A “grandmother cell” is a hypothetical neuron that responds only to a highly complex, specific, and meaningful stimulus, such as the image of one’s grandmother. The term originated in a parable Jerry Lettvin told in 1967. A similar concept had been systematically developed a few years earlier by Jerzy Konorski who called such cells “gnostic” units. This essay discusses the origin, influence, and current status of these terms and of the alternative view that complex stimuli are represented by the pattern of firing across ensembles of neurons. NEUROSCIENTIST 8(5):512–518, 2002. DOI: 10.1177/1073858402237175

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The term “grandmother cell” refers to a neuron that would respond only to a specific, complex, and meaningful stimulus, that is, to a single percept or even a single concept. As originally conceived, a grandmother cell was multimodal, but the term came to be used mostly for representing a visual percept. As we shall see, the term arose because the first such neuron was postulated to represent a grandmother. There might be many grandmother cells responding to a specific stimulus, such as one grandmother, but their response properties would be the same. Because of this redundancy, the loss of a grandmother cell or two might not result in loss of the percept. “Coding by grandmother cells” is at the other extreme from “ensemble,” “coarse,” or “population” coding in which a grandmother or other stimulus is coded by the pattern of activity over a group of neurons. In ensemble coding, there are no “grandmother cells” that detect the unique collection of features that characterize a grandmother. Rather, each member of the ensemble responds somewhat differently, for example, to a granny’s wrinkles, white hair, or to several different old women; the coding of a specific grandmother is done by a unique pattern of activation across the ensemble.

Starting in the early 1970s, the term grandmother cell moved from laboratory jargon and jokes into neuroscience journals and serious discussions of the bases of pattern perception (e.g., Barlow 1972; Blakemore 1973; Anstis 1975; Frisby 1980; Marr 1982; Churchland 1986). The term is now nearly ubiquitous in introductory neuroscience and vision textbooks, where it often plays the role of straw man or foil for a discussion of ensemble or coarse coding theories of sensory representation (e.g., Cowey 1994; Gazzaniga and others 1998; Rozenzweig and others 1999). This essay considers the origins of the term grandmother cell and similar expressions and, more briefly, the roots of ideas about ensemble coding.

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Konorski predicted the existence of single neurons sensitive to complex stimuli such as faces, hands, emotional expressions, animate objects, locations, and so on (see Fig. 2). He called them “gnostic” neurons, and they were virtually identical to what later were called grandmother cells. He suggested that the gnostic neurons were organized into specific areas of the cerebral cortex he termed “gnostic fields.” That is, he predicted (correctly in many cases) the existence of areas of the cortex devoted to the representations of such things as faces, emotional expressions, places, and spatial relations. Destruction of a gnostic field would lead, he predicted, to what were later described as category-specific agnosias. Furthermore, he localized many of these gnostic fields, such as the face field in the ventral temporal cortex and the space...
field in the posterior parietal cortex (Fig. 3). Overall, these gnostic fields and their locations are remarkably similar to contemporary views of the putative functions of extra-striate visual cortex based on monkey single neuron studies and human imaging experiments (e.g., Caramazza 2000; Martin and others 2000).

At the time of their publication, there was nothing in the literature like Konorski’s ideas of highly specialized perceptual neurons in mammals or of areas of the cortex devoted to the representations of particular classes of visual stimuli. In retrospect, however, it is possible to delineate the origins of Konorski’s speculations.

Konorski’s views of the neural organization of perception were a synthesis and extension of three lines of work in the decade before the publication of his book. The first was Hubel and Wiesel’s (1962, 1965) demonstration of the hierarchical processing of sensory information in the geniculo-striate system. In their schema, as one proceeds from center-surround to simple receptive fields and then to complex and then the (now revised) hypercomplex ones, both the selectivity of the cells and their ability to generalize across the retina increase. The possibility that this hierarchy of increasing stimulus specificity continues beyond V2 and V3 was made explicit in their 1965 article, which is repeatedly cited by Konorski. That article ends as follows:

How far such analysis can be carried is anyone’s guess, but it is clear that the transformations occurring in these three cortical areas [V1, V2 and V3] go only a short way toward accounting for the perception of shapes encountered in everyday life. (p. 286)

A second line of inspiration for Konorski’s ideas was the research by Karl Pribram and his students, particularly Mort Mishkin, on the cognitive effects of lesions on what was then called “association cortex” in monkeys. From his close association with Hal Rosvold and Mishkin (both commented on earlier drafts of the book), Konorski was well aware that lesions of the inferior temporal cortex produced specific impairments in visual cognition in monkeys (Mishkin 1966) and that similar areas of association cortex existed for audition and somesthesis. Today, at the annual meeting of the Society for Neuroscience, there are multiple sessions on inferior temporal cortex under the general rubric of “Vision.” However, at that time most visual neurophysiologists had never heard of this area and did not realize that it had visual functions, let alone that it sat at the top of a series of hierarchically arranged extra-striate visual areas. Indeed, although V2 and V3 had been described, no other extra-striate visual areas such as MT or V4 were known until 1971 (Allman and Kaas 1971). Citing Pribram and Mishkin (1955), Konorski (1967) wrote:

