Biosystems II: Neuroscience

Sensory Systems

Lecture 1

Sensation, Perception and Psychophysics

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Outline

1. The relationship between sensory systems and other parts of the brain (Fig.1-1)

2. Sensory systems mediate four basic attributes (modality, location, intensity and timing) of a stimulus that can be correlated with a sensation (Fig.1-2)

3. Sensory modality is determined by the stimulus energy

- a) Modality is encoded by a labeled line code (Fig.1-3)
- b) Receptors transduce specific types of energy into an electrical signal (action potentials) (Fig.1-4)
- c) Each receptor responds to a narrow range of stimulus energy (Fig.1-5)

4. The spatial distribution of sensory neurons activated by a stimulus conveys information about the stimulus location (Fig.1-6,1-7)

5. Intensity of sensation is determined by the stimulus amplitude

Stimulus intensity is encoded by the frequency of action potentials in sensory nerves (Fig.1-8)

- 6. Psychophysical laws govern the perception of stimulus intensity (Fig.1-9)
- 7. Sensory systems have a common plan

a) Sensory information is conveyed by populations of sensory neuron acting together

Examples: *auditory* (Fig.1-10), *somatosensory* (Fig.1-6), *visual* (Fig.1-7)

- b) Sensory systems process information in a hierarchical manner via a series of relay nuclei (Fig.1-11)
- 8. Perception is brain's interpretation of the external world
 - a) Visual example: Perception is different from sensation (Fig.1-12)
 - b) Categorical perception of speech (Fig.1-13, 1-14)

Overview of Sensory Systems



Sensory systems and other parts of the brain

The major components of the system and their nervous functional relationships. Diagram of the major components of the central and peripheral nervous systems and their functional relationships. Stimuli from the environment convey information to processing circuits within the brain and spinal cord which in turn interpret their significance and send signals to peripheral effectors that move the body or adjust the workings of its internal organs.



Sensory systems mediate four basic attributes of a stimulus (modality, location, intensity and timing)

The sensory systems encode four elementary attributes of stimuli-modality, location, intensity, and timing-which are manifested in sensation. The four attributes of sensation are illustrated in this figure for the somatosensory modality of touch.

A. In the human hand the submodalities of touch are sensed by four types of mechanoreceptors. Specific tactile sensations occur when distinct types of receptors are activated. Firing of all four receptors produces the sensation of contact with an object. Selective activation of Merkel cells and Ruffini endings produces sensations of steady pressure on the skin above the receptor. When the same patterns of firing occur only in Meissner's and Pacinian corpuscles, the tingling sensation of vibration is perceived.

B. Location and other spatial properties of a stimulus are encoded by the spatial distribution of the population of activated receptors. Each receptor fires action potentials only when the skin close to its sensory terminals is touched, ie, when a stimulus impinges on the receptor's receptive field. The receptive fields of mechanoreceptors-shown as red areas on the finger tip-differ in size and response to touch. Merkel cells and Meissner's corpuscles provide the most precise localization of touch, as they have the smallest receptive fields and are also more sensitive to pressure applied by a small probe.

C. The intensity of stimulation is signaled by the firing rates of individual receptors, and the duration of stimulation is signaled by the time course of firing. The spike trains below each finger indicate the action potentials evoked by pressure from a small probe at the center of the receptive field. Two of these receptors (Meissner's and Pacinian corpuscles) adapt rapidly to constant stimulation, while the other two adapt slowly.



Modality is encoded by a labeled line code

Various sensory receptors have different morphologies and organization.



Sensory modality is determined by the stimulus energy

Receptors transduce specific types of energy into an electrical signal (action potentials).

