NeuroImage 57 (2011) 1205–1211

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Symbol processing in the left angular gyrus: Evidence from passive perception of digits

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ARTICLE INFO

Article history:
Received 21 March 2011
Revised 6 May 2011
Accepted 10 May 2011
Available online 17 May 2011

Keywords:
Numerical symbols
Symbol mapping
Temporo-parietal junction
Arabic digits
FMRI

ABSTRACT

Arabic digits are one of the most ubiquitous symbol sets in the world. While there have been many investigations into the neural processing of the semantic information digits represent (e.g. through numerical comparison tasks), little is known about the neural mechanisms which support the processing of digits as visual symbols. To characterise the component neurocognitive mechanisms which underlie numerical cognition, it is essential to understand the processing of digits as a visual category, independent of numerical magnitude processing. The 'Triple Code Model' (Dehaene, 1992; Dehaene and Cohen, 1995) posits an asemantic visual code for processing Arabic digits in the ventral visual stream, yet there is currently little empirical evidence in support of this code. This outstanding question was addressed in the current functional Magnetic Resonance (fMRI) study by contrasting brain responses during the passive viewing of digits versus letters and novel symbols at short (50 ms) and long (500 ms) presentation times. The results of this study reveal increased activation for familiar symbols (digits and letters) relative to unfamiliar symbols (scrambled digits and letters) at long presentation durations in the left dorsal Angular gyrus (dAG). Furthermore, increased activation for Arabic digits was observed in the left ventral Angular gyrus (vAG) in comparison to letters, scrambled digits and scrambled letters at long presentation durations, but no digit specific activation in any region at short presentation durations. These results suggest an absence of a digit specific 'Visual Number Form Area' (VNFA) in the ventral visual cortex, and provide evidence for the role of the left ventral AG during the processing of digits in the absence of any explicit processing demands. We conclude that Arabic digit processing depends specifically on the left AG rather than a ventral visual stream VNFA.

Introduction

Investigations into the neural bases of numerical cognition have made significant advances in understanding the neural mechanisms supporting numerical magnitude representation (Dehaene et al., 2003). In contrast, comparatively little progress has been made in understanding the neurocognitive mechanisms underlying the processing of Arabic digits as visual symbols. A detailed understanding of the neural basis of Arabic digit processing is essential to establish a coherent framework of knowledge regarding the neural bases of numerical cognition.

The 'Triple Code' model (Dehaene, 1992; Dehaene and Cohen, 1995) predicts a modality specific 'visual number form area' (VNFA) in the fusiform gyrus (FFG) (Dehaene and Cohen, 1995). According to this model, digits can be processed asemantically, without reference to the numerical magnitudes they represent (e.g. when retrieving simple calculation solutions from memory), or be transcoded into an 'analogue magnitude code' for semantic processing (e.g. during magnitude comparison). However, direct empirical support for an asemantic visual number code in the FFG is presently lacking.

Studies investigating format effects in the processing of numerical magnitude provide some support for a VNFA (e.g. Pinel et al., 1999, 2001; Piazza et al., 2007), showing increased activation in the FFG for digits relative to other numerical stimuli (e.g. number words) in this region. Other studies, however, have reported FFG activation in favour of number words relative to Arabic digits (Cohen Kadosh et al., 2007), making the exact role of this region in the processing of digits unclear.

It is possible that selective activation of a VNFA may be masked by top-down task related brain activations during the explicit processing of numerical magnitude. The majority of neuroimaging studies investigating Arabic digit processing have employed active tasks involving judgments or manipulations of numerical magnitude, making it difficult to disentangle the semantic processing of numerical magnitude from the visual processing of digits. Those few studies which have examined the neural processing of digits in the absence of an explicit numerical magnitude processing task have either not contrasted digits with other symbols (Piazza et al., 2007; Notebaert et al., 2010), or have had, at least some degree of implicit focus on digit identity (Eger et al., 2003; Cohen Kadosh et al., 2007). Thus, no study to date has directly disentangled the neural processing of Arabic digits

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1053-8119/$ – see front matter
doi:10.1016/j.neuroimage.2011.05.035

from other symbol sets in the absence of task demands that require participants to attend to either the identity or magnitude of the digits.

