditory primary and association cortex having differing lifetimes for activation traces, pp. 236–241. Copyright © 1992, with permission from Elsevier Science.
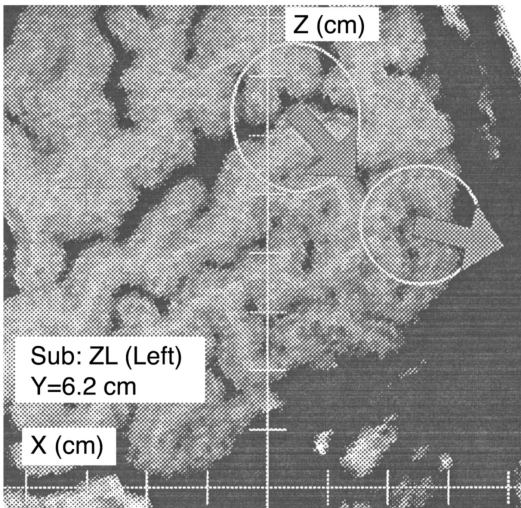

FIG. 13.3. Deduced locations for neuronal sources that are responsible for N100m (upper arrow) and L100m (second N100 source, lower arrow) on sagittal magnetic resonance images of the left hemispheres of 1 subject. Coordinates are expressed in the PPN system, with a distance of 1 cm between adjacent tics on the axes. The base of each arrow indicates the respective positions, with the ellipse indicating the estimated range of uncertainty (95% confidence level), and the direction of each arrow specifies the flow of intracellular current. The N100m source lies within the lateral sulcus, and the L100m source lies within 1 cm of the superior temporal sulcus. Reprinted from *Brain Research, 527,* Z.-L. Lu, S. J. Williamson, & L. Kaufman, Human auditory primary and association cortex having differing lifetimes for activation traces, pp. 236–241. Copyright © 1992, with permission from Elsevier Science.

the primary auditory cortex N100, and the contribution from the association auditory cortex L100.

Peripheral Refractory Effects Versus Central Habituation.

It is also well known that the N100 component exhibits a *rate effect:* It is exceptionally sensitive to the rate at which the stimuli are repeated. Amplitudes diminish if stimuli are presented sufficiently soon after an identical preceding one (Celesia, 1976; Hari, Kaila, Tuomisto, & Varpula, 1982; Naatanen & Picton, 1987). However, it was not clear whether the rate effect arose from peripheral sense organs or from higher cortical regions.

Electrophysiological studies of the auditory system in cats conducted by Wickelgren (1968) and Weinberger et al. (1990) led to four criteria according to which a rate effect could be classified as a central process (habituation): (a) diminished response strength for shorter ISIs (see Fig. 14.4); (b) spontaneous recovery of full response strength after stimuli are withheld for a sufficiently long time (see Fig. 13.5); (c) enhanced response to a different stimulus (probe) which replaces the standard stimulus, thereby ensuring that the weak responses were not due to a state change (e.g., drowsiness; see Fig. 13.6); and (d) enhanced response to a standard stimulus if preceded by a deviant stimulus (dishabituation; see Fig. 13.7). Lu (1992) ob-
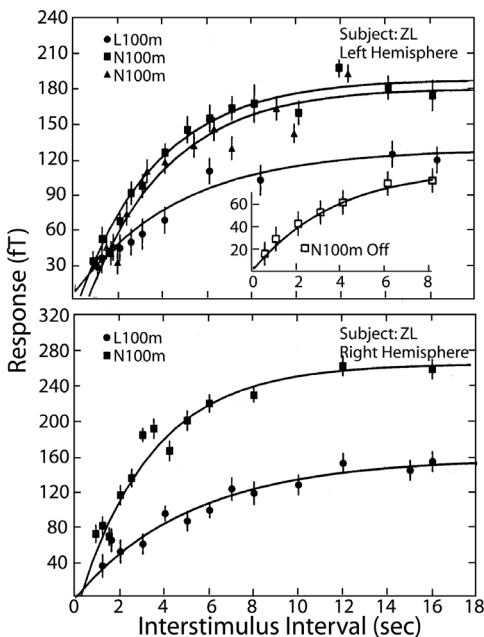

