Current Biology, Vol. 14, R517–R519, July 13, 2004, ©2004 Elsevier Ltd. All rights reserved. DOI 10.1016/j.cub.2004.06.042

Cognitive Neuroscience: Acting on Numbers

Dispatch

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The parietal cortex is a central part of the brain's system for representing numbers and magnitudes. Activity in the parietal cortex might reflect number representation or actions made in response to the numbers.

If you have to decide whether somebody is younger or older than you it might take you a few moments to consider, but it takes longer the closer the person's age is to your own. This is called the numerical distance effect [1]. Whenever people are asked to decide whether a number is bigger or smaller than a reference, response times increase with proximity to that reference (Figure 1). One interpretation of the effect is that it arises because numbers are represented in a spatial format, perhaps along a mental number line. A small proportion of people can explicitly call to mind, or even draw, their mental number lines. The long response times of most subjects when a number is close to the reference is thought to indicate difficulty in discriminating positions that are close together on the number line.

Recently the numerical distance effect has been exploited in several neuroimaging studies aimed at investigating the brain's representation of numerical quantity. Most of the studies have highlighted the importance of the parietal lobes (Figure 2). It is widely agreed that the parietal cortex is critical for our ability to represent space in the world around us. For example, patients in whom the parietal cortex is damaged may find it difficult to move their hand to the correct location when trying to pick up an object. The same patients, however, may have no fundamental disorder of movement or difficulty describing the object's form and appearance.

The critical region for the representation of numerical quantity appears to be the intraparietal sulcus (Figure 2) [2]. Several studies [3–5] have shown that activation here varies with changes in the numerical distance between the compared numbers. Recently, investigators have begun to question how specific activation in the intraparietal sulcus is to number comparison. Rather than being an area for number representation, the intraparietal sulcus could have a general role in magnitude representation. For example, it may be concerned with the representation of magnitudes such as physical sizes [6]. A behavioural distance effect has also been observed in tasks involving non-numerical magnitude comparisons. Response times are also longer when judging smaller differences in size or orientation. Activations of the intraparietal sulcus have been reported when subjects compared angles, lines, physical size or stimulus brightness ([3] and Cohen-Kadosh, personal communication).

A recent functional magnetic resonance imaging (fMRI) study by Pinel *et al.* [7] has investigated this issue in a particularly elegant manner. In their study, the authors presented two single-digit numbers — 2 and 7, for example — concurrently on the screen that could differ in numerical size, physical size and luminance. The subjects had to indicate which number was numerically larger, physically larger or brighter by making one of two responses. A distance effect was found in each case. In general, activations during these three comparison tasks were very similar, with significant overlap in anterior intraparietal sulcus, occipital and infero-temporal areas. It was difficult to identify intraparietal sulcus regions selectively involved in just one type of comparison, but there was a trend for the peak activations associated with number, size and luminance, and with the distance effect in each of these dimensions to be distributed from anterior to posterior along the length of the intraparietal sulcus.

It is possible that proximity of neuroanatomical representations to one another underlies patterns of behavioural interference that were observed when the differences in magnitude were incongruent rather than congruent. An example of an incongruent difference would be when one of the numbers was numerically smaller but physically larger. Incongruent differences in physical size interfered with judgements about number size and *vice versa*. Incongruent differences in physical size and luminance also interfered with one another, but differences in number size and luminance interacted less. Pinel *et al*. [7] suggest that continuous dimensions

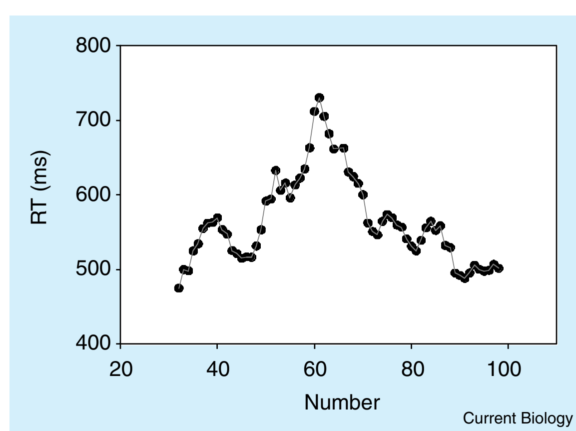

Figure 1. The numerical distance effect.
Subjects were asked to decide whether double-digit numbers (31–99) were larger or smaller than the reference number (65). Their reaction times (RTs) increased the closer the presented number was to the reference.

