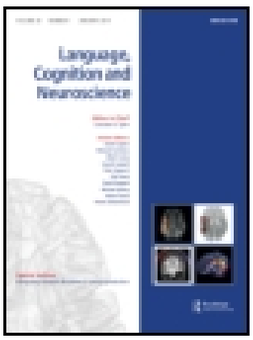

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Grandmother cells: much ado about nothing

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ABSTRACT

We do not dispute the possibility of the existence in the brain of "grandmother cells", which are very finely tuned neurons that fire only in the presence of specific objects or categories. However, we question the causal efficacy of such neurons at the functional or behaviour level. We claim that, even though very familiar items, such as "my grandmother", may well have associated grandmother neurons, these neurons have very little, or no impact on the actual recognition of my grandmother. A study by Thomas, Van Hulle, and Vogels [(2002). Encoding of categories by noncategory-specific neurons in the inferior temporal cortex. *Journal of Cognitive Neuroscience*, *13*, 190–200. doi:10.1162/089892901564252] found finely tuned, category-specific neurons in the inferior temporal cortex of monkeys, but also found that when these neurons were removed from their analysis, this had no effect on categorisation performance. Further, we have found no reported cases of the loss of recognition of single, highly familiar objects, which also argues for a lack of causal efficacy of grandmother-cell neurons.

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Grandmother cells; causal efficacy; tree/non-tree classification; category-specific deficits; category-specific neurons

1. Introduction

The Polish neurophysiologist Jerzy Konorski was the first person to explicitly posit the existence of "gnostic units" that fired exclusively in the presence of specific objects or categories (Konorski, 1967). Two years later Jerome Lettvin coined the term "grandmother cell" for these neurons (personal communication, reported in Gross, 2002). A decade later, Douglas Hofstadter (1979), in a tongue-in-cheek extrapolation from simple, complex, and hypercomplex cells, called them "ultrasuperhypercomplex cells". And evidence is currently piling up that there are, indeed, especially in the temporal lobe, very finally tuned neurons that fire only in the presence of specific, highly familiar categories or objects. The demonstration of ultra-specific "Halle Berry" or "Jennifer Aniston" neurons has caused considerable ink to flow in recent years (Quiroga, Reddy, Kreiman, Koch, & Fried, 2005).

However, the interrogation that forms the core of the present paper is "Grandmother cells, ok. But so what?" Let us start with a very simple analogy. Suppose you had a food-serving machine driven by a multilayer neural network. The inputs to the machine are myriad: it checks your cholesterol and blood sugar levels, it checks your urine, it weighs you, measures your height, calculates your BMI, records how tightly you squeeze a rubber ball, measures your VO_2 level, your lung capacity, your heart-rate, and so on. This information passes through the weights of the network and causes one of four output effectors to get you either a piece of pie, a salad, noodles, or a lean steak. (Assume a dietician had previously trained the machine by giving the machine explicit feedback on the quality of each of its choices.) At the same time, there is a fifth ("grandmother") output, unconnected, or only very weakly connected, to the four effectors. The weights coming into this grandmother output node are learned in exactly the same way as the weights to the effector output nodes. This grandmother node is directly connected to a little light that, depending on how active the node is, will turn red if pie is to be served, green for salad, yellow for noodles, and brown for steak. But, crucially, it does nothing other than light up. In other words, it plays no causal role whatsoever in serving food to people. It simply lights up in a manner that will reflect what the client will be served by the machine. The point, of course, is that the presence or absence of this "grandmother" output is wholly irrelevant to the operation of the machine. Simply put, *it is not causally efficacious* with respect to the functioning of the food-serving machine.

This analogy brings us to the main claim of this paper, which is that, while we accept the possibility of grandmother cells, we are not convinced of their causal efficacy. Just as the coloured light in the above example is

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not causally efficacious with respect to the task of serving the appropriate food to people, we claim that grandmother cells have not been shown to be causally efficacious with respect to the task of category or familiar-object recognition. We will avoid the intractable terrain of consciousness by referring exclusively to an end result of "internal" neural activity as the activity of motor neurons.