The current study tests for the presence of a VNFA by contrasting brain activation during passive, task-irrelevant viewing of digits versus other symbols at both short (50 ms) and long (500 ms) presentation durations. The absence of any type of active digit processing provides the potential to reveal brain regions supporting asemantic processing of digits as predicted by the visual number code. Moreover, by measuring the brain responses to the presentation of digits at both 50 ms and 500 ms presentation times, it is possible to probe brain activation in response to digits under conditions where the amount of possible visual and semantic processing is severely restricted (50 ms) and thereby probe the hypothesis of asemantic, category specific processing of Arabic digits in the ventral stream. In addition to removing any explicit or implicit saliency for Arabic digits, we sought to control for general visual symbol processing and low-level visual processing of complex visual characters. In order to do so, we included three control conditions; Letters, Scrambled Digits and Scrambled letters. The letter control condition allows for the comparison of Arabic digits to another familiar symbol, while the inclusion of two scrambled symbol control conditions allows the comparison of familiar symbols to novel symbols which are exactly matched in terms of number of pixels, and approximately matched in terms of complexity. Furthermore, contrasting single letters to other symbols types allows a deeper examination of the extent to which brain regions preferentially activated for Arabic digits relative to other symbols are responding to a perceptual dimension specific to digits, and not one that is general to familiar visual symbols.

Thus, the current paradigm is engineered to facilitate the elucidation of brain regions which support the perception of Arabic digits as a specific visual symbol set, over and above familiarity and visual complexity.

Materials and methods

Participants

19 neurologically healthy, right-handed (Edinburgh Handedness Inventory, (Oldfield, 1971)) adults participated in this study (mean age = 22.17 years, std dev = 1.74 years, range = 20.51–27.19 years; 13 males). Participants were all enrolled as undergraduate or graduate students at the University of Western Ontario. Participants gave informed consent and the study was approved by the Health Sciences Research Ethics Board (HSREB) at the University of Western Ontario.

Procedure

Task

The experimental task consisted of a fixation/change detection task, during which participants were required to fixate on a centrally positioned hash symbol (#) and press a response key if and when the symbol turned from white to red. Participants were informed that the hash symbol could also change into another symbol, but that these changes were distracters, and no response was required.

Stimuli were presented in white font on a black background at font size 40, at resolution 1024 × 640. Stimuli were presented using E-prime 2 (Psychology Software Tools, Inc., Pittsburg, PA, USA;http://www.pstnet.com) software, running on a windows XP operating system. The paradigm was synchronised with the scanner using a trigger pulse from the scanner, which sent the key response to the computer on which e-prime was running. The key press/trigger pulse initiated the paradigm after collecting 2 EPI volumes which were discarded from further analysis to ensure steady-state magnetization. The paradigm was presented using a back projector (refresh rate 50/60 Hz), projected onto a first surface mirror fixed to the head coil above the participants' eyes. The experiment consisted of two runs of approximately fifteen minutes each. Thus, the experiment, including localiser scans and anatomical scans, lasted approximately forty five minutes in total.

The colour change stimulus was a red hash symbol on a black background. The distracter items were made up of Arabic digits, scrambled Arabic digits, letters, and scrambled letters. For the intact stimuli digits 1–9 were used, and the capitalised letters T, S, N, R, H, E, D, C, and A. These letters were chosen as the 9 most common letters in the English alphabet (Beker and Piper, 1982) excluding those that looked visually similar to a digit (e.g. O and I).The scrambled stimuli were created by segmenting and rearranging the intact letters and digits into a unified but entirely novel shape. Thus, each letter and each digit had an unrecognisable scrambled counterpart with equivalent number of pixels and approximately similar numbers of angles and curves. The average visual angles for each condition were as follows: Arabic digits Width 4.63 (SD = 0.55), Height 9.24 (SD = 0); Letters Width 5.67 (SD = 0.44), Height 9.24 (SD = 0); Scrambled Digits Width 6.18 (SD = 1.00), Height 8.25 (SD = 2.11); and Scrambled Letters Width 6.72 (SD = 1.77), Height 10.83 (SD = 3.5).

The colour change symbol was presented 6 times per run while other symbols were presented twice at a long presentation threshold and twice at a short presentation threshold, resulting in a total of 18 trials for each condition plus 6 trials of button press per run, and a grand total of 150 trials per run, and 300 trials over the whole experiment. Long duration stimuli were presented for 500 ms while short duration stimuli were presented for 50 ms (Fig. 1). There was no gap between stimulus presentation and the fixation hash symbol, therefore, distractor stimuli were forward and backward masked. Inter-stimulus fixation intervals were either 4, 6, or 8 s, with an overall average of 6 s. Different inter-stimulus fixation lengths were equally distributed between stimulus type and presentation duration. A variable jitter (4000 ms, 6000 ms, or 8000 ms, with a mean of 6000 ms) was introduced to allow for both the oversampling (i.e. the onset of events within a TR was varied) of the hemodynamic response function as well the deconvolution of different events from one another. These fixation trials between events of interest were modelled as part of the baseline. In addition, each functional run began and ended with 16 s of fixation to improve the estimation of the baseline. No trials were repeated consecutively at any point in the experiment, ensuring that there was no possibility of adaptation to a given symbol.

