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Are numbers special? The comparison systems of the human brain investigated by fMRI

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Abstract

Many studies have suggested that the intraparietal sulcus (IPS), particularly in the dominant hemisphere, is crucially involved in numerical comparisons. However, this parietal structure has been found to be involved in other tasks that require spatial processing or visuospatial attention as well. fMRI was used to investigate three different magnitude comparisons in an event-related-block design: (a) Which digit is larger in numerical value (e.g., 2 or 5)? (b) Which digit is brighter (e.g., 3 or **3**)? (c) Which digit is physically larger (e.g., 3 or 3)? Results indicate a widespread cortical network including a bilateral activation of the intraparietal sulci for all different comparisons. However, by computing contrasts of brain activation between the respective comparison conditions and applying a cortical distance effect as an additional criterion, number-specific activation was revealed in left IPS and right temporal regions. These results indicate that there are both commonalities and differences in the spatial layout of the brain systems for numerical and physical comparisons and that especially the left IPS, while involved in magnitude comparison in general, plays a special role in number comparison.

Keywords: Intraparietal sulcus; Magnitude; Distance effect

1. Introduction

Are numbers special? Are they represented by a unique brain system? Many accounts of number processing stress the central role of the IPS for number processing (Dehaene, Dehaene-Lambertz, & Cohen, 1998; Dehaene, Piazza, Pinel, & Cohen, 2003). This view is based on patient studies (Dehaene & Cohen, 1997; Lemer, Dehaene, Spelke, & Cohen, 2003) emphasizing the necessity of the IPS of the dominant hemisphere, particularly for number comparison. In addition, electrophysiology studies on monkeys (Nieder & Miller, 2004; Sawamura, Shima, & Tanji, 2002) and neu-

Abbreviations: BOLD, blood oxygen level dependent; CaS, calcarine sulcus; CiS, cingulate sulcus; CoS, collateral sulcus; fMRI, functional magnetic resonance imaging; FEF, frontal eye field; FG, gyrus fusiformis; FOp, frontal operculum; GLM, general linear model; IFG/IFS, inferior frontal gyrus/sulcus; IPL, inferior parietal lobule; IPS, intraparietal sulcus; ITS, inferior temporal sulcus; LS, lateral sulcus; MFG, middle frontal gyrus; MOG, middle occipital gyrus; MTG, middle temporal gyrus; OF, orbitofrontal sulci; OTS, occipito-temporal sulcus; PCS, postcentral sulcus; POS, parieto-occipital sulcus; RS, rolandic (central) sulcus; SFG/SFS, superior frontal gyrus/sulcus; SMA, supplementary motor area; SPL, superior parietal lobule; STS, superior temporal sulcus

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roimaging studies on humans (Pesenti, Thioux, Seron, & De Volder, 2000; Pinel et al., 1999; Pinel, Dehaene, Rivie're, & LeBihan, 2001) revealed bilateral IPS activation during number processing and numerical comparison. Yet, other evidence has suggested that the IPS does not serve as a specialized module for number comparison but is designed to subserve other cognitive processes as well, such as visuospatial analysis (Simon, 1999) or a general magnitude comparison (Walsh, 2003). Moreover, its activity has been reported to be modulated by general task difficulty (Göbel, Johansen-Berg, Behrens, & Rushworth, 2004).

Numbers are claimed to be represented in an abstract fashion on an analogue mental number line (Barth, Kanwisher, & Spelke, 2003; Dehaene et al., 1998; Zorzi, Priftis, & Umilta, 2002). This idea is supported by the *numerical distance effect*, a fundamental behavioral effect that is observed when subjects perform the number comparison task. The distance between two stimuli influences the comparison of the stimuli; the larger the distance between two stimuli, the easier the decision will be and the shorter the reaction time (RT) (Moyer & Landauer, 1967). The number line is generally held to be compressive (Dehaene, 2002, 2003) because comparison times are better predicted when the distance between the two compared numbers are measured on a logarithmic rather than on a linear scale.

