

# The Organization of Brain Activations in Number Comparison: Event-Related Potentials and the Additive-Factors Method

Stanislas Dehaene

I.N.S.E.R.M., E.H.E.S.S. and C.N.R.S., Paris, France

## Abstract

■ Measuring reaction times (RTs) using the additive-factors method provides information about the sequence of processing stages in a cognitive task. Here, I describe how the simultaneous recording of event-related potentials (ERPs) in the same task can provide complementary information that cannot be obtained using RTs alone. Most notably, ERP data can reveal the absolute activation time and the coarse brain localization of processing stages. RTs and ERPs can also be used to cross-validate a serial-stage model. These notions were applied to a study of the temporal unfolding of brain activations in a num-

ber comparison task. ERPs were recorded from 64 scalp electrodes while normal subjects classified numbers as larger or smaller than 5. Specific scalp signatures and timing data were obtained for stages of word and digit identification, magnitude comparison, response programming, and error capture and correction. The observed localizations were compatible with previous neuropsychological and brain imaging data and provided new insights into the cerebral lateralization and timing of number processing. ■

## INTRODUCTION

A goal of cognitive psychology is to understand the organization of information processing in human subjects. Cognitive psychology is still dominated by the functionalist approach, according to which it is possible to describe human information-processing algorithms without consideration of their underlying neural substrate. However, it has been suggested that more accurate psychological theories might be developed by taking into account anatomical and neurobiological constraints on mental processing (e.g., Changeux & Dehaene, 1989; Kosslyn & König, 1992; Posner, Petersen, Fox, & Raichle, 1988; Posner & Raichle, 1994). The emerging field of cognitive neuroscience aims at understanding which brain systems, and ultimately which neuronal circuits and molecular mechanisms, are involved at each step of an information-processing sequence.

Positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) are techniques of choice for the functional localization of cognitive processes in the human brain (Posner & Raichle, 1994). Both can highlight with great accuracy the brain areas active in a given cognitive task. However, PET gives a static picture of brain activity averaged over tens of seconds, and fMRI, although technically faster and spatially more accurate, also remains currently limited by the speed of the hemodynamic response to changes in brain activity (sev-

eral seconds). Electro- and magneto-encephalography, on the other hand, have a very high temporal resolution in the range of milliseconds, and could potentially resolve the temporal sequence of brain activations. However, the problem of reconstructing the large number of electrical sources responsible for the observed event-related potential at any given time remains a major obstacle.

Some limitations of current brain imaging methods can be overcome by using experimental designs that incorporate subtractions of two related tasks and can therefore isolate the contribution of a specific neural processing system (Posner et al., 1988). In the present paper, the subtraction technique is extended to show how the method of additive factors, a classical method of mental chronometry, can be adapted to the recording of event-related potentials. It is then possible not only to decompose a task into a sequence of information-processing stages, but also to estimate the absolute timing of each stage and the localization of the corresponding brain areas. The method is applied here to the electrophysiological analysis of a simple task of number comparison. How do humans decide if a number is smaller or larger than five? Reaction time and electrophysiological results indicate a separation among at least three processing stages with identifiable neural substrates: stimulus identification, semantic access, and motor preparation. The results confirm and extend previous psychological and neuropsychological observations on number processing.

## THE NUMBER COMPARISON TASK

Moyer and Landauer (1967) were the first to measure reaction times (RTs) for number comparison. They presented subjects with pairs of digits and asked them to press a response key on the side of the largest digit (or on the side of the smallest). They reported a *distance effect*: subjects responded more slowly and made more errors when the two numbers were numerically close (e.g., 8 vs. 9) than when they were further apart (e.g., 2 vs. 9). This effect has been extensively replicated and its characteristics have been determined. The curve relating reaction time to numerical distance is a continuously decreasing concave-upward function that is well approximated by a logarithmic or inverse function (e.g., Dehaene, 1989). Even when 2-digit numbers are compared, the distance effect remains continuous with a significant influence of the units and with little or no discontinuity at decade boundaries. For instance, when comparing numbers to a standard of 65, 61 is classified more slowly than 59, which is itself slower than 51 (Dehaene, Dupoux & Mehler, 1990; Hinrichs, Yurko, & Hu, 1981). The distance effect does not disappear with extensive training (e.g., Poltrock, 1989), and is observed early in childhood (Duncan & McFarland, 1980; Sekuler & Mierkiewicz, 1977). Even animals show a distance effect, for instance, when choosing the most numerous of two sets of items (Washburn & Rumbaugh, 1991). Thus the distance effect appears as a universal characteristic of human and animal elementary numerical cognition (Dehaene & Changeux, 1993).

Nothing in the visual appearance of digits betrays that 8 and 9 are conceptually more similar than 2 and 9. Thus the distance effect implies the existence of an abstract mental representation of numbers that recovers numerical relations not obvious in the digital symbols. The classical interpretation of the distance effect supposes that the input numerals are internally transformed into an analogous magnitude representation similar to a mental number line (e.g., Moyer & Landauer, 1967; Restle, 1970; Dehaene & Changeux, 1993). The internal representations of two close numbers would be more similar or would overlap more than those of numbers that are numerically more distant, explaining the distance effect.

For parsimony, some models of number processing have assumed that the same magnitude representation is accessed, regardless of the input format of the numerals (McCloskey, 1992; Dehaene, 1992). According to these models, the semantic representations of the arabic numeral 6, the written word SIX, and the spoken word /siks/ are identical because the meaning of these symbols is represented by the same internal magnitude. Accordingly, the processing steps in the number comparison task can be decomposed into three major operations, depicted in Figure 1: (1) notation-specific stimulus identification, (2) activation of the magnitude representation and retrieval of larger/smaller relations, and (3)

preparation and execution of the motor gesture assigned to the "larger" or "smaller" response.

The present study had several goals: to validate this model of number comparison, to examine which brain areas are involved in each processing step, and to measure the timing of their activations. Two points received special attention: the localization of arabic digits identification processes, and the existence of a notation-independent magnitude representation. First, although there is good agreement that different processes must be postulated for the identification of arabic and verbal numerals, their neural bases remain poorly understood. Brain-lesioned patients have been reported who could read arabic numerals but not words (e.g., Anderson, Damasio, & Damasio, 1990; see Discussion). However, the converse dissociation is quite rare (although see Cipolletti, Warrington, & Butterworth, 1995), and the critical areas for arabic number reading remain unknown. Second, the assumption of convergence toward a common abstract representation of magnitudes has been disputed. Campbell and Clark (1988, 1992, Clark & Campbell, 1991) have suggested that numerals activate a large network of interconnected codes for numbers, including digital, analogical, motor, and imaginal codes, and that this network may systematically differ for arabic and verbal numerals. It was therefore of importance to examine if, as predicted by Figure 1, some common pattern of brain activation associated with magnitude processing of both arabic and verbal numerals could be found.

## THE ADDITIVE-FACTORS METHOD IN ELECTROENCEPHALOGRAPHY

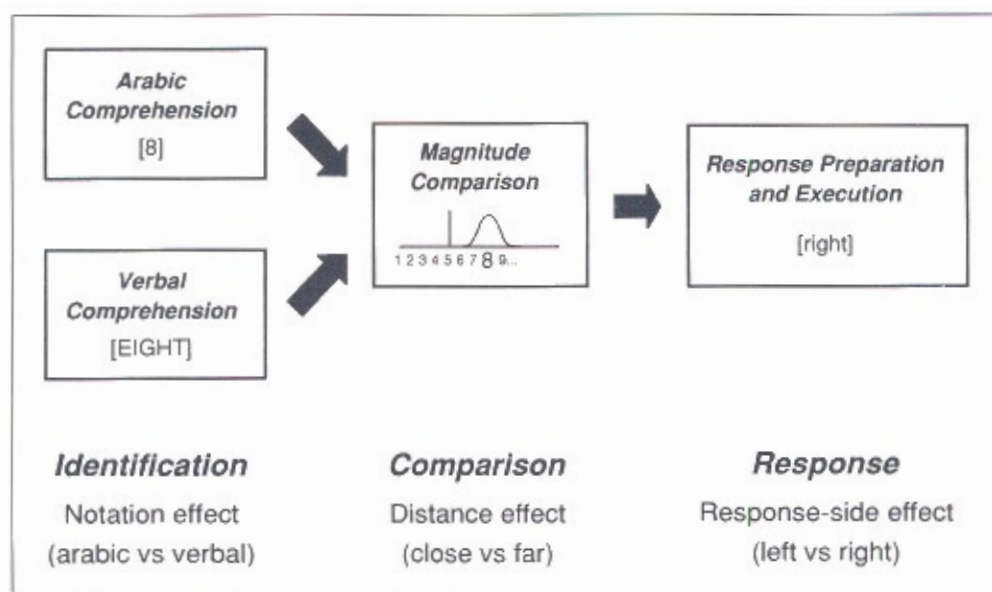
The additive-factors method (Sternberg, 1969) is a classical means of validating a serial-stage processing model using mental chronometry. It is based on the assumption that if mental processing proceeds in a series of successive stages, then reaction time should be the sum of the durations of each stage. The method calls for a factorial experimental design in which several factors  $F_1 \dots F_n$  are varied independently and orthogonally. If each factor  $F_i$  influences only the speed of execution of a distinct stage  $S_i$ , then the factors should have additive influences on RT. The effect of factor  $F_1$ , for instance, should be the same at all levels of factors  $F_2 \dots F_n$ . Deviations from additivity are revealed by significant simple and multiple interactions of some of the factors. Conversely, strong evidence for serial stages is obtained when all the main effects, but none of the interactions, reach statistical significance.

The present experiment used three orthogonal factors that were expected to influence the three processing stages depicted on Figure 1.

1. *Notation*: Numerals were presented visually either in arabic notation (e.g., digit 5) or in verbal notation (e.g.,



**Figure 1.** Model of the stages involved in the number comparison task.



word "FIVE"). This factor should affect the process of stimulus identification.

2. *Distance:* Subjects were asked to decide if each number was larger or smaller than 5. Half of the targets were close to 5 (4 and 6) whereas the other half were numerically more distant from 5 (1 and 9). As discussed above, numerical distance should affect only the magnitude comparison stage.

3. *Response side:* In different blocks, subjects had to respond "larger" with the right hand and "smaller" with the left hand, or the converse. As a result, for each target, RTs were obtained for both right and left key presses. The difference between right-hand and left-hand responses should arise from the motor preparation and execution stage.

In passing, note that a fourth factor of number magnitude was also crossed with the other three. Half of the numbers were smaller than 5 (1 and 4) whereas the other half were larger than 5 (6 and 9). However, magnitude is an ambiguous indicator and, therefore, was not considered in the additive-factors method. While it is generally the case that large numbers take longer to compare than small numbers, this may be attributed either to the lower frequency of larger numerals in the language (Dehaene & Mehler, 1992) or to the greater confusability of larger quantities (Weber's law). Thus both the identification and magnitude comparison stages could be influenced by the number magnitude factor.

In reaction-time analyses, the absence of interactions among the three critical factors of notation, distance, and response side would provide strong evidence for the model of Figure 1. To supplement reaction time measures, event-related potentials (ERPs) were also recorded from 64 electrode sites spread through the entire surface

of the scalp. Using an additive-factor design in combination with topographic ERP recordings offers several advantages over the RT-based method. Once additive factors and stages have been identified in RT analyses, ERPs allow for an approximate determination of the absolute time of onset of each stage as well as their gross brain localization.

### Absolute Timing

ERPs provide a continuous measure of brain activity throughout a trial. Sample-by-sample comparison of two conditions can therefore reveal the earliest point of significance of a given factor. Because of subjects and trials variance, such an onset estimate is only approximate and corresponds to the minimum rather than to the average processing time needed for information to reach the processing stage associated with a given factor. Nevertheless the ordering of onset times for different factors gives an indication of the temporal ordering of the corresponding stages, which is not accessible to the RT-based additive-factor method.

