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Cerebral Bases of the Number Sense in the Parietal Lobe

Lecture Introduction

Ben Backus
First of all, I’d like to thank the current co-director of the Institute for Research in Cognitive Science, that is Mark Liberman, for acting as a consultant in planning this year’s Pinkel, and second I want to point out that the Pinkel Lecture at Penn entails a great deal of work that is not readily apparent. Schedules have to be coordinated, rooms have to be booked, food has to be ordered including the food that will be available after this lecture in the Terrace Room, posters made, paperwork pushed through and I really could go on and on. And for all of that work I’d like to acknowledge Laurel Sweeney from the Institute for doing that work, which she did with great competence and which is really what makes the lecture possible.

And now to explain what Sheila Pinkel had in mind when she set up this lecture and to produce this year’s Pinkel lecturer, I now give you Professor Lila Gleitman, also of the psychology department and a former co-director of the Institute.

Lila Gleitman
Thanks, Ben. It’s been an extraordinary pleasure to introduce Professor Stan Dehaene today, who comes here under the auspices of the Benjamin and Anne Pinkel Endowed lecture fund to the Institute for Research in Cognitive Science. So I want to tell you about the Pinkel fund first, and then I’ll get back to introducing Stan, who as you will see fits the bill so perfectly that it would seem as if the fund was established just for him. The Benjamin and Anne Pinkel Endowed Lecture Fund was established through a generous gift from Sheila Pinkel on behalf of the estate of her parents, Benjamin and Anne Pinkel.
It serves as a memorial tribute to the lives of her parents. Benjamin Pinkel, who received a BSE in electrical engineering from the University of Pennsylvania in 1930, was actively interested in the Philosophy of the Mind and published monograph on the subject: *Consciousness, Matter, and Energy: The Emergence of Mind in Nature* in 1992, the objective of which, and I quote here, is a “reexamination of the mind/body problem in the light of new scientific information”. The lecture series, which has been going for four or five years now, is intended to advance the discussion and rigorous study of the deep questions which engaged Dr. Pinkel’s investigations.

**Speaker Introduction**

And now to Stan Dehaene: he is a mathematician, a computer scientist, a neuroscientist, and a cognitive scientist, and he holds degrees related to all of these areas of his expertise, culminating in a PhD in 1989 – not so very long ago - in cognitive science at the Institute of Advanced Studies in the Social Sciences in France. Stan is the recipient of several highly prestigious international awards, including the 1996 Fannie Emden Prize and in 2000 the Villemot Prize, both from the French Academy of Sciences. He serves as an associate editor of several journals, *Cognition, Neuropsychology*, and *Mathematical Cognition*. He serves on several scientific boards, including the Thyssen Foundation in Paris, and the Trieste Encounters in Cognitive Science in Italy. But despite all of these wonderful awards, post-administrative situations, Stan is very much mainly a working scientist, as you will soon hear. He is the author of literally scores of papers and several books, notably a book called *The Number Sense*, which was published in 1997 and which I’m sure you will all rush out and buy right after the lecture. But by the way don’t leave right away, because after Stan talks there will be a discussion period. He’ll take some questions - he only has to leave at 2 o’clock because the poor man is forced to be in Venice, Italy, tonight. Just a few words to introduce what’s going on here, Stan takes up problems that most people well, after Dr. Pinkel, have been afraid to approach at all because they seem to be so, or were before much of his work, so ill-formulated as to defy rigorous study. For example, his latest interest pertains to the representation of consciousness in the brain. Something I thought we wouldn’t be thinking about seriously at least for decades. And today, a topic which I think is not quite but nearly as awesome, namely what are the mental representations of mathematics – how is quantitative reasoning represented in the brain. So now I turn over the microphone to Dr. Dehaene, speaking on the cerebral bases of the number sense in the parietal lobe.

**Lecture: Cerebral Bases of the Number Sense in the Parietal Lobe**

Dehaene: Thank you very much, that’s a lovely introduction and a great pleasure to be here. I was here several years ago and it’s always wonderful to come back and see how much has been advancing meanwhile. So thank you for this invitation and I’ll start right away. I will be talking today indeed about the cerebral basis of mathematics, a somewhat awesome and implausible topic. I will however very quickly reduce it to much simpler concepts and the idea will be to try to understand how something as simple as an integer,
maybe a small integer like 2 or 4 is represented in the human brain and where does such a concept come from? Why is it that we can entertain such a concept as the concept of the number 2? I would like to say also that much of my talk will be appealing to the new techniques of neuroimaging, and I think it will also serve to illustrate the power of this message of neuroimaging to address questions in cognitive science.

I think many people have a misguided idea of what neuroimaging is for, and that’s illustrated on that slide. Most people have this view in mind: they think that neuroimaging is a form of new phrenology, that the idea is that you are going to make a map of the cortex and that different cognitive functions will map onto different sides and that’s all there is to imaging, the power to localize where are the mental representations of the maps in the brain. Now I think this is one purpose of imaging, but certainly not the most important one. The most important one I think was illustrated in this even older slide which is from the seventeenth century in which you see - this is really from alchemy - but you see someone being scanned in an alchemy oven here, and what comes out of the oven is not localizations but what comes out of this oven is ideas that were in the subjects head but that this machine allows you to read. So I think it illustrates nicely, this person might be thinking of a horse, or a sorcerer, or something like that. And I think it illustrates nicely that I think what the real purpose of neuroimaging is, is to find out about the format of representations in the brain. We have behavioral methods to find out about the representations but they are global, they always incorporate anything between a stimulus and a response, in the case of reaction time. Here we have the power to isolate a few voxels in the brain and ask, well, what is the representation in the neurotissue in these voxels?

So this is what I’ve been trying to do in the domain of numbers: try to dissect out a system and understand what are the formats of representation at each level. So I would like to talk about, to try to pump out your intuition about the domain we’ll be talking about by giving you some examples of numeric intuition. Suppose I ask you number comparison questions, like what is larger, five or nine? You immediately know the answer. Or an approximate calculation: tell me if the following operation is true or false: one plus three equals eight? False. Or twenty one plus sixteen… is ninety seven. I think you get the idea that for all of these examples your mind finds the solution extremely quickly without much introspection and certainly without doing the exact calculation in your mind. I think that’s perfectly clear for the last case. Probably none of you thought first that twenty one plus sixteen was thirty seven, you could reject this operation as false before you were doing the exact calculation. And maybe in terms of introspection you might have a sense of distance, that ninety seven is too far off, or even too far to the right. So you see that special metaphors for this numerical intuition, and as we shall see indeed it is not a bad metaphor for a mental representation to think that numbers are organized on a mental number line, and that we have a sense of distance on this number line so that we can tell when a numerical quantity is too far off a given context. So we’ll be interested in the sources of this intuition.

