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Epistemological evaluation of evidence for ‘number’ neurons in the parietal cortex of macaque monkeys

Laurent Goffart[1]*

[1]Centre Gilles Gaston Granger, UMR 7304 CNRS Aix Marseille Université, Aix-en-Provence, France

Abstract. A contemporary theory holds that mathematical concepts are stored in the long-term memory of mathematicians. This perspective also proposes that the brain has evolved to possess basic “representations” of space, time, and number. These representations are believed to be shared with other animal species and underlie mathematical intuition. To investigate this idea, neuronal recording studies were conducted in monkeys to search for an evolutionary precursor of the human ability to extract and manipulate numerical quantities. A sensitivity to the number of items was reported in the activity of some neurons in the parietal region of cerebral cortex. Area VIP contains neurons whose emission of action potentials is maximum for a specific number of items in the visual field, whereas area LIP contains two classes of cells, 'accumulator' neurons whose firing rate increases with the number of items, and other neurons whose activity decreases with the number of items. In this article, after questioning the reasons that have led to imagining that counting could be biologically inherited rather than culturally transmitted, we shall reveal the shortcomings of these studies conducted with monkeys, and report results that challenge an involvement of their parietal cortex in numerical competence. .

1 Introduction

In a dialogue between Socrates and a slave, Plato narrates how an uneducated person comes to discover geometric relationships from drawings in the sand [1]. Socrates indeed aims at showing that the slave possesses this knowledge, even though he never learned geometry before. According to him, learning geometric concepts is a matter of anamnesis, a recollection of what we have always known.

More than two millennia later, in a dialogue with a mathematician, a neurobiologist reiterates the same fable when he contends that “*mathematics are in the brain of the mathematician, particularly in his long-term memory*” and that “*for achieving a strong materialistic epistemology, the task of the neurobiologist*” would be to “*describe, in particular, how the human brain generates objects, including mathematical objects*” [2]. In the same vein, a neurophysiologist tells us that mathematics are “*neither entities that exist independently in the Universe, waiting to be discovered by the mathematician from the depths of his Platonic cave, nor creations ex nihilo by the brain*”. They would be “*the expression of laws and mechanisms that are at work in the brain*”, “*a language of the brain about the brain itself, that is, since the brain is part of the physical world*, [a language] *about the Universe and its laws*” [3]. The above statements are not considered abusive or speculative, since a few years later, a psychologist takes it even further, explaining that “*numbers, like all mathematical objects, are mental constructs whose roots reach... into the adaptation of the human brain to the regularities of the universe*” [4]. According to him, “*all human brains receive, from birth, sophisticated mental representations, independent of language, which can be qualified as 'proto-mathematical'. In the course of its evolution, our brain has been endowed with elementary representations of space, time, and number, which we share with many other animal species, and which are at the foundation of our mathematical intuitions*” [5]. Likewise, some contemporary neurophysiologists contend that the “*number faculty is rooted in our biological heritage*” [6] or that “*space, time, and number are part of a toolkit that humans share with other nonhuman animals*” [7].

Such speculations illustrate the contemporary merging of biological and psychological approaches to cognition within the developing landscape of cognitive sciences. In fact, it builds on the principles of evolutionary epistemology, a philosophical doctrine according to which “*the external world of any subject as well as the observing subject itself are products of the very same process, that is evolution, and the conformity between patterns of the external world and patterns of subjective thought can be explained intrinsically in terms of evolution and selection ... Through the process of adaptation living systems accumulate more and more information about their environment and, thus, represent the structure of the environment they live in; the better the representation of the environment, the better the chance of survival*” [8].

A few decades earlier, one of the founders of this doctrine, Konrad Lorenz presented adaptation in a similar manner, namely a process by which living organisms conform to the demands of their environment. During the evolutionary history of mankind, “*adaptation has provided our thought with an innate structuralization which corresponds to a considerable degree to the reality of the external world*” [9]. According to the Austrian ethologist, “*our forms of intuitions and categories ‘fit’ to that which really exists in the manner in which our foot fits the floor or the fin of the fish suits the water. The a priori which determines*

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* Corresponding author: laurent.goffart@cnrs.fr

the forms of appearance of the real things of our world is, in short, an organ, or more precisely the functioning of an organ" [9]. Within this theoretical framework, "*the form of thought of numerical quantification is and remains one of the most miraculous apparatuses that nature has ever created*" [9]. Thus, numerical mathematics would be "*an organ, an evolutionarily acquired, 'innate working hypothesis'*" [9]. With regard to its relation to the central nervous system, Lorenz argued that the latter does not dictate the laws of nature any differently than the hoof of a horse treads the ground: "*just as the hoof of the horse is adapted to the ground of the steppe which it copes with, so our central nervous apparatus for organizing the image of the world is adapted to the real world with which man has to cope. Just like any organ, this apparatus has attained its expedient species-preserving form through this coping of real with the real during its genealogical evolution, lasting many eons*" [9].