### Brain Localization

In general, only some electrode sites will show a significant effect of a given factor. The scalp distribution of significant differences gives indications as to the brain localization of the corresponding neural processes. In some cases, the average waveforms recorded in two or more experimental conditions show clearly distinct topographies that can be tentatively related to a neural substrate. To aid in relating distributions of scalp voltages to an underlying generator, it is often useful to relate the ERP results to anatomical studies of the same task, for

instance, using PET. There are several examples of this strategy in the word reading literature (see Compton, Grossenbacher, Posner, & Tucker, 1991; Posner & McCandliss, 1993; Posner & Raichle, 1994). For instance, the left-lateralized focal posterior negativity (N1) observed with word stimuli (Compton et al., 1991; Curran, Tucker, Kutas, & Posner, 1993) has been tentatively related to a left posterior extrastriate activation observed in PET during the presentation of words and pseudowords (Petersen, Fox, Snyder, & Raichle, 1990; see Posner & McCandliss, 1993).

In most cases, however, raw waveforms represent the superposition of the electrical signals generated by a large number of neural sources, only some of which are affected by an experimental factor. In this situation, direct subtraction of the waveforms from two experimental conditions can be used to localize the regions involved. For instance, late components of ERPs in a visuomotor task are often dominated by a large central positivity (late positive complex, P300 or P3), which is only moderately modulated by left vs. right key presses. Direct subtraction of the ERPs to left vs. right key presses eliminates common components and isolates the electrode sites that discriminate most between the two response sides (Kutas & Donchin, 1974; Vaughan, Costa, & Ritter, 1972). The resultant "lateralized readiness potential" is sharply localized to left and right motor and premotor sites.

The subtraction technique is most useful in combination with dipole modeling techniques such as brain electrical source analysis (BESA; Scherg & Berg, 1990). In BESA, the researcher initially provides assumptions about the number, distribution, and symmetry of brain generators. The program then computes the best-fitting dipole model that most faithfully reproduces the observed scalp voltage pattern. Unfortunately, it is well known that the larger the number of dipoles included in a model, the more the results become unstable and dependent on the initial assumptions. Subtraction of ERPs from two tightly controlled conditions, however, can potentially isolate the electrical contribution of a single stage of processing, which may sometimes be modeled by a single dipole or by two symmetrical dipoles. The problem of source localization therefore becomes more tractable.

### Verification of a Serial-Stage Model

ERPs also allow for an internal verification of the hypothesis that each factor affects a different stage of processing. A serial-stage model predicts that the effect of a given factor  $F_1$  should be the same for all levels of the other factors  $F_2 \dots F_n$ . In the present experiment, for instance, the ERP difference between left and right key presses should have the same *magnitude* and the same *scalp topography* whether the stimulus was in arabic or in verbal notation, and whether it was close or far from the standard of comparison.

The *onset time* of each ERP effect should also be delayed by a predictable amount, based on the delays introduced by preceding stages of processing and which can be measured from reaction times alone. For instance, the onset time of the left key/right key ERP difference should itself be an additive function of the notation and distance factors. In this manner, ERP and RT data may be cross-validated. A classical example is McCarthy and Donchin's (1981) analysis of P300 latency. In their experiment, stimulus discriminability and stimulus-response (S-R) compatibility had additive effects on RT, but the latency of the P300 was affected only by discriminability, not by S-R compatibility. McCarthy and Donchin suggested that P300 latency indexes the end of stimulus evaluation and could be used as an alternative to RT, one that would be relatively insensitive to response-related variables.

In principle, the latency of any ERP effect may be substituted for RT in additive-factor analyses. In practice, however, measuring the latency of an ERP effect may be problematic, because an arbitrary threshold of significance must be chosen. This problem worsens when the data are split into small cells defined by the combination of several factors, because the conventional level of significance may not be reached in all cells. Finally, when variance is high, the onset of an ERP effect relates more to the minimum processing time of preceding stages than to its average, and there is no theoretical reason to expect additivity of minimums (Sternberg, 1969). For these reasons, tests of the additivity of ERP onset times are not reported in this paper. Rather, I focus on the predicted similarity of ERP topographies across conditions.

One complication specific to ERP research is that the differential delay introduced by preceding stages can introduce undesirable variance in ERP analyses of the main effect of a given factor. When ERPs are averaged time-locked to stimulus onset, factors related to early processing stages (e.g., arabic vs. verbal notation) will be little affected by the variance of earlier processes. However, later stages can be highly affected by differences in the duration of preceding stages, due either to experimental factors or to trial-to-trial variability. If the effect of interest is late and has a small electrical signature on the scalp, such temporal dilution could render it undetectable. One solution is to use response-locked rather than stimulus-locked ERP averages when examining the effect of factors supposedly related to late processing stages. In the case at hand (Fig. 1), given that there was a large difference in RT to arabic and verbal stimuli, it did not make much sense to study the distance and response side effects on stimulus-locked averages. Rather, the hypothesized convergence toward a common processing stream immediately after stimulus identification suggested that the distance and response side effects would appear more clearly on response-locked averages.

Finally, it should be stressed that the serial stage model

of Figure 1 was used only as a useful heuristic for the description of the temporal unfolding of brain activations. There is no doubt that cortical networks are organized with a substantial degree of parallelism. Thus the serial stage hypothesis is likely to be valid only at very global levels of analysis, and to progressively disintegrate when the data are examined with greater and greater temporal and spatial accuracy. The above ERP techniques would remain useful even if the serial-stage model was found to be invalid. For instance, they might reveal that two effects have simultaneous onsets, perhaps indicating parallel rather than serial execution of psychological processes. Subtraction could then still be used to localize the sources of each effect. In brief, topographical ERP analysis need not be restricted to instances of strictly serial processing, even though the analysis of nonserial models is likely to be more complex.

## SUMMARY AND PREDICTIONS

Event-related potentials were measured while the subjects performed a larger/smaller comparison of arabic digits 1, 4, 6, and 9 and verbal numerals ONE, FOUR, SIX, and NINE to a standard of 5. The model of Figure 1 predicted that (1) the factors of notation, numerical distance, and response side would have additive effects on RTs, (2) the three points in time at which these three factors would first have a significant effect on ERPs would be serially ordered, and (3) these factors would have isolable scalp signatures that would inform about the brain localization of relevant processes. More specifically, the notation factor (difference between digits and verbal numerals) was expected to have an early effect on posterior electrodes, particularly on the N1, reflecting visual identification processes. The distance factor (difference between digits close to 5 and far from 5) was expected to have an effect on posterior electrodes, perhaps near the parieto-occipito-temporal junction since this region is a critical area for number processing impairments (e.g., Benton, 1987). Most importantly, the topography and magnitude of the ERP distance effect were expected to be identical for digits and for verbal numerals. Finally the response side factor (difference between left-hand and right-hand key presses) was expected to yield a lateralized readiness potential on electrodes localized over motor areas (Kutas & Donchin, 1974; Vaughan, Costa, & Ritter, 1972).

## RESULTS

### Reaction Time Results

The overall median correct reaction time in the ERP test was 399 msec. Median correct RTs<sup>1</sup> from the ERP test were computed for each subject in each cell, and submitted to an ANOVA with Notation (arabic or verbal), Distance (close or far from 5), Magnitude (larger or

smaller than 5), and Response side (left or right) as within-subject factors.

Main effects were found for Notation [arabic 38 msec faster than verbal;  $F(1, 11) = 88.3, p < 0.0001$ ], Distance [far 18 msec faster than close;  $F(1, 11) = 21.0, p = 0.0008$ ], and Response side [right hand 10 msec faster than left hand;  $F(1, 11) = 7.05, p = 0.022$ ]. These three effects were additive (Fig. 2a). All two- and three-way interactions between these factors did not reach significance (all  $F$ s  $< 1$ ). There was, however, a triple interaction of Notation, Distance, and Magnitude [ $F(1, 11) = 27.0; p = 0.0003$ ], which indicated the presence of a processing difference between arabic and verbal numerals (see Fig. 2b). Follow-up analyses showed that the Magnitude  $\times$  Distance interaction reached significance only in verbal notation [ $F(1, 11) = 47.8, p = 0.0001$ ], but not in arabic notation [ $F(1, 11) = 2.24, p = 0.16$ ]. Thus in arabic notation, the distance effect was similar for small and large numbers: target 1 was 22 msec faster than target 4 ( $p = 0.0002$ ), and target 9 was likewise 14 msec faster than target 6 ( $p = 0.012$ ). In verbal notation, by contrast, the distance effect appeared large and very significant for numbers smaller than 5 (ONE 37 msec faster than FOUR,  $p < 0.0001$ ), but it seemed altogether absent for numbers larger than 5 (NINE 1 msec slower than SIX,  $F < 1$ ).

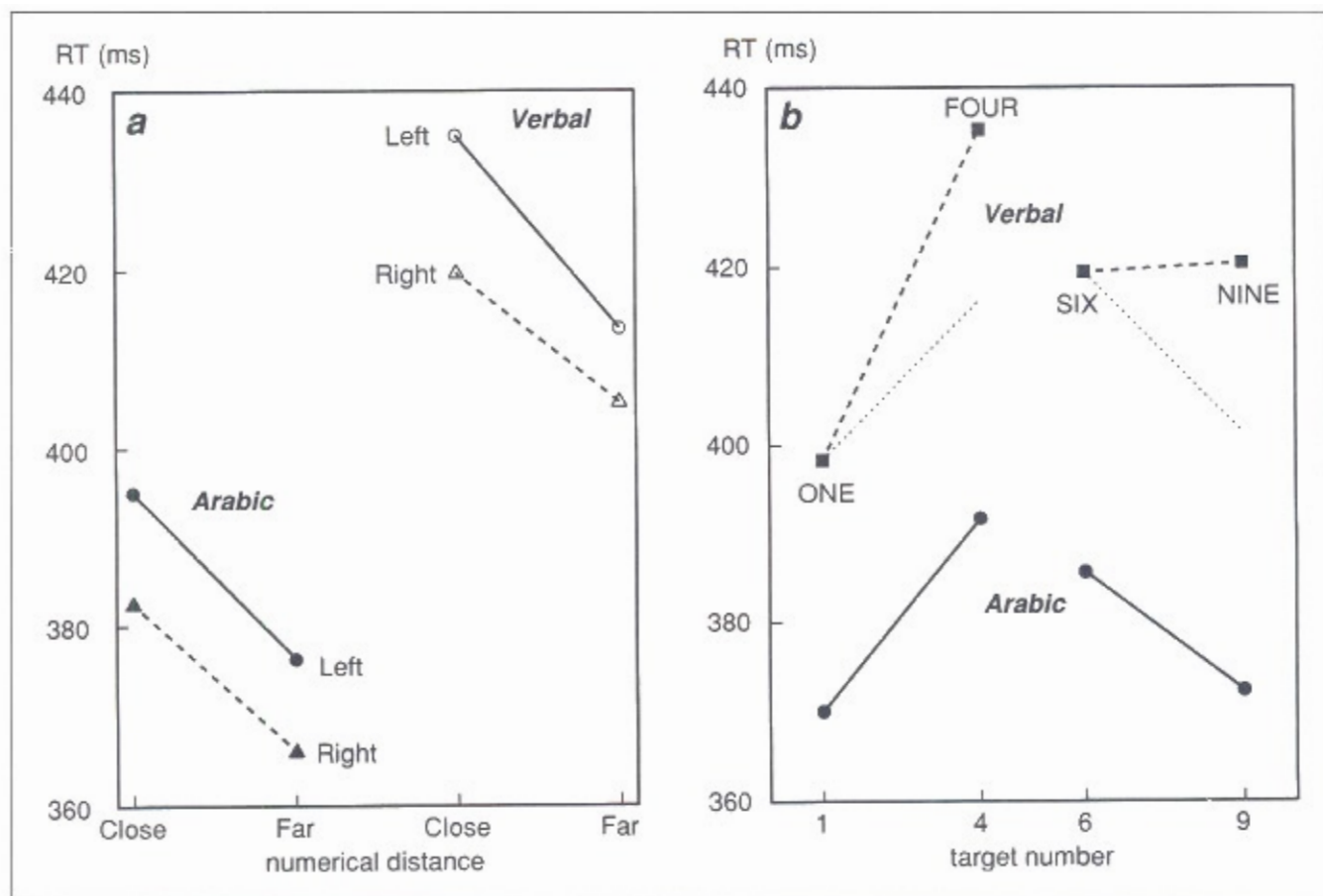
Fundamentally similar results were found in a similar analysis of error rates. Subjects made fewer errors with arabic digits than with verbal numerals [3.6 vs. 5.2%;  $F(1, 11) = 6.38, p = 0.028$ ], and there was a significant distance effect [close = 6.2%, far = 2.6%;  $F(1, 11) = 21.0, p = 0.0008$ ] of equal magnitude in both notations (interaction  $F < 1$ ). Neither the effect of response side nor the Notation  $\times$  Distance  $\times$  Magnitude interaction was significant in the error analysis (both  $F$ s  $< 1$ ).