FIG. 13.4. Response amplitudes versus interstimulus interval over the left and right hemispheres for subject ZL, for tones of 0.5 sec (N100m: squares; L100m: circles), 1.2 sec (N100m: triangles), and 2 sec (N100m: inverted triangles) duration. Insets illustrate the dependence for the N100m offset response for tones of different duration indicated by the horizontal axis. Reprinted from *Brain Research, 527,* Z.-L. Lu, S. J. Williamson, & L. Kaufman, Human auditory primary and association cortex having differing lifetimes for activation traces, pp. 236–241. Copyright © 1992, with permission from Elsevier Science.
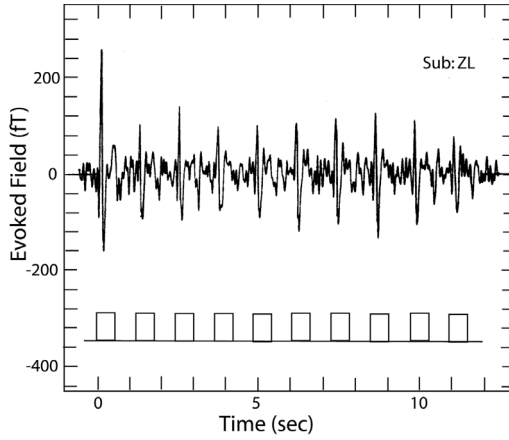
FIG. 13.5.   Average evoked magnetic field to trains of tones of the same frequency and intensity. One stimuli train is shown under the waveform. Sub = Subject.
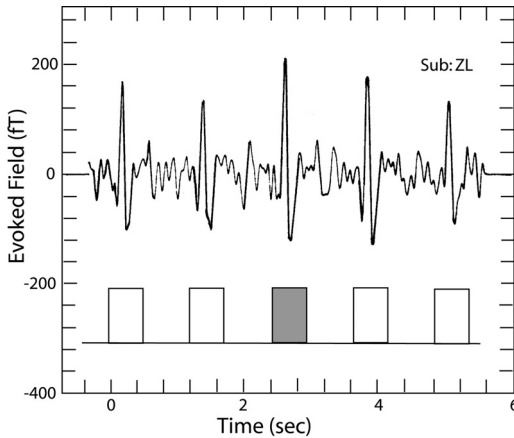

FIG. 13.6.   Recording of the probe response. The shadowed block represents the probe stimulus; the other four blocks denote the standard stimuli. Sub = Subject.

tained the first evidence that the N100 and L100 rate effects satisfy all the criteria from habituation and thereby reflect cortical processes.

Modeling Neural Activity With Exponential Decay Functions

As noted earlier, one can separately measure magnetic fields arising from the primary and association auditory cortical areas. Figure 13.4 shows that response strengths increase systematically with increasing ISI for both cortical areas. Maximum responses are not attained until ISIs ex-
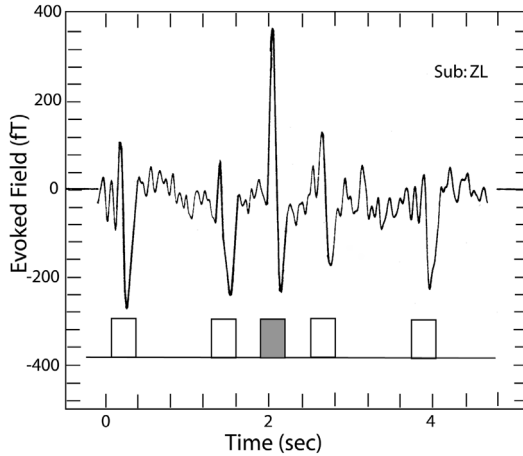
FIG. 13.7.   Recording of dishabituation. The shadowed block represents the probe stim-
ulus (which is of a different temporal frequency); the other blocks denote standard stim-
uli. Sub = Subject.

ceed a few seconds, with the primary cortex approaching its asymptote
sooner than the association cortex. Because of the similarity in the ISI
trends, each set of data was fit with an exponential function. The solid
curves in Fig. 13.4 are obtained with the function $A\ (1 - e^{-(t-t_0)/\tau})$, whose pa-
rameters are determined by a least-squares fit to the data. All the data are
well fit by this expression (τ = 3.5 sec for N100 and 5.1 sec for L100).