Data acquisition

Scanning was performed on a 3T Siemens Tim Trio MRI system with a Siemens 32-channel head coil (Erlangen, Germany) at Robarts Research Institute, London, Ontario. An anatomical scan was performed encompassing the whole brain after the functional runs were completed. This was achieved by collecting 192 one-mm thick slices using a 3-D T1-weighted acquisition sequence (TI = 900 ms, TE = 4.25 ms, TR = 2300 ms, flip angle = 9°). The in-plane resolution of the anatomical scans was 256 pixels × 240 pixels. To collect functional data, we used a T2-weighted echo-planar imaging sequence (TE = 30.0 ms, TR = 2000 ms, flip angle = 90°) for BOLD acquisition (Ogawa et al., 1992). The field of view was 21.1 cm × 21.1 cm with an in-plane matrix size of 64 pixels × 64 pixels. Each image covered the whole brain (isovoxel size = 3.3 mm). There were no gaps between slices and 488 volumes were collected in a run.

Data analysis

Both structural and functional images were analysed using Brain Voyager QX 2.1.2 (Brain Innovation, Maastricht, Netherlands). The functional images were corrected for differences in slice time acquisition, head motion, and linear trends. In addition, functional images were spatially smoothed with a 6-mm full width at half

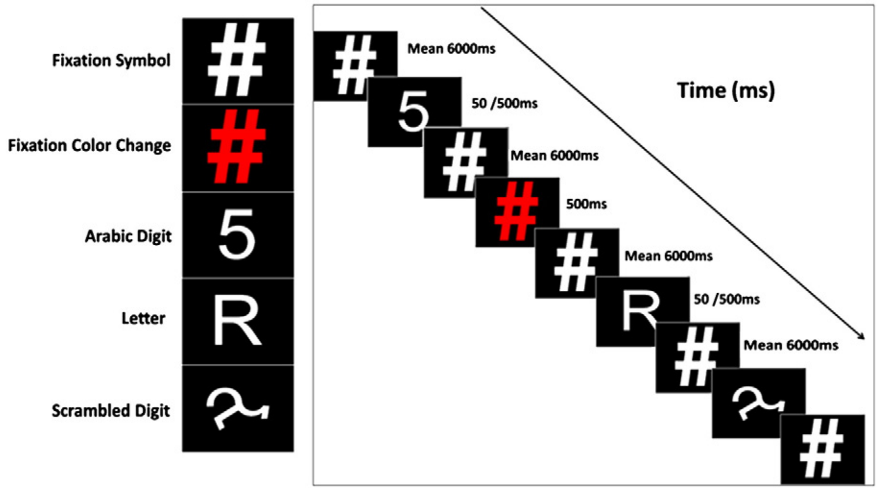

Fig. 1. Example of stimuli and experimental timing parameters.

maximum (FWHM) Gaussian smoothing kernel. Following initial automatic alignment, the alignment of functional images to the high resolution T1 structural images was manually fine-tuned. The realigned functional data set was then transformed into Talairach space (Talairach and Tournoux, 1988). A two gamma hemodynamic response function was used to model the expected BOLD signal (Friston et al., 1998). Baseline was calculated using the 16 s rest periods at the beginning and end of each run, as well as the between trial fixation periods.

Whole-brain random-effects conjunction analyses were conducted to examine differences in BOLD response to the three symbol types (i.e. Arabic digits, letters, and scrambled digits) at short and long presentation durations. As the primary goal of this study was to investigate brain regions sensitive to Arabic digits to a greater extent than other symbols and low-level perceptual features (such as the total number of black and white pixels), conjunction analyses were set to reveal brain regions which showed greater activation for Arabic digits relative to both novel (scrambled digits) and familiar non-numerical symbols (letters). It would have been possible to explore this question by employing either first order contrasts (e.g. Digits > Letters) or interaction analyses (e.g. stimulus type (digit vs letter) × condition (intact vs scrambled)). However, we feel that simple first order contrasts would not adequately control for visual differences between conditions, while interaction analyses have the potential to reveal regions whose interaction terms would be driven by differences in the scrambled symbol conditions, and these differences are of no theoretical relevance to the current study, and would thus dilute the focus of the analysis structure. Thus we opted for a more conservative double conjunction analysis which focuses on the theoretical hypotheses addressed by this study. As button press trials were of no empirical interest to the current study and were merely included to ensure that participants were attending to the stimuli, they were modelled as predictors of no interest and excluded from further analysis.