Delving deeper into the history of ideas, we encounter Herbert Spencer, the founder of the misnamed social "Darwinism". Spencer's ideas on the relationship between intelligence and evolution are particularly relevant to our discussion. He explained that "*the spatial relationships have been the same, not only for all humans, but also for all primates and all orders of mammals from which we descend, as well as for all lower orders of beings. These constant spatial relationships are expressed in defined nervous structures, which are congenitally constituted to act in a certain way, and are unable to act in a different way*" [10]. A more recent statement echoes Spencer's ideas, suggesting that "*in the course of their evolution, humans and many other animal species have internalized basic codes and operations isomorphic to the physical and arithmetic laws that govern the interaction of objects in the external world. Indeed, there is now considerable evidence that space, time and number are part of the essential toolkit that adult humans share with infants and with many nonhuman animals*" [11]. This statement illustrates the persisting influence of the Spencerian thesis on contemporary thought.

The invitation by evolutionary epistemologists and psychobiologists to search for mathematical objects in the brain contrasts with the sociological thesis. According to this thesis, the categories of human thought are neither universal nor set in stone, but constantly evolving across cultures and time. They are "*like sophisticated tools of thought, which human groups have laboriously forged over the centuries and in which they have accumulated the best of their intellectual capital*" [12], and not "*locked in the physiology or biology of Homo sapiens*" [13]. Next to sociologists, philosophers confirm that mathematics is a "*collective work of art that derives its objectivity through social interactions*" [14]. They also argue that the persons who managed to constitute abstract objects and mathematical theories, are "*men* [and women] *in the plural, concrete men* [and women] *acting in historically determined conditions, and not some kind of outgrowth of a 'cognitive subject'*" [15]. In fact, the fallacy of the putative innate 'number sense' arises from the fact that comparing two quantities does not necessitate assigning a numerical value to each one [16].

While socio-historical perspectives offer valuable insights, a plethora of researchers investigate mathematical thinking through the lens of brain function. This is where studies on eye movements come in. These people believe that recording eye movements opens "*a window onto the mathematical mind*" [17] and assesses the "*subconscious aspects of mathematical thinking*" [18]. According to some brain imaging studies, the activation pattern in the parietal region of cerebral cortex "*would resemble the activation pattern associated with rightward eye movement, whereas subtraction would resemble a leftward eye movement*" [19]. At the same time, some neurophysiologists trained monkeys to various kinds of tasks in order to provide evidence for the presence of so-called "number neurons" [20] in this region of cerebral cortex. We propose to evaluate the scientific value of the data that are claimed to support the existence of such neurons in the parietal cortex of monkeys. We shall not discuss neurons in frontal regions of the cerebral cortex because of the lack of inactivation studies and because of the dependence of their activity on prior learning (as explained in the conclusion section).

2 Critical assessment of 'number' neurons in the simian parietal cortex

Before discussing the evidence for 'number' neurons in the parietal cortex, we shall describe the experimental procedure that led to their discovery and review the basics of activity propagation in neuronal networks.

Monkeys were trained to detect whether two visual stimuli displayed on a video monitor contained the same number of items. Each training session consisted of a series of trials, with each trial beginning when the monkeys grasped a lever and fixated a target at the center of a visual display. After a short fixation interval (500 ms), a first sample of small disks appeared for 800 ms around the central target. A delay interval of 1000 ms followed during which the monkeys had to maintain fixation of the central target. This interval was then followed by the display of a second sample of small disks for 1200 ms. The monkeys were rewarded if they released the lever after detecting that the number of disks contained in the second sample was identical to the number in the first one. If the number of disks did not match, the monkeys were required to continue holding the lever until the appearance of a sample in which the number of disks was the same as in the first one. For each trial, the small disks were randomly placed within a circular gray zone at the center of the video monitor. Their position, their size and their total area varied also from trial to trial. After the training of monkeys was completed, the activity of neurons was recorded in their parietal cortex to test the presence of neurons whose firing rate would be modulated by the number of items.