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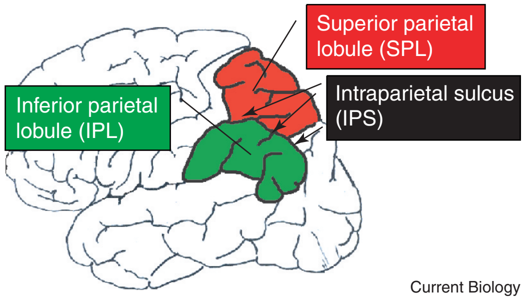

Figure 2. The parietal lobe.
The parietal lobe can be divided into two lobules: a lower part, the inferior parietal lobule (IPL, green) and an upper part, the superior parietal lobule (SPL, red). The intraparietal sulcus (IPS) is the sulcus between these two lobules (see arrows).

— such as luminance, size and number — are processed neither by specialised cortical subregions nor by a single general comparison module, but instead by a distributed, overlapping set of codes dependent on tissue spanning the length of the intraparietal sulcus.

There is a potentially more troublesome aspect of Pinel *et al.*'s [7] findings and of others that have been made with the same number comparison approach [3,4,5,8], which has so far provoked little comment. Activations and single cell activity patterns in the intraparietal sulcus have also been related to basic processes of attentional selection of one stimulus amongst many and intentional selection of a particular response amongst possible alternatives [9]. Simply selecting responses, such as a left or right hand key press, regardless of whether a judgement is being made about numerical magnitude, has been shown to activate similar bilateral intraparietal sulcus regions [10,11]. It is therefore possible that the activity in the intraparietal sulcus reported by Pinel *et al.* [7] is a reflection of basic response selection processes that were common to all three comparison tasks.

One recent fMRI experiment [8] directly contrasted number comparison with a perceptual task with very similar but non-numerical stimuli and with matched responses. As expected, imaging during number comparison, relative to rest, revealed activity in a large bilateral parietal-posterior frontal network. But, as in Pinel *et al.*'s [7] study, no areas showed more activation during number comparison than during the control tasks, although in this study [8] the control tasks lacked any element of continuous magnitude comparison. Activation in a left-lateralised parietal-posterior frontal network varied significantly as the difficulty of response selection (indexed by response times) increased, but this occurred in both number and control tasks. Changes in activation in the intraparietal sulcus may therefore more directly reflect the difficulty of selecting responses in a number judgement task, and only indirectly reflect the nature of the number representation itself.

The results of another fMRI study [12] argue against the idea that intraparietal sulcus activation is entirely driven by response selection. In this case, greater activation was found within an intraparietal sulcus region when subjects were making judgements about numbers, as opposed to letters, even on those trials in which no response was made. Such a result would seem to rule out any confounding effect of response selection, but still some caution is warranted. Studies of both the human and monkey intraparietal sulcus have emphasized that, unlike the premotor cortex, it is not concerned with selection *per se* but with the representation of the possible response alternatives that might be selected [13–15]. Even if ultimately the response is withheld, intraparietal sulcus neurons are active [13,16].

Issues of experimental design and possible artefacts make it difficult to separate number representations from response representations, but there may also be a more fundamental issue of whether we should actually expect the two types of representation to be intertwined [6,17]. There is behavioural evidence that numbers, response codes and space might be closely linked: subjects are faster to respond to smaller numbers with a left button press and to larger numbers with a right button press — the 'spatial numerical association of response codes' effect [18]. Furthermore, there is evidence for a link between the representation of number magnitude and response selection at the single neuron level. Some neurons on the medial bank of the intraparietal sulcus in the macaque monkey were reported to code aspects of numerical magnitude [19]. The neurons were interspersed within the representation of the proximal forelimb that the animals used for making the responses.

It is established that number processing problems are seen after damage to the parietal cortex [2,17], but the nature of the parietal cortex's representation of number is still elusive. It may have been particularly difficult to disentangle from response selection in recent studies. Alternatively, as is the case with other parameters, such as space, numerical magnitude may be represented in the context of response selection in the parietal cortex.

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