Here’s a little bit of advertisement but one of the basic ideas in my book, *The Number Sense*, was that the foundation for this numerical intuition lies in the presence of a
So I'm not going to follow all that program today in the lecture but I'll give you a few points and I'll be talking specifically about the dedicated cerebral substrate, the automaticity, and the presence in animals, and a little bit about genetics, so new experiments we've done. All of this is extremely new experiments, I thought it was more fun to talk about ongoing research than, you know, the old results, so first let's talk about the format of representation of numbers in the parietal lobe and the basic involvement of the parietal lobe in number processing. So an experiment of number comparison: imagine you are a subject in this task: You are viewing a computer screen and on this computer screen there will be Arabic numerals, and you are asked to decide if they are larger or smaller than 65. So 52 you press left because it's smaller, 84, etcetera. When you do this sufficiently long you measure reaction time to all of the numbers you have this beautiful curve which was already observed several decades ago, which is called a distance effect. This is your reaction time, the time it takes to press the key, and these are the different numbers that can be presented with sixty five the reference in the middle here. What you can see is that the reaction time is a beautifully decreasing function of the distance between the numbers to be compared. And this is a very smooth curve as you can see, it has no discontinuity, it extends beyond the range of the sixties in which you have a six here on the left. And there is no discontinuity between 59 and 60. In other words what seems to be happening is that you're no longer dealing with the symbols on the screen, what you are dealing with is the working with the semantics of the number and in particular the continuum, which is behind the number: the continuum of numerical quantity. That's on this substrate that you do the comparison.

So the idea here is that you might have a conversion operation. First you have, of course, your brain has to identify those Arabic symbols but then you convert them into a quantity. What could be a model for this distance effect? Here is a little figure showing a tentative model that they have proposed with Jean-Pierre Changeux in 1993. This is a
model in which your brain might contain a number detector, a numerosity detector in neurons. The idea is there might be neurons or columns of neurons specially tuned to a certain number of objects in the outside world, so that this neuron might react, for example, when there are about seven objects, but there would be a distribution of activation as is usual, a tuning curve if you want, for neurons, so that that neuron would also [activate] a little bit to six, a little bit less to five, and so on. If you have multiple detectors and you think about comparing, say, number fifteen with number twenty, the overlap between those curves would determine under this proposed model the speed with which you can discriminate the numbers. The closer the numbers, the more overlap they have in your mental representation.

So that would predict the distance effect that we are empirically observing. There are behavioral data that fit extremely beautifully with this model, for instance the data from [- - ] in 1982 when they were working with displays of dot patterns and asking subjects to discriminate their numerosity so given a block of trials you might have twenty as a reference and you are asked to decide whether the particular number you have under your eyes, number of dots, is twenty or something else than twenty. What you see here is the curve for the subjects' responses, and you can see that as the number gets closer to twenty the subjects respond more and more. They make errors for numbers that are close to twenty but not exactly twenty, and the profile of errors is exactly that tuning curve that we are postulating here. But that's indirect behavioral evidence. Could we look more directly at the brain and find evidence for such a representation of quantity in the form of numerosity detectors?

Well, first we find evidence for the substrate of the distance effect here. This is an experiment where we simply measure the fMRI activation to each of the two-digit numbers that I showed you earlier leading to a behavioral distance effect. So this is a single subject image here of a subject taking this number comparison task. In orange you have the same distance curve I was showing earlier. Distance is now plotted horizontally from small distances to large distances and you have reaction time decreasing. What is wonderful is that there are a few brain areas, or actually a whole network, that shows exactly the same distance effect. So the percentage of activation that you see in blue here in these different regions is decreasing with numerical distance in exactly the same way as the behavior is. And the areas where they are located, what you see here the slice of the brain, horizontal slice, is the front, the back, the left, and right, okay? What you have is activation concentrating in the banks of the interparietal circuits. So this is the parietal cortex here, on the back of the head, and these regions seem to be systematically activated whenever you do calculation. We have found them in many different calculation tasks. I'll come back to them. Notice that there is a large network here and there must be several components here that are not concerned specifically with number processing. We can be a little bit more selective about which regions are the most interesting by looking at variants for notation.

In this experiment what we did again was to present Arabic numerals and ask the subjects to compare then with sixty five, but some of the numbers will appear as words. And we ask what is happening. Is there a parallel between the responses to Arabic numerals and
to words? Well, in behavior there certainly is. So here's the behavior as a function of the distance; close, medium, far numbers to be compared, and you can see that there is a distance effect in both verbal and Arabic notation with an additive effect of notation. A possible interpretation is that it takes a long time for your visual system to identify the verbal notation, but once you've past that stage the comparison itself is performed on this quantity continuum which is common and therefore gives an additive distance effect. So you can use that in imaging to ask, well what are the voxels that show the distance effect completely independently of notation? These are voxels that should be associated with quantity processing other than notation processing. So we did this experiment, and the data is a little bit noisy, this is also averaged across subjects but you can see that these voxels are largely concentrated in the left and in the right parietal lobes. In these regions what you find is a distance effect without an effect of notation. Unlike reaction times where you find the sum of the two effects here you can tell that voxel cares about distance, but does not care about notation at all, apparently. So you can dissect the additive factors method into voxels coding for each of the parameters of your additive factors method. So we are going to talk largely about these regions in the parietal lobe here. Are they a good candidate for quantity representation? What can we tell about them?

Well one thing that I was very interested in, as Lila mentioned, is whether there could be processing occurring without consciousness in those regions. Given that we have this extremely fast numerical intuition that I showed you at the beginning, is it possible that even without consciousness we might be activating that system and having an intuition about the distance between numerical quantities? So we did studies with subliminal priming.

This is work done with Lionel Naccache - he did his PhD on that. Here is the basic paradigm: you present a letter string, a random letter string, then a number, for a very short period, forty three milliseconds; then another letter string, and finally another number for a longer period of two hundred milliseconds. When you do this at the same location on a computer screen the subject does not see the first number. Even the experimenter does not see the first number. I'm still blind to those stimuli after such a long time experimenting with them. So what you see is a blinking of letters and then the final number nine. We don't tell the subject there is a hidden number, by the way, we just tell them there is a signal and then there will be the number. So we can show on rigorous tests that they have essentially no discrimination ability for this hidden number. They can not discriminate it from a random consonant string, for instance. We ask the subjects to compare the last number with five, so they have to press the right hand key if it's larger, for instance here.

I'll be reporting today - we did many experiments with this paradigm - but I'll be reporting today only on one contrast here which is the contrast between repeating twice the same quantity versus on the right here presenting two different quantities to the system. So the subject thinks that this is the same trial, right, it sees only the nine, but unbeknownst to him there is a repetition of the same number twice, possibly in different notation in this example here. In the other situation there is the presentation of two
different quantities. If you think about this numerosity detector model again, the prediction would be that there would be more activation if you have to process two different quantities because there would be two different [-] of activation evoked by two different numbers, compared to the situation in which there is only one number to be processed, like on the left here. Say we predict a difference in brain activation; we would also predict a difference in reaction time, with faster processing when you have to process on a single quantity.