### Discussion of Reaction Time Results

In agreement with their putative intervention at separate identification, comparison, and response stages, the factors of notation, distance, and response side had additive effects on RTs. Most importantly, the distance effect was of similar size whether the numerals were presented in arabic or in verbal notation (exactly 18 msec in both cases). In the literature, when more levels of numerical distance were used, the curve for RT as a function of distance was found to have exactly the same concave-upward shape whether the numbers were presented in arabic or in verbal notation (Foltz, Poltrock, & Potts, 1984; Tzeng & Wang, 1983). Such additivity of notation and distance effects supports the hypothesis of a convergence of processing toward a common representation of magnitudes, regardless of input notation (Dehaene, 1992; McCloskey, 1992).

However, an unexpected interaction of Notation, Distance, and Magnitude was observed. This interaction could be damaging to the model of Figure 1 if it meant





**Figure 2.** Reaction times in the number comparison task. (a) Additivity of notation, distance, and response side effects. (b) Interaction of the notation, distance, and magnitude factors, suggesting an additional effect of word length specific to verbal notation. Dotted lines show the RTs after subtraction of a 19 msec correction from RTs to four-letter words.

that the distance effect, and therefore the process of numerical comparison, significantly varied with number notation. However, a simpler and more convincing explanation may be found. The interaction may be interpreted as a word length effect for verbal stimuli: four-letter words (FOUR and NINE) were 19 msec slower than three-letter words (ONE and SIX). Such a word length effect, when combined with the classical distance effect, can explain the entire pattern of results with verbal stimuli. RTs to FOUR were considerably slower than RTs to ONE because target FOUR is both one letter longer and numerically closer to the standard of comparison. Conversely, RTs to SIX and to NINE did not differ because, in this case, the distance and word length effects cancelled each other: target NINE is one letter longer than SIX, but it is numerically more distant from the standard of comparison. Once a correction for word length was applied to RTs, the distance effect was again found to be strictly identical for arabic and for verbal numerals (Fig. 2).

Under the hypothesis that only the verbal comprehension stage is affected by word length, the serial model of Figure 1 predicts that the word length effect (i.e., the

Distance  $\times$  Magnitude interaction for verbal notation) should be additive with Distance and with Response Side. This prediction was verified in the ANOVA (both interactions  $p > 0.20$ ). The model also predicts that word length should have a measurable influence on ERPs recorded from posterior sites, which should first be found significant early in time, *before* the emergence of a difference between close and far targets. This prediction was verified below.

In summary, four effects significantly affected performance in the number comparison task. Two of them, notation and word length, could be attributed to an early notation-specific identification stage. A third, the distance effect, was attributed to a later stage of magnitude comparison. Finally the fourth, the response side effect, compatible with the right-handedness of the subjects, was attributed to a motor stage. Whenever interactions were testable, effects attributed to different processing stages were found to have additive influences on RTs and errors. Thus, the performance results were fully compatible with a sequential stage model of number processing, with convergence at the level of a common semantic representation of number magnitude.

## Electrophysiological Results

For the sake of simplicity, the effects are described in the order in which they appeared as measured from stimulus onset. For reference, the grand-average stimulus-locked waveforms recorded at each of the 65 electrode sites appear in Figure 3.

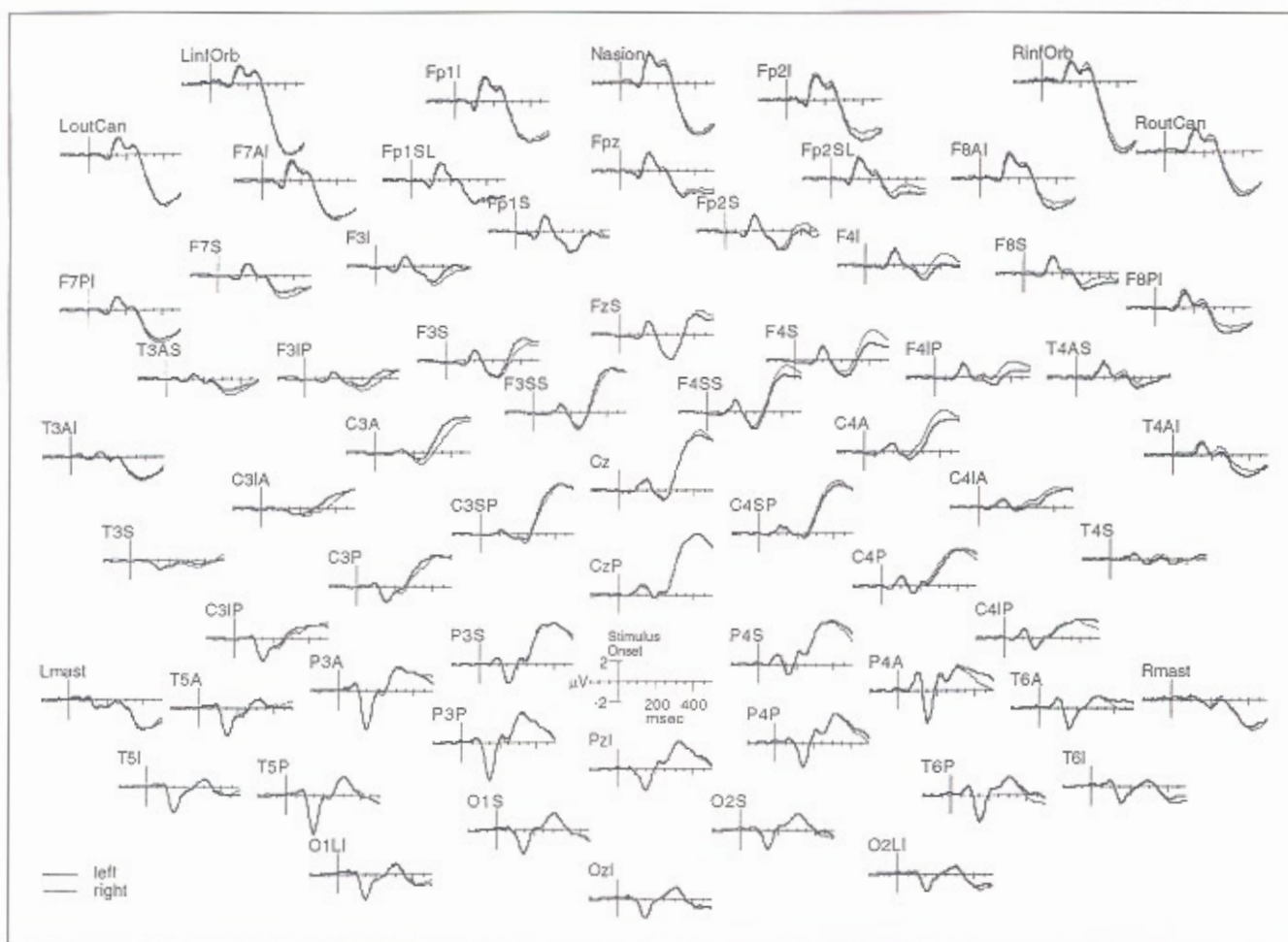
### Early Visual Processing and the P1

The first measurable electrophysiological event was the P1, which culminated 104 msec after stimulus onset. Topographically, the P1 was characterized by a small focal positivity over the left and right posterior electrode sites surrounding the parieto-occipito-temporal junction, accompanied by a posterior medial negativity (Fig. 6). No significant differences among the experimental conditions were found at this stage. The amplitude of the P1 simply tended to be larger on the right than on the left ( $p = 0.051$  on channels P3A/P4A).

### Notation Effects on the N1

The next major electrophysiological event, the N1, was characterized by two sharp foci of negativity over symmetrical temporo-parietal sites, accompanied by a simultaneous fronto-central positivity (P2). The peak of the posterior negativity was reached 148 msec after the onset of verbal stimuli, and 160 msec after the onset of arabic stimuli. In sample-by-sample analyses, this delayed onset of the N1 for arabic stimuli yielded a significant divergence of the arabic and verbal waveforms, which first reached significance at 106 msec post-onset.

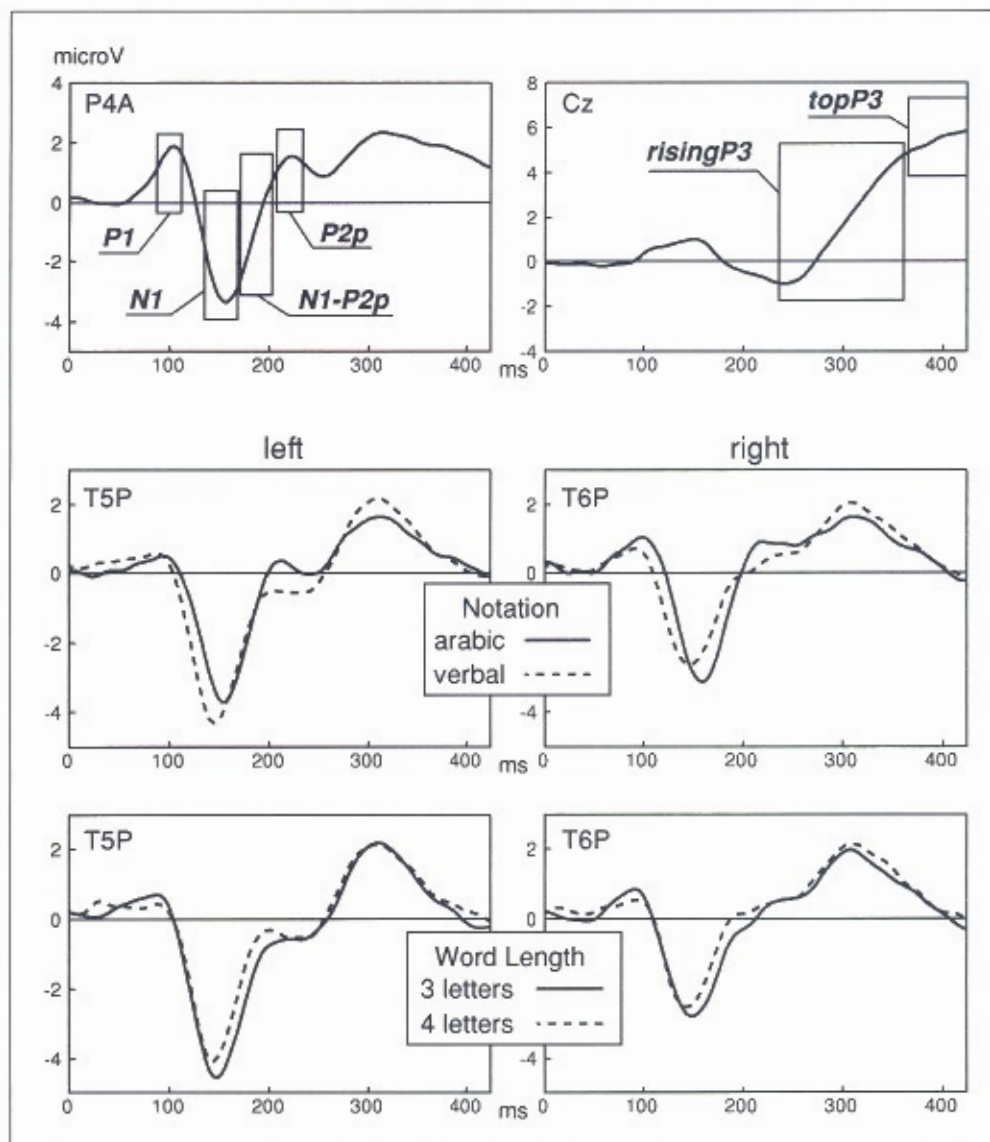
Notation also had a significant effect on the asymmetry of the N1 (Figs. 4 and 6). Globally, the N1 was of significantly higher amplitude on the left than on the right [ $1.06 \mu\text{V}$  asymmetry on sites T5P/T6P;  $F(1, 11) = 5.49, p = 0.039$ ]. However, this interacted with notation [ $F(1, 11) = 5.91, p = 0.033$  for sites T5P/T6P;  $F(1, 11) = 7.44, p = 0.020$  for sites P3A/P3P]: the N1 was highly asymmetrical for verbal stimuli [ $1.45 \mu\text{V}$  asymmetry;



**Figure 3.** Stimulus-locked grand-averaged ERPs from 12 subjects in the number comparison task. Data from correct trials have been averaged separately for left-hand (thick curve) and right-hand (thin curve) responses. Each graph shows a 650 msec epoch, including a 150 msec baseline prior to stimulus onset (see middle scale bar), at a given electrode site (top = anterior, bottom = posterior, left = left hemisphere sites). Note the divergence of the waveforms at sites C3A/C4A overlying motor areas.