A complex network of neurons is involved in the brain to transform a sequence of disks samples displayed in the visual field into coordinated muscle contractions and relaxations, leading the monkey to release a lever. Between the ganglion cells in the retina, from which the optic nerves originate, and the motor neurons at the origin of the nerves innervating the muscles, signals consist of action potentials that propagate along their axon before exciting or inhibiting post-synaptic neurons. These influences depend on the neurotransmitters released at the points of contact between the neurons, the timing of pre-synaptic action potentials and the "sensitivity" state of post-synaptic neurons. It is also important to know that each neuron receives inputs from numerous pre-synaptic neurons and that its axon forms synaptic contacts with numerous post-synaptic neurons. The probability of firing action potentials increases with the synchrony of pre-synaptic excitatory inputs, whereas inhibitory neurotransmitters decrease it by reducing the sensitivity to pre-synaptic excitations.

2.1 The case of 'number' neurons in area VIP

Figure 1 shows the average firing rate of five example neurons as a function of the number of items that were displayed on the video monitor while a monkey fixated the central target. The firing rate of neurons A, B [20] and E [21] were recorded while the monkeys had to detect whether the number of items contained in the second sample was identical to the number in the first sample. For the neurons A and B, the firing rate was maximum when 3 items were displayed in the first sample. The neuron E "preferred" 4 items. The neurons C and D were recorded in monkeys whose task was to detect whether the items in the second sample were of the same color as the items in the first sample [22]. They exhibited a maximum firing rate when the first sample contained 3 and 4 items, respectively.

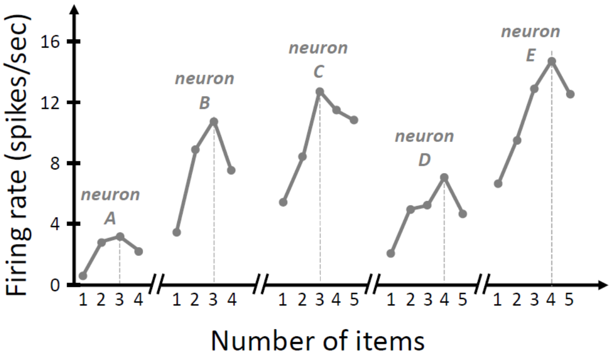

Fig. 1: Sensitivity of example neurons to the number of items in the perifoveal field. The neurons were recorded in the parietal cortex of monkeys fixating a central target. The graph is a reconstruction of data collected in three different studies [20-22].

A close examination of the sequences of action potentials emitted by these neurons reveals that the duration during which their firing was higher for a specific number of items (conventionally called 'preferred number') was brief. For the neurons C and D, the interval lasted approximately 600 milliseconds (ms), corresponding to a difference of three to six action potentials between the preferred number and the neighboring numbers of items. For the neuron E, it lasted approximately 400 ms. The same conclusion can be drawn from neurons A and B because of their very low firing rate. Assuming that the synapses between the recorded neurons and their post-synaptic targets are excitatory, how is it that so few action potentials, out of hundreds or thousands of others, can lead the post-synaptic neurons to emit different numbers of spikes as a function of the number of items? The authors fail to explain how the post-synaptic neurons can "distinguish" (i.e., discharge differently), the 1-3 action potentials from 'number neurons' against the multitude of action potentials they receive from other neurons, during an interval of 200-500 ms. Furthermore, they do not explain how these post-synaptic neurons transmit a number of action potentials that ultimately change the muscle contraction and produce different responses depending on the number of items presented (2, 3 or 4).

2.2 The case of 'number' neurons in area LIP

Neurons sensitive to the number of items in the visual field have also been found in the lateral intraparietal (LIP) area of cerebral cortex [24]. Their firing rate is higher than that of neurons in area VIP. Two groups of neurons have been identified: neurons whose firing rate increases with increasing number of items in their response field ('accumulator' neurons) and neurons whose firing rate decreases with increasing number of items. However, a close examination of the graphs plotting the firing rate of example neurons as a function of the number of elements reveals that the presumed influence of the number of items on their activity is not consistently observed. Indeed, the graphs reveal that the firing rate of some neurons is not affected by the number of items, and this is even blatant in several cases. The example neuron shown in Figure 4A of this study does not respond differentially to the presentation of 2, 4, 8 and 16 items. Thus, it is not certain whether the post-synaptic cells can relay any signal related to the number of items, given that the recorded neuron does not fire differentially as a function of the number of items (blue and green symbols). Similarly, it is uncertain whether the post-synaptic targets of the example neuron shown in Figure 4C respond differently to its firing rate when the number of items is larger than 4 (purple symbols). Finally, the decline of firing rate with the number of visual items is not obvious in the graph plotted in their Figure 4D. In other words, based on the firing rate of single neurons, it is not certain that post-synaptic neurons receive signals that allow them to respond differently to different numbers of items. The firing rate of individual neurons does not guarantee that post-synaptic neurons receive signals that enable them to discriminate between different numbers of items.