The remainder of this paper is organised as follows. We will begin by presenting neurobiological evidence for grandmother cells. We will then discuss a study by Thomas, Van Hulle, and Vogels (2002) who used machine-learning techniques (specifically, a Kohonen network, also called a self-organising map (SOM; Kohonen, 1990, 1993) to analyse recordings from 219 neurons in the inferior temporal cortex of a monkey as they performed a tree/non-tree categorisation task. This analysis showed how the elimination of a subset of these neurons which were category-specific (i.e. grandmother cells) did not affect categorisation performance of the Kohonen network. We then shift to discussing evidence from agnosia patients. If grandmother neurons were causally efficacious, we should find in the literature, reports of subjects who have lost their ability to recognise one face, a single type of object or one object, while their capacity to recognise everything else remained fully intact. We have not seen any such reports, even in cases of focal or locally restricted neuron loss.

2. Evidence for grandmother cells

There is an ever-growing body of evidence for the presence of neurons in the brain that can be very selective for the presence of complex stimuli. Young and Yamane (1992), analysing 850 unit recordings in the temporal cortex in response to the presentation of 27 faces, concluded that sparse population coding is used to represent faces. Quiroga et al. (2005) reported how neurons in the medial temporal lobe can respond selectively to different pictures of the actress Jenifer Aniston. Vogels (1999a, 1999b), carrying out recordings in the inferior temporal cortex of the monkey during a tree, non-tree categorisation task, reported the presence of neurons that responded to only one category or the other. Gross, Roche-Miranda, and Bender (1972) reported the presence of neurons in the monkey inferior temporal cortex that showed a preference for stimuli in the shape of a human or monkey hand. This response was even specific with regards to hand orientation. The neuronal responses decreased greatly when the hands were oriented in directions which did not correspond to those of the preferred hand direction (Gross et al., 1972). In short, there are several reports of single neurons whose responses indicate which element of the stimuli set was presented. Since the selective neurons described above fired even in conditions of changing features, such as stimulus size, position or exact representation, the activity of such neurons appears to be indicating the presence of *one familiar thing*.

Hair-splitting, back-and-forth – and generally unenlightening – arguments abound on the question of what, exactly, constitutes a "grandmother cell". Would it be a neuron that does not respond *at all* to any other elements in the presented stimuli set? What would define *at all*? Do the indices for measuring neuronal selectivity, in many cases, sparseness, change with the stimulus set that is used? Perhaps this would explain why Rolls and Tovee (1995), Rolls and Treves (2011), or Franco, Rolls, Aggelopoulos, and Jerez (2007), recording in the inferior temporal cortex, came to the conclusion that encoding for faces in these areas is distributed, while Young and Yamane (1992) conclude that it is sparse? And most of all, when does sparse become so sparse that it is localist? (Plaut & McClelland, 2010; Quiroga & Kreiman, 2010 and a reply by Bowers, 2010.)

Bowers (2009) has dismissed, correctly in our opinion, many of the arguments that trivialise what constitutes a grandmother cell or a localist encoding:

- a localist encoding does not imply that one and only one neuron represents "my grandmother". There could be several units encoding for "my grandmother". The activities of any one of these units would be sufficient to confirm if my grandmother had walked into the room.
- perceptual events such as grandmother crying or grandmother weeping are not represented by single neurons.
- complex propositions such as "Have a nice day" are not encoded by single units but constructed from the convergence of several local representations.

Bower's key claim is for a localist encoding scheme is that one neuronal unit encodes for *one familiar thing*. It is possible to interpret the output of a single unit in the network (Bowers, 2009).

We will, instead, argue that it is not unreasonable that a small number of neurons downstream from a chain of feature extraction, come to represent *one familiar thing*. It is a generally accepted idea in neuroscience that the convergence of neuronal input observed from lower areas in the visual cortex, serves to gradually build up neurons with more and more complicated receptive

fields as one goes up the hierarchy of visual processing. And so it is that while the neurons in V1 are tuned for specifically oriented light bars, the convergence of several neurons from V1 to V2 and V3, constructs neurons that show a similar preference for the orientation of bars of light but are less selective for their precise position in space (Hubel & Wiesel, 1962, 1965). There is then a further convergence of input from these lower areas to the neurons in the inferior temporal cortex. The inferior temporal cortex has long been thought to play an important role in object recognition and categorisation as cells in the area have a preference for complex images (Sary, Vogels, & Orban, 1993; Tovee, Rolls, & Azzopardi, 1994). Their selectivity is invariant to alterations in position, size, colour, and mode of definition. The last feature refers to how an object can be defined by features such as motion or texture differences (Sary et al., 1993; Tanaka, 1993; Vogels & Orban, 1996). This complexity is thought to result from progressive information processing in the ventral pathway as visual input makes its way from V1 to V2 and then V4 (Tanaka, 1993; Vogels & Orban, 1996).