However, it is important to note that the reaction time data for the comparison of physical magnitudes across a wide range of domains (e.g., line length, pitch, weight) show exactly the same effects as the comparison of numerical size. Accordingly, the RT profiles for the comparison of both numerical and physical magnitudes are best described by the same logarithmic equation (Welford, 1960). This has led some authors to argue that the mechanism for comparing numerical magnitudes is equivalent to that for the comparison of physical stimuli (Gallistel & Gelman, 1992, 2000; Moyer & Landauer, 1967), a view that is further supported by simulations of number comparison with a recent computational model (Zorzi & Butterworth, 1999).

Therefore, the activation found for number comparison might indicate the operation of a magnitude comparison network rather than a specific numerical network. No study that investigated IPS involvement in number comparison, neurophysiological and neuropsychological alike, examined this possibility. A few recent imaging studies attempted to address the question of whether the way in which the human brain represents numbers is similar to the way in which physical features (Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003) or other semantic information (Le Clec'H et al., 2000) are represented. Yet, none of these studies manipulated the to-be-compared features (e.g., numerical and physical) and their distances within the same experimental design. Only the latter approach, as taken in the present study, can control for the non-specific activations of other brain areas due to attention, difficulty, semantic content, and the like. For example, Wiese (2003) suggested that language and numerical abilities are dependently linked. Thus, one may suggest that the differences between comparisons are not due to the comparison per se, but are due to the content of the stimuli that are presented. In order to determine commonalities and differences between the numerical and physical comparison systems it is essential to adopt such a design that will manipulate and combine the comparison type and distances. We manipulated three different features, numerical value, luminance, and size, of similar stimulus material and varied the distance in each of these features. Pinel, Piazza, Le Bihan, and Dehaene (2004) addressed the same question with a similar design. They scanned normal subjects with fMRI while they compared size, number, and luminance, which varied orthogonally. They found the expected behavioral interference effect and, in their brain activation data, distributed and overlapping cerebral representations for size, number, and luminance. However, their results could have been influenced by the processing of the irrelevant features that were manipulated as well. Our design was different in that, for each manipulation, we kept the other features constant (e.g., all stimuli for the numerical comparison had the same size and luminance) in order to avoid interference effects and thus be more sensitive to effects specific for the respective comparison. Note that Stroop-like interference between physical size and numerical values (Henik & Tzelgov, 1982; Schwarz & Ischebeck, 2003; Tzelgov, Meyer, & Henik, 1992), and luminance and numerical values (Cohen Kadosh & Henik,submitted for publication) has been documented in previous work. Accordingly, in the current experiment, any overlap between comparison conditions in brain imaging data would then indicate a common magnitude comparison network rather than reflect the implicit and automatic processing of the irrelevant magnitude.

We expected that task-specific[1] areas would show increasing activity with decreasing distance, corresponding to the increasing difficulty (cortical "distance effect"). On the basis of the clinical studies, we expected the cortical specific-distance effects for numbers in the parietal lobe to be unilateral (in the dominant hemisphere) rather than bilateral. Hence, we hypothesized that while a widespread network of areas would be commonly activated by all comparison tasks, a subset of them, particularly along the left IPS, would show a task-specific modulation by number comparison.

[1] We use the term "specific" through this paper to indicate an area whose activation is stronger for a given process relative to other processes. This does not mean necessarily that this area is solely active in response to the given process. This fits the view recently presented by Posner (2003). Posner refers to activations observed under different tasks in the same brain area: "*Although it is not always easy to distinguish between a brain area being specific for a domain or performing a computation that is of particular importance for some domains, either can underlie a form of modularity . . .. Thus these areas and many others that have been described are modules in the sense that they perform specific mental operations . . . sometimes the operations are within a single domain, but sometimes they are more general. In the case of face perception, and for word reading and attention described below several such modules work together in a network to carry out cognitive tasks*." (p. 450)