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When Brightness Counts: The Neuronal Correlate of Numerical–Luminance Interference

Roi Cohen Kadosh[1,2], Kathrin Cohen Kadosh[1,3] and Avishai Henik[1]

[1]Department of Psychology and Zlotowski Center for Neuroscience, Ben-Gurion University of the Negev, Beer-Sheva, Israel, [2]Institute of Cognitive Neuroscience, University College London, London, UK and [3]Centre For Brain and Cognitive Development, School of Psychology, Birkbeck College, University of London, London, UK

Previous studies showed that the processing of numerical information and spatial information such as physical size causes a mutual interference. The neuronal correlate of such interference was suggested to be in the parietal lobe. However, a previous study showed that such interference does not occur between numerical information and nonspatial dimensions such as luminance level (Pinel P, Piazza M, Le Bihan D, Dehaene S. 2004. Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. Neuron. 41:983–993). Here it is shown that numerical value and luminance level do cause a behavioral interference and that this interference modulates the activity in the parietal lobe. The current results support the idea that the parietal lobe might be equipped with neuronal substrates for magnitude processing even for nonspatial dimensions.

Keywords: conflict task, functional magnetic resonance imaging, intraparietal sulcus, magnitude, numerical cognition, size congruity

Introduction

How do we compare numbers and other magnitudes? Moyer and Landauer (1967), in their seminal study on numerical comparison, noted that "... a comparison is then made between these magnitudes in much the same way that comparisons are made between physical stimuli such as loudness or length of line." (p. 1520). Because this observation almost 40 years ago, many studies have been dedicated to key issues in numerical cognition, such as the representation of numbers (Restle 1970), its cognitive architecture (McCloskey et al. 1985; Dehaene 1992; McCloskey 1992; Campbell 1994; Cipolotti and Butterworth 1995; Dehaene and Cohen 1995; Noel and Seron 1997), and with the rise of sophisticated imaging techniques, also its neuronal correlates. The latter were found mainly in the intraparietal sulcus (IPS) (Dehaene et al. 1996, 1999, 2003; Pinel et al. 2001; Piazza et al. 2002, 2004; Delazer et al. 2003; Fias et al. 2003; Cohen Kadosh et al. 2005; Ansari et al. 2006; Cantlon et al. 2006; Wood et al. 2006). Evidence for similarity in the decision processes of different types of magnitudes, as was noted by Moyer and Landauer (1967), motivated research that examined whether the neuronal substrate for numerical processing is common to other types of magnitude processing (Schwarz and Heinze 1998; Fias et al. 2003; Pinel et al. 2004; Cohen Kadosh et al. 2005; Kaufmann et al. 2005; Castelli et al. 2006; Cohen Kadosh and Henik 2006a, 2006b; Cohen Kadosh, Cohen Kadosh, Linden, et al. 2007). In addition, these studies were further stimulated by "a theory of magnitude" (ATOM), which postulates that different magnitudes such as number, space, and time, or any other dimension that can be classified by "more/less than," are computed according to a common metric in the parietal lobe (Walsh 2003). Based on human and animal (mainly monkeys) studies, Walsh suggested that the neuronal substrate of the common magnitude system is located in the parietal lobe, mainly in the right hemisphere, and that this mechanism operates already at birth.

