Double Dissociation of Format-Dependent and Number-Specific Neurons in Human Parietal Cortex

Roi Cohen Kadosh\(^1\), Neil Muggleton\(^2\), Juha Silvanto\(^3\) and Vincent Walsh\(^2\)

\(^1\)Department of Experimental Psychology, University of Oxford, Oxford OX1 3UD, UK, \(^2\)Institute of Cognitive Neuroscience, University College London, London, UK and \(^3\)Brain Research Unit, Low Temperature Laboratory, Helsinki University of Technology, Finland

Address correspondence to Roi Cohen Kadosh. Email: roi.cohenkadosh@psy.ox.ac.uk.

Based on neuroimaging methods, it is a commonly held view that numerical representation in the human parietal lobes is format independent. We used a transcranial magnetic stimulation adaptation paradigm to examine the existence of functionally segregated overlapping populations of neurons for different numerical formats and to reveal how numerical information is encoded and represented. Based on 2 experiments, we found that right parietal lobe stimulation showed a dissociation between digits and verbal numbers, whereas the left parietal lobe showed a double dissociation between the different numerical formats. Further analysis and modeling also excluded pre- or postrepresentational components as the source of the current effects. These results demonstrate that both parietal lobes are equipped with format-dependent neurons that encode quantity.

Keywords: brain stimulation, neuronal specialization, numerical cognition, parietal lobes, representation

Introduction

The question of how we represent numbers, the basic component for more sophisticated numerical and arithmetical skills, is a matter of central concern for researchers from various disciplines such as neuroscience, psychology, philosophy, education, linguistics, and anthropology (Wiese 2003; Gordon 2004; Cohen Kadosh and Walsh 2009; Nieder and Dehaene, 2009).

Numbers can come in many forms; we can represent the same quantity, as a word (ONE), a digit (1), in Roman numerals (I), nonsymbolically as on a dice (\(\bullet\)), with our fingers, in a temporal series (e.g., a drum beat) or with other words (eins, uno) or symbols with agreed meanings (\(\downarrow\)) that carry semantic and numerical meaning. The question of how we represent numbers and whether there is a unitary cognitive and neuronal basis for all forms of numerical representation is therefore an important problem. In this paper, we examined the commonly held view that numbers are represented in an abstract fashion in the intraparietal sulcus (Dehaene et al. 1998; Eger et al. 2003; Cohen Kadosh and Walsh 2009; Nieder and Dehaene, 2009), a core area for numerical representation. This is a critical testing ground for models of numerical cognition (Verguts and Fias 2004), education (Ansari 2008), and remediation from dyscalculia (Wilson et al. 2006; von Aster and Shalev 2007).

Previous studies have used functional magnetic resonance imaging (fMRI) to examine the numerical representation for numbers as a function of modality or notation in the human intraparietal sulcus (IPS) (Eger et al. 2003; Cohen Kadosh, Cohen Kadosh, Kaas, et al. 2007; Piazza et al. 2007; Jacob and Nieder 2009; Cantlon et al. 2009). In the current study, we combined transcranial magnetic stimulation (TMS) with an adaptation paradigm (TMSA) (Silvanto et al. 2008). This combination enables improved functional resolution by differential stimulation of distinct but spatially overlapping neural populations within a stimulated region (Silvanto et al. 2008).

The paradigm is based on findings that the effects of TMS are determined by the initial neural activation state, with attributes encoded by the less active/excitable neural populations within the stimulated region being more susceptible to the effects of TMS. Thus, by using adaptation to manipulate neural activation states prior to the application of TMS, one can control which neural populations are preferentially activated by TMS (Silvanto et al. 2008). For example, following color adaptation, it was found that phosphenes induced from the early visual cortex selectively took on the color qualities of the adapting stimulus (Silvanto et al. 2007). This behavioral facilitation of the adapted neural populations by TMS suggests that, at the behavioral level, the effects of TMS are akin to microstimulation of the adapted neural populations (Silvanto and Muggleton 2008a).

This state dependency can be used to reveal receptive field properties of the stimulated region: if TMS applied over a given area facilitates the detection of the adapted attribute, this indicates that neurons in that area were adapted by and, thus, to some degree tuned to the adapting stimulus.

By using TMSA, we tested whether, in the human IPS, number-sensitive neurons code numbers in an abstract, that is, format-independent fashion (Dehaene et al. 1998) or rather in a format-dependent fashion (Cohen Kadosh and Walsh 2009; Fig. 1). Moreover, single-cell neurophysiology studies in monkeys have revealed neurons with preferences for specific nonsymbolic numbers (e.g., an array of 4 dots) in the IPS, and a decrease in sensitivity as the numerical proximity to this number decreases (Nieder et al. 2002; Diester and Nieder 2007). Therefore, we used the improved functional resolution of TMSA to examine whether in the human IPS there are neurons with greater preference for a specific symbolic numerical quantity, such as the digit 7, but not the number word “SEVEN.”