The following assumptions define a model of neural activation. (a) It
is generally accepted that a stimulus produces a neural activation trace
that decays after the stimulus is withdrawn (Fig. 13.1). We further pro-
pose (b) that neural activation decays exponentially and (c) that a subse-
quent identical stimulus resets the trace to its full strength. Thus, the
observed response strength indicates how much the trace has decayed
since the preceding stimulus. The assumptions provide a method for
quantifying the strength of the neural activation trace in terms of the
peak magnetic field strength that is observed from the responding popu-
lations of cortical neurons.

Within the framework of the preceding model (see Fig. 13.1), three pa-
rameters need to be estimated for empirical fits to data: A, t_0, τ. The pa-
rameter A determines the maximum response strength, t_0 denotes the
time when the activation trace begins to decay, and τ specifies the life-
time of the decay. Lu et al. (1992s) found that t_0 for the primary auditory
cortex is very close to the offset of the previous tone, indicating that the

activation trace reflects the offset response to that tone. Indeed, it is well known that the offset of a tone evokes a response in the primary auditory cortex. It appears that the activation traces established by the onset and by the offset of a tone burst are very similar. In support of this notion, Lu et al. (1992a) showed that the offset response of a tone is habituated by the onset response to the same tone. A graph identical to those illustrated in Fig. 13.4 is obtained if the horizontal axis represents tone duration instead of ISI.

However, the situation is different in the association cortex: The value of t_0 matches the onset of the previous tone, not its offset. The response of association cortex consequently distinguishes between onset and offset in the sense that the offset of a tone does not establish a new activation trace or enhance the activation trace left by the onset. It may well be that the primary auditory cortex cannot "tell" the difference between the onset and offset of a tone, because the activation traces are so similar. However, both onset and offset are clearly distinguished from each other when one takes into account the additional information provided by association cortex. Because neuronal activity is nearly simultaneous in the two cortical areas, the need for higher centers in the brain to rely on the output of the two areas in such a way would seem to impose no temporal disadvantage.

Lifetime of Neural Activation Predicts Duration of Echoic Memory

It is quite remarkable that the lifetimes obtained by fitting the exponential function to the MEG ISI data for the N100 component vary considerably across the 4 subjects who were studied in detail. The values are: $\tau = 0.8, 1.4, 1.6$, and 3.4 sec, a range that spans a factor of 4. Approximately the same lifetimes were found for habituation of another component, with 180-msec latency, suggesting that the lifetime is characteristic of the specific cortical area. It is also noteworthy that the lifetime best accounting for the ISI data for the magnetic field arising from the association cortex is longer by about 2 sec for each subject. These ranges of values suggest that the activation trace in the primary auditory cortex may well be associated with very short term echoic memory. Lu et al. (1992b) carried out behavioral studies on the same subjects to determine whether a correlation could be found for individual subjects between their MEG habituation time constants and the behaviorally measured duration of their echoic memories.

Measuring Duration of Echoic Memory

Early in this century, Hollingworth (1910) discovered the central tendency: A few seconds after experiencing a stimulus, the judged magnitude of the stimulus approaches the mean magnitude of all the stimuli used in the experiment. Lu et al. (1992b) were able to exploit this tendency to measure the decay of very short term echoic memory. They used a two-alternative forced-choice paradigm for the same subjects who had been studied using MEG. A test tone was provided to one ear, and after a delay a probe tone was provided to the other ear (see Fig. 13.8). The subject responded by indicating whether the probe tone was louder or softer than the test tone.