Whereas several neuroimaging findings support the assumption of a shared mechanism for magnitude by reporting that different dimensions show a common activation in the left posterior IPS, rather than the right IPS (Fias et al. 2003; Cohen Kadosh et al. 2005), others do not (Castelli et al. 2006). Several studies used the size congruity paradigm in order to investigate the possible shared mechanism for magnitude (Schwarz and Heinze 1998; Pinel et al. 2004; Kaufmann et al. 2005). In this Stroop-like paradigm, 2 numerical quantities such as digits (Henik and Tzelgov 1982; Tzelgov et al. 1992; Schwarz and Ischebeck 2003), number words (Foltz et al. 1984; Cohen Kadosh, Henik, et al. 2007), or dot arrays (Pansky and Algom 2002; Hurewitz et al. 2006) appear on a screen and are varied in their numerical magnitude as well as in their physical sizes. The stimuli can be incongruent (e.g., the physically larger digit is numerically smaller; 2 4) or congruent (e.g., the physically larger digit is also numerically larger; 4 2). It is commonly found that reaction times (RT) to incongruent trials are slower than to congruent trials ("size congruity effect"). This slowing down of responses, due to the influence of the irrelevant dimension, suggests that the processing of numerical and physical dimensions overlap up to a certain point. In light of the suggestion proposed by ATOM (Walsh 2003) that magnitude is processed by a general mechanism in the parietal lobe, it is highly important to pinpoint when selection of the relevant dimension occurs. Previous studies found that the interaction between numerical quantity and physical size occurs in the IPS (Pinel et al. 2004; Kaufmann et al. 2005; Cohen Kadosh, Cohen Kadosh, Linden, et al. 2007). These results suggest that the interference between numerical value and physical size occurs due to a shared representation of magnitude, but this does not seem to hold true for the relation between numerical and other magnitudes. Namely, Pinel et al. (2004) examined whether luminance levels interfere with numerical values. Although they reported mutual interference of numerical value and physical size at the behavioral level and in the parietal lobes, they failed to find symmetrical interference between luminance level and numerical value at the behavioral level. Moreover, there seemed to be no interference at the neuronal level. Pinel et al. (2004) suggested that there is a shared neuronal substrate for numbers and space, but not for other types of magnitude that are nonspatial. Note that this suggestion impacts the ATOM's idea that magnitude has a shared neuronal substrate in the parietal lobe (Walsh 2003). Pinel et al.'s conclusions are in contrast to other studies that found the distance effects for numerical value, physical size, and luminance level overlap in the left IPS (Cohen Kadosh et al. 2005). In addition, we recently reported a mutual behavioral interference between numerical value and luminance level (Cohen Kadosh and Henik 2006a). Namely, we found that the level of brightness influences the performance in numerical comparison; RTs were slower when the larger numerical value was associated with a smaller level of luminance (as compared with the background). In contrast, faster RTs were observed when the smaller numerical value appeared in a smaller level of luminance. The reverse also held true; numerical value affected processing of luminance comparison. That is, slower RTs were associated with a smaller level of luminance when it appeared with the larger numerical value, as compared with the smaller numerical value. In contrast, faster RTs were observed when the smaller numerical value appeared in a smaller level of luminance. Moreover, the interference was quite similar to the one observed between numerical value and physical size. Thus, we assumed that the interference between numerical value and luminance value (i.e., nonspatial magnitude) recruits the parietal lobe, which is involved also in interference between numerical value and physical size (i.e., spatial magnitude).

These results are in contrast to the null results reported in Pinel et al.'s (2004) study. It might be that the irrelevant luminance dimension was masked by the irrelevant physical size that was manipulated in the same experimental design. That is, although our study manipulated only 2 dimensions as in the classical size congruity paradigm, Pinel et al.'s design included 3 dimensions: physical size, numerical value, and luminance level, which varied orthogonally. Thus, it might be that the irrelevant physical size masked the luminance dimension due to greater saliency. In addition, the stimuli in Pinel et al.'s study were adjusted to equalize the difficulty level between comparisons on a subject-by-subject basis (although there were differences in the error rates). This in turn added another factor to the design which is training. In contrast, Cohen Kadosh and Henik (2006a) selected their stimuli, and equalized the difficulty level between comparisons based on a pilot study with different subjects. These methodological differences might at least partly explain the differences in the results.

The current study aimed to find out whether numerical and luminance comparisons share a neural structure, which in turn produces interference.

Materials and Methods

Participants

Sixteen participants (6 males, all right-handed, mean age: 26.14 years, standard deviation [SD]: 1.47 years) were recruited from an academic environment and gave written informed consent to participate in the study. The study was approved by the local ethics committee. None of the participants reported significant neurological or psychiatric disorders.