Sensory system	Modality	Stimulus energy	Receptor class ¹	Receptor cell types ²
Visual	Vision	Light	Photoreceptor	Rods, cones
Auditory	Hearing	Sound	Mechanoreceptor	Hair cells (cochlea)
Vestibular	Balance	Gravity	Mechanoreceptor	Hair cells (vestibular labyrinth)
Somatosensory	Somatic senses: Touch Proprioception Temperature sense Pain	Pressure Displacement Thermal Chemical, thermal, or mechanical	Mechanoreceptor Mechanoreceptor Thermoreceptor Chemoreceptor, thermoreceptor, or mechanoreceptor	Dorsal root ganglion neurons Cutaneous mechanoreceptors Muscle and joint receptors Cold and warm receptors Polymodal, thermal, and mechanical nociceptors
	Itch	Chemical	Chemoreceptor	Chemical nociceptor
Gustatory	Taste	Chemical	Chemoreceptor	Taste buds
Olfactory	Smell	Chemical	Chemoreceptor	Olfactory sensory neurons

Each receptor responds to a narrow range of stimulus energy

Each receptor responds to a narrow range of stimulus energy. Tuning curves of sensory receptors measure the minimum amplitude of stimulation needed to activate a sensory receptor over a range of stimulus energies. Each sensory receptor responds optimally to a narrow range of intensities of a single type of energy. The tuning curve shown here is for an auditory receptor most sensitive to sound at 2.0 kHz Higher and lower frequencies require stronger amplitude stimuli to evoke a response from the receptor. The tuning curve also illustrates the range of stimulus energies that can excite the receptor when presented at a given intensity In this example, as the loudness of the tone rises, the receptor responds to a greater range of auditory frequencies. However, the receptor provides a stronger response at the preferred frequency than at other frequencies. Graded responses over the energy band- width provide a mechanism for sensory neurons to signal the particular type of stimulus energy that is presented. The auditory system tunes receptors in distinct parts of the sensory epithelium to different frequencies of sound. The relative response amplitude of these receptors to tones signals the sound frequency.

100 75 Sound intensity (dB) 50 25 Threshold **Characteristic Frequency** 1.5 2.0 5.0 0.5 1.0 10 Sound frequency (kHz)

Tuning curve (receptive field) of an auditory neuron

The spatial distribution of sensory neurons activated by a stimulus conveys information about the stimulus location

Structural basis of the receptive field of receptors for the sense of touch. The receptive field of a touchsensitive neuron in the skin includes the sensory transduction apparatus in the terminals nerve ant the surrounding skin in which the terminals are located. A patch of skin contains many overlapping receptive fields individual innervated by sensory nerve fibers. When this region is touched, action potentials are initiated at the node of Ranvier closest to the nerve terminals in the skin They are conducted past the cell body, located in the dorsal root ganglion, to the synaptic terminals in the spinal cord or medulla



The density of sensory receptors and the size of receptive field determine the resolution of sensory systems

The density of sensory receptors in the retina and the size of the receptive field for each receptor deter- mine the resolution of a visual image. Each square or pixel in these images represents a receptive field. The gray scale is proportional to the average light intensity in that region of the image. White pixels represent receptors with the highest firing rate, while black pixels represent receptors with the lowest firing rate. If there are a small number of receptors and each spans a large area of the scene, the result is a fuzzy, very schematic representation of the scene (A). There is no cue from this representation what the picture actually shows. As the density of receptors increases, and the size of the receptive field of each receptor decreases, the spatial detail be- comes clearer (B-D). Clouds, mountains, trees, grasslands, and water emerge, until the scenery is identifiable as Yosemite valley. However, the increased resolution comes at the cost of enlarging the total size of the receptor population.

The brain resolves the conflict between information over-load from a huge number of receptors and the need for resolution of spatial detail by having a higher density of receptors in regions of the body where high resolution of detail is behaviorally important and using progressively lower numbers of receptors in surrounding regions. Spatial resolution for vision and touch parallels the density of receptors in the retina and skin. Spatial resolution on the finger-tips approaches that of the image in **D**. Receptor density and tactile sensitivity on the palm is similar to the resolution in **C**. Resolution of spatial detail on the forearm approaches that in image **B**, while on the trunk it is similar to that in image **A**.



C 14,400 receptors

D 160,000 receptor





The firing rates of sensory nerves encode the stimulus magnitude.