   The frequency of the probe was always the same as the test tone, but its intensity was randomly chosen with equal probabilities from one of two lists. One list had a mean loudness that, together with the test tone, is 2.9 dB lower than the loudness of the test tone, and the other list had a mean loudness that is 2.5 dB greater (see Fig. 13.9). Subjects were unable to determine which list was presented in a given session. The hypothesis was that, for short delays, the subject would judge the loudness of the probe tone relative to the test tone. However, for long delays the subject would have lost the very short term echoic memory of the test tone and make judgments based on a "longer term" memory representing the long-term mean loudness of all tones. A total of 6,000 trials were col-
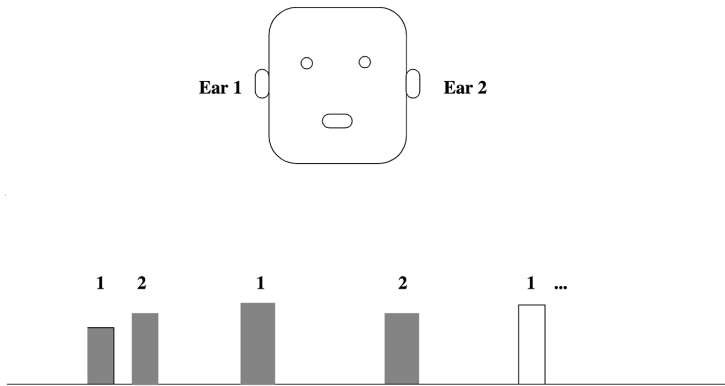

FIG. 13.8.   Loudness match paradigm. The loudness of test tone and the time between each pair of stimuli is fixed. Test and probe tones are of the same frequency and duration. For each pair of stimuli, the frequency is randomly chosen from 800, 900, and 1100 Hz with equal probability. The time delay between test and probe tones is randomly chosen from 0.5, 2.3, 4.3, 6.3, and 11.8 sec with equal probability.
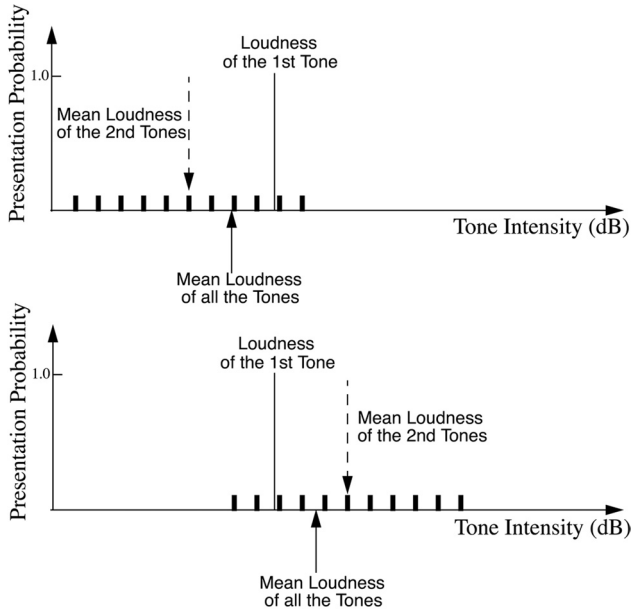
FIG. 13.9.   Two histograms of probe tone loudness distributions. One list had a mean loudness that together with the test tone is 2.9 dB lower than the loudness of the test tone, and the other list has a mean loudness that is 2.5 dB greater. Only one list was used in a given experimental session.

lected for each subject. One of the challenges in carrying out studies of this kind is to determine how long it takes at the beginning of a session for the subject to acquire accurate judgment of the average loudness. In practice, several hundred of the initial trials were discarded without the subject's knowledge, so that stable results could be obtained.

Representative results for the decay of echoic memory are illustrated in Fig. 13.10. When the mean loudness of the probe tones is biased higher than that of the test, the subject's loudness judgments shift toward greater loudness as the delay between presentation of the test and probe increases. When the mean loudness of probe tones is lower than the test, the opposite trend is observed.