Stimuli

Stimuli consisted of 2 digits that appeared at the center of a screen. The center-to-center distance between the 2 digits subtended a horizontal visual angle of 5°. The digits subtended a horizontal visual angle of 1.85°. Numerical and luminance comparisons were performed in separate blocks. Two types of pairs were used; congruent and incongruent. In a congruent pair the numerically larger digit was also brighter (e.g., 2 4). In an incongruent pair the numerically larger digit was darker (e.g., 2 4) (Fig. 1). As in previous studies (Cohen Kadosh and Henik 2006a, 2006c; Cohen Kadosh, Cohen Kadosh, Linden, et al. 2007; Cohen Kadosh, Henik, et al. 2007) we used the digits between 1 and 9, excluding digit 5. In order to present each number an equal number of times we presented pairs 1–2, 3–4, 6–7, 8–9, 1–6, 2–7, 3–8, and 4–9. This way each number appeared an equal amount of time.

For the degree of luminance we used the same stimuli as in Cohen Kadosh et al. (2005). Namely, we created 8 different stimuli that varied only in brightness with constant hue and saturation. Their photometric luminances were 20.9, 27.7, 35.8, 46.5, 58.4, 82.5, 108, and 175 cd/m^2. The selection of the luminance levels was made in order to create a logarithmic-like function of intensity as reported previously for the representation of numerical quantity (Dehaene 1989). As with the numerical stimuli, in order to present each luminance level an equal number of times, we presented pairs 20.9–27.7, 35.8–46.5, 58.4–82.5, 108–175, 20.9–58.4, 27.7–82.5, 35.8–108, and 46.5–175 (in cd/m^2).

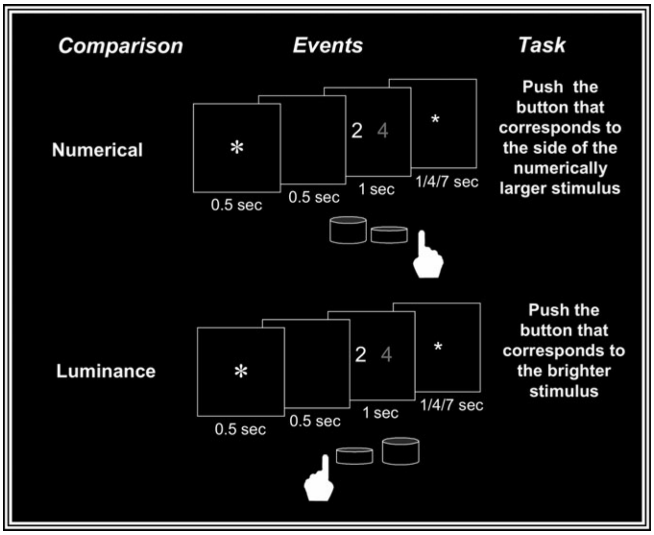

Figure 1. Paradigm design for 2 different tasks containing numerical and luminance comparisons. Each pair of stimuli was preceded by a fixation point and a blank screen (500 ms each) and remained visible for 1 s. After 1, 4, or 7 s (ITI) a new trial began with the presentation of a larger fixation point that indicated the beginning of a new trial. The participants had to decide which stimulus was numerically larger or brighter while ignoring the irrelevant dimension. The correct response was indicated by a button press on the side that corresponded to the larger numerical value (numerical comparison) or brighter stimulus (luminance comparison).

Procedure

Participants were asked to decide which of 2 stimuli in a given display was numerically larger (numerical comparison) or brighter (luminance comparison). All participants took part in one session of 4 runs. Each run was composed of 2 blocks of numerical comparisons and 2 blocks of luminance comparisons. Participants were asked to respond as quickly as possible while avoiding mistakes, and to attend only to the relevant dimension. They indicated their choices by pressing one of 2 keys corresponding to the side of the display with the selected digit (i.e., right hand for the right side, left hand for the left side). The order of the runs was counterbalanced in a Latin square design, whereas the presentation of the blocks in each run was counterbalanced in ABBA/BAAB order. The stimuli were randomly sampled, and correct responses were made equally often with the left and right hand.

Each experiment was preceded by a short training session of 24 trials for each comparison task. The presentation of the experiments and the collection of the behavioral data were controlled by E-prime software (Psychology Software Tools Inc., Pittsburgh, PA).