Combining the activity of multiple neurons does not provide a better understanding of how the firing rate of LIP neurons contributes to discriminating different numbers of items in the visual field. Indeed, when examining the population response of each subgroup of neurons (the 'accumulator' neurons and those "preferring" small number), it takes approximately 400 ms to distinguish the population responses corresponding to each number of items. As a result, post-synaptic neurons may differentiate between distinct signals from the population of LIP neurons in two ways: either by integrating the number of action potentials over a 400 ms time interval, or through an additional process that attenuates their sensitivity to action potentials emitted during that interval. The first option is complicated by post-synaptic neurons receive numerous action potentials from other neurons. The integration process must select the action potentials emitted by 'number' neurons and ignore those emitted by other neurons. The second option implies, at the level of post-synaptic neurons, a kind of procrastination that may have to be repeated at the subsequent stages. After all, the central question that remains to be answered is how post-synaptic neurons selectively distinguish action potentials emitted by 'number' neurons from those emitted by a multitude of other afferent pre-synaptic neurons. In other words, how do post-synaptic neurons manage to separate relevant signals from irrelevant signals?

3 Evidence against parietal cortex involvement in numerical discrimination

A correlation between the firing rate of a group neurons and an external event, such as the number of items in the visual field, does not necessarily mean that the neurons' action potentials play a causal role in the behavioral response (releasing a lever or making an eye movement). In fact, to establish a causal relationship, we need to manipulate the neurons' firing rate or the number of emitted action potentials and assess whether this affects performance. For example, would artificially increasing the firing rate of 'accumulator' neurons lead monkeys to overestimate the number of items in their visual field? To date, such experiments have not been conducted. However, one study has investigated the effect of suppressing the activity of all neurons using a pharmacological agent on performance during a numerical discrimination task [25].

In this study, two monkeys were trained to perform a numerical discrimination task and a color discrimination task. The experiment consisted of a series of trials that began with the presentation of a small target at the center of the visual display. The monkeys were required to fixate the central target until its disappearance. Seven hundred milliseconds after central target onset, two large stimuli appeared for a duration ranging from 70 to 300 ms, in the left or right visual hemifield. The two stimuli were presented in different parts of the hemifield, one in the upper part and the other in the lower part. In the numerical discrimination task, the stimuli consisted of sets of small red or green disks. To obtain a reward, the monkeys had to continue fixating the central target during the presentation of stimuli and for an additional delay of 400 ms, after which they had to make a saccade toward the location of the stimulus that contained the larger number of red disks. In the color discrimination task, the small disks were of the same color within each stimulus, but of different color between the upper and lower hemifields. Similar to the numerical task, to obtain a reward, the monkeys had to fixate the central target during the presentation of stimuli and an additional delay interval of 400 ms, then make a saccade toward the location of the stimulus that contained disks whose color was closer to red.

Injection of an inhibitory pharmacological agent (muscimol) in area VIP did not alter the performance of monkeys, either during the numerical discrimination task or during the color discrimination task. Muscimol injection in area LIP led to marginal impairments during both discrimination tasks. The proportion of correct trials was reduced by less than 5% during the numerical discrimination task and by less than 10% during the color discrimination task.

Surprisingly, the authors of the study do not question numerical processing in the parietal cortex of monkeys, either in VIP or in LIP. According to them, "*if inactivation resulted in similar deficits in the two tasks, it would endorse the view that number processing in LIP and VIP is merely one application of a general purpose circuit for ordinal comparison, visual attention, or perceptual decision making*". However, such a statement is not consistent with the absence of deficit in the numerical discrimination task after VIP inactivation. Moreover, if the LIP area is involved in counting the number of visual items, then its inactivation should have a greater impact on the monkeys' ability to discriminate different numbers of items than on their ability to discriminate colors. Given that the experimental results do not confirm this prediction, it is logical to conclude that in monkeys, neurons in LIP are not specifically involved in the comparison of quantities. The small declines of performance in the numerical and color discrimination tasks may result merely from a visual deficit, such as diplopia or blurred vision. Indeed, it has been shown that area LIP contains a large percentage of neurons (about 72 %) whose firing rate depends upon the target depth relative to the plane of fixation [26]. Despite acknowledging that any factor affecting vision or motor skills could have caused similar deficits in both discrimination tasks, the authors argue that their results are "*consistent with the idea that the IPS* [intraparietal sulcus] *is specialized for the perception and comparison of various magnitudes, such as time, space, and size, as well as numerosity and area*".