**Figure 4.** Selected waveforms of stimulus-locked grand-averaged data. X-axis is milliseconds from stimulus onset. Top: Major features of the posterior (P4A) and central (Cz) stimulus-locked ERPs, showing the time windows used in analyses of variance. Middle: Variation of N1 latency and N1 asymmetry with number notation. Bottom: Variation of N1 amplitude and duration with word length.



$F(1, 11) = 7.06, p = 0.023$ ], but not significantly so for arabic stimuli [ $0.66 \mu\text{V}$  asymmetry;  $F(1, 11) = 2.72, p > 0.13$ ]. The notation  $\times$  hemisphere interaction first appeared significant at 146 msec post-onset.

In agreement with the serial-stage model of Figure 1, there was yet no effect of distance on the N1 time window ( $F < 1$ ). The only additional effect was an obscure interaction of hemisphere and response-side on sites T5P/T6P [ $F(1, 11) = 5.16, p = 0.044$ ]. However, the very small size of this effect ( $0.08 \mu\text{V}$ ), the fact that it was not found at the neighboring electrode sites P3A/P4A, and that it seemed highly unlikely for a motor effect to emerge so early following stimulus presentation suggested that this was a type I error rather than a genuine effect.

### Second Posterior Positivity

Following the N1, a second focal posterior positivity was observed at the same sites where the P1 previously culminated (electrodes P3A/P4A; Fig. 6). It culminated at 220 msec after stimulus onset and was therefore clearly separable in time and in space from the earlier broad fronto-central positivity, simultaneous with the N1, which is classically called the P2 (Curran et al., 1993). Curran et al. (1993) have termed the second posterior positivity the P1 reprise to emphasize the fact that it is peaking at the same sites as the initial P1. Here, however, I have preferred to use the more neutral term "second posterior positivity" (abbreviated as P2p) because there is yet no evidence for a functional link with the P1 and



because important differences with the P1 were seen. Most notably, the left and right foci of the P1 were separated by a posterior medial negativity, which was not present at the time of the P2p and suggests that the two peaks have different generators (Fig. 6).

The P2p, like the P1, tended to be larger over the right hemisphere than over the left [ $F(1, 11) = 3.56, p = 0.086$  on sites P3A/P4A]. More importantly, the transition from the N1 to the P2p and the size of the P2p were modulated by several experimental variables: word length, distance, and response side. These effects are considered in their order of appearance following stimulus presentation.

#### *Word Length and the N1-P2p Transition*

On a time window isolating the transition from N1 to P2p (174–198 msec post-onset), the asymmetry of the N1 to verbal stimuli and the symmetry of the N1 to arabic stimuli continued to be perceptible [e.g.,  $F(1, 11) = 4.91, p = 0.049$  for the hemisphere  $\times$  notation interaction on sites P3P/P4P]. At this point, however, the effect of word length reached significance [ $F(1, 11) = 25.8, p = 0.0004$  for sites P3P/P4P;  $F(1, 11) = 16.1, p = 0.002$  for sites P3A/P4A]. Three-letter words were more negative than four letter words by 0.6–0.8  $\mu V$  over symmetrical parieto-temporal electrode sites (Fig. 4). No such effect was found for the corresponding arabic digits. Traces of the word length effect were found on the N1 itself [ $F(1, 11) = 3.56, p = 0.086$  for sites T5P/T6P], and sample-by-sample analyses indicated that the effect first reached significance 162 msec after the stimulus onset.

**Distance Effect.** Windows centered on the transition from N1 to P2p (174–198 msec) and on the P2p itself (206–230 msec) also revealed the first significant effects of numerical distance on ERPs. During the N1-P2p transition, numbers close to 5 yielded a significantly greater posterior positivity than numbers far from 5, over both sites P3P/P4P [ $F(1, 11) = 9.75, p = 0.0097$ ] and P3A/P4A [ $F(1, 11) = 6.22, p = 0.030$ ]. At this point, there was no hemispheric asymmetry in the distance effect. However, slightly later, in the P2p time window, a significant interaction of distance and hemisphere emerged on sites P3A/P4A [ $F(1, 11) = 5.50, p = 0.039$ ], showing that the difference in P2p amplitude between numbers close to 5 and numbers far from 5 was larger over the right hemisphere than over the left hemisphere (0.42 vs. 0.03  $\mu V$ ).

The model of Figure 1 predicted that a similar distance effect would be found in both arabic and verbal notation, but with a different latency reflecting the faster identification of arabic stimuli. Indeed, on the N1-P2p window, a significant interaction of distance and notation [ $F(1, 11) = 7.80, p = 0.018$ ] on sites P3P/P4P indicated that the distance effect was already present for arabic

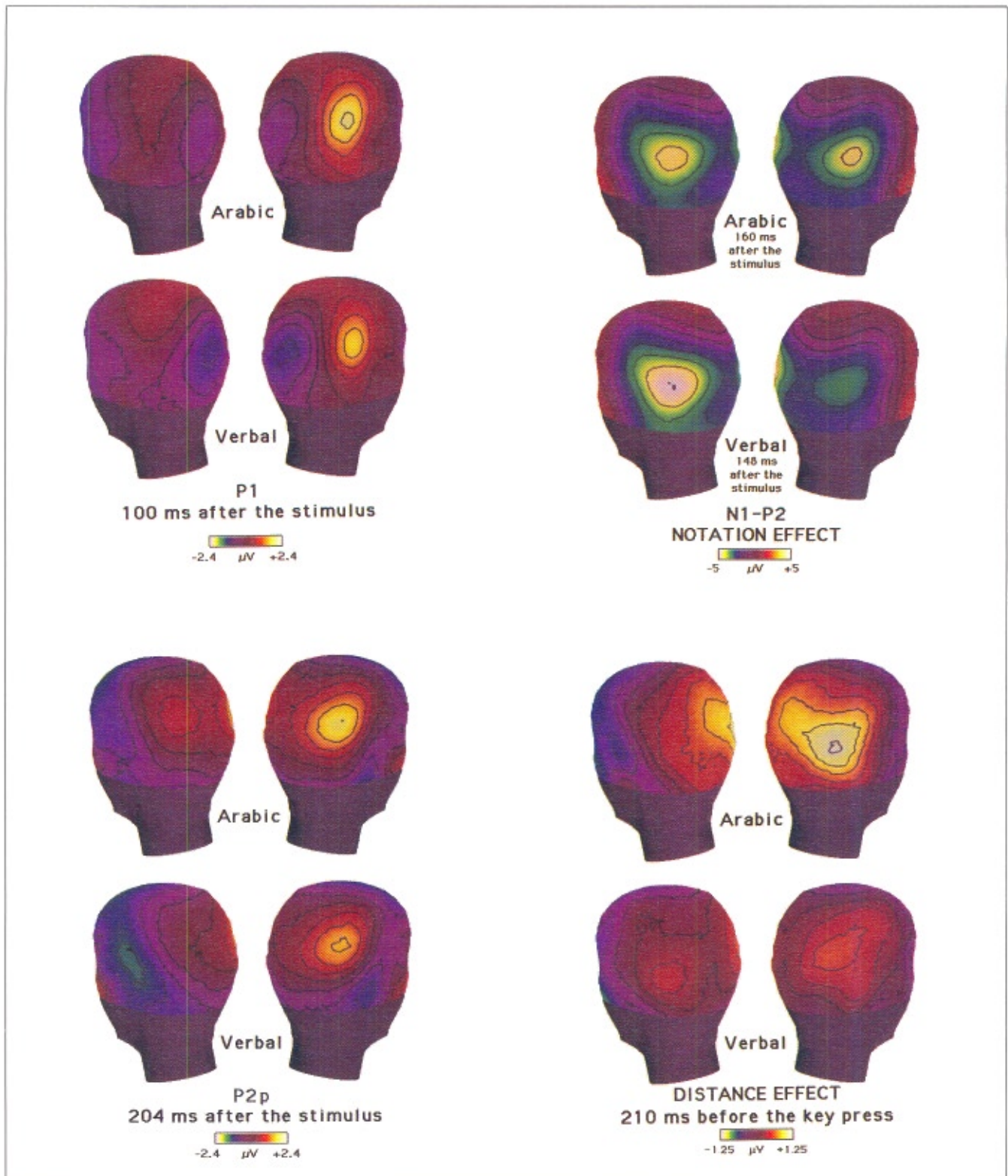
stimuli [ $F(1, 11) = 10.3, p = 0.008$ ; 0.82 V difference], but not for verbal stimuli [ $F(1, 11) < 1$ ]. By 200 msec post-stimulus, however, on the P2p window, interactions of distance and notation had vanished. Sample-by-sample analyses confirmed that the first significant effect of distance emerged at 174 msec for arabic notation and at 190 msec for verbal notation, a difference consistent with the faster RTs to arabic stimuli.

To get rid of stimulus identification delays and therefore to provide a better test of the similarity of the distance effect in the two notations, response-synchronous averages were computed. Figure 5 shows that on response-synchronous averages, subtracting the ERP to close digits from the ERP to far digits again revealed a right-lateralized parieto-occipito-temporal positivity. The difference was maximal at 210 msec before the key press, whether the numbers had been presented as digits or as words. ANOVAs on the response-synchronous data from sites P3A/P4A on windows N1-P2p and P2p showed a significant main effect of distance [respectively,  $F(1, 11) = 14.5, p = 0.0029$ ; and  $F(1, 11) = 8.22, p = 0.015$ ]. The distance effect appeared slightly smaller in verbal notation than in arabic notation (Fig. 6). However, this did not reach significance on either time window (both  $F$ s  $< 1$  for the interaction of notation and distance).

Response-synchronous analyses also confirmed the asymmetry of the distance effect [ $F(1, 11) = 8.93, p = 0.012$  for the N1-P2p window;  $F(1, 11) = 5.95, p = 0.033$  for the P2p window]. As seen on Figure 6, the voltage difference between close and far numbers was two to three times larger over the right hemisphere than over the left (0.30 vs. 0.84  $\mu V$ ), even though it reached significance on both sides [ $F(1, 11) = 6.01, p = 0.032$  on the left;  $F(1, 11) = 15.4, p = 0.0024$  on the right].

The BESA program was used to model the topography of the distance effect, averaged across notations, in response-synchronous averages. A single-dipole model, placed by the program near the right parieto-occipito-temporal junction, accounted for 87.7% of variance. When two symmetrical dipoles were introduced, the residual variance was further reduced and 92.9% of variance could be accounted for. The two dipoles were placed within the left and right parieto-temporo-occipital junctions, with the right activation being about twice greater than the left (Fig. 7). Allowing for nonsymmetrical dipoles did not further improve the model.