Each trial began with an asterisk as a central fixation point (visual angle of 1.85°) presented for 500 ms at the center of a computer screen. Five hundred milliseconds after the fixation point disappeared, a pair of digits appeared for 1 s. A small fixation point (visual angle of 1°) appeared during the intertrial interval (ITI) for 1, 4, or 7 s (each ITI appeared an equal number of times). The interblock time interval was 21 s. At the beginning of a new block a message appeared for 3 s, indicating the relevant dimension.

Design

The variables manipulated were comparison (numerical, luminance) and congruity (congruent, incongruent). Thus, we had a 2 × 2 factorial design, with all variables manipulated within subjects.

FMRI Scanning and Analysis

Whole-brain functional magnetic resonance imaging (fMRI) data were acquired with a 1.5-T scanner (Philips Intera, Eindhoven, The Netherlands) using a gradient-echo echo planar imaging sequence (18 axial slices; repetition time/echo time = 2,000/60 ms; flip angle = 90°, field of view = 210 × 210 mm, voxel size: 3.28 × 3.28 × 5 mm). Stimuli were presented on a 7.5″ LCD monitor (IFIS-SA, MRI Devices, Waukesha, WI). Each run comprised the acquisition of 161 volumes and contained 48 trials (12 trials × 2 comparison tasks × 2 congruity). Stimulus presentation was synchronized with the fMRI sequence. Each scanning session included the acquisition of a high-resolution T_1-weighted 3-dimensional volume (voxel dimensions = 1 × 1 × 1 mm) for coregistration and anatomical localization of functional data. Data were preprocessed and analyzed using the BrainVoyager QX 1.7 software package (BrainInnovation, Maastricht, The Netherlands). The first 2 volumes of each run were discarded to allow for T_1 equilibration. 3D motion correction and Talairach transformation (Talairach and Tournaux 1988) were performed on the remaining set of functional data of each participant. Two participants were dropped from the analysis due to excessive head movements of more than a voxel. The 3D functional data set was resampled to a voxel size of 3 × 3 × 3 mm, and further preprocessing was applied, such as spatial smoothing with a Gaussian kernel (full-width at half-maximum [FWHM] = 8 mm), linear trend removal, temporal high pass filtering (high pass: 0.00647 Hz) and autocorrelation removal. For the general linear model (GLM) analysis, we applied a voxel-by-voxel analysis of variance (ANOVA) on the beta weights (2-way ANOVA with factors "comparison" [2 levels: luminance and numerical] and "congruity" [2 levels: congruent and incongruent]). Error trials were modeled separately. The GLM, with predictors convolved with a gamma distribution to account for the shape and delay of the hemodynamic response, was computed from the 56 z-normalized volume time courses. A random effects analysis was employed. An area was considered as significant if at least one of the conditions' beta values was significantly greater than 0 (in order to not include effects due to deactivation). To enforce an a priori threshold of $P < 0.05$ (corrected for multiple comparisons), a cluster extent threshold procedure was used (Slotnick et al. 2003). This procedure is based on the fact that the probability of observing clusters of activity due to voxel-wise type I error (i.e., noise) decreases systematically as cluster size increases. Therefore, the cluster extent threshold can be determined to ensure an acceptable level of corrected cluster-wise type I error. In order to implement such an approach, we ran Monte Carlo simulation with 1000 iterations using the same parameters as in our study (i.e., acquisition matrix, number of slices, voxel size, FWHM, resample voxel size) to model the brain volume. An individual voxel threshold was then applied to achieve the assumed voxel-wise type I error rate ($P < 0.001$). The probability of observing a given cluster extent was computed across iterations under $P < 0.05$ (corrected for multiple comparisons). In the present study, this translated to a minimum cluster extent threshold of 16 resampled voxels.