So let’s look at reaction time first. The results came out nicely. The reaction time here on the y-axis is slower on the different quantity trials than on the repeated quantity trials. Here are the different notations for the target. We have trials in which the same physical stimulus, two words, verbal/verbal here, or two Arabic digits represented consecutively; and here you could say its a physical priming phenomenon, but you see that there is the same difference between different quantity and repeated quantity trials even when you change the notation used for the numbers. And there is nothing similar between the word nine and the digit nine aside from the quantity, the quantity that they represent. So we think that this effect is rising indeed from a notation-independent representation of quantity. Now we went to imaging with this task and again collected fMRI activation patterns to each of those trial types, and asked the imaging software to show us all of the voxels in which there was more activation for two different quantities than for the same quantity twice. And those are the voxels here.

The results came out beautifully again. It’s only the left and the right intraparietal regions, at the same location as before, that show this priming effect. Let me show you the curves, and they are like this. What you have here is the percentage of bold signals for those for you who know fMRI, the signal that we are measuring, which is something like the amount of blood flow that there is in the neural tissue, and blood flow will vary as a result of neural activation. All this is very slow and that explains why the time is in seconds here. It takes about five or six seconds to have a maximal effect in fMRI in a single event here. But you can see on events with the same quantity the peak was much less high than on events with a different quantity. That’s this reduction in activation on repeated trials so you can describe it as a greater activation when there are two quantities to be processed. The two curves are for same-notation versus different-notation trials, and you can see again that region does not care about notation at all. It seems to be able to extract a common quantity even when it’s conveyed by two different notations.

In passing I should note that this is a very powerful method. We call it the priming method, and its uses go way beyond the uses in the number domain. You can use this just like people have used priming in psychology: to ask exactly what is being represented in a given brain area, because you can ask what it is sensitive to, what counts as repetition, and what it is not sensitive to. It’s in that sense that I think we can use imaging to decode brain representations, and this has been used by various people. Now, a more difficult question: I’ve shown you parietal activations, they are quite nice and they tend to be a little bit extended and many people have expressed skepticism about the specificity for the numerical domain, after all this is probably working memory or spatial representation or attention or something like that. I think this is a big problem and I won't pretend I will
solve it today. The parietal lobe is engaged in many different tasks, and we don't know which region, if any, is specific for arithmetic. In order to try to approach this problem, it’s a huge problem, because the problem of specificity I think is one of the biggest problems with imaging, because potentially you could always think of one more task that has not been tried and which could potentially show that the region is not specific. But at least we tried six different tasks that are quite classical. We didn't invent new tasks. Our purpose was to try tasks that have been known to activate the parietal lobe and see whether there is any overlap with our number activations.

It is important to do that within the same subjects because there is a little bit of inter-subject variability. So here is this subtraction task which was used to locate the number activations. In this task you see digits and you have to subtract each of them from eleven or from five, fifteen – from some reference. The contrast task was a control task where you see some symbols that are letters and you just have to name them. So you have similar inputs and outputs but you have internal operation that differs, which is a calculation operation. When we do that, you see the subtraction here isolates a large network which is biparietal, bifrontal and midline interior cingulate supplementary motor area here. I focus exclusively on the parietal lobe in that talk and we are extremely interested in those bilateral activations here, which again, are in the same location - are they specific for number? Here is another task where you have to move your eyes. You find very clear activations of the parietal lobe in this situation that have been reported for a long time. As soon as you move your eyes you have activations here as well as in the frontal eye fields and the supplementary eye fields there and you overlap with the calculation task. Same for movements of visual attention.

This task was derived directly from the work of Maurizio Corbetta, who has shown that the networks of movements of attention in the absence of eye movements activate networks that are quite similar to those that you have when you simply move your eyes. So you see there is a lot of resemblance with the previous slide here. But there are also some interesting differences. Finger pointing is a very good activator of the parietal lobe, which is very concerned with the transformation between vision and action. So in this task we ask subjects to point their fingers to little targets that appear in the periphery. Just move their finger like that, not move their eyes, and we contrasted that with a situation where the same targets would appear but the subjects would have to fixate their fingers. And see this huge pattern of activation, this subtraction of course included motor cortex and somatosensory cortex but there is a lot of dorsal superior parietal activation here. Here is another task of grasping where you have to grasp objects. This task has been studied a lot in monkeys by Rizzolatti and collaborators. Here this was simple mimic grasping, and you can see again that this task will activate a lot of the parietal lobe, with some resemblance to the subtraction pattern we had observed before. Is there anything specific to number again? We know that the left angular gyrus region is concerned a little bit with language processing, we don't know yet exactly what it's doing but it seems to be active when converting orthography to phonology. So here we presented words and asked subjects to detect phonemes in these words, like the sound “e” here in concert, in French. We contrasted that with a situation where we simply had to decide the case of a letter string. When you do that you find this network of activation that includes the left angular
gyrus quite clearly here, and the issue is if this is the same region that we find active in number processing.

So when we put it all together, here is what we find: we can make all the intersections of these different tasks, now there are $2^6-1$ possible intersections so it is not an easy task but we think that we have isolated the right intersections, the ones that are reproducible from subject to subject, and here is what we find. If we start by the inferior parietal lobe, we find these areas in green here which is quite interesting which is relatively specific for grasping operations. In our situation that was the only task that activated that area. It is in connection in the monkey with field F5 where Rizzolatti is finding mirror neurons, so this area must be engaged in the action of grasping, and is similar to area AIP in the monkey; I will come back to that. Now the area in blue is engaged in saccades - that has been known also for a little while - and may also contain LIP, a homologue of area LIP in the monkey. As we move upwards we start to see interesting activations for number processing, so the area in red here was an area that we could only activate by number processing, compared to those five tasks, again. This is not eliminating the possibility that with some other task we would find that this area is actually non-specific, but for the moment at least it appears to be relatively specific compared to all of these other five operations. The area in yellow however was interesting because it showed an overlap between number and language tasks. These were the only two tasks that will activate these regions, so you can say that you can decompose the network of number processing... (tape ends)

I'll come back to that. Let me continue to show you the topography. We move upwards we see a lot of activation relatively specific to number processing but we also see the beginning of two other activations. There is this activation relatively specific to attention movements in the precuneus, there is this activation specific to manual movements whether pointing or grasping. This of course contains, as I said, probably somatosensory and motor regions but also more complex regions in the parietal lobe. There is also this very dorsal region which is quite interesting, which was activated only by the four visual-spatial tasks. So grasping, pointing, eye-movement, attention all activate that area here and this makes it all relatively abstract.

This is the same area, or at least part of the same area that [-] and collaborators have found to be associated with high-level attention including temporal attention, so it must have an interesting role in attention to space or something like that. I'll come back to that also. So let's comment these results a little bit. First we have interesting evidence I think that the number circuit is not a homogenous circuit. When you look at the subtraction task, the subset of it is shared with the phonological task and this allows us to decompose this network into a relatively perhaps more specific network, and network shared with language on the back. This is a result that fits very well with the literature, and in particular with the previous work I did with Elizabeth Spelke, and the dissociation between exact and approximate task. What we found was that the more interior and superior part in interparietal circuits was more activated by approximation tasks, like I gave you in the beginning, whereas the angular gyrus was more activated by exact calculation tasks that seemed to be more dependent on language and require a rote
storage of arithmetic tables. So the idea is that this region here might be more engaged in processing of quantity whereas this one would be coding numbers just like other words, and you would know your multiplication table and your addition table simply by reciting the corresponding words.