In the present study, uncorrected thresholds for conjunction analyses were set at $p < 0.005$. For a conjunction analysis, the effective p-value is the square of the p-values for each component (in our case 0.005^3), thus making the current uncorrected thresholds conservative. The resulting statistical maps were subsequently corrected for multiple comparisons using cluster size thresholding (Forman et al., 1995; Goebel et al., 2006). In this method, an initial voxel-level (uncorrected) threshold is set. Then, thresholded maps are submitted to a whole-slab correction criterion based on the estimate of the map's spatial smoothness and on an iterative procedure (Monte Carlo simulation) for estimating cluster-level false-positive rates. After 1000 iterations, the minimum cluster-size that yielded a cluster-level false-positive rate (α) of 0.05 was used to threshold the statistical maps. Put another way, this method calculates the size that a cluster would need to be (the cluster threshold) to survive a correction for multiple comparisons at a given statistical level. Only activations whose size meets or exceeds the cluster threshold are allowed to remain in the statistical maps.

Results

The only behavioural response required in the current experiment was to press a response key when the fixation symbol changed colour. As these trials were of no empirical interest, they were modelled separately and excluded from further analysis. Two subjects made 2 errors each and one subject made one error thus 5 errors of omission were made (i.e. the red colour change stimulus was only missed 5 times out of 114 trials across all participants). The average reaction time for the catch trials was 527 ms (standard error of the mean = 26 ms).

Symbols versus scrambled symbols

To investigate brain regions involved in the perception of familiar symbols (digits and letters) over novel symbols (scrambled digits and scrambled letters), we ran two whole brain random effects (RFX) General Linear Model conjunction analyses testing for regions which showed stronger activation for digits than for scrambled digits as well as stronger activation for letters than for scrambled letters: (Arabic digits > Scrambled digits + Letters > Scrambled Letters). Separate conjunctions were computed for the short and long presentation duration conditions.

For the short presentation condition, the results of this analysis revealed no regions which showed a greater response to familiar versus unfamiliar symbols.

For the long presentation condition, the conjunction analysis revealed one region in the left dorsal Angular gyrus (Tal −37, −64, 42; Cluster size = 792 Voxels) (see Fig. 2).

Letters versus digits and unfamiliar symbols

To investigate brain regions involved in the perception of letters over and above Arabic digits and physically matched meaningless symbols and thereby to test for category specific processing of single letter in the brain, we ran two whole brain random effects (RFX) General Linear Model conjunction analyses testing for regions which