In addition, we also conducted an analysis of the lateralized blood oxygen level–dependent (BOLD) response (LBR) (Dehaene et al. 1998; Cohen Kadosh, Cohen Kadosh, Linden, et al. 2007). Similar to the lateralized readiness potential (Coles et al. 1985; Gratton et al. 1988), the LBR can be obtained by subtracting ipsilateral activity (of the nonresponding hand) from contralateral activity (of the responding hand) in the primary motor cortex (M1). If the irrelevant dimension is processed throughout response initiation (e.g., response selection, motor preparation, and response execution), the LBR for the conflict condition (i.e., incongruent in the current study) will yield less activation than the LBR for the no-conflict condition (i.e., congruent in the current study). Indeed, by using the LBR it has been shown recently that the interaction between numerical value and physical size (in a numerical and physical comparison task) occurs not only in the IPS but also in the motor cortex under certain conditions (Cohen Kadosh, Cohen Kadosh, Linden, et al. 2007), thus indicating that the irrelevant dimension can be processed up to the motor level. In the current study we calculated the LBR using the following equation (Cohen Kadosh, Cohen Kadosh, Linden, et al. 2007):

$$\mathrm{LBR} = \frac{(\beta_{\text{Left hand}} - \beta_{\text{Right hand}})_{\text{right M1}} + (\beta_{\text{Right hand}} - \beta_{\text{Left hand}})_{\text{left M1}}}{2}$$

We anatomically defined the hand knob in the primary motor cortex according to the procedure described by Yousry et al. (1997), masked it and extracted the beta weights of each condition for each hemisphere in each participant. Later we calculated the LBR as mentioned above, and subjected it to an ANOVA of the beta weights (2-way ANOVA with factors "comparison" [2 levels: luminance and numerical] and "congruity" [2 levels: congruent and incongruent]) by using an off-line statistical software (Statistica 6.0).

Results

Behavioral Data

Similar behavioral results have already been reported extensively elsewhere (Cohen Kadosh et al. 2006a). The current results replicated these results when we included other factors (e.g., distance effect). However, these factors were not of main interest in the current study, and thus were not discussed.

For every participant in each condition the mean RT was calculated for correct trials only. These means were subjected to a 2-way ANOVA with comparison and congruity as within-subject factors. The main effect for comparison was not significant ($F < 1$), whereas the main effect of congruity was significant ($F_{1,13} = 78.62$, $P < 0.001$). Moreover, the interaction between comparison and congruity was also significant ($F_{1,13} = 22.72$, $P < 0.001$, Fig. 2). It seems that this effect was due to a greater congruity effect under numerical comparison as compared with luminance comparison. To further our understanding regarding the sources of the interaction between comparison and congruity, we conducted simple effects analyses for numerical and luminance comparisons separately (Keppel 1991). The simple congruity effect of 81 ms under numerical comparison (incongruent condition, mean: 593 ms, SD: 21.42; congruent condition, mean: 512 ms, SD: 16.22) ($F_{1,13} = 89.14$, $P < 0.001$) as well as the simple congruity effect of 42 ms under luminance comparison (incongruent condition, mean: 563 ms, SD: 20.19; congruent condition, mean: 521 ms, SD: 20.07) ($F_{1,13} = 30.93$, $P < 0.001$) were significant. The congruent

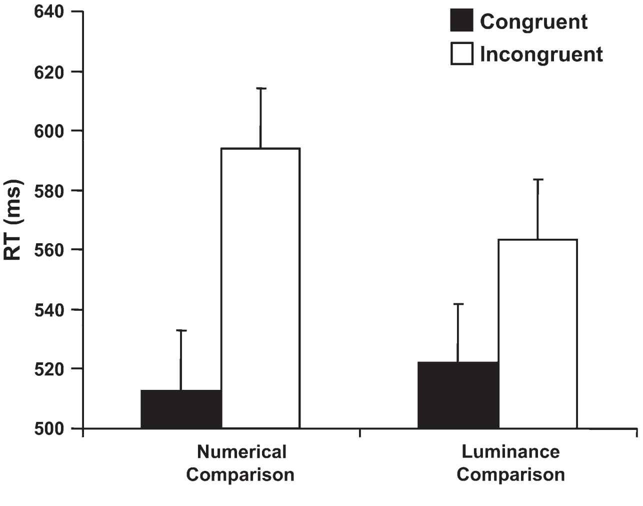

Figure 2. Mean RT as a function of congruity and comparison. Error bars depict one standard error of mean.

condition, as well as the incongruent condition, did not differ between the 2 comparison tasks ($F_{1,13} = 0.42$, $P = 0.52$, and $F_{1,13} = 2.52$, $P = 0.13$, respectively).