A. The number of action potentials per second in a slowly adapting mechanoreceptor action the amount of skin indentation. This receptor required a minimum indentation of 80 um to respond. The relationship between increases in frequency of firing and pressure or the skin is linear.

B. Estimates made by a human subject of the magnitude of sensation produced by pressure on the hand increase linearly as a function of skin indentation. The relation between a subject's estimate of the intensity of the stimulus and its strength resembles the relation between the discharge frequency of a sensory neuron and the stimulus strength. These data suggest that the neural coding of stimulus intensity is faithfully transmitted from the peripheral receptors to the cortical centers that mediate sensation.

Psychometric Function



Sensory thresholds and the just noticeable difference (JND) between stimuli that differ in intensity, frequency, or other parametric features are quantifiable.

A. The psychopathic function plots the percentage of stimuli detected by a human observer as a function of stimulus intensity. Threshold is defined as the stimulus intensity detected on 50% of the trials.

B. The absolute sensory threshold (curve b) is an idealized relationship between stimulus intensity and the probability of stimulus detection. If the sensory system's ability to detect the stimulus is increased or the subject's response criterion is decreased, curve a would be observed; curve c illustrates the converse.

Sensory thresholds are modified by psychophysical and pharmacological factors

Sensory thresholds depend upon psychological factors and the context in which the stimulus occurs. The threshold for pain is often heightened during competitive sports or in childbirth, as reflected in a shift in the psychopathic function to higher stimulus intensities (Fig.1-9B, curve c). Similarly, sensory thresholds can be lowered. Consider a runner at the starting line prepared to respond to the starter's shot. It is advantageous to respond as rapidly as possible, and the slightest noise resembling the start gun may trigger a leap to action. The runner's response to a lower stimulus intensity is represented as a shift in the psychopathic function to lower stimulus intensities (Fig.1-9B, curve a).

The modifiability of sensory thresholds can be under- stood by considering two aspects of sensation: (1) the absolute detectability of the stimulus and (2) the criterion the subject uses to evaluate whether a stimulus is present. Detectability measures the capacity of a sensory system to process a stimulus, whereas the response criterion reflects an attitude or bias of the subject toward the sensory experience.

In the 1950s Wilson Tanner and John Swets developed the signal detection theory to explain the observation that subjects often report a sensory experience (i.e, detection of a stimulus) when no stimulus is actually presented. A consequence of this decrease in response criterion (or bias) is that a subject is more likely to make mistakes. For example, the runner at the starting block is likely to make a false start in a crucial race. Similarly, elderly patients with sensory loss may falsely report feeling stimuli tested in a neurological examination as a denial of aging. The opposite condition-ignoring the occurrence of a stimulus such as pain-is also common.

The separate measures of stimulus detectability and response criterion can be combined with the concept of thresh- old to explain the mechanisms of drug action. For example, morphine, a potent analgesic, elevates the pain threshold both by reducing the detectability of a painful stimulus and by elevating the criterion the subject uses to determine whether a stimulus is painful or not. Marijuana also increases pain thresholds, but does so by increasing the response criterion rather than decreasing stimulus detectability-the stimulus is just as painful but the subject is more tolerant.

Sensory information is conveyed by populations of sensory neurons

Sensory information is conveyed by populations of sensory neuron acting together: Examples of auditory nerve fibers.

Frequency tuning curves of six different fibers in the auditory nerve. Each graph plots, across all frequencies to which the fiber responds, the minimum sound level required to increase the fiber's firing rate above its level. The lowest spontaneous firing point in the plot is the intensity to which the neuron will respond. The frequency at this point is called the neuron's characteristic frequency.



Sensory systems process information in a hierarchical manner

Sensory systems process information in a hierarchical manner via a series of relay nuclei. The functional and anatomical organization of sensory processing networks is hierarchical. Stimulation of a population of receptors initiates signals that are transmitted through a series of relay nuclei to higher centers in the brain (only one relay is shown). At each processing stage the signals are integrated into more complex sensory information.