In MEG studies characterizing the dependence of N100 amplitude on ISI, an exponential function was used to achieve the data fit shown in Fig. 13.11. The behavioral measurements for the temporal dependence of remembered loudness are also well described by an exponential decay. A causal relation between the two phenomena would be suggested if the lifetimes of the two, behavioral and brain, were the same for each subject
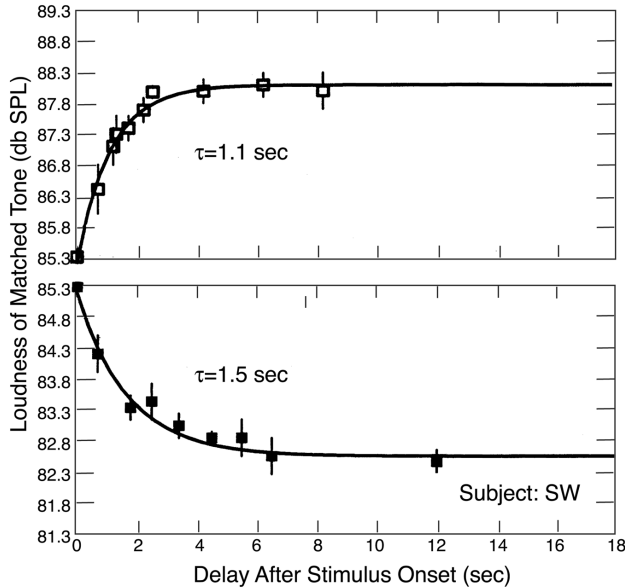
FIG. 13.10.   Remembered loudness of a tone as determined by a forced-choice match with
a probe tone presented at various delays after the test tone. Data represented by the open
symbols were obtained when the mean loudness of the test and probe tones was 2.5 dB
greater than that of the test tone. Data represented by closed symbols were obtained with
the mean loudness 2.9 dB lower. Error bars denote the standard deviation for each delay. Re-
printed with permission from Lu, Z.-L., Williamson, S. J., & Kaufman, L. (1992). Physiologi-
cal measurements predict the lifetime for human auditory memory of a tone. *Science, 258,*
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but differed between subjects. Figure 13.12, based on the data of 4 sub-
jects, shows a correlation of .97 between the brain and behavioral echoic-
memory lifetimes. The high correlation suggests that noninvasive mea-
surements of the lifetime for cortical activation traces may provide an ob-
jective and meaningful characterization of sensory memory lifetime for
individual subjects. This interpretation of the activation trace also pro-
vides a possible neural mechanism for very short term echoic memory.

Other Auditory Sensory Memories

Cowan's (1995) review concluded that there are at least two forms of au-
ditory sensory memory: (a) a very short-lived memory, such as the mem-
ory for tonal loudness just described, and (b) a second auditory sensory
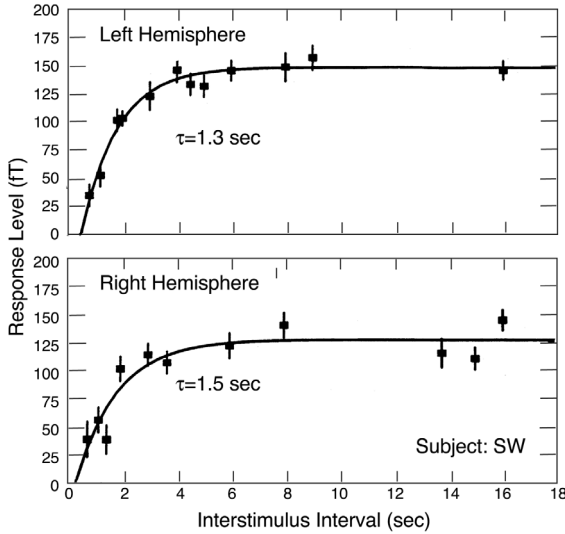memory with a duration on the order of seconds.

FIG. 13.11.   Peak magnetic field strength near the scalp approximately 100 msec after the onset of a tone burst stimulus (the magnetic counterpart to the N100 component in the event-related potential) increases with interstimulus interval, as shown, in both hemispheres of Subject SW. The field sensor was placed over each hemisphere at a location where it monitors activity in the primary auditory cortex. Reprinted with permission from Lu, Z.-L., Williamson, S. J., & Kaufman, L. (1992). Physiological measurements predict the lifetime for human auditory memory of a tone. *Science, 258,* 1668–1670. Copyright © 1992 American Association for the Advancement of Science.