In other words, there is considerable experimental evidence for the presence of very narrowly tuned neurons, and given our knowledge of neuronal convergence from lower to higher areas in the visual hierarchy, it is not hard to imagine that such units exist. We will not argue about whether these units really represent information about *one and only one familiar thing*, and where on the localist-sparse-distributed continuum this representation lies. We will, instead, argue that the presence of such selective neurons is of little consequence either functionally or behaviourally (i.e. these neurons are not causally efficacious).

3. Three scenarios for grandmother cells

Assuming that we accept the existence of grandmother cells – and we do – we believe that there are three reasonable scenarios that would explain the empirical data that has been presented in the literature to date. We illustrate these three scenarios in Figure 1(a–c).

4. Causal efficacy

The first example we will use to explore this notion of *causal efficacy* is a study by Thomas, Van Hulle, and Vogels (2002) in which the authors explored the effect of the loss of category-specific neurons on the capacity to discriminate between tree and non-tree stimuli. For the second example, we will look at visual agnosias and category-specific semantic deficits. We will briefly explore the literature on category-selective deficits to show that there are no reported losses as specific as that of *one familiar thing* or exclusively of one person, like "my grandmother". We will suggest that, even if such narrowly tuned neurons did exist, their contribution to cognition would appear to be minimal, since we do not find any evidence of such narrow recognition loss.

4.1. Grandmother cells for "tree/non-tree" categorisation

The first results that clearly support the main hypothesis of the present paper – that is, the lack of causal efficacy of grandmother cells – come from studies on the encoding of tree and non-tree categorisation in the inferior temporal cortex of monkeys. In a behavioural study, Vogels (1999a) reported that monkeys are well capable of distinguishing between images of approximately 200 tree and 200 non-tree stimuli. The non-tree category consisted of several natural and non-natural objects. Among the non-natural objects were images of various objects and places. Also included in the non-tree category, were plants such as flowers and ferns. The monkeys were able to distinguish these plant images from those of the trees. The stimuli in both categories were carefully selected to have matching sizes and luminance. Recordings were made from 219 neurons in the inferior temporal cortex of the monkey during the study (Vogels, 1999b). He found that some neurons were broadly tuned and responded to both tree and non-tree categories. Some neurons on the other hand only responded to the tree or non-tree images. In other words, they were category selective. Even among the category-selective neurons however, none of the neurons responded to all the exemplars of the favoured category.

A Kohonen network (Kohonen, 1990, 1993) was used to analyse these neuronal recordings. This is a machine-learning method that is able to classify data, assuming sufficient information is available in that data. Using this technique, Thomas et al. (2002) attempted to identify, using the neuronal responses, whether the monkey had seen a tree or non-tree. They were able to do so with a mean success rate of 83%. What is crucial to the discussion concerning causal efficacy, however, is the effect on categorisation performance of the elimination of information from the category-selective neurons: There was no significant deterioration in the discrimination performance of the Kohonen network, indicating that the presence of the category-selective or narrowly tuned neurons was irrelevant to the tree/non-tree discrimination. Moreover, an analysis of the weight vectors in the Kohonen network revealed that the neurons contributing the most to the