A. In the somatosensory system excitatory synaptic connections from each receptor in the skin are widely distributed to a large group of postsynaptic neurons at each relay nucleus. 1). Each relay neuron receives sensory input from a large group of receptors and therefore has a bigger receptive field than any of the input neurons. 2). Receptors closest to the stimulus respond more vigorously than distant receptors.

B. 1). The addition of inhibitory interneurons (gray) narrows the discharge zone. 2). On either side of the excitatory region the discharge rate is driven below the resting level by feedback inhibition.



Perception is brain's interpretation of the external world

(Visual Example)

Categorical perception of speech.

(*left plot*) Stimuli from a voiced-voiceless continuum varying in voice onset time (VOT). Humans perceive the 0-msec VOT stimulus as /da/, whereas the +40-msec VOT and +80-msec VOT stimuli are perceived as /ta/. The onset of voicing (V) and the onset of the burst (B) are marked.

(*right plot*) Humans' and animals' identification functions for two series ranging from a voiced to a voiceless phonetic unit (/d/ to /t/ and /g/ to /k/) showing that animals' perceptual boundaries correspond to humans' phonetic boundaries.



Linguistic experience alters phonetic perception in infants

(Lecture 1 reading: Kuhl et al. Science 1992)



Fig. 1. Six-month-old infants from America and Sweden were tested with two sets of vowel stimuli, American English /i/ and Swedish /y/. Each set included an exceptionally good instance of the vowel (the prototype) and 32 variants that formed four rings (eight stimuli each) around the prototype (8).



Fig. 2. Results showing an effect of language experience on young infants' perception of speech. Two groups of 6-month-old infants, (A) American and (B) Swedish, were tested with two different vowel prototypes, American English /i/ and Swedish /y/. The mean percentage of trials in which infants equated variants on each of the four rings to the prototype is plotted. Infants from both countries produced a stronger magnet effect (equated variants to the prototype more often) for the native-language vowel prototype when compared to the foreign-language vowel prototype. (Error bars = standard error.)

Summary of Lecture 1

- Sensory systems have a common plan
 - Sensory information is conveyed an array of receptors, each of which responds to a narrow range of stimulus energy
- Sensation and perception can be quantitatively studied by psychophysics
- Perception is brain's interpretation of the external world

Readings:

(1) *Principles of Neural Science*, by E.R. Kandel, J.H. Schwartz and T.M. Jessell, 2000.
4th Ed. (Chapter 21)
(2) Kuhl et al. Linguistic experience alters phonetic perception in infants by 6 months of age. *Science* 255(5044):606-8, 1992

We propose the following model for the role of Sos in R7 development (Fig. 5). The Sos gene product may be activated by the tyrosine kinase encoded by sev. This facilitates the activation of Ras. Ras, in turn, acts upon as yet unidentified substrates and leads to a commitment to the R7 cell fate. A GAP-like molecule has not yet been found in this pathway but is proposed in this model by analogy to other Ras pathways. The data presented here do not rule out the possibility that sevenless also acts through a molecule other than Sos.

Previous work in mammalian systems suggests the Ras pathway might operate downstream of receptor tyrosine kinases. A dominant-negative ras gene, for example, was able to interfere with oncogenic transformation by several tyrosine kinase-encoding oncogenes (21). Furthermore, genetic analysis has demonstrated a function for Ras in Caenorhabditis elegans vulval development. A ras gene, let-60, has been shown to act downstream of a receptor tyrosine kinase encoded by the let-23 gene (22, 23). Results presented here implicate Ras in Drosophila neuronal development as well. Thus the Ras pathway may be a general component of many developmental systems.

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namely, the child's understanding that pho-

netic units are used contrastively to specify

well before the acquisition of language (4),

infants' phonetic perception has been altered

by exposure to a specific language. Infants in

America and Sweden were tested with both

native- and foreign-language vowel sounds.

Infants from both countries exhibited a lan-

guage-specific pattern of phonetic percep-

tion. Thus, linguistic experience alters phonetic perception at an unexpectedly early

age, and this has implications for theories of speech perception and the development of

The present test focused on phonetic "prototypes," speech sounds that are identi-

fied by adult speakers of a given language as

ideal representatives of a given phonetic

category. Experiments with adults have

shown that phonetic prototypes function

like "perceptual magnets" in speech percep-

tion (5). The magnet effect causes other

We show here that by 6 months of age,

different word meanings (3).