For errors, only the main effect for congruity was significant ($F_{1,13} = 6.13$, $P = 0.03$) (other Fs < 1). The percentage of errors was larger for incongruent than congruent conditions (9.2, and 2.0, respectively) and thus excluded any RT-accuracy trade-off.

In previous studies it was found that participants are faster to respond to small numbers with left hand responses, and to large numbers with right hand responses (the so-called "spatial numerical association of response codes"; Dehaene et al. 1993, see Fias and Fischer 2004; Gevers and Lammertyn 2005, for reviews). One might argue that luminance also has similar spatial characteristics (although we are not familiar with any evidence for it). That is, participants might associate higher levels of luminance with the right and smaller levels of luminance with the left side. In order to examine this possibility we added the factor hand (responding with the left or right hand) to the factorial design. In this case, because the task was to select the larger/brighter stimulus, responses with the right hand were considered spatially compatible, whereas left hand responses were considered spatially incompatible. Importantly we found a marginally significant interaction between task and hand ($F_{1,13} = 4.45$, $P = 0.055$). This result was due to a significant effect for hand under numerical comparison ($d = 20$ ms, 544 ms for compatible, 564 ms for incompatible, $F_{1,13} = 7.51$, $P = 0.01$), but a nonsignificant difference in the case of luminance comparison ($d = -7$ ms, 546 ms for compatible, 539 ms for incompatible, $F < 1$).

FMRI Data

One area in the parietal lobe showed a main effect for congruity. This area was the right IPS (Fig. 3*A*). In addition, the right middle frontal gyrus (MFG) showed also a congruity effect. Importantly, neither of these areas showed a trend toward a main effect of comparison, nor interaction between congruity and comparison (all Ps > 0.23). Moreover, the descriptive activation pattern of the right IPS (Fig. 3*A*) was opposite to the behavioral results (Fig. 2). That is, in contrast to the RT data, there was a smaller congruity effect under numerical comparison as compared with luminance comparison. Thus, the possibility that this activation was driven by differences in task difficulty (Göbel et al. 2004) was excluded. No area showed a main effect for task or an interaction between congruity and comparison. However, when we examined the data under a less conservative P value ($P < 0.005$) we observed an interaction between congruity and comparison in the right IPS at a posterior site to the area that showed a congruity main effect (Fig. 3*B*). In contrast to the interaction between congruity and comparison in the behavioral data, the current interaction was due to a significant congruity effect under luminance comparison, but not under numerical comparison. In other words, the interaction was due to automatic processing of the numerical dimension, but not the luminance dimension.

When we computed the LBR it was not significant. Namely, there was no modulation of motor cortex activation by congruity, or congruity and task (Fs < 1, Ps > 0.2).

The cluster size for the congruity effect in the right IPS was small. Thus, one might argue that our results might be due to a type I error (but see our Monte Carlo simulation in the Method section). Nevertheless, in order to further examine this possibility we conducted an additional independent analysis. We located each area in the parietal lobe that showed significant activation for all conditions versus rest ($P < 0.001$, uncorrected). This way, the analyses of interest (e.g., congruity effect) are independent of the threshold that was set for the region of interest selection, and are not biased to one of the experimental conditions. Next, we performed an ANOVA on the extracted beta weights (2-way ANOVA with factors "comparison" [2 levels: luminance and numerical] and "congruity" [2 levels: congruent, and incongruent]). We again found a congruity effect in the right IPS (45, −34, 43, 1262 voxels). Moreover, in the current analysis the left IPS also was modulated as a function of congruity (37, −36, 34, 1716 voxels).