When we put it all together, this is work we did very recently we reviewed the literature and we were able to obtain images in many cases which we could intersect and we ended up with this map of the relevant activations in the parietal lobe. The area which is in red which we call the HIPS, the horizontal interparietal sulcus, is really an area that is activated by all numerical tasks but particularly comparison, calculation and approximation more than exact calculation. This is an area that shows quantity priming, it shows a number/size effect, it is more active for larger numbers than for smaller numbers, so we think really that this area is a good candidate for a core semantic area. It has all the properties of a good core semantic area. The area in green again is the left angular gyrus. It is left-lateralized and it is very related to language dependent tasks in the number domain. So it is more active for exact calculation, which we know is related to language processing; it is more active for multiplication which is the one operation that you really learn to solve by rote learning. It is also activated non-specifically for the number domain but in tasks of word processing like non-word reading. So we think that this is plausible that all arithmetic tables are engaged in this region.

Finally the area in blue is also active in number processing tasks. Now this is a bit more fuzzy. There is only a subset of numerical tasks that activate the area in blue; they are in the bilateral posterior superior parietal lobule. Those tasks are subtraction, approximation, and the distance effect. And what could be common to all of these regions is that they involve some form of internal attention on the space of numbers. This is the intuition that I was trying to develop in you in the beginning - the intuition that you were orienting your attention and you found that eight was too far to the right as a solution to one plus three. It could be that you have this very abstract attention process that you orient either to space, and you definitely find that this area is activated during spatial attention processes, but you can also orient it in more abstract domains like time and number. That’s the speculation we have now. But at least with this subdivision now we are able to clearly isolate an area in red here which seems to be for the moment at least a good candidate for specificity in the number domain. I guess I'm going to skip that part with the map that we did.

We can explain to some extent the conjunction of deficits that are found in patients with lesions to the parietal lobe. Often they are [-] in the midst of other deficits and they all seem to fit together with this map. But I really want to talk about the evolutionary precursors of this number sense in the parietal lobe. Really if we have this dedicated representation and it’s laid down in the genes it must have an evolutionary precursor in animals. Of course animals would not be processing numbers symbolically, this would be the prerogative of the human mind, but there might be an ability to extract number from numerosity of sets of items, and is this present in animals? Well there is a lot of evidence, actually, and before going to that evidence I think we can use the map that we made to
make a little prediction about exactly where, if there is a sense of number in animals, to which brain area it should relate to. In fact this experiment was made especially on purpose so that we could compare the map in humans to the map that is known in monkeys. So if we look at this map, the area in green which is involved in grasping is a very plausible homologue of area AIP which is in grasping in monkeys. The area in orange plausibly contains among other things a large composite activation but it must contain a homologue of area MIP in the monkey. Then the area in pink might be homologous to area V6A which contains neurons that are related to arm movements as well as eye movements, with neurons that decode for the direction of those in space. Finally, area LIP is engaged in saccades and attention in monkeys and it's a good plausible homologue for the area in blue. So we have a map, you can see it makes a little arch. There is a very nice geometry in the left parietal lobe here.

The same arch in a sense can be found in the monkey brain. What are the differences? Well the differences are that we see those two areas in the middle here that occupy a lot of space, whereas there is relatively little space, if any space at all, between this corresponding areas in the monkey. So we have an incredible process of expansion, non-linear expansion, because you require, at least, as shown by David [Vanessen] you must have has at least a twentyfold, probably more than that, more than twentyfold increase in the size of the parietal lobe to move from this monkey map to this human map here. But given that we have this homologue map well if there's something homologous to this area in red which is activated for number processing – is there anything like that in the monkey? The behavioral evidence is quite good to show that monkeys can do some form of number processing.

So here's an experiment for instance by Marc Hauser and colleagues, in which they show that rhesus monkeys in the wild could select the larger of two numbers. In this experiment the experimenter presents food item by item in one of these wells. For instance the experimenter may be putting three pieces of food here, and two pieces of food here, and then turns away and the monkey is allowed to go and take some of this food, and you look at where the monkey goes first. The finding is that the monkey goes first to the place where there are more items of food. And with good controls you can show that this is really number that they look for. These experiments are very nice because it is done on a single trial basis in monkeys that are free on an island, and monkeys that are not trained. They participate in this experiment, and they accept to come and be subject in this experiment. So what is nice is you know this is a basic ability, it has not been inculcated in them by training.

But with training you can do more in the lab, of course and here is a beautiful experiment by Brannon and Terrace in Science a few years ago, where they were looking at the ordering of numbers. What they asked subjects to do was to press on a touch screen in the appropriate numerical order, four cards that bore the numbers one, two, three and four - numbers of objects. So the monkey would be presented with those cards randomly arranged on the screen and would first find the one then the two then the three then the four. Monkeys would learn to do that very accurately and very quickly. Seeing them behaving is incredible; they're much faster than we are, actually, probably because they're
smaller brain smaller connection smaller everything. They just did this task (makes sounds) like this – extremely fast. Now what was interesting was that after training when they reached performance of something like sixty persons, which is much better than a chance level, a chance level would be one success in twenty four trials if you look success for an entire sequence, so they already got much better than chance. They generalized two new sets in which various parameters were controlled but most importantly they generalized this knowledge even to new numbers that had never been trained, and I think that's crucial. So the monkeys were transferred without reward onto a task where they had to discriminate and order numbers five to nine. What they did was transfer spontaneously and press the smaller first and the larger second, without training. So this indicates that even though there was a lot of training in this experiment, what the monkeys that acquired went beyond what was necessary to acquire the initial task, and they brought to bear on this task a sense of number.

Now I come to the more exciting part I think which was two weeks ago. This paper in *Nature* from a Japanese group of Jun Tanji and collaborators, this is a group that has looked at action and sequences of action in the past and they found a way to test number with sequences of action, and to do neurophysiology on those monkeys. So the behavioral task was that the monkeys were learning to make a sequence of five actions. For instance: pushing a knob five times. And after the fifth they would have to switch to a new action of turning. They would turn five times and then they would have to switch to pushing again. So there were long temporal intervals between the pushing and the turning, between each individual action I mean, and these intervals were determined by the experimenter so that they could be randomized and decorrelated with number but the monkeys quickly learned to change the action after the fifth action. That's what you see here. You have the distribution of the frequency of changing as a function of the number of consecutive movements and you see the monkeys switch mostly after five. Interestingly there is a little distribution of errors here. So after that what they did was go to record with a single electrode penetration, various neurons in particular in the parietal cortex. And the great finding was that there are indeed in the parietal cortex of monkeys just like we predicted by the model I showed you initially, there are neurons that are tuned to a specific number.