Linguistic Experience Alters Phonetic Perception in Infants by 6 Months of Age

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Linguistic experience affects phonetic perception. However, the critical period during which experience affects perception and the mechanism responsible for these effects are unknown. This study of 6-month-old infants from two countries, the United States and Sweden, shows that exposure to a specific language in the first half year of life alters infants' phonetic perception.

guage?

language.

T THE BEGINNING OF LIFE, HUMAN infants exhibit a similar pattern of phonetic perception regardless of the language environment in which they are born (1). They discern differences between the phonetic units of many different languages, including languages they have never heard, indicating that the perception of human speech is strongly influenced by innate factors. However, by adulthood, linguistic experience has had a profound effect on speech perception. Exposure to a specific language results in a reduction in the ability to perceive differences between speech sounds that do not differentiate between words in one's native language (2, 3). Adult native speakers of Japanese, for example, have great difficulty in discriminating between words containing English /r/ and /l/, phonetic segments that belong to the same underlying category in Japanese (2). Adults thus exhibit a pattern of phonetic perception that is specific to their native language, whereas infants initially demonstrate a pattern of phonetic perception that is universal. At what point in development does linguistic experience alter phonetic perception, and

Downloaded from www.sciencemag.org on January 5, what is the nature of the change brought about by experience with a particular lan-Previous studies suggested that the effects of linguistic experience on phonetic perception occur at about 1 year of age (3), coinciding with the age at which children begin to acquire word meanings (4). It was thus proposed that the change from a language-universal pattern of phonetic perception to one that is language-specific was brought about by the emergence of a milestone in the child's linguistic development,

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Fig. 1. Six-month-old infants from America and Sweden were tested with two sets of vowel stimuli, American English /i/ and Swedish /y/. Each set included an exceptionally good instance of the vowel (the prototype) and 32 variants that formed four rings (eight stimuli each) around the prototype (8).

nonprototypic members of the category to be perceived as more similar to the category prototype than to each other, even though the actual physical differences between the stimuli are equal (5).

It has been shown that 6-month-old American infants tested with a prototype and a nonprototype of an American English vowel duplicate the magnet effect shown in adults (5). A critical question for theory is whether this infant effect reflects languagespecific or language-universal perception. Is experience with a specific language necessary, or would 6-month-olds show the magnet effect for all vowel prototypes regardless of language experience? We examined this question by conducting a cross-language study in 6-month-old infants from two countries using both native- and foreignlanguage sounds.

We tested infants in the United States and Sweden on two vowels. One vowel (American English /i/, the front unrounded vowel in the word "fee") constituted a nativelanguage prototype for American adults and a nonprototype for Swedish adults; the other vowel (Swedish /y/, the front rounded vowel in the Swedish word "fy") constituted a native-language prototype for Swedish adults and a nonprototype for American adults (6). If experience with language in the first half year of life alters phonetic perception, a specific pattern is predicted in which the two groups of infants differ: (i) American infants would treat the American English /i/ as a prototype and the Swedish /y/ as a nonprototype, exhibiting a stronger magnet effect for American English /i/, (ii) Swedish infants would treat the Swedish /y/ as a prototype and the American English /i/ as a nonprototype, exhibiting a stronger magnet effect for Swedish /y/. However, if the results show any other pattern (if both groups of infants exhibit the magnet effect equally for both vowels or more strongly for the same one of the two vowels), then we would have no evidence that linguistic experience alters phonetic perception by 6 months.

We computer-synthesized prototypes of the American English /i/ and Swedish /y/vowels (7). Each prototype was then modified to create 32 additional variants that were acoustically similar, but not identical, to each prototype (Fig. 1) (8). The magnet effect was assessed by testing infants' perception of the similarity between each prototype and its variants.