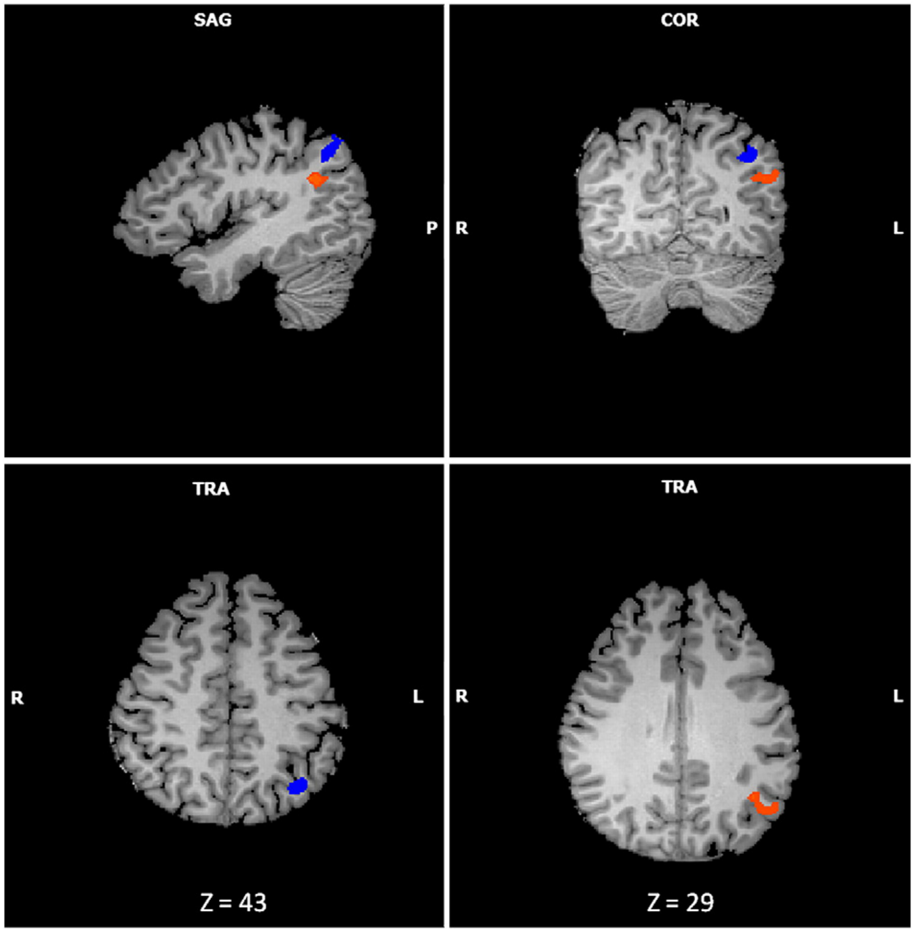

Fig. 2. Activation clusters in the left dorsal AG (shown in red) resulting from the long presentation condition conjunction analysis: Digits>Scrambled Digits + Letters>Scrambled Letters and the ventral AG (shown in blue) resulting from the long presentation condition conjunction analysis: Digits>Scrambled Digits + Digits>Letters + Digits>Scrambled Letters.

showed stronger activation for letters than for digits and scrambled letters: (Letters>Arabic digits + Letters>Scrambled Letters). Separate conjunctions were computed for the short and long presentation duration conditions.

For both the short and the long presentation conditions, the results of the above conjunctions revealed no brain regions that were more active for letters than all other conditions.

Digits versus letters and unfamiliar symbols

To investigate brain regions involved in the perception of digits over and above frequency matched letters and physically matched meaningless symbols, we ran two whole brain random effects (RFX) General Linear Model conjunction analyses testing for regions which showed stronger activation for digits than for letters and scrambled digits: (Arabic digits>Letters + Arabic digits>Scrambled digits). Separate conjunctions were computed for the short and long presentation duration conditions.

For the short presentation condition, the above analysis revealed no brain regions which exhibited preferential activation for Arabic digits.

For the long presentation condition, the above analysis revealed a single region exhibiting preferential activation for Arabic digits over other symbol types in the left Angular gyrus. The locus of this Angular gyrus region was ventral to the dAG region observed for familiar vs unfamiliar symbols (Talairach: −45, −61, 29; Cluster size = 1014 Voxels) (see Fig. 2).

The results of the conjunction analysis indicate that intact Arabic digits activate the vAG to a greater extent than scrambled Arabic digits, but that intact and scrambled Letters do not yield differential activation of this region. To further confirm this distinction, we extracted parameter estimates from the vAG region and conducted a 2 × 2 repeated measures ANOVA testing for an interaction between Stimulus (Digits vs Letters) and Condition (Intact vs Scrambled). The results of this ANOVA revealed a significant Stimulus × Condition interaction [$F(1,18) = 11.35$, $p = 0.003$], thereby supporting the results of the whole-brain conjunction analysis. Post-hoc one sample t-tests revealed that only intact Arabic digits activated the vAG region significantly above baseline [$t(18) = 3.93$, $p = 0.001$]. Furthermore, post-hoc paired samples t-tests revealed that while the vAG was significantly more active for intact Arabic digits relative to scrambled Arabic digits [$t(18) = 4.2$, $p = 0.001$], intact and scrambled letters did not differ in their activation of this region [$t(18) = 0.04$, $p = 0.97$] (Fig. 3).

Discussion

The current study investigated the neurocognitive architecture underlying the processing of Arabic digits and tested the hypothesis proposed in the 'Triple Code Model' (Dehaene, 1992; Dehaene and Cohen, 1995), that the fusiform gyrus (FFG) houses a modality specific 'visual number form area' (VNFA) that subserves the asemantic processing of Arabic digits.