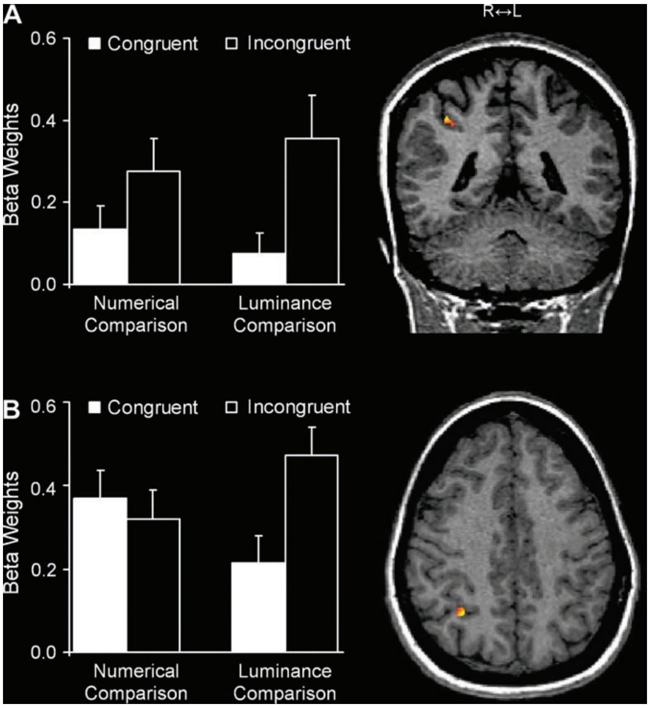

Figure 3. (*A*) Main congruity effect in the right IPS ($x = 35$, $y = -43$, $z = 35$) from a sagittal point of view and a plot of the congruent and incongruent beta weights for each comparison task. (*B*) Interaction between congruity and comparison in the right IPS ($x = 32$, $y = -53$, $z = 39$) from a transverse point of view and a plot of the congruent and incongruent beta weights for each comparison task. L = left; R = right. Error bars depict one standard error of mean.

Discussion

The results of the current study replicated the behavioral interference between numerical value and luminance level that was found in a previous study (Cohen Kadosh and Henik 2006a). Moreover, in contrast to another previous study (Pinel et al. 2004), we found that the right IPS exhibited activity modulation as a function of the interaction between luminance and numerical magnitude, independent of the comparison type. These findings are in agreement with the ATOM (Walsh 2003), which predicts that the parietal lobes, and especially the right IPS, might play a role in magnitude processing, independent of spatial characteristics. The congruity effect in the right IPS was observed both in a voxel-by-voxel ANOVA, and in a power analysis (e.g., Slotnick 2005; Slotnick and Moo 2006; Cohen Kadosh, Henik, Rubinsten 2007; Cohen Kadosh, Cohen Kadosh, Linden, et al. 2007). Compared with the former analysis, in the latter analysis the activation for the congruity effect in the right IPS was larger, more anterior, and was also observed in the left IPS. This result, not

Table 1.
Talairach coordinates for foci that showed significant effects

	Stereotaxic coordinates					
Effect	*x*	*y*	*z*	No. of voxels	Hemisphere	Region (BA)
Size	35	−43	35	22	Right	IPS (40)
Congruity	34	13	34	25	Right	MFG (9)
Comparison × congruity	32	-53	39	42	Right	*IPS (40)

Note: BA = Broadmann area; *in contrast to $P = 0.001$, this area was detected under $P = 0.005$.

surprisingly, indicates that the method of analysis can alter the exact area of activation, and might have different sensitivity in detecting effects (e.g., Cohen Kadosh Cohen Kadosh, Kaas, et al. 2007). Nevertheless, we found a right IPS activation in both analyses, thus, increasing the trust in a main congruity effect in the right IPS.