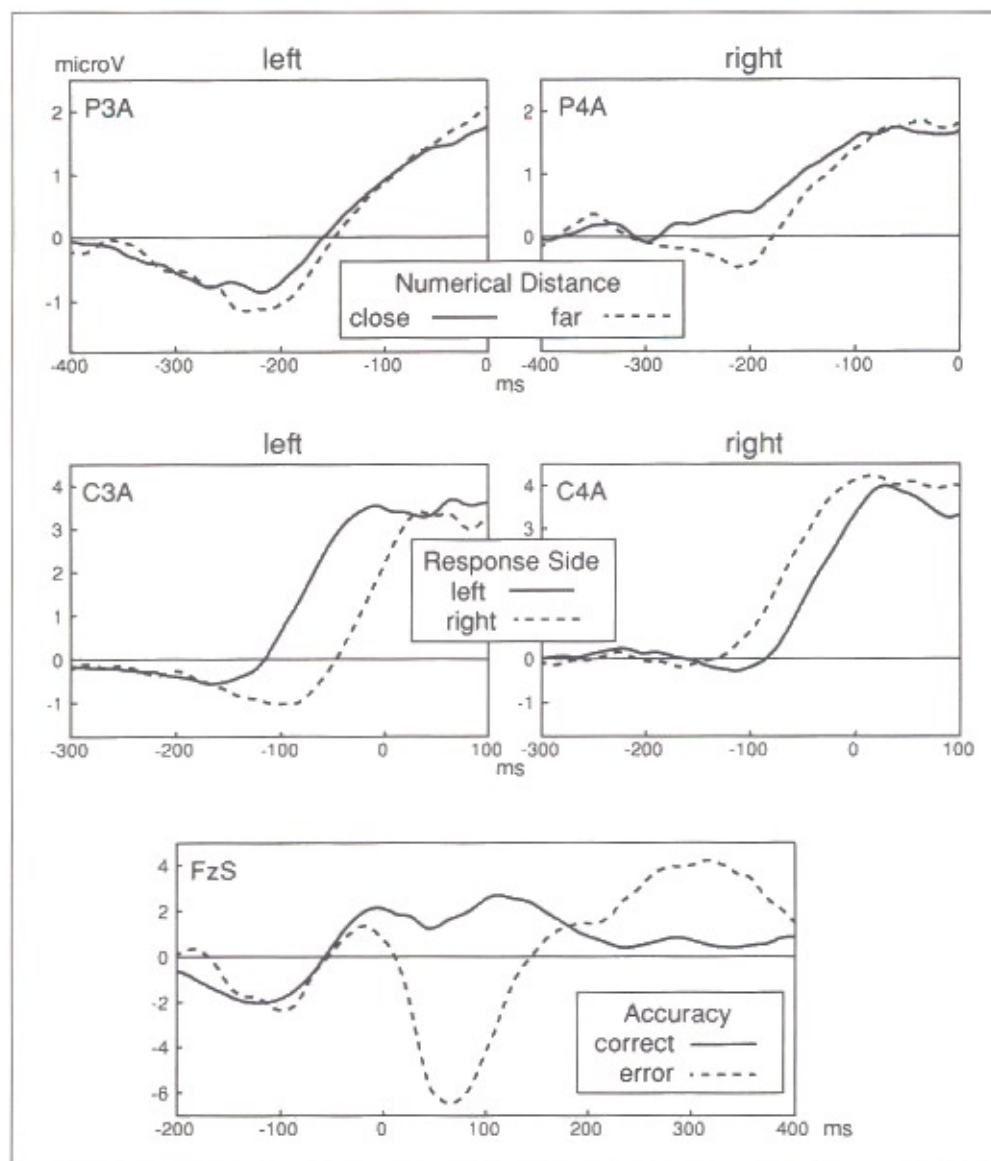
**Motor Effect.** On stimulus-synchronous averages, the first reliable difference between left and right key presses emerged on the P2p window over sites C3A/C4A, which are located over the central part of the left and right primary motor areas. The response side effect took the form of a significant interaction of hemisphere and response-side [ $F(1, 11) = 10.5, p = 0.0078$ ]: ERPs were more negative on the side contralateral to the



**Figure 5.** Three-dimensional reconstructions of instantaneous scalp voltage at different times in the epoch, as a function of number notation. Each pair of images shows left and right posterior views of the same head. Voltage is color-coded using the linear color scale shown (colors and scaling vary for each set). Images marked 'msec after the stimulus' were computed from stimulus-locked averages, whereas those marked 'msec before/after the key press' were computed from response-locked averages. Top left: Topography of the P1 to arabic and verbal numerals. Note the higher amplitude over the right hemisphere and the medial negativity. Top right: Topography of the N1, which was bilateral for arabic digits and left-lateralized for verbal numerals. Bottom left: Topography of the second posterior positivity (P2p). Bottom right: Topography of the voltage difference between numbers close to 5 and numbers far from 5. Note the similar scalp distribution of the distance effect for arabic and verbal numerals, with a nonsignificant tendency toward a larger effect in arabic notation.



**Figure 6.** Selected waveforms of response-locked grand-averaged data. X-axis is milliseconds before (–) or after (+) the key press. Top: Effect of numerical distance on left and right parietal sites. Middle: Response-side effect on left and right motor sites before the response (lateralized readiness potential). Bottom: Error-related negativity observed on a medial prefrontal site following erroneous key presses.

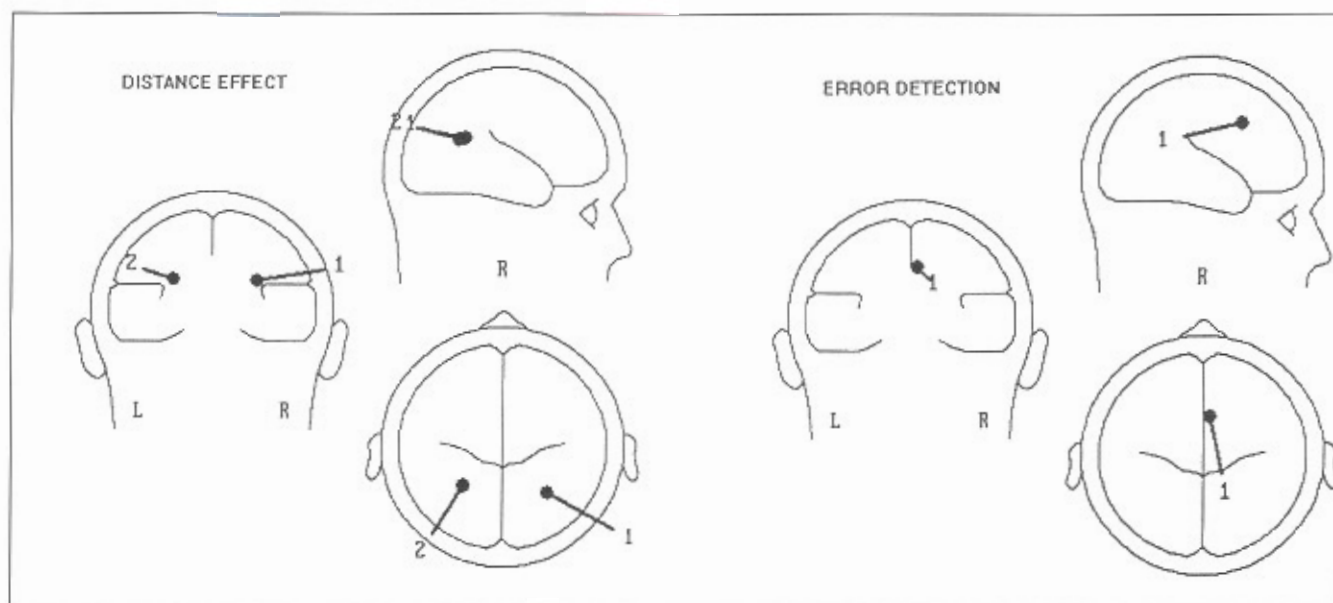


upcoming response (Fig. 3). This effect grew stronger as a major positivity (P3) developed over the central and frontal sites, culminating at the time of the response (Figs. 3 and 5). The size of this lateralized readiness potential was  $0.85 \mu\text{V}$  on a time window isolating the rising part of the P3 (236–360 msec) and  $1.05 \mu\text{V}$  on a time window for the top of the P3 (364–424 msec).

The first significant response-side effect was found at 208 msec post-onset on channel C3A. Such an early onset, however, is probably due mainly to a small proportion of exceptionally fast trials. On response-synchronous averages, the lateralized readiness potential showed a sudden onset at 140 msec prior to the key press on site C3A (Fig. 5). Three-dimensional reconstruction illustrated its sharp localization to premotor and motor regions (Fig. 8), in agreement with its purported origin within primary motor cortex (e.g., Requin, 1985). How-

ever temporal animations of these images showed that this topography was not static, but shifted from anterior prefrontal/premotor sites toward more central motor sites as one approached the time of the key press.

On response-synchronous averages, a response-side effect was also found over *parietal* sites at a much earlier time (200 msec prior to key press on site P4A). This appeared as a main effect of response side [ $F(1, 11) = 20.9, p = 0.0008$  on sites P3A/P4A]. The ERP for left-hand responses was  $0.52 \mu\text{V}$  more positive than the ERP for right-hand responses. The effect was in the same direction over the left and right hemispheres, which distinguished it clearly from the cross-over interaction of the lateralized readiness potential. There was only a small interaction with hemisphere [ $F(1, 11) = 5.19, p = 0.044$ ], indicating a larger effect over the right parietal lobe than over the left.



**Figure 7.** Dipole solutions obtained using brain electrical source analysis (BESA; Scherg & Berg, 1990). Left: 92.9% of the variance in the topography of distance effect (see Fig. 7, top left) was accounted for by a model with two dipoles occupying symmetrical locations near the left and right parieto-temporo-occipital junctions, with an asymmetry favoring the right hemisphere. Right: 89.7% of the variance in the topography of the error-related negativity was accounted for by a single dipole located on the midline in the vicinity of the anterior cingulate and the supplementary motor area.

*Effects of Experimental Variables on the P3.* The latency of the P3 component is known to reflect in part the termination of sensory or cognitive processing (Kutas, McCarthy, & Donchin, 1977; McCarthy, & Donchin, 1981). Indeed, on response-synchronous averages, the rising of the P3 was differentially delayed in a manner consistent with the effects of notation, distance, and word length observed in the reaction time analysis. First, the rising portion of the P3 was significantly more positive for arabic stimuli than for verbal stimuli [ $F(1, 11) = 8.49, p = 0.014$ ], reflecting a shorter rise time for arabic stimuli. Second the peak of the P3 itself was more positive for far digits than for close digits [ $F(1, 11) = 14.4, p = 0.0029$ ] and also for three-letter words as compared to four-letter words [ $F(1, 11) = 7.80, p = 0.018$ ]. This modulation of P3 amplitude may reflect at least in part a decreasing time-locking of the P3 on stimulus-synchronous averages as processing time increases.

On response-synchronous averages, the P3 was found to be virtually unaffected by variables other than the side of the upcoming response. The sole exception was a small but significant effect of distance on the rising part of the P3 [ $F(1, 11) = 6.44, p = 0.028$ ], indicating a 0.23  $\mu V$  greater positivity for far numbers as compared to close numbers.

*Error-Related Negativity.* All the above analyses concerned trials in which the correct response key had been pressed. On such correct trials, the P3 peaked rather sharply around the time of the key press and later de-