Here is an example of one such neuron that responded very strongly prior to the action when the monkey was doing the second the third or the fourth action, but not when the monkey was doing the first or doing the fifth. So there is a little bit of a tuning curve here. There were neurons tuned to different numbers like this, in fact to all the relevant numbers in the experiment one through five, and you know we don't know if there are neurons tuned to any other numbers or not. What was most interesting to me was where those neurons were. And here is where they are: the author says that this is a well-delimited area, if you move millimeters further you simply don't find those neurons any longer. Most of the neurons are concentrated then in this little area of the interparietal sulcus. Fascinatingly, I think, this is an excellent, very good homologue for the area in red on the map that I showed you earlier, relative to the other [areas] that are known in the monkey like the AIP and LIP and so on. It is also a good relative location. These neurons were not solely found in the parietal cortex. There were also similar neurons in
the frontal cortex and in the midline supplementary motor area cortex. This is similar to what we find, but the authors found that they were more numerous proportionately speaking in the parietal lobe. So this is really a good candidate for one or the other that really represents the parameter of number. And it shows that there is a real possible homology here. We might be starting in life with a nearly [innate] response to the numerosity of actions, objects, addition. It remains to be shown that these neurons would have these multi-modal properties, but we are starting life with such an area and then learn to connect it with the appropriate signals: digits and words.

So I’ll finish the talk by talking a little bit about the genetics. If really what I said is correct then there should really be a connection to genetics which should be possible. That is to say, the area is not landing there by chance; it’s landing there because there is a genetic predisposition in the buildup of the brain to provide neurons that have this appropriate property. So we should be able to find genetic diseases that affect this laying down of the organization of the parietal lobe and that perhaps leads to [-] and this is called in the developmental domain developmental dyscalculia. So we are doing a little bit of work – this is really work in progress that I’m going to show you, preliminary data. But we have done some work with Nikolas Molko and Marie Bruandet to scan for a genetic disease called Turner Syndrome, which may have the appropriate properties.

To introduce the subject I’d like to say that there is a little bit of work on the developmental dyscalculia already but not of genetic origin, and again this work points to the parietal lobe as a likely source of impairment for developmental dyscalculia. On this slide she has put together the activations that we see for instance in subtraction, the lesions that we see in adult subjects that lead to dyscalculia, an inability to calculate, I should say a word about what these patients are like. Some of these patients can look fairly normal, have normal reading abilities, have normal planning abilities, and working memory, but be totally unable to do simple calculations, and in fact they seem not to understand what a number means. So we found some patients that could not do three minus one for example. Or that couldn’t say what’s between two and four - operations that are so simple that they aren’t really a calculation any longer. They already top, I think, I argue this basic numerical intuition that I’ve been talking about. Now it’s an interesting issue if you can find the same thing in the developmental domain. There are at least some cases that are quite intriguing of children that seem to be born with a similar deficit in which they are gifted at school, they learn to read, they have normal command of language, they have normal attention, they don’t have attention disorder, but they have this isolated difficulty in understanding calculation and number.

There have been very few good studies I think in this domain, and there have been even fewer studies where people have looked at the actual brain abnormalities behind this deficit. So we already have not much data, but recently there’s been two studies of the brain basis of this deficit, one if which is shown here. This is the study of Levy, Reis and Grafman. What they did was to use spectroscopy to look at the metabolism of a slice that was going from the front to the back of the brain and through the parietal lobe in a subject that was showing this very striking selective dyscalculia. I should say first that the anatomy of this subject as shown on a normal T1-weighted anatomical image was
normal. It didn’t seem to be abnormal at all. There was a folding pattern of the sulci. Maybe with zooming in we might have found something but it seemed to be normal. However the metabolism was not normal. You can see that there was a little hole here, if you want, of abnormally reduced metabolism that was found on the left but not on the right in the parietal lobe but not in other regions of the brain. To close such a deficit in metabolism it seems that at least this was what the authors postulated there must have been an abnormal neuronal migration very early on that would have caused both this abnormal metabolism and also the condition of developmental dyscalculia.

More recently there’s been a very nice study in the journal *Brain* by the group of Isaacs and collaborators in Great Britain where they looked at premature children. Premature children often have dyscalculia but not always so what they did here was to take a large group of premature children when they were adolescents and sort them as a function of whether or not they had had dyscalculia during their development. Half of them had dyscalculia, the other half did not have dyscalculia. And what they did here was to compare the percentage of brain matter in the whole brain trying to see whether there are decreases in the amount of brain matter in different regions. What they found when they did this is that there is a single region that discriminated between the two groups of dyscalculics versus non-dyscalculics, well there was decreased brain matter in the dyscalculics and this was in the interparietal circuits on the left here, almost exactly at the right coordinate where we find the activations in normal subjects. So loss of gray matter in that region seemed to be responsible, at least was a plausible cause, for the fact that these children were developing dyscalculia. Now here we are probably talking about an [injury] just before birth, so at the time of the birth, but probably not of genetic origin.

However now I’m going to talk about this Turner syndrome which is a genetic disease where we have been looking for similar observations. Turner syndrome is caused by a partial or total deletion of one X chromosome in girls. So normally you have two X chromosomes if you are a girl but these girls only have one X chromosome. Either it’s a total deletion, or it can be a partial deletion of part of one arm of the X chromosome, and it can be present in all cells or it can be a mosaic pattern in which some cells show this loss but not all. It’s a relatively frequent deficit, one in 2500, the phenotype is relatively complex. It includes a small size, recognizable facial features, [above all] there is an aplasia in the pubertal development, so these girls are sterile and they are deficit in estrogen and progesterone that needs to be compensated by medicine. But I think we are really interested in their cognitive abilities and their cognitive abilities are quite subtly abnormal. They have normal verbal IQ, they are not retarded. Some of them can be very bright, actually. Performance IQ may be a little bit reduced, and they do show visual and perceptual deficits, especially spatial deficits. Interestingly there have been reports of difficulties in arithmetic, and the few anatomical studies that are available to that suggest some amount of occipital parietal atrophy. So we started from this point, and you know it’s a fairly ambiguous pattern. We were hoping that this could be a case where the quantity of a presentation would be affected but of course you’ve seen it there are multiple representations in the parietal lobe and so that is an interesting thing to try to decide exactly what is the nature of the deficit here. Is it in the verbal domain? Does it affect things like multiplication? Or is it more in the quantity domain?
Well, we have a fairly ambiguous answer. Here for instance is the behavior of subjects in multiplication, both their response time and their error rates. What we did here is compare the Turners in yellow and the controls in green for different types of numerical facts. Trials are things like 2x2, 3x3; rules are things like x1 and x0 which can be done by knowing a little rule, these are small facts, x2, x3, x4, that very often you learn by rote very easily, and finally these are larger facts, x5, x6, x7, that studied in normal subjects show that these are the facts where you begin not to know them so well, indeed you can see that normal subjects begin to have difficulty with those facts. An interesting finding is that the Turners were essentially identical to the controls except for this particular category of larger number facts. Larger number facts [create] a situation where we find there is a coordination of these two systems, of quantity processing and verbal processing. Larger facts, certainly you try to access your verbal memory, but it is an empirical finding that you don’t always succeed in returning the result from your verbal memory, therefore this is where you start to see subjects using strategies that have a quantitative nature. For instance, you might find the result of seven times nine, therefore you might do, well nine is just one below ten so I’m going to do seven times ten and I’m going to subtract seven. Or is it nine? I’ll let you think about that.