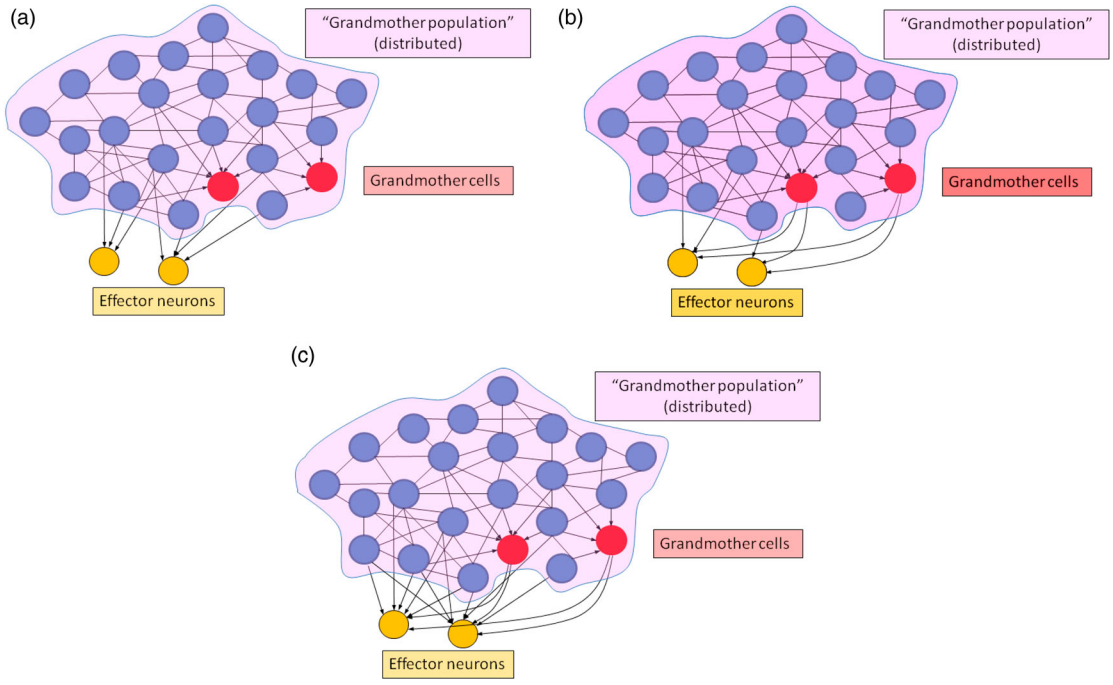

Figure 1. (a) "Dead-end" grandmother cells with no connections to effector neurons. Our "grandmother" is distributed over a large collection of neurons (blue/pink) that feed down to a relatively small number of grandmother cells (red), as well as to the effector neurons that allow us to say, "Hi, Grandma" (orange). The grandmother cells in this scenario are leaf-nodes (i.e. have no downstream connections) in the network and they do not connect to the output effector neurons. They do, indeed, fire in the presence of grandmother, and only grandmother, being downstream from the distributed collection of neurons that represent grandmother. This type of grandmother cell fits the standard definition of what we mean by such a cell. However, they are not causally efficacious, (b) "bottleneck" grandmother cells are largely the only neurons that feed into the effector neurons. Here the grandmother cells act as a bottleneck to the effector neurons. While there may be a few connections from the distributed "grandmother" cells, there are not many. The key connections are from the grandmother cells to the effector cells. These grandmother cells fit the definition of what is meant by a grandmother cell and are causally efficacious. Losing a small number of these cells would have dramatic effect on the recognition of our grandmother, but nothing else. For the moment, as we discuss later in the article, there is no current evidence for this configuration in real neural structures where the ablation of a small number of neurons would cause the complete loss of our recognition of one familiar person or object, and (c) "integrated" grandmother cells connected to the effector neurons along with the neurons from the distributed grandmother population. This, in our opinion, is the most likely neural organisation that allows for both the existence of grandmother cells and their concomitant lack of causal efficacy. In this case, ablation of the grandmother cells will have no, or only a very small, effect on the recognition of a category or a familiar object, because the output neurons are already fully activated by activation coming from the distributed neurons representing our grandmother.

categorisation were a group of more broadly tuned neurons that responded to both categories, but which showed a preference for one category over the other. The elimination of this latter group of neurons from the input vectors for the Kohonen network led to a very significant deterioration in classification performance. This difference in the performance could not be ascribed to differences in the number of category-selective and non-category-selective neurons, as there were 57 category-selective neurons and 49 neurons that belonged to the more successful non-category-selective population.

The more likely explanation for the poor contribution of the category-specific neurons in the tree discrimination task was, instead, the low sparseness index of these neurons. The average sparseness of all the category-specific neurons was 0.15, while it was 0.37 for all the recorded neurons in the study. Sparseness is an index of the proportion of samples to which a neuron showed a response (Rolls, Treves, Tovee, & Panzeri, 1997). The overlap between the responses of the category-specific responses was probably insufficient to represent the entire tree category. When it comes to the individual non-category neurons, their responses were insufficient to assign a class to the presented stimulus. However, as even the broadly tuned neurons had a preference for one class or the other, individual responses did provide a probability index concerning the stimulus class. With a population of broadly tuned neurons, the collective probabilities provided sufficient information for a more reliable class distinction.

Thomas et al. (2002) clearly demonstrates the main claim of this paper – namely, that while there may well be units which are very narrowly tuned, they do not make a significant contribution to the encoding of the familiar thing, in this case, the category tree. Furthermore, we were able to identify a simple additive algorithm with the non-category-selective neurons that revealed which type of stimulus the monkey had seen.