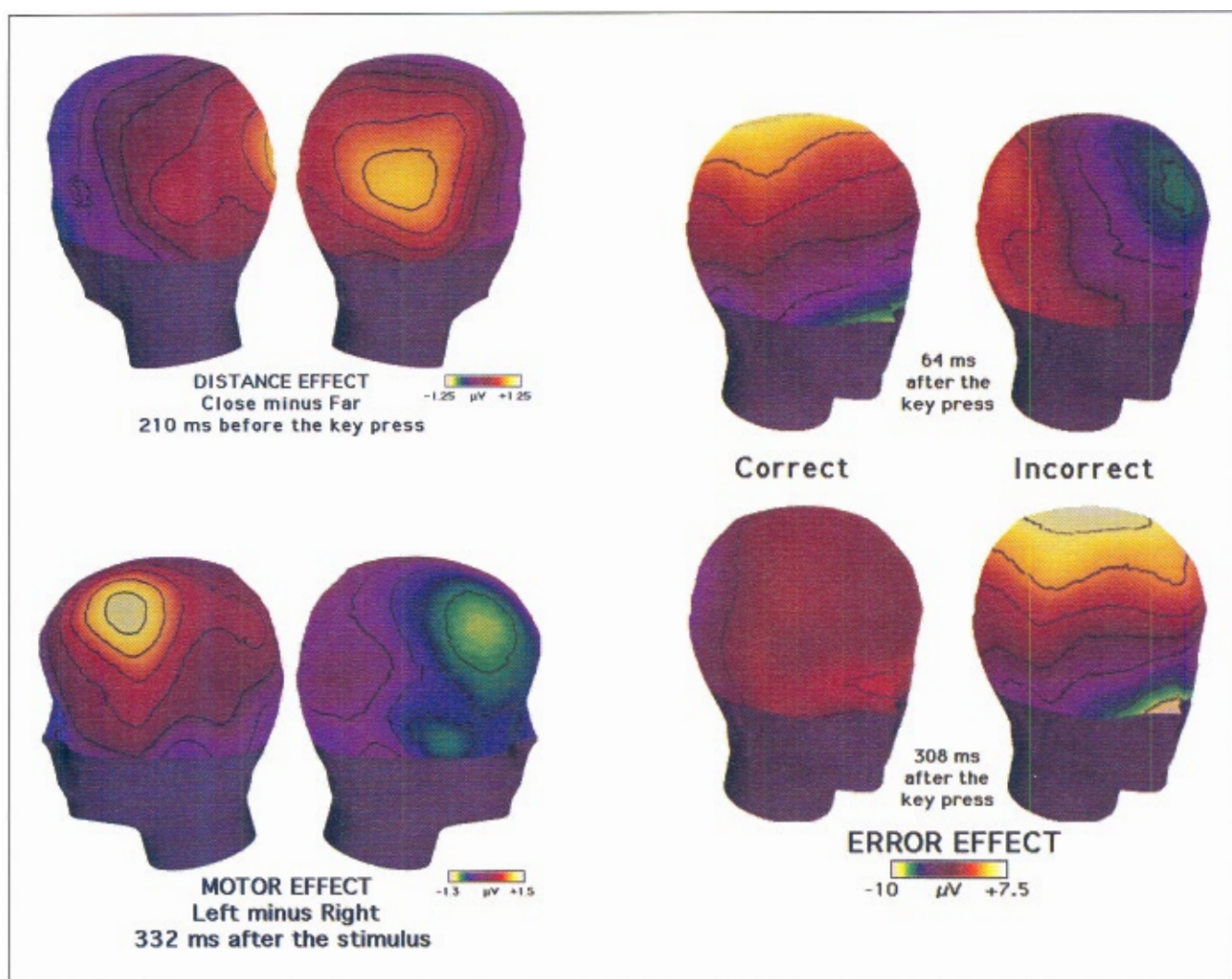
creased over an interval of several hundred milliseconds. On erroneous trials, however, the decrease of the P3 was suddenly interrupted by a major focal negativity sharply localized to electrode FzS (halfway between Fz and Cz) and a few neighboring sites (see Fig. 7). Although this error-related negativity was seen on stimulus-synchronous averages, it was clearly better time-locked to the response and peaked sharply at 64 msec following an erroneous key press (Fig. 5). The first significant divergence between correct and error trials was found exactly at the time of the key press on site FzS (0 msec post-response).

The BESA program was used to model the neural generators of this error-related negativity. A single-dipole solution accounted for 89.7% of variance in the voltage surface observed on error trials. Regardless of initial conditions, the dipole was always placed by the program along the midline within the anterior cingulate cortex (Fig. 8). Multidipole models did not improve this solution. A similar, though somewhat deeper, localization was obtained when the difference between correct and incorrect trials was used for input (see Dehaene, Posner, & Tucker, 1994).

## DISCUSSION

Three major points are considered in the discussion. First, I examine the extent to which the additive-factors methodology succeeded in analyzing the information-processing sequence in number comparison. Second, the





**Figure 8.** Same as Figure 6. Top left: Left and right posterior views of the topography of the distance effect averaged across notations. Bottom left: Left and right views of the topography of the lateralized readiness potential, computed as the difference between ERPs for left-hand and right-hand responses. The voltage was systematically more negative over premotor and motor regions contralateral to the oncoming movement. Right: Right anterior views of the topography of ERPs following correct and incorrect responses. On incorrect trials, a sharp medial prefrontal negativity was observed, followed by a broad positivity quite similar to the P3 seen earlier on correct trials.

serial stage model is applied to a post-hoc analysis of the information-processing sequence when the same stimulus was repeated on two consecutive trials. Third, the compatibility of the inferred number processing areas to previous neuropsychological and brain-imaging findings is discussed.

#### The Information-Processing Sequence in Number Comparison: Evaluation of the Additive-Factors Methodology

The experiment was initially designed to decompose three stages of the number comparison task: stimulus identification, magnitude comparison, and response preparation and execution. However, several additional observations were made that led to a much richer tem-

poral analysis of the number comparison process. What follows is a summary and tentative interpretation of this information-processing sequence.

First, a posterior right-lateralized P1, culminating at 104 msec postonset, was noted. No effects of experimental conditions were observed at this stage. Previous researchers (Compton et al., 1991; Posner & McCandliss, 1993; Posner & Raichle, 1994) have tentatively linked this right-lateralized P1 to a right posterior extrastriate activation observed in a PET experiment in which subjects saw words, nonwords, or false-font stimuli (Petersen et al., 1990). There would be a right posterior specialization for the early processing of visual features. The short latency of the P1 and the absence of any notation or distance effect at this stage are indeed compatible with early nonspecific visual processing.



The *notation effect* was reflected in ERPs by a left-lateralized N1 to verbal numerals contrasting with a bilateral N1 to arabic digits. The notation effect was first significant at 106 msec post-onset, suggesting that by 100–150 msec, notation-specific identification processes have become activated. Note that surprisingly, the N1 latency was inversely related to reaction time. The N1 reached its maximum faster for verbal than for arabic numerals, yet RTs were 38 msec slower for verbal than for arabic numerals. Inasmuch as the N1 reflects visual processing, it is possible that at least part of the visual analysis starts earlier for verbal than for arabic stimuli. This onset difference would be later compensated by the longer duration of word identification as compared to digit identification.

*Word length* may contribute to the slow identification of verbal numerals. Indeed, RTs indicated that three-letter words were compared 19 msec faster than four-letter words. In ERPs, a significant bilateral parieto-temporal divergence was found between three- and four-letter words. The word length effect was first significant at 162 msec after the stimulus, which places it after the divergence of notation-specific arabic and verbal identification processes (106 msec) and before the first effect of numerical distance (190 msec). Taken together, these results suggest that word identification processes incorporate a substage implemented in posterior cortical areas and sensitive to word length.

The *distance effect* (RTs 18 msec faster for numbers far from 5 than for numbers close to 5) was reflected in ERPs by a right-lateralized parieto-occipito-temporal positivity to close numbers as compared to far numbers. Importantly, the topography was similar whether the numbers were presented in arabic or in verbal notation (Fig. 6). These results provide strong evidence for a critical aspect of the model of number processing presented in Figure 1, which is that the same representation of number magnitudes should be accessed regardless of input number notation (McCloskey, 1992; Dehaene, 1992). The distance effect first arose at 174 msec post-onset for arabic digits and at 190 msec for verbal numerals. This difference is in the same direction as that found in RTs, and again suggests that the comparison stage was preceded by a stimulus identification stage that took longer for verbal than for arabic stimuli. Dipole reconstruction indicated that the distance effect could be modeled as originating from the left and right parieto-occipito-temporal regions, with larger activity on the right. Such localization must remain tentative because the observed scalp topography was relatively nonspecific and not entirely noise free. Converging results from PET and neuropsychological studies of number processing are discussed further below.

The *response-side effect* (RTs 10 msec faster with the right hand than with the left) was observed mainly as a negative deflection over the motor sites contralateral to the moving hand, starting 140 msec before the key press.

This contralateral response-related negativity is known as the lateralized readiness potential (Kutas & Donchin, 1974; Vaughan et al., 1972). Interestingly, the lateralized readiness potential shifted slightly in time from an anterior to a more central position. An earlier bilateral parietal difference between left and right key presses was also observed. Further work should tell whether these effects are replicable and reflect a parietal/prefrontal/motor sequence in response preparation.

A major central positivity, traditionally called the P3 (or P300), was also found to culminate at the time of response and may reflect in part nonspecific motor preparation. In agreement with previous studies (Kutas et al., 1977; McCarthy & Donchin, 1981), the P3 was affected by the same variables of notation and distance that also affected RTs. However, on response-synchronous averages the P3 was largely unaffected by experimental variables. This suggested that, as predicted by the serial stage model, the response pattern was largely invariant, though differentially delayed, across the experimental conditions. The sole exception was a small effect of distance on P3 amplitude. One may speculate, in agreement with the subjects' introspection, that the response was selected somewhat less confidently and less forcefully when the target number was close to the standard of comparison than when it was far.

Finally, after the key press, the comparison of correct and erroneous trials isolated a significant negativity peaking at 64 msec after the key press, sharply localized to the medial superior prefrontal region, and specific to erroneous trials. This is known as the *error-related negativity* (ERN) and has been reported in several experimental situations (Falkenstein, Hohnsbein, & Hockmann 1995; Gehring, Goss, Coles, Meyer, & Donchin, 1993; Dehaene et al., 1994). It is thought to reflect an attempted inhibition of the upcoming incorrect response as well as its correction by the opposite hand. The short delay between the erroneous key press and the ERN was clearly too short for sensory or kinesthetic feedback to operate, and suggested an internal process of error capture.

Brain electrical source analysis indicated that the error-related negativity could be accurately modeled by a single dipolar generator located along the midline within the anterior cingulate cortex (Fig. 8). There are inherent difficulties in localizing brain activity from surface recordings. In the present case, however, the voltage surface showed a characteristically dipolar field with an extremely focal negativity and an opposing broad positivity. Furthermore this pattern was replicated in two independent experiments in which essentially identical single-dipole solutions were obtained (Dehaene et al., 1994). Thus the localization to the anterior midline seems reliable. The depth of the activation, however, is less reliably estimated from ERP recordings. Although BESA located the dipole deep into the anterior cingulate, it seems equally likely that the source was a more superficial and spread-out region of activity within the



supplementary motor area. Both the supplementary motor area and the anterior cingulate have been shown by previous studies to play a role in error processing and response inhibition (Gehring et al., 1993; Gemba, Sasaki, & Brooks, 1986).

In summary, the results suggested the following organization of activations:

1. a posterior activation, possibly right-lateralized, related to early visual processing;
2. a posterior occipito-temporal activation related to stimulus comprehension, which was left-lateralized for verbal stimuli and bilateral for arabic stimuli;
3. a bilateral temporo-parietal effect of word length;
4. a right-lateralized parieto-occipito-temporal activation affected by the distance effect;
5. an activation over motor sites contralateral to the response key;
6. a medial superior prefrontal activation related to error processing.

That all these events took place within 500 msec underlines the ability of the ERP additive-factors methodology to decompose a simple series of brain activations. In addition, a critical prediction of the serial stage model of Figure 1 was that factors affecting different stages should have independent effects. In RT analyses, the independence assumption implied that factors should have additive effects on total reaction time. This was verified by the absence of factor interactions in an analysis of variance. In ERPs, independence implies that the divergence of waveforms reflecting the effect of a factor should have the same sign and topography regardless of manipulations of the other factors, but that its latency should vary with the duration of preceding stages. Both predictions were verified for the distance and the response-side effect. Most notably, the distance effect showed a similar topography regardless of input notation (Fig. 6), but its onset was delayed for verbal numerals as compared to arabic digits.

A number of caveats should nevertheless be mentioned. That stages of stimulus identification, semantic access, and motor execution should be activated sequentially and in this order is, of course, rather trivial. It remains to be seen if the additive-method will prove useful for analyzing less predictable processing sequences. The present results are also neutral concerning the temporal overlap and the transmission of information between consecutive stages. Information might be transmitted only after a computation is completed, or it could be sent, continuously or by discrete packets, even before a unique answer has been reached (e.g., McClelland, 1979; Miller, 1982). In the latter case, the activations of two consecutive stages may overlap in time. No attempts were made here to distinguish between these further refinements of the serial stage model (but see, e.g., Coles, Gratton, Bashore, Eriksen, & Donchin, 1985; Coles, Gratton, & Donchin, 1988; de Jong, Wierda, Mulder,

& Mulder, 1988; Miller & Hackley, 1992). In the general case, temporal variability and smearing due to averaging still pose considerable obstacles to the precise determination of stage onsets and offsets.

Finally, exact source localization remains a major problem for ERP techniques. Most often, the effects could be localized only in relatively vague terms such as "left posterior occipito-temporal." Nevertheless, significant differences between two conditions occasionally yielded sharply localized voltage patterns on the scalp. One example is the error-related negativity (Fig. 7), which peaked sharply on a single electrode site (FzS) and had a much reduced effect on electrodes located as little as 4 cm away. In this situation, the generator of the effect must be relatively superficial and close to the scalp location of FzS (see also Dehaene, Posner & Tucker, 1994). Such inferences can be made even before dipole reconstruction is attempted.