Materials and Methods

Subjects

Seven native English speakers (20-27 years, mean age = 22.71 years, standard deviation [SD] = 2.37, 6 females, all right handed) took part in Experiment 1 and 6 participants (20-28 years, mean age = 24.33 years, SD = 2.35, all females, all right handed) took part in Experiment 2. None reported any neurological illnesses or mathematical learning difficulties. Subjects received monetary compensation for their participation. The study was approved by the local ethics committee and all gave informed consent.
During the task, we delivered biphasic TMS pulses through a figure-of-eight coil and Magstim Super Rapid machine at 180, 280, and 380 ms after trial onset (Fig. 1). This timing was chosen for 2 reasons. First, the most effective timing to deliver a disruptive TMS pulse has been suggested to occur before the peak of the event-related potential (ERP) component that relates to the mental operation of interest (Walsh and Cowey 2000; Cohen Kadosh, Cohen Kadosh, Kaas, et al. 2007). Therefore, the timing of the TMS pulses (180, 280, and 380 ms after stimulus presentation) were chosen based on previous ERP studies that found modulation of the P2p and P3b during numerical processing (Dehaene 1996; Turconi et al. 2004; Cohen Kadosh, Cohen Kadosh, Linden, et al. 2007; Libertus et al. 2007; Szucs et al. 2007). Second, this timing makes it unlikely that we would induce a perceptually related effect (cf., timings of parietal cortex TMS on perception [Ashbridge et al. 1997; Kalla et al. 2008]).

Prior to the experiment, a T1-weighted structural image (1 mm3 resolution) was acquired to allow neuronavigation of the TMS coil to the coordinates of interest in each individual IPS by using Brainstims software (Magstim, UK). TMS pulses were delivered at 60% of maximum stimulator output (maximum stimulator output equals ~2 Tesla). The site of IPS stimulation was localized based on coordinates from a meta-analysis of fMRI studies of numerical representation (Cohen Kadosh et al. 2008). To increase sensitivity and to compensate for the large individual difference in the IPS anatomy (Zilles et al. 2003; Sack et al. 2009) when the foci fell on a gyrus, the foci were moved to the nearest portion of the IPS. The vertex was localized according to the EGG 10-20 system.

**Stimuli and Procedure**

To adapt number-tuned neurons, the digit 7 (Experiment 1) or the verbal number “SEVEN” or “TWO” ( Experiment 2) was presented to subjects at different locations, fonts, and sizes for 45.5 s on a monitor. In the adaptation phase, the number being adapted to appeared for 300 ms with 350 ms interstimulus interval (ISI). The number was presented 70 times during each adaptation period (Fig. 1A).

Following this adaptation phase, the subjects performed 12 trials of a physical same-different task on pairs of digits or verbal numbers that contained the numbers 1, 2, 7, and 8 (Van Opstal et al. 2008). The numbers 1, 2, 7, and 8 were selected as they are well controlled for differences in perceptual similarity (Verguts and Van Opstal 2005). In this task, a fixation appeared for 200 ms, followed by a blank screen for 300 ms. The stimulus then appeared for 900 ms. The ISI was 1800 ms. We used a physical same-different task as it provides an examination of the default mental representation, independent of subjects’ strategies (Tzelgov and Ganor-Stern 2004; Fischer and Rottmann 2005; Shuki and Fischer 2008; Cohen Kadosh and Walsh 2009). All stimuli appeared in white on a black background.

Ten blocks of adaptation-task pairs were presented for each stimulation site (left IPS, right IPS, vertex). In order to estimate the effect of the TMSA, the same procedure was applied without TMS although the subjects were adapted to the # symbol in the place of numbers (baseline task).

The order of the session (left TMS, right TMS, vertex, and baseline), as well as the buttons used for same and different decisions (the buttons P and Q on QWERTY keyboard), was counterbalanced across subjects.