Infants sat on a parent's lap and watched an assistant, seated on the infant's right, manipulate silent toys. Each infant listened to one of the vowel prototypes (either American English /i/ or Swedish /y/), continuously repeated every 2 s from a loudspeaker located on the infant's left. In the training phase infants learned to produce a head-turn (HT) toward the loudspeaker when they heard the prototype vowel change (9). Two kinds of 6-s trials occurred. During change trials the prototype vowel was changed to one of its variants and infants' HT responses were rewarded by the activation of a toy bear that pounded a miniature drum. An equal number of control trials occurred in which the prototype vowel was not changed and infants' falsepositive HTs were tabulated. Safeguards against bias on the part of the parent, the experimenter, and the assistant were stringent to ensure that these individuals did not influence infants' HTs (5). The test phase consisted of 64 trials, 32 change trials (one for each variant), and 32 control trials, presented in random order. The perceptual magnet effect was indicated by the degree to which infants responded to each prototype's variants as though they were identical to it, that is, trials in which infants did not detect a difference between a prototype and its variants.

Sixty-four 6-month-old infants were tested, 32 in the United States and 32 in Sweden. In each country, 16 infants were trained and tested with the American English /i/ prototype, and 16 were trained and tested with the Swedish /y/ prototype (10). Except for the critical variable of the language experience of the infants, all components of the experimental test remained the same in the two countries. The speech testing apparatus, computer equipment, and the three experimenters were physically moved from one site (the University of Washington, Seattle, Washington) to the other (Stockholm University, Stockholm, Sweden) for the duration of the tests. The same

test protocol and stimuli were used.

The results confirmed that linguistic experience in the first half year of life alters infants' perception of speech sounds. Infants from both countries showed a significantly stronger magnet effect for their native-language prototype (Fig. 2). American infants perceived the American English /i/ prototype as identical to its variants on 66.9% of all trials; in contrast, they perceived the Swedish /y/ prototype as identical to its variants on 50.6% of the trials. Swedish infants perceived the Swedish /y/ prototype as identical to its variants on 66.2% of all trials; in contrast, they treated the American English /i/ prototype as identical to its variants on 55.9% of the trials. Infants' responses to the two sets of stimuli were submitted to a two-way analysis of variance to assess the effects of infants' language environment (American English versus Swedish) and the prototype vowel tested (American English /i/ versus Swedish /y/). The interaction to tween the two factors was highly significant



Fig. 2. Results showing an effect of language experience on young infants' perception of speech. Two groups of 6-month-old infants, (A) American and (B) Swedish, were tested with two different vowel prototypes, American English /i/ and Swedish /y. The mean percentage of trials in which infants equated variants on each of the four rings to the prototype is plotted. Infants from both countries produced a stronger magnet effect (equated variants to the prototype more often) for the native-language vowel prototype when compared to the foreign-language vowel prototype. (Error bars = standard error.)

[F(1, 60) = 20.107, P < 0.0001]; neither of the main effects was significant [language environment: F(1, 60) = 0.526, P > 0.40; vowel: F(1, 60) = 0.978, P > 0.30] (11).

The findings demonstrate that by 6 months infants exhibit a strong magnet effect only for native-language phonetic prototypes. By this age foreign-language prototypes have begun to function like nonprototypes in the native language (12). The results show that the initial appearance of a language-specific pattern of phonetic perception does not depend on the emergence of contrastive phonology and an understanding of word meaning. Rather, infants' language-specific phonetic categories may initially emerge from an underlying cognitive capacity and proclivity to store in memory biologically important stimuli (13) and from the ability to represent information in the form of a prototype (5).

The findings also suggest the process by which linguistic experience alters phonetic perception. Linguistic experience shrinks the perceptual distance around a nativelanguage prototype, in relation to a nonprototype, causing the prototype to perceptually assimilate similar sounds (5). The nativelanguage prototype's magnet effect may help explain why older children and adults fail to discriminate two speech sounds from a foreign language when both sounds resemble a native-language prototype for the subject (such as /r/ and /l/ for native Japanese speakers) (2, 3).