So you see that if subjects adopt such a strategy they will both be retrieving from verbal memory but also using quantitative strategies like knowing that nine is close to ten. So this is a complicated pattern and it seems to suggest that rote verbal memory per se may not be so much affected as the coordination with quantity-based strategies. We did an imaging study with those subjects, we had a relatively small number of subjects now that number keeps changing all the time but I think now we have 14 patients with Turner’s syndrome not all of them with the simplest karyotype where a full X chromosome is missing and controls much for age and sex. The imaging, there are lots of things you can do of course. We did anatomical scans that allowed us to look at the distribution of white matter and gray matter, we did functional imaging that allowed us to look at the activation patterns in those subjects in an exact versus approximate calculation task. And we did diffusion tensor imaging, a technique which allows us to look at the microstructure of white matter. I’ll come back to that in a second. So here’s the functional test: you see an addition like four plus five, and you are asked to select between two results, like nine and seven. In this situation the two results are close, so you cannot really use approximation, and one of them is correct which you can retrieve from your memory and this is the nine. So you are asked to select the nine. This is what we call the exact calculation task. In the approximate case you are shown the similar addition four plus five, two results, both of which are false now but one is grossly false, it’s a three here, so you can very quickly reject it using approximation and you’re asked to select the one which is closest to the correct result, eight. We also have a letter matching control, I’m not going to talk too much about that but that’s a situation where we have to detect a repeated letter. So we think this is tapping the verbal system of calculation and this is tapping the quantity system. So here is the behavior of the controls in the Turners in this test, and again we find a relatively selective deficit first, not too many errors. I think this is a good situation because it means that those subjects are not hugely impaired, they are simply slowed. Then we find that the slowness is again confined to large numbers during exact calculation.
What is quite interesting is that in approximate calculation they really have no deficit at all. But then neither do they have any problem with exact small problems. So it seems to be when you engaged a combination of – having to do an exact calculation but having to do quantity manipulations because these are large numbers that you don’t know to well, that seems to be where they have the deficit. What about imaging? Well imaging is complicated and it’s only a developing story, but I wanted to give it to you. See how [many] differences there are between the brains of the Turner subjects compared to control subjects. This is a huge difference. There are differences in used gray matter, in very many different locations. However some of them are interesting and there is in particular left lateralized this loss of gray matter very close to the area where we see activation during exact calculation. So it’s possible that this reduced gray matter here would be directly correlated in the left angular gyrus with this difficulty that they seem to show in exact calculation with large numbers. If we look at the reduced white matter the picture is also complicated because there are large areas of loss of white matter in those subjects. But you see that there is nothing in the parietal lobes here, however we think that that image may not be very sensitive. It’s simply sensitive to the presence of white matter and therefore it can only show areas where there is loss of an entire fiber track for instance. But it is not sensitive to subtle disorganization of these fiber tracks.

So we went to another technique which is called diffusion which allows you to measure very finely the properties of the fiber tracks. The diffusion phenomenon is that there are water molecules throughout the cortex in the white matter and you can measure how far those water molecules are moving, they are moving constantly in Brownian motion, you can measure how far they are moving in different directions and every voxel of the brain. Now when you do that in water, just in a glass of water you find that diffusion is isotropic and it’s a well-known Brownian motion that goes in all directions. But if you do that in white matter like it’s doing here, you find that the water molecules, they are trapped either inside the cell or between the cells. And because they are trapped they will not move as easily in all directions. In fact they will move relatively easily along the fibers because there are no membranes in this reaction, but they will have much more difficulty moving in the opposite direction, perpendicular to the membranes. So what you have then when you measure the MR signal in diffusion is a signal which reflects the direction of the fibers. For instance here you have a big fiber track plunging vertically here in the brain. And this is colored in blue because blue was used to color the vertical direction. So you suddenly have images that are highly sensitive to the microstructural properties of the tissue and particularly in the white matter. They are extremely useful. So we used those techniques, and with those techniques indeed again we can find that there is an abnormality of the white matter now in the left angular gyrus; with two different techniques I’m not going to go into that too much but its two different measures here. We have a clear decrease in the signal from white matter in those regions. So it’s clear that this region is abnormal, and that this might correlate with the deficit in exact calculation. However, the other region, the interparietal circuits the HIPS region which seems to be more associated with quantity is not normal either, and this was very clear in the activation pattern of the subjects.
Normally I showed you that we are doing exact versus approximate calculation and we still have to analyze all the details of the experiment but I just wanted to show you one result, which is that in control subjects, as you increase the size of the numbers you find that there is additional activation in those left and right regions. This is the number/size effect, and this is found only in exact calculation. It seems to reflect the fact that suddenly as I said you have to resort to quantity-based strategies, and you see this interparietal system lighting up again. That’s in control subjects. There is no such effect in patients. So they’re going to have abnormal effect of number size in those regions. They seem to compensate it a little bit by having increased activation here in the left and in the right inferior prefrontal regions. That results in this interaction that you see where there is a number size effect in controls but not in patients. So those regions are not normally activated either and this was also the case in the approximate situation, we could show that even though the performance of Turner’s subjects and the controls were identical in terms of reaction times and error rates, they were not distinguishable, the patterns of activation that were behind that performance seemed to differ. Which is perhaps an ideal situation for imaging, because if you have a difference in performance, of course it’s normal that you should find a difference in brain activation. It’s still interesting to see where it is but it’s quite expected. But if you have no difference in performance and a difference in brain activation then it really means that you have spotted an abnormality without the possibility of alternative explanations in terms of length of reaction time or something like that.

So I’d like to conclude. This is a temporary conclusion I changed as we continue to analyze this very complex data set, but I’d like to conclude that the patients with Turner’s syndrome do exhibit behavioral deficits which are largely confined to a slowing down of exact calculation with large numbers, and this is associated with microstructural anomalies of the left angular gyrus, not the quantity area that we are finding in other studies but more this language related area which plays a crucial role in exact calculation. However the abnormal fMRI activations in interparietal circuits, and this might suggest that there is an abnormal lack of coordination of quantity-based and language-based calculations. (tape ends) … the circuits that we find laid down normally, systematically in the same way indifferent individuals in normal subjects.