4.2. Category-specific deficits

If single cells or groups of cells were individually responsible for encoding all the percepts associated with a single object or person, we should see cases of isolated memory loss, that is, the inability to identify individual items or persons, while we continue to be able to identify other members of that class. Instead, what is observed in agnosia and semantic deficits is the inability to recognise broad classes of objects.

When category-specific semantic deficits occur, they involve an entire category or a broad class of objects (Camarazza & Mahon, 2003; Capitani, Laiacona, Mahon, & Camarazza, 2003; Warrington & Shallice, 1984). Capitani et al. (2003) conducted a review of 79 case studies and found that most of them involved the loss of biological categories. A small minority of patients showed a selective incapacity to recognise artefactual categories. An appendix in Capitani et al. (2003) lists the categories of semantic deficits for each patient on a case-by-case basis. Finer grained losses could be found within the group of patients with the loss to identify biological objects. Some showed more specific semantic deficits with respects to the fruit/vegetable (inanimate biological) category than the animal category (animate biological) and vice versa. Curiously, the impairment in the biological category was also sometimes associated with deficits in recognising manufactured foods and musical instruments. The authors also reported that there was no interaction between the type of knowledge missing (e.g. perceptual or functional) and the deficit category. None of the reported cases involved the loss of just one familiar thing

One type of agnosia does appear to be more selective than that of the other categories. Prosopagnosia is a cognitive disorder in which subjects are unable to recognise faces including familiar ones despite intact primary visual processing and other intellectual functions (De Renzi, 1997). Once again, there is controversy concerning the specificity of the deficits for face recognition. Some researchers have reported agnosias for categories of certain objects, without corresponding difficulties in face recognition (Moscovitch, Winocur, & Behrmann, 1997). Others have reported cases in which there is a deficit in face recognition without corresponding difficulties in the recognition of classes of objects (Busigny, Graf, Mayer, & Rossion, 2010; Duchaine & Nakayama, 2005; Rezlescu, Pitcher, & Duchaine, 2012).

This point of view on the specificity of facial processing is in contrast to one in which it is thought that one general-purpose visual system underlies the processing of both face and non-face stimuli. The difficulties with identifying faces therefore simply arise from the fact that identifying individuals is a more detailed task in which subjects have to identify within-category exemplars while the identification of other objects takes place at a more basic level (Grill-Spector, 2003; Tarr & Gauthier, 2000). Proponents of such a point of view report that prosopagnosic patients also have difficulties when asked to distinguish between non-face items with subtle variations (Damasio, Damasio, & Van Hoesen, 1982; Etcoff, Freeman, & Cave, 1991; Gauthier, Behrmann, & Tarr, 1999). Once again, there are no reports of a loss of capacity to recognise just one or a few persons, as we might expect with a grandmother cell coding

4.3. Familiar-object loss

We will not embark on a philosophical discussion of what constitutes a category versus an exemplar of a category. Suffice it to say that the distinction between categories and category exemplars is far from clear cut. However, for the purposes of the present article what is of crucial importance is how they are learned. Virtually all real-world categories are learned by seeing many different instances of members of the category in many different contexts. This is no different from how we learn highly familiar category exemplars.

For example, grandmother is a category, one learned by seeing many instances of grandmothers, reading about grandmothers in stories, and so on. But what about my grandmother? We learn about our own grandmother in the same way we learn the category grandmother. One sees his/her grandmother from many different angles, doing many different tasks, in many different clothes, in many different contexts, and so on, which is precisely how we learn the category grandmother. And as a result of this in-depth learning, we would expect that there would be "my grandmother"-specific neurons. And if these "my grandmother"-specific neurons (grandmother cells) are causally efficacious, we would expect there to be recorded cases of people who can recognise everyone except their grandmother. We know of no such cases. The same applies to other highly familiar objects.

4.4. Neuronal damage

We have argued above that a localist encoding would result in very specific losses of recognition and memory. Rather than having a general loss of the capacity to recognise faces or all animals, we should be able to find cases of patients who have lost their capacity to recognise one, or a few individuals. Rather than observing semantic deficits with an entire category, such as animals or vegetables/fruit, there should be reported cases of people who had lost their capacity to recognise just "zebra" or "apple". We have not read or heard of any such cases.