### Analysis of the Repetition Effect

The success of a sequential analysis of the number comparison task prompted examination of the effect of one final factor: the repetition of some target numbers on two consecutive trials. Because of the random ordering of the four numbers 1, 4, 6, and 9 within each block, on one-fourth of the trials, the same stimulus that had been compared on the previous trial was repeated on the next trial. Reaction time and ERP analyses showed that the processing sequence was reorganized in a predictable manner on such repeated trials, providing another demonstration of serial stage decomposition using RT and ERP measures.

To analyze the repetition effect, average RTs, error rates, and ERPs were compared across two conditions: exact repetition of the same stimulus (and therefore of the same response) versus presentation of a different stimulus, which nevertheless yielded the same response (e.g., 1 followed by 4, both requiring a "smaller" response). Both of these categories involved a similar number of trials (one-fourth of the data). Only correct trials that were themselves preceded by a correct trial were included in these analyses.

As expected, repeated trials yielded faster responses [38 msec effect;  $F(1, 11) = 52.7, p < 0.0001$ ] and lower error rates than nonrepeated trials [1.7% vs. 5.6 errors;  $F(1, 11) = 13.9, p = 0.003$ ]. What modifications in information processing could account for this facilitation on repeated trials? Based on an analysis of the model of Figure 1, the following sequence of processing can be predicted. First, the subjects must recognize that the stimulus was repeated. This presumably implies that they apply the same stimulus identification routines as in nonrepeated trials. Thus the identification stage should not vary much with repetition, except perhaps for some amount of repetition priming. Second, once they have identified the stimulus and noticed the repetition, the

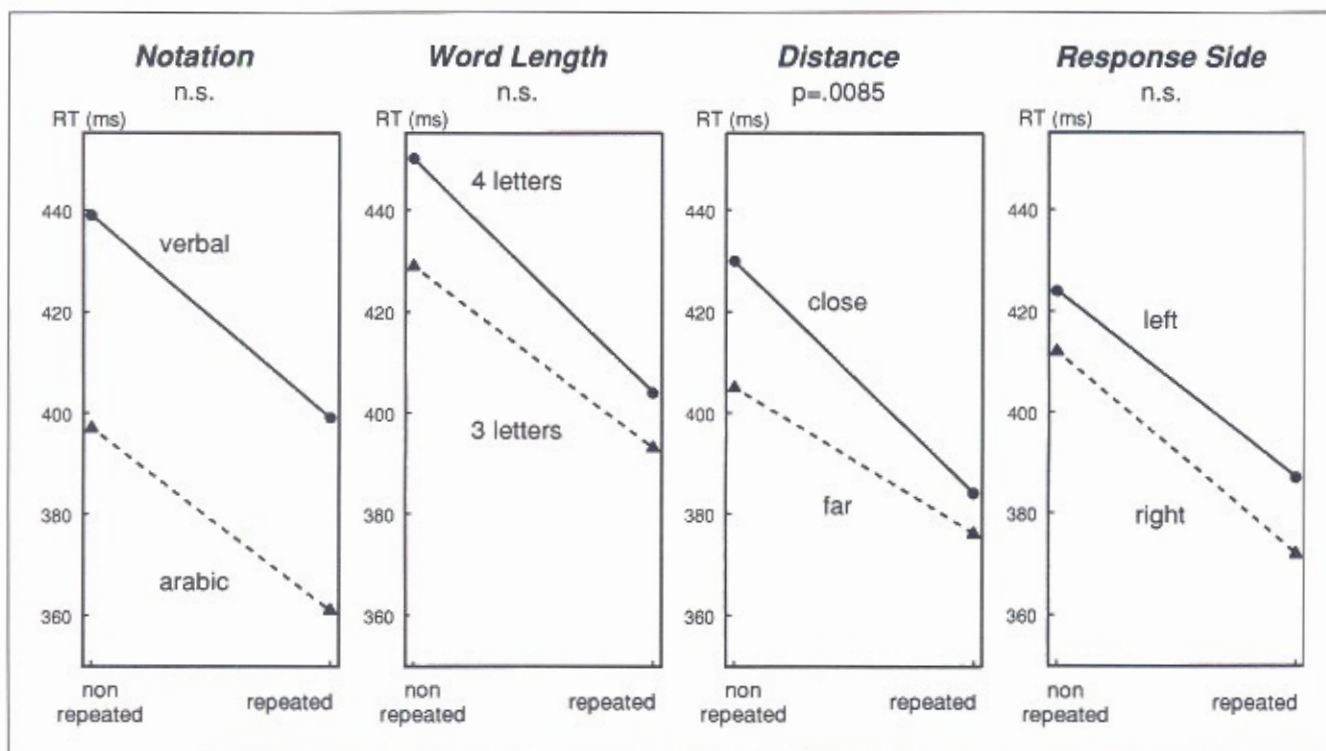


subjects may presumably short-circuit the comparison operation itself and directly recall the response that was made on the previous trial. Third, motor preparation and execution must obviously proceed in much the same way on repeated and nonrepeated trials. Repetition priming of motor processes is not expected here because the repeated and nonrepeated trials that were contrasted both involved the same motor response as the preceding trial.

In brief, repeated trials should behave as if a single processing stage (magnitude comparison) had been deleted. According to the logic of additive-factors, repetition should therefore interact with distance (both factors affecting the same magnitude comparison stage), but not with any other experimental factor. Analyses of variance on reaction times confirmed this prediction (see Fig. 9). First, there was no interaction of repetition and notation ( $F < 1$ ). Arabic numerals always yielded faster responses than verbal numerals, whether the stimulus was repeated or not (both  $ps < 0.0001$ ). Second, there was no interaction of repetition with word length ( $F < 1$ ). Responses were faster for three-letter words than for four-letter words in both repeated and nonrepeated trials (both  $ps < 0.016$ ), although the difference tended to be smaller on repeated than on nonrepeated trials (11 vs. 21 msec). Third, there was a significant interaction of repetition and distance [ $F(1, 11) = 10.2, p = 0.0085$ ]: the distance effect dropped from a highly significant 25

msec on nonrepeated trials [ $F(1, 11) = 62.6, p < 0.001$ ] to a nonsignificant 8 msec on repeated trials [ $F(1, 11) = 2.40, p = 0.15$ ]. Finally, there was no interaction of repetition and response side ( $F < 1$ ). Subjects were faster with the right hand than with the left hand on both repeated [ $F(1, 11) = 10.2, p = 0.009$ ; 15 msec effect] and nonrepeated trials [ $F(1, 11) = 4.27, p = 0.063$ ; 12 msec effect]. As predicted, the distance effect associated with magnitude comparison was the only effect to disappear on repeated trials (Fig. 9).

Analysis of the ERPs to repeated and nonrepeated trials essentially confirmed this picture, with some additional complexities. No effect of repetition was perceptible on the P1. The first effect of repetition was found on the N1 [ $F(1, 11) = 5.96, p = 0.033$ ]: the N1 was smaller on repeated than on nonrepeated trials. This can perhaps be attributed to repetition priming, because repetition of a stimulus has been found to decrease posterior brain activation in a PET study by Squire et al. (1992). However, the qualitative shape of ERPs was not modified by repetition: on repeated trials, the N1 remained equally left-lateralized for verbal targets and symmetrical for arabic targets. By contrast, the distance effect was largely reduced on repeated trials. It remained significant at only one right parietal electrode site (P4A). The clearest evidence that the magnitude comparison stage was largely short-circuited on repeated trials came from an examination of the motor effect (lateralized



**Figure 9.** Influence of stimulus repetition over two consecutive trials on the number comparison task. There was no interaction of repetition with notation, word length, or response side. However, the distance effect was reduced to a nonsignificant trend on repeated trials, suggesting skipping of the magnitude comparison stage.



readiness potential). The difference between left and right key presses showed exactly the same topography on repeated and nonrepeated trials. In both cases, a negativity contralateral to the responding hand was observed. The onset of the effect, however, was quite different. The first significant difference between left and right key presses was observed at 220 msec postonset on repeated trials and at 290 msec postonset on nonrepeated trials. Thus, the onset of motor preparation appeared to have shifted to a much earlier point in time, almost to the point where the distance effect was found to culminate.

In brief, the serial stage model of number comparison could also explain, without modification, the effect of repeating a given trial. The results indicated, as predicted, that stimulus identification and response processes were relatively unaffected by stimulus repetition, but that the magnitude comparison stage was largely short-circuited. This situation is a particular case of the additive-factor methodology in which a psychological manipulation (here stimulus repetition) has the effect of shortening the information-processing sequence by deleting one of its stages (Donders, 1969).

### Brain Areas Related to Number Processing

How do the present results illuminate our understanding of number processing in the brain? Two points will be emphasized here: the existence of a bilateral system for identifying arabic digits, and the convergence of activation toward a right posterior system for magnitude comparison.

#### *Bilateral Numeral Identification Systems*

The observation of a symmetrical N1 to arabic digits and of a left-lateralized N1 to verbal numerals suggests that arabic digits are initially processed bilaterally, whereas verbal numerals seem to be primarily identified in the posterior left hemisphere. In other experiments, all sorts of words, not just numerals, have elicited a left-lateralized N1 (e.g., Curran et al., 1993; Dehaene, 1995; Neville, Kutas, Chesney, & Schmidt, 1986). PET studies have identified a left ventromedial extrastriate area activated by the presentation of real words and pronounceable pseudowords, but not by consonant strings or false-font stimuli (Petersen et al., 1990). A lesion in this area produces pure alexia with letter-by-letter reading, suggesting a deficit of the visual word form (Shallice, 1988). Thus PET, ERP, and patient data seem to converge in isolating a left posterior ventral system related to word identification. This system would first become specifically activated by words as opposed to digits around 110–160 msec postonset. Additional evidence indicates that words and consonant strings are not discriminated until about 150–200 msec post-onset (Compton et al., 1991; Dehaene, 1995; Posner & McCandliss, 1993).

Why then is the activation bilateral with arabic digits? In the left hemisphere, it seems likely that the same brain area (or perhaps two nearby areas) is responsible for the identification of words and strings of digits. Indeed, alexic patients with left-hemispheric lesions often have difficulties naming multi-digit arabic numerals. However a number of cases on record indicate that the identification of arabic digits may be preserved when word identification is impaired (e.g., Anderson, Damasio, & Damasio, 1990; Cohen & Dehaene, 1995; Dejerine, 1891, 1892). Some abilities for digit identification have been observed after massive left-hemispheric lesions (e.g., Dehaene & Cohen, 1991; Barbizet, Bindefeld, Moaty, & Le Goff, 1967), left hemispherectomy (e.g., Patterson, Vargha-Khadem, & Polkey, 1989), or in the right-hemisphere of callosal patients (e.g., Gazzaniga & Smylie, 1984). The right N1 observed in the present experiment with arabic digits, which was much weaker with words, may therefore reflect, in part, the functioning of a right-hemispheric digit identification system.

Word alexia without digit alexia is a relatively frequent deficit. The opposite deficit, however—impaired naming of arabic numerals with preserved word naming—is quite rare (although see Cipolotti et al., 1995; Hécaen, Angelergues, & Houillier, 1961). This neuropsychological asymmetry can be explained by the hypothesis of a bilateral system for digit identification. If a posterior left-hemispheric lesion impaired word reading, the right-lateralized digit identification system might be able to take over. Conversely, it would take a bilateral posterior lesion to eliminate both digit identification processes, and such a lesion would be likely to affect word naming as well.<sup>2</sup>

Are the left- and right-hemispheric identification processes strictly redundant? Neuropsychological data rather suggest that they may play slightly different roles. The left-hemispheric processes seem to play a special role in accessing a phonological representation, whereas the right-hemispheric processes are involved in accessing number meaning without necessarily permitting to read aloud. For instance, patients NAU (Dehaene & Cohen, 1991) and GUI (Cohen, Dehaene, & Verstichel, 1994) both suffered massive posterior left-hemisphere lesions and subsequent reading deficits. Both patients had to laboriously count in order to name arabic numerals, yet both were excellent in determining which of two two-digit numerals was the largest. Patient GUI suffered from deep dyslexia and could not read aloud nonwords or unfamiliar arabic numerals, indicating impairment of a surface reading route. Yet he could still understand and occasionally name familiar numerals such as 1789 (French Revolution) or 1918 (World War I), indicating preserved access to number meaning. More recently, two cases of pure alexia have confirmed that a small lesion restricted to the left posterior ventral region, while sufficient to impair digit naming, leaves digit comprehension virtually intact (Cohen & Dehaene, 1995). These



cases fit well with the notion of two systems for digit identification, one biased toward phonological retrieval and the other toward semantic access.