Indeed, it is not obvious that the next-higher auditory memory can be characterized by a time constant in seconds. It might be a limited-capacity memory based on retroactive interference in which new inputs push older material out of memory. In the absence of new auditory input (i.e., silence), periods of silence might themselves be recoded as memory events. This is a much more complex process than simple, exponential passive decay with time, although it may be difficult to distinguish from passive decay when new stimuli arrive at a constant rate. We consider here two instances of higher level auditory memory: one related to the loudness experiment and another that illustrates exponential decay based on retroactive interference and the kinds of significant complications that arise.

Memory for the Mean Loudness of a Tonal Sequence

In the loudness experiment described earlier, the very short term auditory sensory memory decayed in a second or two to the average loudness
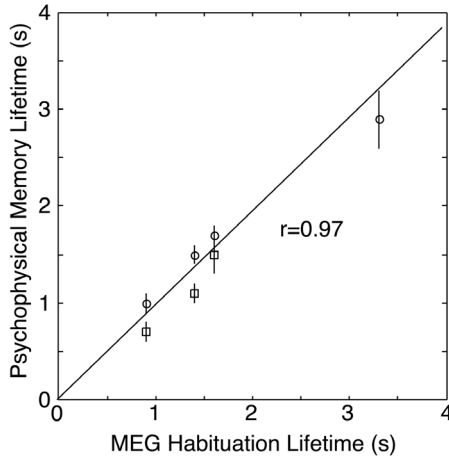
FIG. 13.12.   Agreement across 4 subjects between behavioral lifetimes for the decay of the loudness of a tone following its presentation and physiological lifetimes for the decay of the neuronal activation trace in the primary auditory cortex. Squares denote behavioral lifetimes measured in blocks when the mean loudness of the probe tones was higher that of the test tones, and circles denote the results when the mean loudness was lower. MEG = magnetoencephalography. Reprinted with permission from Lu, Z.-L., Williamson, S. J., & Kaufman, L. (1992). Physiological measurements predict the lifetime for human auditory memory of a tone. *Science, 258,* 1668–1670. Copyright © 1992 American Association for the Advancement of Science.

of the previous tonal sequence. Thus, the very same tone, after a 2- or 3-sec interval during which the very short term auditory memory trace decayed to insignificance, would be judged as louder following a sequence of loud tones and softer following a sequence of less intense tones. Obviously, the memory for the loudness of the previously heard tones in a test block is an auditory memory. In the context of tonal sequences, it has a time constant of many seconds. Using the memory for tonal sequence to establish the baseline to which the probe tones decayed was one of the critical design elements that made the measurement of very short term auditory memory decay so successful.

Short-Term Phonemic Memory

Exponentially Defined Capacity Limit.   We describe here a simple model of an auditory memory (Sperling, 1968) that can be reasonably approximated as a memory for phonemes, and we indicate how it might be studied using MEG. This memory model explains the effect of acoustic similarity in short-term memory experiments (Conrad, 1963; Sperling

& Speelman, 1970): why sequences of similar-sounding letters (such as B, C, D, E, G, P, T, V, and Z) are remembered much less well than sequences of different sounding letters (such as A, B, F, O, Q, R, and Y).

The phonemic short-term memory model is illustrated in Fig. 13.13. Items enter memory and are stored in sequence. A spoken letter sequence "X, Y, Z" would enter memory as six phones: $1 = e$, $2 = ks$, $3 = w$, $4 = ii$, $5 = z$, $6 = ee$. Let i be the index number of a phoneme, counting backward in time from the last phoneme heard. The probability of retrieving recalling the ith most recent phoneme is proportional to $e^{-i/\alpha}$, where α is the memory capacity (in phonemes). The brief silence that separates spoken letters is assumed to be stored without requiring additional space and without loss. A model with discrete, indexed phonemes is appropriate for an experimental procedure in which letters are distinct utterances (as opposed to continuous speech). The probability of correctly recalling a letter depends on which of its constituent phonemes are retrieved. If all constituent phones are retrieved, the letter is recalled correctly. If they are not, an informed guess is made on the basis of the phoneme (if any) that was retrieved. In a stimulus constructed
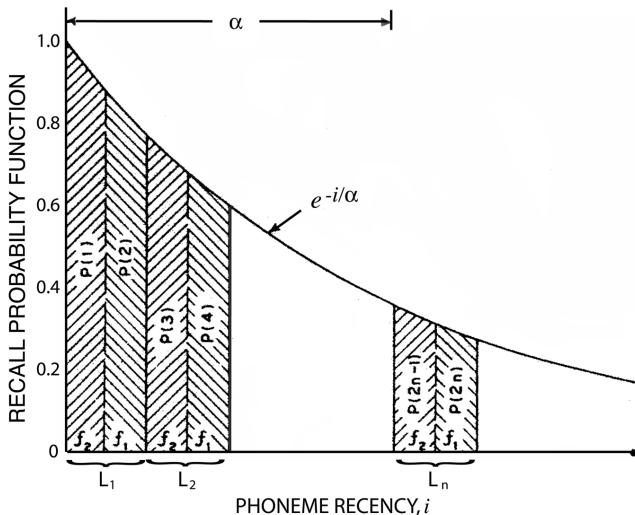