From a logical point of view, given the equivalence between the proposition "if A then B" and its contrapositive "if not B then not A", the absence of a deficit in the numerical task after parietal lesion ("not B") should lead one to question, or even reject, the postulate that neurons in VIP and LIP areas of monkeys are involved in "numerosity" processing.

4 Conclusion

In this article, we presented and discussed the evidence that some neurophysiologists brought to support the involvement of neurons in the parietal cortex in the numerical performance of monkeys. Unit recording studies reported neurons whose firing rate exhibits some modulation in their firing rate according to the number of items in their response field. Unfortunately, none of them explained how post-synaptic neurons detected, among input from numerous other pre-synaptic neurons, the few spikes difference that 'number' neurons emitted between two different sets of items, and how in turn, these differences are signaled to subsequent post-synaptic neurons. This shortcoming applies to the activity of single neurons as well as to the population activity. Finally, when the activity of these neurons was suppressed by the local injection of a pharmacological agent, the monkeys exhibited no deficit (VIP inactivation) or a marginal one (LIP inactivation).

If the primate brain is *"predisposed to acquire a number system"* and "*the symbolic number faculty cannot be reduced to simply a product of culture"* [6], then this biological heritage does not seem to rest upon the activity of neurons in the parietal cortex. Against the thesis that numerical competence is "*rooted in our biological heritage*" and precedes cultural influences, the cognitive scientist Rafael Nunez explains that the ability to practice snowboarding, similar to mathematical practice, cannot be considered as a result of natural selection. Although snowboarding requires a set of biological sensorimotor functions (such as bipedal posture, balancing, and optic-flow navigation), it is obvious that it is not a part of "our biological heritage" [27-29].

Beyond the fact that the analysis of data presented in the previous two sections seriously challenges the suggestion that "number" neurons provide the neurobiological substrate of "*the intuitive sense of number*", the idea that this putative "sense" would be "*present at birth* [i.e., innate] *in both humans and monkeys*" is not supported by any data, since all studies were conducted on trained juvenile or adult monkeys. The other major concern of these studies is the lack of information about the procedures used to train the monkeys prior to testing the sensitivity of their neurons to the number of items. The duration and number of sessions required are not documented either, raising the question of whether this "sensitivity" depends on the training rather than being present prior to it. As shown in frontal premotor regions of the cerebral cortex [30-32], such a dependence on learning would indicate a mere artefactual sensitivity.

By reducing the socio-historical aspects of the mind to the neurobiological development, the intellectual evolution of ideas to the maturation of the central nervous system, cognitive neuroscientists have created a confusion between the neurobiological functioning of an individual and the historical and collective evolution of a scientific discourse that has been transmitted through language, memorized in books (stored in libraries) and obeying the principle of non-contradiction. This confusion results from the tendency to equate the intellectual evolution of ideas with the maturation of the central nervous system. There is no justification for assuming that the brain is wired to obey classical logic [33] or that space, time and number "naturally" emerge from its functioning [27-29,34].

The evidence of an internal "representation of space" in the brain must be reevaluated in light of studies on saccades toward the memorized location of visual targets [35]. Regarding the notion of time, if it is a convenient epistemological shortcut used to avoid the complex task of detailing the multiplicity of factors generating any measured physical event, then the question of its representation in the brain is nonsensical. Finally, how can one ignore the fact that intellectual development involves a multitude of cognitive structures that are external to the individual? "*These structures have evolved through the intellectual technology of writing and rely on external instruments such as books, libraries, and calculation and observation tools, as well as social structures for knowledge production and accumulation, including encyclopedias, learned societies, and cultural networks for knowledge creation and dissemination. The cognitive process is inextricably linked to social structuring, just as wealth production is*" [36].

At the final conclusion of our epistemological inquiry, Novalis' words still resonate: "*hypotheses are nets, only he who casts will catch*". Indeed, but we must be aware of the risk that some catches correspond to abandoned old myths, creations of human imagination or mere copies, which may be mistaken for facts by the public when it is not informed of their socio-historical origin.

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