By contrasting brain activation during the passive, task-irrelevant viewing of digits relative to letters, scrambled letters and scrambled

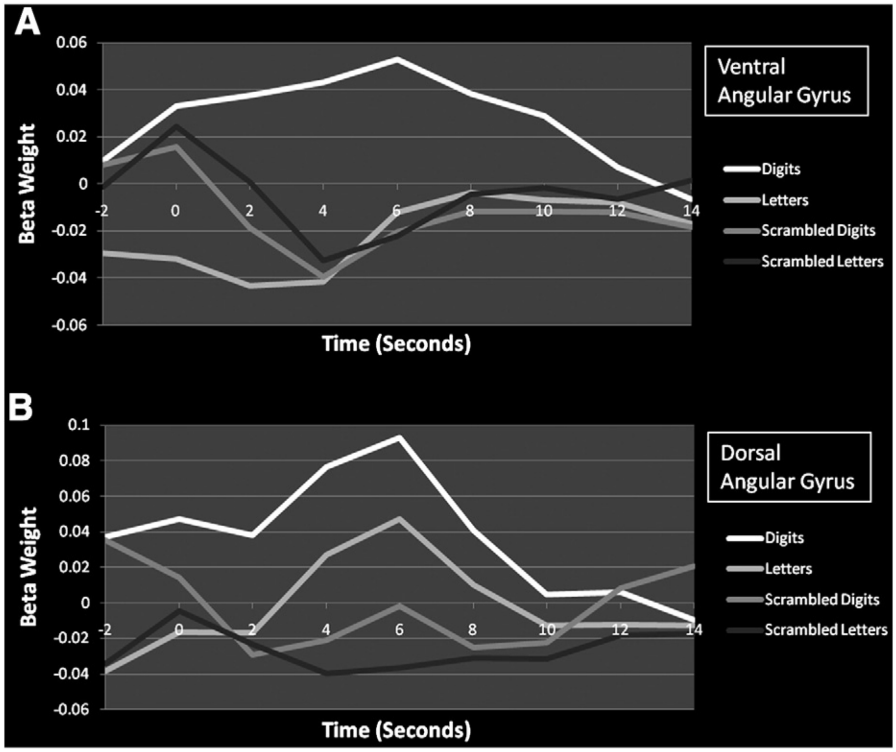

Fig. 3. BOLD response profiles for each condition at 500 ms presentation duration in (A) ventral left Angular gyrus and (B) dorsal left Angular gyrus.

digits, we examined which regions support stimulus driven processing of Arabic digits. Furthermore, by investigating this question using both short and long presentation times, we were able to probe the degree to which such neural substrates vary as a function of the extent to which conscious perceptual processing is possible. If a VNFA exists in the ventral visual stream, it should respond during the passive perception of Arabic digits. This should be expected to be particularly the case in the short presentation condition, during which any top-down effects of conscious semantic processing are severely restricted, if not absent.

The results of the present study, however, did not reveal category specific activation of the FFG in response to Arabic digits, either at short (50 ms) or long (500 ms) presentation durations. Instead, digit specific activation was observed only in the long presentation condition in a ventral section of the left angular gyrus (AG). These results do not support the hypothesis of a VNFA located in the FFG, and instead suggest the AG plays a fundamental role in Arabic digit processing, but only at presentation durations that allow some degree of conscious perceptual processing. It should be noted that one potential explanation for the lack of ventral visual differentiation of stimuli types is that the visual angles subtended by the stimuli in the current paradigm were larger than would be experienced in everyday reading and perception of letters of digits, thus raising the possibility that in concert with the short presentation durations, holistic perception of the images was not maximised. However the effect of this variation in visual angle can only be assessed by direct investigation, and thus remains a question for future research. Furthermore, such an explanation does not sufficiently account for the differences in category-specific activation observed between the Arabic digits and letters.

It should also be noted that although the present data do not reveal evidence of category specific processing of Arabic digits in the FFG, it does seem necessary for there to be some involvement of the ventral visual stream in the processing of Arabic digits that most likely precedes the involvement of the Angular gyrus. It is possible that this ventral visual processing is simply not category specific, as suggested by the current results. However, it is also possible that a) spatial smoothing and Talairach transformation blur fine grained regional distinctions, thus masking any category specific effects, or b) that the relatively large visual angles discussed above somehow interfere with the revelation of category specific effects in the FFG. The current data do not allow us to take a strong position on either of these explanations and so, future research should seek to experimentally address these issues.

Another parietal region, the intraparietal sulcus (IPS) has frequently been shown to be involved in the representation and processing of numerical magnitude (Dehaene et al., 2003). The widely accepted role of the IPS in processing numerical magnitude, in concert with evidence that numerical magnitude representations can, under certain experimental conditions, be found to be automatically activated (Henik and Tzelgov, 1982; Rubinsten et al., 2002), might prompt the expectation that even the passive perception of Arabic digits would elicit preferential activation in the IPS. However, the current results do not reveal any IPS activation in favour of digits versus other symbols. This lack of automatic IPS activation is, however, supported by recent behavioural evidence suggesting that Arabic digits do not automatically activate numerical magnitude representations during a numerical same/different task (Cohen, 2009) and a parity judgement task (Naparstek and Henik, 2010).