FIG. 13.13. Phonemic model of short-term auditory memory. The abscissa is phonemic recency; the most recent phoneme is numbered 1. The ordinate is the memory strength function; the area under the function describes the phoneme's strength in memory. As a simplification, recall probability (of a phoneme) is taken to be directly proportional to its memory strength. From "Phonemic model of short-term auditory memory," by G. Sperling, 1968, *Proceedings of the 76th Annual Convention of the American Psychological Association*, 3, p. 63. Copyright © 1968 by American Psychological Association.

out of an ideal acoustically unconfusable alphabet, retrieval of just one of a letter's two phonemes suffices for recall of that letter. In an acoustically confusable stimulus (B, T, V, P, Z, T) the phoneme *ee* is useless but nevertheless occupies space in memory. The initial consonant must be retrieved to recall the letter.

The simple phonemic model gives a good account of the acoustic-similarity phenomenon and of the relative difficulty of lists composed of different alphabets. It works especially well when the capacity of memory is tested by *partial reports* in which the listener reports only a subset of characters that is requested by a randomly selected poststimulus cue. The phonemic capacity of this short-term auditory sensory memory is relatively independent of presentation rate in the range of 1 to 4 items per second. This indicates that memory capacity is described in terms of number of phonemes rather than in units of time.

Complications.   When listeners have to make whole reports of the entire presented list, matters get more complicated because of subvocal rehearsal and because of *destructive readout*—a long response interferes more with the items still in memory than does a brief response. Matters get still more complicated when comparing memory for pseudodigits with real digits. Pseudodigits are carefully constructed nonsense syllables than have phonemic properties identical to real digits but are unfamiliar. Memory for pseudodigits is worse than memory for real digits. This indicates that a simple phonemic model of auditory short-term memory cannot give a full account of human performance, because familiarity, a much higher level process than echoic memory, plays a significant role.

The advantage of a reasonably good quantitative description of an auditory short-term memory is that it lends itself to MEG analysis by means of habituation paradigms. In this case, one would be presenting not repetitions of the same tone but repetitions of the same or similar phonemic sequences. If one could localize the phonemic memory illustrated in Fig. 13.13, would that memory use the same mechanisms as the memory for the mean loudness of the tonal sequences used to discover very short term auditory sensory memory? Indeed, to what extent does short-term memory for melodic sequences or for noise bursts share resources with short-term memory for phonemic sequences? These are precisely the sorts of questions that are extremely difficult to answer by means of psychophysics alone and that would benefit from collateral MEG brain-imaging data.

VISUAL SENSORY MEMORY

Visual Iconic Memory

Although this chapter deals primarily with auditory memory, it is useful to compare auditory with visual sensory memory. An unpublished experiment carried out by Sam Williamson's student Wei Yang (1999) is especially relevant. Yang measured the time course of the decay of visual very short term sensory memory (iconic memory) and compared it with the time course of recovery in a visual habituation procedure—a close parallel to Lu et al.'s (1992a) experiment, reviewed earlier.