Infants demonstrate a capacity to learn simply by being exposed to language during the first half year of life, before the time that they have uttered meaningful words. By 6 months of age, linguistic experience has resulted in language-specific phonetic prototypes that assist infants in organizing speech sounds into categories. They are in place when infants begin to acquire word meanings toward the end of the first year. Phonetic prototypes would thus appear to be fundamental perceptual-cognitive building blocks rather than by-products of language acquisition.

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- Many detailed studies of language acquisition have shown that infants first begin to comprehend and produce words after 9 months of age [E. Bates, I. Bretherton, L. Snyder, From First Words to Grammar (Cambridge Univ. Press, Cambridge, 1988)]. For word production, the mean age for acquiring ten words = 15.1 months (SD = 1.76), for 50 words = 19.6 months (SD = 2.89) [K. Nelson, Monogr. Soc. Res. Child Dev. 38, 1 (1973)]; for word comprehension, the mean age for acquiring ten words = 10.5 months (SD = 0.92), for 50 words = 13.2 months (SD = 1.53) [H. Benedict, J. Child Lang. 6, 183 (1979)].
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- 6. The status of the two vowel prototypes in American English and Swedish was experimentally assessed. Adult native speakers of American English and Swedish were asked three questions about each prototype: (i) whether it was a sound used in their language, (ii) the category it belonged to, and (iii) its representativeness as a member of that category using a scale from "1" (poor) to "7" (good). American listeners unanimously judged the *i*/i prototype as an English vowel, giving it an average rating of 5.4 as a member of the English *i*/i category. They unanimously rated the Swedish /y/ prototype as not in their language. Swedish adults unanimously judged the /y/ prototype as not in their language. Swedish adults unanimously judged the /y/ prototype as 1 average rating of 4.7 as a member of the category /y/. They rated the American English *i*/i

prototype as present in the language but ambiguous with regard to category; /i/ was given an average rating of 2.6 as a member of the Swedish /e/ category and 1.8 as a member of the Swedish /i/ category. These ratings are typical of native-language nonprototypes (5).

- The five formant frequencies of English /i/ were 270, 2290, 3010, 3300, and 3850 Hz; for Swedish /y/, 220, 1980, 2640, 3340, and 3720 Hz.
- 8. Variants were created by manipulating the first two formant frequencies [scaled in mels (5)] in uniform, psychophysically equal steps. The variants formed four rings that were 30, 60, 90, and 120 mels, respectively, from each prototype.
- 9. During change trials in training, the prototype vowel was changed to a variant from the fourth ring around the prototype and this stimulus change was paired with the reinforcer, causing infants to turn toward the reinforcer. Once infants were producing HTs reliably on change trials, control trials were introduced. Infants had to meet a criterion of seven out of eight consecutive correct trials (including both change and control trials) during training, and produce no more than 35% false-positive responses once the test started, to be included in the study.
- 10. Mean age of infants: 6.5 months (range = 6.1 to 6.9) for American infants tested on /i/; 6.5 months (range = 6.0 to 7.0) for Swedish infants tested on /i/; 6.7 months (range = 6.2 to 7.1) for American infants tested on /y/; 6.6 months (range = 6.1 to 6.9) for Swedish infants tested on /y/.
- 11. Follow-up tests indicated that for both the American and Swedish infants there was a significant difference between the vowels, P < 0.05.
- 12. We have not yet determined whether prototypes for all vowels (or a subset of them) exist at birth and are modified by 6 months due to linguistic experience or whether prototypes are initially absent and subsequently formed by 6 months as a result of language experience.
- Studies suggest that infants under 3 months are capable of remembering faces, voices, and certain acoustic characteristics of speech [M. E. Barrera and D. Maurer, Child Dev. 52, 714 (1981); A. J. DeCasper and W. P. Fifer, Science 208, 1174 (1980); J. Mehler et al., Cognition 29, 143 (1988); A. N. Meltzoff, P. K. Kuhl, M. K. Moore, in Neuborn Attention, M. J. S. Weiss and P. R. Zelazo, Eds. (Ablex, Norwood, NJ, 1991), pp. 377-411].
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