To confirm the anatomical distinction between the AG region reported in the present study and the IPS, we calculated the Euclidian distance between the dorsal and ventral left AG regions reported in the current study and left IPS and left AG regions reported in a meta-analysis of neuroimaging studies of number processing (Dehaene et al., 2003). The results of these comparisons are listed in Table 1. The results indicate that the currently reported left AG regions are clearly distinct from the IPS region as defined in a meta-analysis of the functional neuroanatomy underlying number processing.

It should be noted that previous studies (Naccache and Dehaene, 2001) have demonstrated that subliminally presented digits can influence parietal activation in numerical priming tasks. It appears, therefore, that subliminally presented digits can activate semantic

Table 1
Beta Weights for each predictor at the 500 ms presentation duration in the left dorsal and ventral AG regions plus Euclidian distances between the ventral and dorsal AG regions reported in the current study and the IPS and AG regions reported in the Dehaene et al.'s (2003) meta-analysis of neuroimaging studies of numerical cognition.

		Left ventral Angular gyrus	Left dorsal Angular gyrus
Beta Weights	Digits	2.169	3.317
	Letters	0.296	2.153
	Scrambled digits	0.281	0.839
	Scrambled letters	0.273	0.06
	Euclidian distance from left IPS (mm) (Dehaene et al., 2003)	22.23	18.17
	Euclidian distance from left AG (mm) (Dehaene et al., 2003)	9.49	7.48

number representations, presumably housed in the IPS (Dehaene et al., 2003). In the case of the subliminal priming work, however, participants were engaged in magnitude comparison tasks, and such top-down task related processing may impact the neural processing of numerical stimuli (Peelen et al., 2009). The present findings suggest that when no explicit attention is being directed to Arabic digits, numerical magnitude processing mechanisms in the IPS may not be invariably activated.

The present findings raise the question of what role the left AG plays in Arabic digit processing, and in numerical cognition more generally. A growing body of data suggests an important role for the left AG in symbolic numerical processing and calculation in particular. Damage to this region impairs calculation ability (Gerstmann, 1940), and activation in this region has been associated with arithmetic fact retrieval (Delazer et al., 2003, 2005; Grabner et al., 2009a, 2009b) and exact versus approximate calculation (Dehaene et al., 1999; Venkatraman et al., 2006). However, the left AG is also associated with an extensive literature in the reading domain, which has led several researchers to suggest that the role of the AG in arithmetic lies in the linguistic processing demands of verbally mediated numerical processing, such as retrieval of arithmetic facts versus subtraction (for a review see Dehaene et al., 2003), or phonological processing (e.g. Delazer et al., 2003; Simon et al., 2002).

Thus, it could be suggested that the current finding of activation of the left AG during the viewing of Arabic digits reflects phonological processes, such as sub-vocal naming, rather than any form of category specific semantic processing. However, it is unlikely that the digit-related activation of the left AG in the present study reflects phonological processing given that digits were presented as frequently as letters, and there is no reason why digits should be sub-vocally named any more than letters.

An alternative interpretation for the current left AG activation can be drawn from recent neuroanatomical models of language processing suggesting that, rather than phonological processing, the left AG is instrumental in the domain general processing of semantically weighted stimuli (Ben Shalom and Poeppel, 2008; Mechelli et al., 2007; Price, 2000; Vigneau et al., 2006). Recent work in the field of numerical cognition suggests that the specific role of the AG in semantic processing may be related to processing the mappings between visual symbols and their semantic referents (Grabner et al., 2007; Holloway et al., 2010) or in other words, identifying Arabic digits as visual symbols of semantic information. Consistent with this interpretation, Seghier et al. (2010) have recently demonstrated three functional subdivisions of the left AG: 1. a dorsal section shown to be activated above fixation for all stimuli, 2. a medial region that was deactivated relative to fixation, and 3. a ventral region that was activated above fixation for semantic matching only. The authors suggest that while the dorsal AG is involved in searching for semantic representation in all visual stimuli, the ventral AG subdivision reflects a later stage of conceptual identification. These functional subdivisions represent an interesting framework by which to interpret the results of the current study. Conjunction analyses testing for brain regions which were more responsive to familiar symbols than novel symbols (i.e. digits and letters > scrambled digits and scrambled letters) revealed a dorsal left AG region proximal to the dAG region reported by Seghier et al. We suggest that the visually familiar Arabic digits and letters activate the dAG region suggested by Seghier et al. to be involved in "searching for semantics in all visual stimuli" (pp 16815).