One might argue that this is not surprising as the neuronal damage underlying such problems can be extensive. Associative visual agnosias are usually associated with damage to the anterior left temporal lobe (De Renzi, 2000; Goldberg, 1990; Greene, 2005). This damage, as it is often caused by strokes or head injuries, would not be associated with cell loss restricted to one cortical column. However, category-specific semantic deficits indicative of more focalised damage have also been observed in patients with Alzheimer's disease (Capitani et al., 2003). This is a progressive disease in which the presence of the amyloid plaques and neurofibrillary tangles gradually increases (Francis, Palmer, Snape, & Wilcock, 1999; Meyer, Xu, Thornby, Chowdhury, & Quach, 2016; O'Brien & Wong, 2011). At early stages of the disease, when the plaque volume is still very restricted, we should find cases where patients lose their capacity to recognise a single person or a single category of objects.

One might argue that this type of loss could be greatly reduced by having grandmother gnostic units that are distributed throughout the brain, hence preventing a single small lesion from resulting in the total loss in the capacity to recognise one's grandmother. However, it is highly unlikely that the grandmother neurons would be distributed throughout the brain. A bedrock principle of neural organisation is that similar information is encoded by neurons with similar spatial locations. Thus, for example, neurons that respond to similar orientations of light bars are in the same cortical column of the visual cortex. In the auditory cortex, this is referred to as a tonotopic organisation (Bear, Connors, & Paradiso, 2001). Similarly, there appears to be a columnar organisation of information in the inferior temporal cortex in which neurons within a column show a similar preference for complex stimuli (Fujita, 2002; Fujita, Tanaka, Ito, & Cheng, 1992; Tanaka, 1993). We would, therefore, expect to see all the grandmother "gnostic units" in an approximately similar location. Category-specific semantic deficits caused by Alzheimer's disease result are due to focalised damage. Since the disease is progressive, it should in some cases eliminate all the grandmother neurons of one column thereby eliminating the capacity to recognise grandmother. Instead, what is observed is the loss of broad, rather than very narrow categories, thus providing further support for the idea that grandmother neurons are of little functional/behavioural relevance.

5. If grandmother cells serve no purpose, why do they exist?

Assuming causally inefficacious grandmother cells do exist, why would evolution or development not have culled these cells, or at least put them to some other use? There are many reasons for this. First, evolution is hardly an optimal culling mechanism, as can be seen from the presence of staggering quantities of non-functional ("junk") DNA in our genome or from the presence of vestigial organs like the appendix. The disappearance – or in this case, the non-disappearance – of grandmother cells cannot be likened to the disappearance of sight in fish that live in caves. First, the changes in these fishes' eyesight took place over very long periods of time, literally hundreds of thousands of generations, rather than in individual brains, for individual neurons coding for particular categories or familiar objects. Do all individuals have the same narrowly tuned, category-specific neurons for the same categories? This is dubious, at best. Second, would the cost associated with leaving these neurons in place be such that an evolutionary disadvantage would be created with respect to those individuals without grandmother cells? This, too, is hard to imagine. Certainly, at the behavioural level (i.e. recognition of one's grandmother), there would be no disadvantage whatsoever to the continuing presence of these cells.

6. Sparse or semi-distributed encoding

So, is information in the brain represented in a localist or distributed fashion? It is difficult to characterise such a complex system in such a black-and-white manner. At least in the inferior temporal cortex, it is clear that the encoding is something between a fully distributed code in which all the neurons participate in the representation of *one familiar thing* and a strictly localist code in which the firing patterns of individual neurons would signal its presence. In the inferior temporal cortex, there is now much evidence for a sparse encoding in which the neurons respond to several but not all members of a given category (Rolls & Treves, 2011; Vogels 1999b). Several theoretical studies have now

shown that such a sparse encoding is more robust to the loss of neurons than a localist representation (Field, 1994; Rolls & Treves, 1990). Rather than attempting to label such a complex system as being either strictly localist or strictly distributed, it is almost certainly more useful to use the sparseness index as an informative measure of the degree of distributed/localist coding.

7. Conclusion

In conclusion, we do not dispute the idea that there may, indeed, be neurons in the brain that are very narrowly tuned (i.e. grandmother cells). Not only are there numerous experimental reports of such neurons, but in addition, the hierarchical processing of information in the brain makes the presence of such cells a logical possibility. However, the causally efficacious nature of such neurons at the functional or behaviour level remains to be demonstrated.

Disclosure statement

No potential conflict of interest was reported by the authors.

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