**TMS Apparatus and Stimulation Parameters**

During the task, we delivered biphasic TMS pulses through a figure-of-eight coil and Magstim Super Rapid machine at 180, 280, and 380 ms after trial onset (Fig. 1). This timing was chosen for 2 reasons. First, the most effective timing to deliver a disruptive TMS pulse has been suggested to occur before the peak of the event-related potential (ERP) component that relates to the mental operation of interest (Walsh and Cowey 2000; Cohen Kadosh, Cohen Kadosh, Kaas, et al. 2007). Therefore, the timing of the TMS pulses (180, 280, and 380 ms after stimulus presentation) were chosen based on previous ERP studies that found modulation of the P2p and P3b during numerical processing (Dehaene 1996; Turconi et al. 2004; Cohen Kadosh, Cohen Kadosh, Linden, et al. 2007; Libertus et al. 2007; Szucs et al. 2007). Second, this timing makes it unlikely that we would induce a perceptually related effect (cf., timings of parietal cortex TMS on perception [Ashbridge et al. 1997; Kalla et al. 2008]).
numbers in the left IPS, we conducted a second experiment, in which the subjects were adapted to verbal numbers rather than digits. The analysis for Experiment 2 followed the same steps as for Experiment 1. The adaptation effect was not significant for RT (all \( P > 0.2 \)). However, the effects were clearly observed for errors; as numerical distance increased errors increased. Following left IPS TMS, digits significantly differed from verbal numbers and zero (verbal numbers vs. digits \( t(5) = 2.9, P = 0.01 \); verbal numbers vs. zero, \( t(5) = 3.27, P = 0.01 \); digits vs. zero, \( t(5) = -1.17, P = 0.3 \)). This effect was consistent across the adapted values, and all the subjects showed the same trend. In the right IPS, vertex numerical formats did not differ significantly from each other (all \( P > 0.4 \) ) and did not differ from zero (all \( P > 0.2 \) ) (Fig. 3).

TMSA affected different indices of information processing. In Experiment 1, the effect was observed for RT, whereas in Experiment 2 it was present for accuracy. These results can be caused by differences in the required amount of accumulated evidence before a response is activated (Pachella 1974). Fast responses will lead to error rate effects, whereas slow responses will lead to RT effects (Pachella 1974). To assess if and how these results related to one another, we used a diffusion model (Wagenmakers et al. 2007). This approach is very similar to classical signal detection theory in its aim, scope, and method. Based on accuracy, mean RT, and RT variance, the model yields 3 different parameters: 1) drift rate, which combines respond speed and response accuracy to quantify subject ability and can be interpreted as an index for the signal-to-noise ratio (the equivalent of \( d' \) prime in the signal detection theory framework) of the information processing system (Wagenmakers et al. 2007), 2) boundary separation, which indicates response conserva-
tiveness (the equivalent of beta in the signal detection theory framework), and 3) mean of nondecision time. Thus, this model allows one to examine whether the results in Experiments 1 and 2 were derived from a common mechanism that affected the signal-to-noise ratio of the numerical representation (drift rate) but not other non-numerical processes (boundary separation or nondecision time). The results from the diffusion model supported this view. In Experiment 1, TMSA to the left IPS, but also the right IPS, led to increased drift rate (a better signal-to-noise ratio) as numerical distance from the adapted digit decreased. This beta value differed from the beta value for verbal numbers and from zero (all \( P < 0.03 \)). In Experiment 2, TMSA to the left IPS revealed a beta value between drift rate and numerical distance for verbal numbers. This beta value differed from zero and from digits (all \( P < 0.005 \)). Neither boundary separation nor mean nondecision time was modulated by the numerical distance in any of the experiments (all \( P > 0.1 \)).

The double dissociation between Experiment 1 (TMSA to the left IPS affect digits but not verbal numbers) and Experiment 2 (TMSA to the left IPS affect verbal numbers but not digits) was statistically confirmed by subjecting the drift rate data from the left IPS in both experiments to a 2-way analysis of variance with the format (digits, verbal numbers) as the within-subject factor and Experiment (Experiment 1, Experiment 2) as the between-subject factor. The only significant effect was the 2-way interaction between format and experiment, \( F(1,11) = 17.23, P = 0.001 \), thus, confirming a double dissociation between the different numerical formats in the left IPS.

We also analyzed the results without subtracting the RTs and accuracy for each pair in the TMSA conditions from its
Discussion

TMSA selectively affected information processing of numbers in a format-specific manner in the IPS, an area that is believed to hold the putative abstract representation (Dehaene et al. 1998; Eger et al. 2003; Cohen Kadosh, Cohen Kadosh, Kaas, et al. 2007; Piazza et al. 2007; Cohen Kadosh and Walsh 2009; Cantlon et al. 2009). This was reflected by a dissociation between digit and verbal numbers in the right IPS and a double dissociation between the different formats in the left IPS. These effects specifically affected the mental number line (Restle 1970) when neurons were adapted for numerical value, processing of numerical information was made easier by TMS, the closer the numbers were to the adapted number. However, this effect was specific for the format in which it was adapted.