Conjunction analyses testing for Digit specific activations revealed a ventral AG region at the long presentation duration (500 ms). We contend that this reflects activation of the vAG region proposed by Seghier et al. to be involved in the "conceptual identification from visual inputs" (pp 16815). We suggest that Arabic digits, more than single letters, engage this domain general semantic classification mechanism because they carry a richer semantic content than single letters do. In fact, it is difficult to think of any set of single symbols (rather than strings of symbols, such as words) which carry as much semantic information as single digits. Thus, while we do not suggest that the vAG represents a VNFA, we do suggest that of simple visual symbols, Arabic digits are very well suited to tap this region's hypothesised mechanistic properties due to their high level of familiarity and their rich semantic content. This framework would explain why, in the current study, the left AG does not show digit specific activation when short presentation times preclude conceptual identification, and why at longer presentation durations, it is active specifically for digits, which carry richer semantic content than single letters or scrambled digits.

In most reports of the involvement of the angular gyrus in numerical processing, relative states of deactivation of this brain region have been observed (Rickard et al., 2000; Zago et al., 2001). Often relative states of deactivation of the AG are interpreted as reflecting differential degrees to which the so-called 'default-mode network' (DMN) is suppressed during ongoing task demands (Raichle et al., 2001). The AG represents one of the nodes of this DMN and, therefore, legitimate questions have been raised concerning the extent to which this region's role during numerical and arithmetic processing is reflective of domain-specific processes (Wu et al., 2009). In the present study, however, the activation of the left AG was above baseline for all conditions, suggesting that the current activations in the AG do not reflect activity in the DMN (see Table 1).

The results of the present study do not reveal any brain regions which exhibit preferential activation for letters versus other symbol types. Although such letter specific activations were not explicitly hypothesised, since the theoretical motivation of this study was to explore the processing of digits in the brain with letters serving as a control condition, the lack of any letter preferential region was surprising given the extant literature showing activation in response to letters versus other symbols, in particular in the left fusiform gyrus (e.g. Flowers et al., 2004; Longcamp et al., 2003; James et al., 2005). The reasons for the lack of letter specific activations in the current study are unclear. However, previous studies which observed preferential brain activation during letter processing in the ventral visual stream, even those containing passive viewing conditions (e.g. Longcamp et al., 2003), included at least one active letter processing condition. It is possible that the inclusion of such active processing conditions created an implicit saliency for letter stimuli, and thereby affected neural responses in the passive conditions. However, this is a purely speculative suggestion, and empirical investigation would be required to substantiate it.

Conclusions

In summary, the present results show that even in the absence of top-down task demands, at longer presentation durations, passive viewing of Arabic digits was associated with activation of the left ventral AG, possibly reflecting the activation of a domain general semantic system involved in the conceptual identification of digits as semantically meaningful visual symbols (Seghier et al., 2010). Furthermore, familiar symbols (i.e. digits and letters) activated a region of in the left dorsal AG more than unfamiliar symbols (i.e. scrambled digits and scrambled letters). These findings suggests that different parts of the left AG are involved, as predicted by Seghier et al., 2010, in different levels of symbolic processing. Digit specific activation was not observed in the IPS, however, suggesting that some measure of cognitive focus on number identity or magnitude may be necessary for the activation of magnitude-related processing in the IPS. Thus, while the IPS is involved in the representation and manipulation of semantic quantity information carried by digits, the left ventral AG appears to be crucial for the conceptual identification of digits as semantically-weighted symbols. The left dorsal AG, on the other hand, appears to play a more general role in the perception of familiar symbols.

In view of the above, the present findings do not support the existence of a 'visual number form area' located in the ventral visual stream, thus speaking against the localization prediction of the 'visual number code' hypothesis of the Triple Code Model (Dehaene and Cohen, 1995). Instead, these findings strengthen the notion that the AG plays a critical role in symbolic number processing, and suggest that this role is of a semantic, not phonological nature. Since Arabic digits are culturally-mediated representations of numerical magnitude and order, future studies should investigate how, over the course of learning and development, the brain comes to fluently identify them as semantically meaningful symbols, and whether this process is compromised in individuals suffering from deficits in the ability to use digits to compare magnitudes and transform them in the process of calculation.

Acknowledgments

This research was supported by funding from Canadian Institutes of Health Research (CIHR) Operating Grant and Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to DA, and Ontario Ministry of Research and Innovation (OMRI) Postdoctoral Fellowship to GRP. Additionally we would like to thank Marty Rotenberg for his assistance in creating the stimuli.

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