Stimuli and Results

Yang (1999) chose to measure iconic memory for a brief flash of 8 sine wave patches arrayed in an annular fashion around the fixation point (see Fig. 13.14). Each patch had one of four randomly chosen slants. At a variable interval T after the presentation, a report cue (a pointer) appeared over the fixation point, and it directed the observer to report the slant of the pointed-to sine wave patch. The probability $p(T)$ of a correct report declined with increasing T. To a reasonable approximation, $p(T)$ decayed exponentially (with time constant α_ψ) from an initial level of 91% (which represents memory for seven locations) to a value of 43% that represents a residual memory for about two locations. The average value of α_ψ was about 470 msec. A very interesting ancillary observation was that, with extensive practice, the value of α_ψ appeared to increase, doubling in some cases. Contrary to intuition, very short term visual memory for sine wave patches improves with practice.

For brain recording, Yang (1999) used a two-electrode EEG system of one reference electrode and one occipital placement. To measure recovery from habituation, Yang presented a stimulus consisting of eight sine wave patches (see Fig. 13.14) at various rates. Although there was a problem with noise level in the EEG recording that made determination of the habituation recovery time constant α_ϕ somewhat problematic, Yang reported a high correlation between the time constant of iconic memory decay and the time constant of recovery from habituation. Remarkably, the habituation time constant measured by EEG appeared to increase with practice by the same amount as the time constant of the psychophysically measured decay of iconic memory, suggesting that, indeed, the same neurons were involved in psychophysical memory performance and in physiological habituation.
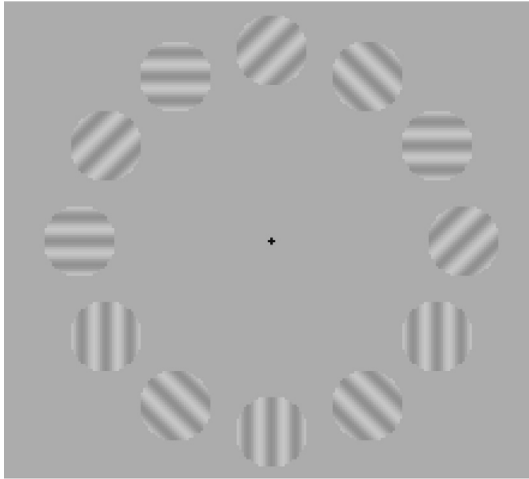
FIG. 13.14.   An array of sine wave patches displayed to the observer in Yang's (1999) psychophysical partial report and electroencephalography habituation procedures. The four orientations are horizontal, vertical, and 45° to the left and right of vertical. The background luminance is 20 cd/m$_2$. The contrast of the sine wave patches is 0.20.

Complications

There are a number of problems not resolved in Yang's (1999) study. For example, although the stimuli to measure the psychophysical and physiological time constants were the same, the habituation was not slant specific (Yang, Kounios, & Bachman, 2000); the EEG recording method did not permit Yang to separate possibly different sources; and there was the EEG noise problem, to which we already alluded. Nevertheless, Yang's thesis represents a promising beginning and suggests that a combined psychophysical and MEG approach to measuring very short term visual sensory memory would very likely succeed.

Higher Level Visual Sensory Memories and MEG

As in the determination of very short term auditory sensory memory, the asymptote to which the very short term visual memory decayed represents a form of longer duration visual sensory memory. In vision, even more than in audition, numerous paradigms have evolved to measure and characterize short-term visual memories (some of which we mentioned in the introductory paragraphs). Combining these paradigms with MEG (and EEG and fMRI) would seem to offer bountiful possibili-

ties for the differentiation of the systems. Obviously, these methods of studying sensory memory have not been fully exploited.

CONCLUSIONS

The sensory memory mechanism suggested by our studies is basically a strength model that has appeared in the psychology literature quite frequently (Loftus, Duncan, & Gehrig, 1992; Reeves & Sperling, 1986). Recent research applying the habituation methods to the human visual system found that each responding area of the brain habituates, indicating memory for past stimulation, and the lifetimes are organized in a hierarchy with lifetimes ranging from a few hundred milliseconds in the sensory areas to 10–30 sec in the parietal, temporal, and prefrontal areas (Uusitalo et al., 1996). The links between the psychological functions and the MEG response strengths of these cell populations remain to be established.

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