So I think I’m reaching my conclusion here, I think there are, I give you quite a bit of evidence that numerical quantities, the number parameter, are represented in a non-verbal format independent of the particular symbols in the left and in the right interparietal sulci. I think that this representation is the foundation for our numerical intuition, I think there is good proof of that in the fact that if you lack it because you have a vascular accident, prematurity, or some kind of abnormal development of that region then this interferes and you have developmental dyscalculia. So I gave you also evidence that this representation is present early on in phylogeny and ontogeny. I’d like to stress that you should not some out of this room thinking that this is some form of new phrenology. It is very clear. I wouldn’t like you to think that arithmetic is associated with a single brain area. That would be actually the exactly the contrary to what I’ve tried to say. There are multiple networks, you’ve seen the extent of those networks and I’ve been talking solely about the parietal lobe but there is a lot of activation in the frontal lobe as well. So it’s a collective
phenomenon, multiple brain areas are collectively engaged. But this does not mean that we cannot isolate specific functions associated with specific brain areas. Simply they are very simple functions. They are not like having numerosity detector neurons that would help for a specific coding level, but of course it’s not doing the whole job of calculation all by itself. Finally I’d like to conclude that here we have I think growing and growing evidence that the number domain is a domain that is biologically determined. I think that it would be nice to apply the same message to other domains of semantic knowledge and here is a potentially very fruitful research program. I think numbers [form] a very simplified model for the acquisition of semantic knowledge and how it is represented in the brain. I’ll stop here and take your questions. Thank you very much.

Questions & Answers

Q.: (inaudible)

Dehaene: That’s a good question. There is a little bit of a paradox here which I don’t think is fully resolved, because on the one hand we see that the activations in this HIPS region are largely bilateral, on the other hand the lesions in patients that are clinically reported tend to be on the left side exclusively for acalculia. And there are many different problems here. One could be a problem of report. A problem that aphasia patients with left hemispheric lesions tend to go to the clinic much more than patients with right hemisphere lesions who might even have anosognosia, so they might not be aware of the deficits. But aside from that it’s possible also that a lesion to the right hemisphere would have more subtle effects, because the view here is that you have redundant quantity representations in the left and in the right. So if you have a lesion on the left why would it have such a big effect since you still have this representation on the right? Well it might be because even though that representation is still there it is functionally disconnected from the language regions in the left hemisphere. This left-hemispheric quantity region will also serve as a pivot through which you can connect the right quantity representation with the language system. So that would predict that the region on the left would have a much stronger effect than the region on the right. What is for sure is that we split brain studies. We can show that both hemispheres have access to a quantity representation and the properties of the left and the right for the moment have been shown to be largely similar, and there is a little bit of evidence that the right hemisphere alone can approximate calculation even though it cannot do exact calculation.

Q: (inaudible)

Dehaene: It was inspired by memorizing telephone numbers, so actually it started when – I should say that all of these behavioral experiments on exact versus approximate calculations are all Liz’s experiments with [-]. But her intuition was the same as mine. We had been to each other’s countries and we had to memorize telephone numbers, and I know my American telephone number but I know it only with American words. So I know it’s 503 485 9831 I think, but I don’t know it in French words. And if I have to say it in French it’s a terrible experience. So there are facts that concern numbers that we know in a specific language. So she set out to test that formally but there was training
involved in both the exact and the approximate case. The idea was that subjects would learn an operation like you say fifty three plus eighty one so they would come on one day and they were bilingual subjects, they knew Russian and they knew English. They would come in one day and learn precise facts like 53 plus 81 is – what is it? 114. I can even do that in English! That’s unusual, it’s a counterexample. But they would learn this in one of their languages, English for instance. Then the next day they would come in and they would also learn, so there was learning in both cases, but they would learn now approximate facts. So they would come and these would be taught in Russian, for instance. So they would learn that 53 in Russian plus 81 in Russian is approximately 110 and they would be given a choice between 110 and say, 150. And they would learn to select 110. They were identical learning curves in the two situations - that’s important. So in both cases they were acquiring something. But then in order to know exactly what they had acquired, Liz tested them in a last test session without reward, without feedback, they were tested on the same facts as before presented either in the same language or in a different language. This way you can see whether there is a cost to changing the language in which you’ve learned the facts. And a beautiful finding was that if you’ve learned the exact facts, 53 plus 81 is 114, I guess its 134! Ah, okay. If you learn that fact then you have a huge cost to switching to Russian. It’s a one second cost, a large cost which implies some kind of internal translation process. So you’ve really learned it with the specific words in which it was presented. But the other situation in which you also learned, in which the subjects improved and became faster and so on, there was absolutely no cost for switching the language. So if you learned that 51 plus 83 is about 130 then you’ve learned it once and for all if you already know the languages in which one can ask the question. There is no cost. So that was the origin of the experiment. It’s not just a matter of learning versus not learning, but it’s the format in which you’re learning from. Both systems can learn but this gives evidence that they have not learned in the same format. Does that answer the question?

Q.: (inaudible)

Dehaene: No. And that’s work that needs to be done. We don’t know what angular gyrus really is doing in language. However we have some neuropsychological evidence that constrains very tightly I think at what level these kind of language effects could be occurring. John [Wellon] has performed some very nice work, showing that – I’m not sure if I can reproduce that so easily, but actually John could you give a one minute summary of what the argument was for a non-phonological contribution? It was very striking, actually, in the patients. (response inaudible) So initially we took this data as going completely against what I was saying. The fact that you could have the phonology wrong but still could be retrieving the results seems to be complicated. But then there could be – and that’s still what I’m arguing – is that there could be sources of error in the phonological naming pathways that would be beyond the stage which is common to language and calculation and one such stage might be the stage of the lemma, in a model like Levelt’s model of word processing. So at some level like this there could still be mapping between calculation processes and language processes. So it would be very interesting to try to decode what that angular gyrus agent is doing exactly to language and the prediction would be that it might be related to the lemma level.
Q.: (low volume)…increased response with magnitude of number. This can’t go on forever… But that also leads to the question of whether our number system is well chosen to interact with our native abilities to think about numbers, in the same way that we have designed graphical elements in our alphabet that are easy to discriminate, we have seven digit phone numbers because eight [-]. Do we have a base ten number system where we count up to hundreds of ones and hundreds of thousands and hundreds of millions for example because this formal structure in the Arabic number system and the way we [-] is convenient for our native number sense?

Dehaene: I’ll start with the first question which was number size. I think I can clarify that a little bit because it’s not the case that if you simply present larger and larger numbers you have more and more activation in all tasks. So if I am doing the number comparison task I add similar amount of activation for comparing one with five, relative to comparing nine with five. So there was a symmetrical activation pattern like this. So you have increasing activation with number size in tasks that are known to show an increase in reaction time with number size. Probably what is happening is that larger numbers yield more difficult processing and therefore activations that last longer. So this is the case in multiplication for instance where five times nine really lasts longer and there must be longer lasting activations that show up as increased signal in the fMRI. So you know, we still have to sort out exactly the tasks in which there is such a number size effect and exactly for what reason there is a number size effect. But I don’t think it’s a mechanistic thing in which the greater the number the larger the amount of neural activation. It has more to do with the strategy that the subject is bringing to the task. Now your question was very interesting: what properties of the language of numbers reflect the properties of our number sense? I think there are many properties of the number sense that are reflected in language, actually. James Herford published two books listing the exceptional properties of the small numbers one, two and three, which are also the numbers that the quantity system can recognize relatively easily and precisely, and so in language these numbers are special. They don’t have the same properties of declination, with grammatical context. They don’t have the same properties of ordinality, you have words for second and third that have radically different properties from the other words: fourth, and fifth and so on. So that’s one property. And then you mentioned the base. I think the base is an invention that was invented to circumvent this approximation sense that we have when you move to larger and larger numbers. So it’s a way to recycle the same numbers again this time by multiplying them by something else as if we were saying ‘three tens’ just like we say ‘three apples’. It allows us to use the same numbers in small quantities to refer to much larger numbers. So I think that’s how the syntax of numbers started and there’s good evidence from the evolution of languages that the word for ten for instance might be ‘two hands’ in several languages so it really started very concretely when subjects were using their fingers to refer to numerosity. So all of this is a bit mysterious still but I think we can see some properties there.