### *A Right-Lateralized Area for Magnitude Comparison*

The present data also speak to the nature and brain localization of an abstract representation of number magnitude. Subjects were slower and made more errors when comparing two close quantities than when comparing two more distant ones. In ERPs, a significant difference between close and far trials first emerged on sites located close to the parieto-occipito junction, with a significant right lateralization. Most importantly, a similar voltage pattern was found whether the numbers were presented in arabic or in verbal notation. This suggests that the distance effect originates from a level of representation that abstracts away from the physical and notational characteristics of the stimulus (Dehaene, 1992; McCloskey, 1992), in contrast with the predictions of the encoding-complex model (Campbell & Clark, 1988, 1992).

The left parieto-occipito-temporal junction is a critical site for acalculia in brain-lesioned patients (e.g., Benton, 1987; Henschen, 1919; Hécaen et al., 1961; Warrington, 1982). It is therefore perhaps surprising that a similar localization was obtained here with a significant *right* lateralization. Several findings are, however, consistent with a right-hemispheric contribution to magnitude comparison. First, as mentioned above, in patients with massive left posterior lesions, knowledge of number magnitudes, larger-smaller relations, and approximation of quantities is often preserved (e.g., Dehaene & Cohen, 1991; Cohen et al., 1994; Assal & Jacot-Descombes, 1984). Second, functional brain-imaging studies in normal subjects have revealed an activation of both left and right inferior parietal areas during calculation (Appolonio et al., 1994; Dehaene et al., submitted; Roland & Friberg, 1985). Third, a recent model of the development of numerical abilities in animals and in human infants has underlined the natural relation of number perception to object localization and size perception abilities (Dehaene & Changeux, 1993). Since the latter two depend on the integrity of right parietal areas, it is perhaps plausible that number representations should follow a similar pattern. It is noteworthy that the few number-coding neurons recorded in the cat by Thompson, Mayers, Robertson, and Patterson (1970) were all found within the posterior association cortex, near the parieto-occipito-temporal junction.

In conclusion, the right hemisphere appears to possess both the ability to identify a digit and to represent its magnitude relative to other numbers. This conclusion, far from being in contradiction with neuropsychological findings, may explain the frequent preservation of digit identification, number comparison, and approximation abilities in acalculic patients with left-hemisphere le-

sions. It also suggests that more attention should be paid to number processing impairments following right posterior lesions. Such patients should be able to read arabic numerals and perform rote calculations, but may not understand the numerical quantities and the approximate relations involved.

## **METHODS**

### **Task**

Subjects were presented with a random list comprising only the numbers 1, 4, 6, and 9, which in different blocks appeared either in arabic notation or in capitalized verbal notation. They had to decide whether each number was larger or smaller than 5, and to depress one of two corresponding response keys using the left or right hand. Responses were measured via two microswitches, 2 cm apart, connected to the millisecond timer of a National Instruments NB-DMA-8 card. In one half of the experiment, the "larger" response was assigned to the right-hand key and the "smaller" response to the left-hand key. This assignment was reversed in the other half. Instructions emphasized both speed and accuracy.

### **Stimuli**

The arabic digits 1, 4, 6, 9 and the verbal numerals ONE, FOUR, SIX, NINE were presented on a standard black and white Macintosh monitor (white on black) equipped with a Polaroid CP-50 circular polarizing filter to reduce glare and stimulus persistence. Arabic digits were presented in a Geneva Bold 48-point font and subtended about 12 × 16 mm (1.1 × 1.5° at the viewing distance of about 60 cm). Verbal numerals were presented in a Geneva bold 36-point font and subtended at most 35 × 12 mm (3.3 × 1.1°). Stimuli were presented for 105 msec, synchronous with the 15 msec refresh cycle of the monitor, and preceded and followed by an empty screen. The interval between a key press and the next stimulus was fixed at 1935 msec. Given an average RT of 399 msec, the average interstimulus interval was 2334 msec or about 26 trials per minute.

### **Procedure**

Subjects first participated in a pretest without ERP recording, whose purpose was to familiarize the subjects with the task, to align them on a fixed level of performance, and to reject exceptionally slow or fast subjects. The pretest comprised 4 consecutive blocks, each including 10 training trials followed by 20 presentations of each target number, for a total of 90 trials. Notation (arabic or verbal) and response assignment (larger-right or larger-left) were fixed within each block, and varied systematically in counterbalanced order across blocks. After each block, the experimenter examined the results and asked the subject to respond faster if the mean RT



was larger than 500 msec, or slower if the error rate exceeded 10%. Subjects that still exceeded these criteria after the fourth block were not included in the study. The results of the pretest were not analyzed statistically because the four blocks were differentially affected by feedback from the experimenter.

On a subsequent day, the remaining subjects came back for the ERP test, in which the same blocks were now run in the converse order. Each ERP block included 10 training trials and 40 presentations of each target number, for a total of 170 trials. During the ERP test, the subjects were not given feedback until the experiment was over. However, the pretest proved quite successful in reducing intersubject differences in speed, since the individual median RTs in the ERP test all fell in a tight interval from 383 to 441 msec (average = 399 msec,  $SD = 15.2$  msec). The individual error rates were slightly more variable (average = 4.4%,  $SD = 2.5\%$ , range 0.9–9.5%).

### Subjects

Sixteen right-handed students participated in the selection pretest. One failed to meet the inclusion criterion. The others participated in the ERP test, where one subject was rejected for experimenter error and two for having less than 50% artifact-free trials after editing. The remaining 12 subjects (6 females) were aged between 18 and 23 (average 21.3).

### Scalp Electrical Recording

Scalp voltages were collected using a 64-channel Geodesic Sensor Net (Tucker, 1993). This device consists of 58 Ag/AgCl electrodes encased into sponges soaked in a saline electrolyte. The electrodes occupy the vertices of a triangular mesh of elastic lines, which ensures their regular repartition on the surface of the scalp with a spacing of about 4 cm. The Net was applied in anatomical reference to the canthomeatal line and was supplemented with 8 independent electrodes at mastoid, nasion, seventh cervical vertebra, infraorbital, and external canthus locations. The electrode on the seventh cervical vertebra was connected to the ground, and the right mastoid electrode to the reference input of 64 custom-built AC-coupled high-impedance amplifiers with a band-pass of 0.1–50 Hz (3 dB/octave attenuation) and a 60-Hz notch filter. Amplified scalp voltages were digitized by a Macintosh II computer using National Instruments multiplexor card AMUX-64, 16-bit analog-to-digital converter card NB-MIO-16, and direct memory access card NB-DMA-8. A total of 256 samples were collected at 250 Hz starting 150 msec before stimulus onset.

### Data Reduction

Each subject's 640 trials of 64-channel voltage data were stored on disk and later edited manually. A trial was

rejected whenever eye blinks, eye movement, muscular activity, movement, or electrical artifacts were detected, or when the subject had responded incorrectly. In the 12 subjects included in the analysis, at least 68.4% of trials were kept (average 80.7%). An ANOVA on the number of rejected trials revealed no major difference in rejection rates across the different experimental conditions.

The artifact-free trials were then averaged either synchronous to the stimulus onset or to the key press. In the latter case, trials with a response time under 250 or over 600 msec were also excluded. The resulting averages were baseline corrected on the 150 msec prestimulus period and low-pass filtered at 40 Hz using a two-pole double Butterworth filter. The average reference transform was applied to provide a reference-free estimate of voltage at each electrode site (Bertrand, Perrin, & Pernier, 1985; Curran et al., 1993; Tucker, Liotti, Potts, Russell, & Posner, 1993). Eventually the data, including the reconstructed right mastoid reference, were reduced to 65 epochs of 256 samples for each of 12 subjects in each of the 16 experimental conditions (4 numbers  $\times$  2 notations  $\times$  2 response assignments).

### Statistical Analysis

Two approaches were taken to the statistical analysis. First, nonparametric statistics for comparisons of interest were applied to each time sample and at each electrode site. The Wilcoxon matched pairs signed-rank test was used to reveal consistent differences among two conditions (e.g., arabic vs. verbal notation). An effect was deemed significant if significant differences at the 0.05 level were found for at least five consecutive samples (20 msec). The onset of the effect was then determined as the first sample when a significant divergence was found. Specific effects were studied on stimulus-synchronous averages, response-synchronous averages, or both.

In addition, some bilateral electrode pairs showing significant effects were selected for parametric analysis. The selected electrode pairs were T5P/T6P (posterior superior temporal), P3P/P4P (posterior inferior parietal), P3A/P4A (anterior inferior parietal), and C3A/C4A (primary motor area). These sites were selected based on a pilot study of arabic number comparison involving repeated testing of three subjects. This study, although it did not incorporate manipulations of notation and response side, already showed that the N1 peaked on sites T5P/T6P, the distance effect around sites P3P/P4P and P3A/P3P, and the motor effect on sites C3A/C4A, at times similar to those reported in the present study.

For each electrode pair, nonoverlapping time windows were selected to cover the entire time range in which nonparametric analyses had revealed significant effects. Individual windows were selected to analyze separately the amplitude of major observable ERP events such as the P1, the N1, the P2p, and the P3. On stimu-



lus-synchronous averages, the windows of interest were 86–110 msec poststimulus (peak of the P1; channels T5P/T6P, P3A/P4A), 134–166 msec (peak of the N1; same channels), 170–202 msec (N1–P2p transition; channels P3P/P4P, P3A/P4A, C3A/C4A), 206–232 msec (peak of the P2p; same channels), 236–360 msec (rising of the P3; channels C3A/C4A), and 364–424 msec (peak of the P3; same channels). On response-synchronous averages, the same windows N1–P2p, P2p, rising of the P3, and top of the P3, now defined, with respect to the *average* time of stimulus presentation, were applied to the electrode pairs P3A/P4A and C3A/C4A.

For each electrode pair and each time window, average-reference voltages averaged over the entire time window were then entered into an ANOVA with factors of notation (arabic vs. verbal), magnitude (large vs. small), distance (close vs. far), response key (left vs. right), and laterality (left/right hemisphere). To restrict the number of tests, only the following effects of theoretical significance were tested: notation, distance, response key, word length (which appeared as the interaction of magnitude and distance for verbal stimuli), and interaction of distance and notation. Interactions of these effects with the laterality factor were also tested to examine hemispheric asymmetries.

### Graphical Rendering and Dipole-Fitting

The average-reference voltage data were interpolated across the surface of the scalp using spherical splines (Perrin, Pernier, Bertrand, & Echallier, 1989). The reconstructed voltage surface could then be visualized from any angle as a three-dimensional object, using color coding for the different levels of voltage on the head (Figs. 6 and 7). In a few simple cases, a forward-search dipole localization algorithm, brain electrical source analysis (BESA; Scherg & Berg, 1990), was also used to generate single- or double-dipole models of the observed scalp voltages. This approach should be considered only indicative, however, because it relies on a number of implausible assumptions (sphericity of the head, punctual dipole sources, etc.). Dipole reconstruction requires some *a priori* decisions from the experimenter (number of dipoles, symmetries, etc.) and is thus more akin to modeling than to straightforward data analysis (Tucker et al., 1993).

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Reprint requests should be sent to Stanislas Dehaene, Laboratoire de Sciences Cognitives et Psycholinguistique, C.N.R.S.-E.H.E.S.S., 54 Boulevard Raspail, 75270 Paris Cedex 06, France. Electronic mail may be sent to stan@lscp.msh-paris.fr.

### Notes

1. Mathematically speaking, additivity of factors is predicted only when the dependent measure is the average RT of all observations (Sternberg, 1969). However, this requirement conflicts with the need to exclude from the analysis exceedingly short or long RTs that are commonly believed to reflect inadequate task processing (e.g., anticipation or inattention). Median RT was used here to limit the influence of such outliers. ANOVAs on mean RTs gave essentially identical results.
2. Note that the ERP data do not indicate strictly unilateral processing of words. There was a small right-lateralized N1 to verbal numerals. That the right hemisphere may have some mediocre ability for word recognition is compatible with the preservation of 'whole-word' identification abilities in pure alexia (review in Coslett, Saffran, Greenbaum, & Schwartz, 1993) as well as the inferred role of the right hemisphere in deep dyslexia (Coltheart, 1980; Patterson et al., 1989).

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