The right IPS activation is in contrast to the activation in the left posterior IPS, which we and others have suggested plays a role in magnitude processing (Fias et al. 2003; Cohen Kadosh et al. 2005). How can this apparent contradiction be settled? The current study showed right IPS activation, which in other studies was due to *automatic* magnitude processing of quantifiable dimensions such numerical value, and physical size (Pinel et al. 2004; Kaufmann et al. 2005; Cohen Kadosh, Cohen Kadosh, Linden, et al. 2007). In contrast, left posterior IPS was found to be involved in *intentional* magnitude processing (Fias et al. 2003; Cohen Kadosh et al. 2005). It is possible that separate neuronal substrates are dedicated to intentional and automatic magnitude processing. Accordingly, in a recent transcranial magnetic stimulation (TMS) we found that TMS to the right, but not the left IPS, impaired automatic magnitude processing (Cohen Kadosh, Cohen Kadosh, Schuhmann, et al. 2007). Note that the suggestion of dissociated automatic and intentional magnitude processing is in contrast to the viewpoint of some theoreticians (Tzelgov and Ganor-Stern 2004), but is in line with studies on automaticity and intentional processing in other domains (e.g., time measurements, Lewis and Miall 2003; visuomotor functions, Rossetti et al. 2003). However, we do not intend to claim a complete dissociation between both parietal lobes. Both the left and right parietal lobes were found to play role in automatic processing of magnitudes (Piazza et al. 2004, 2007; Pinel et al. 2004; Kaufmann et al. 2005; Ansari et al. 2006; Cantlon et al. 2006; Cohen Kadosh, Cohen Kadosh, Kaas, et al. 2007; Cohen Kadosh, Cohen Kadosh, Linden, et al. 2007), and both parietal lobes were also activated during intentional processing (Chochon et al. 1999; Pinel et al. 2001; Ansari et al. 2005). The activation in the right parietal lobe during intentional processing might, at least partly, be due to automatic processing, which operates autonomously during intentional processing. Nevertheless, the left parietal activation during automatic processing in other studies shows that the left parietal is capable at least to some extent to process magnitude in an automatic fashion. However, we believe that in the case of automatic processing the right parietal lobe is *more* dominant. The observation of right parietal activation under both analyses, and the results of the TMS study that we described previously support this idea, which will need to be examined further in future studies.

In addition, several areas outside the parietal lobe were modulated as a function of congruity. The MFG in the prefrontal cortex showed a main effect for congruity. This activation is probably due to the need of cognitive control (e.g., MFG, Miller and Cohen 2001), which is involved during conflict tasks. The right IPS (under a less conservative *P* value), at a posterior location to the area that showed a congruity main effect, was activated due to automatic numerical processing, but not due to automatic luminance processing. The size congruity for luminance comparison might indicate that *part* of the parietal lobe is involved in numerical processing rather than in general magnitude processing. These results support the idea that aside from commonalities between different magnitudes, numerical processing is partly subserved by a specialized neuronal substrate (Fias et al. 2003; Cohen Kadosh et al. 2005). Moreover, it suggests that numerical magnitude is processed in a more automatic fashion than luminance.

The absence of an effect in the LBR analysis indicates that the irrelevant dimension was not processed up to the response selection stage as in a previous study that manipulated numerical and physical size (Cohen Kadosh, Cohen Kadosh, Linden, et al. 2007). A possible explanation for the lack of effect in the LBR analysis might be the different response codes for number (which stimulus is larger?) and luminance (which stimulus is brighter). Hence, it is less likely that these 2 dimensions would compete with one another at a late postcategorization level (such as the motor level). In contrast, numerical value and physical size have a shared response code (which stimulus is larger?). The shared response code might lead to a conflict after the comparison stage such as at the level of response selection and to the observance of LBR (see Koechlin et al. 1999, for a similar model for numerical processing).

RT and functional data produced a different pattern of congruity effect. In the RT data we found a larger congruity effect under numerical comparison than under the luminance comparison. The reverse pattern was observed in the functional data. Currently, there is growing understanding that the relationship between functional data and traditional behavioral indices that underlie the same mental states is not always straightforward (see Wilkinson and Halligan 2004, for a review). The current results add important evidence for this suggestion.

All in all, the current study found that the right IPS is activated due to automatic processing of magnitude such as numerical value or luminance level. This finding supports the idea of a common neuronal basis for magnitude processing as suggested by the ATOM (Walsh 2003). Such processing of magnitude is not restricted to spatial characteristics (Pinel et al. 2004), and is not only due to intentional processing of magnitude (Fias et al. 2003; Cohen Kadosh et al. 2005).

Notes

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Address correspondence to Roi Cohen Kadosh, University College London, London WC1N 3AR, UK. Email: r.cohenkadosh@ucl.ac.uk

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