Q.: (inaudible)

Dehaene: Ah. Well there’s been a few but only one that used imaging, there was two years ago in Nature or Science. It was only using positron emission tomography which is
not a very precise technique, so they were not able to find differences in the parietal lobe. And maybe that’s okay. It has always been my point of view actually in the number sense I was talking [in] one chapter about that. It has always been my point of view that these people are not so different from the rest of us. They are not outlandish completely. I think they have the same basic representations and then they have all sorts of learned strategies and expertise which they have learned to use which are really quite simple if you are a mathematician. They are mostly using $a^2 - b^2 - a - b(a+b)$ and stuff like that. Its not hugely complicated. In this one scanning study it was interesting to show that there was no difference in the parietal lobe activation. There were differences in the network for episodic memory, which involve in particular the parahippocampal areas. Common introspection of these people is that they’re so expert with numbers that they have a kind of personal relation with those numbers. They say that. They say, “numbers are my friends”, alright, “I met 1872 in a calculation three weeks ago and now I’m meeting it again”; so it’s really episodic memory that they are using here and it was nice to see that that circuit was becoming active more than in some other control subjects. So that would be the story. Now the real thing to explain with them is why they are so passionate about calculation, which is such a dull subject, eh? And that relates to the fact that many of them are autistic.

Q.: (inaudible)

Dehaene: Ah interesting. Yeah, we had been suggesting that for retrieval of arithmetic facts the basal ganglia on the left play a particular role. This was based on lesion evidence that can be discussed, there’s a little bit of activation in those regions, it’s not always so easy to detect. So yeah we had suggested that there could be automatisms in the verbal sphere but this has nothing to do with number really, it has to do with the storage of rote verbal facts, and here the left basal ganglia only play a role. We had this nice patient that was a dyscalculic, but really dyscalculic for the multiplication table, largely, more than for any other operation. There was an association between this dyscalculia and knowledge of rote verbal facts like prayers, poems for instance. She would mix them up in a similar way that she would mix up the multiplication tables. So that would be where the basal ganglia plays a role, it’s relatively trivial. But there are so many multiple loops that I have no doubt that they are part of the basal ganglia, maybe involved in more quantity processing. I have no evidence for that for the moment but I wouldn’t be surprised if it was the case. Yes. You had a question for a long time, too.

Q.: (inaudible)

Dehaene: Yeah we are doing that right now, actually. So I don’t have the results to give you. Of course there are several reasons why we didn’t want to start with that. One was that the task that we selected was selected to resemble the task that had been used in monkeys, so that we could make that connection to monkey. The second is that you may be right, and we wanted to focus first on possible differences between other areas. But it would be equally interesting I think if numbers and continuous quantities like distances would be represented by the same system. Finally I think I was always worried by the specificity issue and it can even become and artifact issue, whether there’s any artifact in
this task that explains your parietal activation but has nothing to do with number. But I was really pleased to see that the monkey evidence for number neurons, when you have number neurons like this it becomes very hard to think of an artifact of space or something like that.

Q.: (inaudible)

Dehaene: Yeah I agree with you there must be a problem at some point. This was mentioned before. Right. So we don’t know the answer to that question. All I can say is there have been some experiments in animals that go to relatively large numbers, like 45 versus 50 in the pigeon for instance. They do better than chance on 45 versus 50. Better than? Ah, I don’t think so, and that could be interesting. It’s possible that those properties are modified and in a rich and interesting way in humans. Because we have words than can refer to precise numbers and that could change the pattern of activation even in nonverbal regions. There is perhaps a little bit of evidence again from John [Wellon] and colleagues in that the verbal faction if you measure the imprecision in the perception of numbers, well the verbal faction seems to be smaller in humans than in animals. Would you confirm that, John? Yeah. So it’s twice smaller of something like that? Yeah. It could be that we are able to have intuitions about larger numbers because the language allows us to refer to those numbers first. (long inaudible response) Oh well, I think that it would be really naive to expect that there should be a single gene that, all by itself, lays down number neurons, and I also think it would be a mistake to think that there would be a single gene that would be specific to a particular number area. All we know about the patterns of gene expression is that they manage to specialize areas for intersections of gradients of the effects of different genes. So I think this is why it’s going to be hard to find an extremely specific deficit just in the number sphere without affecting the neighboring parietal areas. In all the patients that you listed I really think the Turner’s are the most selective. But even they have difficulty in the visual-spatial sphere. And that’s natural, because it would be extremely implausible to have the effects of a gene stop really sharply at the boundary between number areas and other visual-spatial areas. So these genes together I think they only build biases locally and all that we see here, and I think even in young babies if we are able to see the organization of those areas, is already influences by epigenetic factors. The genes laid out a biased architecture that then gets laid out by epigenesis. So genetics is going to be a very complex enterprise. But I think it’s interesting to show at least the logical proof that there is a link between genetics and those areas. It’s not going to be a simple one gene, one area thing.

Q.: (inaudible)

Dahaene: That’s a good question. We don’t know that. All the images we’ve done, they were done with small groups of subjects and we did not find a difference between males and females but we have not looked very hard. This would require relatively large experiments that we have not done. There are reported differences in the broader, richer, [pool] of tests, international comparisons and so on, but this is a fairly ambiguous area, fairly difficult to discuss. I have a few pages on that in the book but these are some of the most careful pages in it. Because it’s so ambiguous you really don’t know what
proportion is due to the social pressures and what proportion might be due to a biological basis. Now still I wouldn’t be surprised if there were biological differences in those areas. One of the biggest differences between males and females is in mental rotation, that’s where you find the most reliable difference. It still is a difference of less than one standard deviation, so there is a lot of overlap between males and females, of course, but it’s a large difference and it’s in the parietal systems as well. I wouldn’t be surprised if the parietal lobes turn out to be one of the origins of a relatively big sexual dimorphism. At most this is going to give you a little bit of a bias, initially. This is shown very clearly in the international studies. This is what I like to quote the most, I think: you know that there is a huge difference on the very same test in international studies between, say, America and Japan, for instance, or China, with China and Japan being way in advance in terms of performance at the same age. So what you can do is compare American males and females to the Chinese males and females. What you find is that the Chinese females are much higher in scores than the American males. And the difference between the countries is much bigger than the sex difference. So that means that there may be a little bit of a bias and it’s bigger than the sex difference. But the effect of education on this is huge, and the two are very hard to separate. And I’m sorry for the American students… but the French are not so good as well, we have to learn from Asia, I think, in that respect. Thank you very much.