The current results therefore support the idea that numerical representation is notation dependent and the computation of the numerical information is not necessarily abstract (Cohen Kadosh and Walsh 2009). The current study also shows that both the left and the right IPS are equipped with notation-dependent numerical representations.

Results from computational models, neuroimaging in adults and children, and neuropsychological studies suggested that nonverbal numerical abilities served as the foundation for later, symbolic numerical representation, by mapping spoken and written numerals into the nonverbal core representation (Dehaene 1997; Butterworth 1999; Cantlon et al. 2006; Piazza et al. 2007). According to this idea, the effect of stimulation on symbolic notations, such as digits and verbal numbers in this study, should have yielded similar results independent of the adapted notation. In contrast, the results suggested that numerical information is accessible in a notation-dependent fashion.

Another theory that does not hold in the face of the current results is that digits are mapped into verbal numerals (Carey 2004). If that were the case, again adaptation for digits following TMS to the left IPS should have yielded a similar effect also for verbal numbers as digits in the adaptation stage was mapped into verbal numerals. From the same reason, in Experiment 2, adaptation for verbal numbers following TMS to the left IPS should have led to similar effects for digits. The double dissociation seen poses a challenge to this theory. Although this theory might hold for children, it seems that it does not receive support from our study with adults.

Although the current results demonstrate the specificity of neuronal substrates for numerical representation, this does not mean that the affected neuronal substrates in our experiments are active solely for digits or verbal numbers, and no other function, as they may be involved also in other parietal lobe functions (see Posner [2003] for a similar idea on the usage of the term "specific" in cognitive neuroscience). Indeed, previous single-cell neurophysiology showed that even if neurons are tuned to a specific quantity, they are still sensitive to other features such as motion direction (Nieder et al. 2006) or other magnitudes such as space and time (Walsh 2003a, 2003b; Bueti and Walsh 2009).

In the current study, we initially found that different dependent variables are affected in different experiments. Namely, in Experiment 1, the effect was observed in RT, whereas in Experiment 2 the effect was observed in error rates. Although we stressed both accuracy and reaction time to our subjects, it is possible that different subjects might adopt different criterion for responding. Pachella (1974) suggested that if one adopt a conservative criterion for responding, then any effect will be observed mainly in RT, whereas if one adopts a more liberal criterion for response the effect will be present mainly in error rates. For this reason, in the current paper, we used diffusion modeling. The important point, however, is that diffusion modeling not only confirmed the findings in Experiments 1 and 2, but by taking both RT and error rates into account, we were able to show that the right IPS was also affected by the TMSA in Experiment 1.

In the current study, we used a combination of meta-analysis coordinates and anatomical MRI to localize the site of stimulation (see Materials and Methods). It is likely that a localization based on functional MRI would have been superior, most likely by reducing the variance between subjects, as was shown also in the case of parietal lobe stimulation and numerical cognition (Sack et al. 2009). However, in the current study, we found a differential effect both in Experiment 1 and Experiment 2, including a double dissociation, which indicates that our localization method was sufficient with the amount of subjects.

The current study extends the feasibility of TMSA paradigms in examining neuronal specialization from perceptual processes (Silvanto et al. 2008) to high-level cognitive processes. The results in Experiment 2, showing that the verbal numbers modulate the left IPS only, are in line with a previous fMRI results (Cohen Kadosh, Cohen Kadosh, Kaas, et al. 2007). However, the important findings are the double dissociation in the left IPS. Several previous fMRI studies have failed to find specific numerical representation in the IPS (Eger et al. 2003; Cohen Kadosh, Cohen Kadosh, Kaas, et al. 2007; Piazza et al. 2007; Jacob and Nieder 2009; Cantlon et al. 2009). It is noteworthy that recent evidence has demonstrated that fMRI can show regional blood oxygenation level-dependent change in the absence of activated neurons (Sirotin and Das 2009), thus obscuring the detection of functional specialization in the brain. There are also other methodological reasons for some of these absence of difference (see Cohen and Walsh 2009). In contrast, TMSA has clearly been shown to be capable of segregating functionally distinct but anatomically overlapping neuronal populations (Silvanto et al. 2007; Silvanto et al. 2008; Silvanto and Muggleton 2008b; Cattaneo et al. 2009) and, thus, reveal format-dependent numerical representations in both IPS. Thus, TMSA offers an attractive method to uncover neuronal specialization in the human brain in addition to providing causal inference about the neuronal populations that are involved in cognitive and perceptual domains (Price and Friston 2002; Walsh and Pascual-Leone 2003; Allen et al. 2007).

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.
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