In monkeys the gnostic visual area seems to be localized in inferotemporal cortex, as judged from numerous experimental results in which ablations of this region produced impairment of visual discrimination. (p. 123)

The third line of evidence for his theories of gnostic neurons and areas came from Konorski’s familiarity with the various agnosias that follow cortical lesions in humans from his own clinical experience, from the Western neuropsychological literature, and from Luria’s work in the Soviet Union. He was aware of both the symptomatic specificity of some cases of agnosia and their tendency to be localizable. Furthermore, unlike most contemporary neuropsychologists and neurophysiologists, he was aware of the similarity of human agnosias to the effects of experimental lesions in monkeys. For example, he directly related prosopagnosia or face agnosia after ventral temporal lesions in humans to the visual learning deficits in monkeys after inferior temporal lesions.
In summary, Konorski's prophetic ideas on gnostic neurons and gnostic fields came from a bold extension of Hubel and Weisel's findings to account for specific cognitive effects of specific lesions in monkeys and humans. Konorski's book received a long and laudatory review in Science (Gross 1968). However, for at least the next decade virtually all the many citations to the book were to the parts concerned with learning rather than perception; learning theory still dominated American psychology. As described in the next section, the ideas on gnostic neurons did influence one laboratory, namely, the laboratory that first reported (the predicted) neurons in the IT cortex that selectively respond to faces and hands.

In the last decade, gnostic cells have begun to be commonly mentioned in textbooks and in the vision

Fig. 2. “Particular categories of visual stimulus-objects probably represented in different gnostic fields” (Konorski 1967).
and pattern recognition literature, usually as synonyms for grandmother cells and usually in the context of inferior temporal cortex cells.

**The Discovery of Face and Hand Selective Cells in the Inferior Temporal Cortex**

In the early 1970s, my colleagues and I working at M.I.T. in Cambridge, Massachusetts, reported visual neurons in the inferior temporal cortex of the monkey that fired selectively to hands and faces (Gross and others 1969, 1972; Gross 1992a). These observations were probably primed by our familiarity with Konorski’s gnostic units as well as the propinquity of Lettvin’s work on detectors in the frog’s eye (Lettvin and others 1959, 1961) also at M.I.T., Hubel and Weisel’s discoveries on the hierarchical processing in cats and monkeys across the river in Boston at Harvard Medical School, and local talk about grandmother cells. Starting 10 years later, these findings were replicated and extended in a number of laboratories (e.g., Perrett and others 1982; Rolls 1984; Yamane and others 1988) and were often viewed as evidence for grandmother cells. Konorski (1974) himself saw them as confirming his ideas of gnostic cells. For some time, these cells were the strongest evidence for the existence of grandmother/gnostic cells. However, there was little good evidence for cells from monkeys that are selective for other visual objects important or common for monkeys such as fruit, tree branches, monkey genitalia, or other features in their natural environments. Nonetheless, inferior temporal cells can be trained to show great specificity for arbitrary visual objects, and these would seem to fit the requirements of gnostic/grandmother cells (e.g., Logothetis and Sheinberg 1996; Tanaka 1996). Furthermore, there is now good evidence for cells in the human hippocampus that have highly selective responses to gnostic categories (Gross 2000; Kreiman and others 2000) including highly selective responses to individual human faces (Kreiman and others 2001).

However, most of the reported face-selective cells do not really fit a very strict criteria of grandmother/gnostic cells in representing a specific percept, that is, a cell narrowly selective for one face and only one face across transformations of size, orientation, and color (Desimone 1991; Gross 1992). Even the most selective face cells usually also discharge, if more weakly, to a variety of individual faces. Furthermore, face-selective cells often vary in their responsiveness to different aspects of faces, suggesting that they form ensembles for the coarse or distributed coding of faces rather than detectors for specific faces. Thus, a specific grandmother may be represented by a specialized ensemble of grandmother or near grandmother cells (Desimone 1991; Gross 1992).

There are two reasons why the members of face-coding ensembles may appear more specialized than the members of other stimulus-encoding ensembles, that is, why there are many more face cells than banana cells. First, it is more crucial for a monkey (or human) to differentiate among faces than among any other categories of stimuli such as bananas. Second, faces are more similar to each other in their overall organization and fine detail than any other stimuli that a monkey must discriminate among. If there had been...
The idea that there might be convergence of neural input onto a single cell, which would provide that cell with the ability to represent a com-
plex and specific percept, seems to have arisen independently several times, first as the gnostic cells elaborated in detail by Konorski and then as the grandmother cells deriving from Lettvin’s parable. Cells with properties that are similar to those of gnostic and grandmother cells have been found in both the inferior temporal cortex and the hippocampus. Grandmothers (and other complex objects) may be represented by ensembles of “grandmother” cells, which vary in their responses to different aspects of the stimulus. Finally, contemporary human brain imaging studies have yielded specialized regions of the cortex that closely resemble the gnostic fields proposed by Konorski.

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