

A theory of magnitude: common cortical metrics of time, space and quantity

Vincent Walsh

Institute of Cognitive Neuroscience and Dept of Psychology, University College London, 17 Queen Square, London WC1N 3AR, UK

Research into the perception of space, time and quantity has generated three separate literatures. That number can be represented spatially is, of course, well accepted and forms a basis for research into spatial aspects of numerical processing. Links between number and time or between space and time, on the other hand, are rarely discussed and the shared properties of all three systems have not been considered. I propose here that time, space and quantity are part of a generalized magnitude system. I outline A Theory Of Magnitude (ATOM) as a conceptually new framework within which to re-interpret the cortical processing of these elements of the environment.

It is the purpose of this paper to bring together, as A Theory Of Magnitude (ATOM), disparate literatures on time, space and number, and to show similarities between these three domains that are indicative of common processing mechanisms, rooted in our need for information about the spatial and temporal structure of the external world. Some of the proposals follow on from work by Gallistel and Gelman who argued that 'countable and uncountable quantity (numerosity and amount, duration, etc.) should be represented with the same kind of symbols (mental magnitudes), because there are many cases in which the two kinds of quantity must be combined...to determine behaviourally important decision variables.' (Ref. [1], p.62; see also [2]). My starting point is complete agreement with their statement, although I am more concerned with proximal sensorimotor consequences of processing magnitude. In the context of this article, then, the 'important decision variables' are short 'action-time' durations in the millisecond-to-seconds range, spatial information used for action, and co-ordinate transformations for action or predictions about the immediate sensorimotor consequences of action [3]. This position addresses the question of why the parietal cortex, of paramount importance here, should contain subregions that are important for reaching, grasping, space, quantity and time. Cajal noted that 'All natural arrangements, however capricious they may seem, have a function' ([4], p.119), and here I argue that the arrangement of the inferior parietal cortex reflects the common need for space, time and quantity information to be used in the sensorimotor transformations that are the main goal of these areas of cortex [5,6].

Hints at common mechanisms

Connexions between time and number perception have been noted since at least 1890 [7] and are echoed in other parallels between time and space, or space and quantity. Similar behavioural functions in estimating temporal duration and numerical quantity have also been observed in non-human species. Church and Meck [8] for example, tested rats on their ability to discriminate small quantities (between two and eight tones) and short durations (between two and eight seconds). On both duration and number tasks, the rats showed similar generalization behaviour indicating that they estimated four (tones or seconds) to be halfway between two (tones, seconds) and eight [2]. Evidence linking time and space can also be found in the neurological literature. Critchley, reviewing neuropsychological studies [9], noted the overlap between time, space, size and number deficits following parietal cortex damage, after which 'Pure temporal disorientation...occurring independently of spatial disorders, is a rarer phenomenon, for more often, the two are combined' (p.352).

Links between space and number have also been recognized in developmental psychology, but as Bryant and Squire [10] comment, when thinking of number and space, psychologists have usually treated the link '...in a negative way. Space, for them, is part of the problem in children's mathematics, not part of the solution' (p.175). In other words, the tendency has been to emphasize the differences between these sources of information rather than informative similarities that limit the cognitive strategies one might be able to use in spatial behaviour and later in mathematics and reasoning.

The missing links

The above hints at correspondences suggest a common basis for the three particles of ATOM: space, time and quantity (see also Box 1). These suggestions have rarely been pursued and certainly not to the extent that the spatial representation of number has stimulated research (e.g. [11]). The contention of ATOM is that an understanding of the common basis of these three systems requires a description of what they share in terms of

Box 1. Two schemas for magnitude processing

The generalized magnitude system applies to those dimensions that were described as 'prothetic' by Steven [61], meaning dimensions that can be experienced as 'more than' or 'less than'. Quantity, space and time are all prothetic dimensions – one speaks of more/longer time, more objects and larger/smaller spaces etc. The possibility that the link between space and quantity is action has been emphasized and demonstrated recently [62,63]. As Figure I illustrates, the information about different magnitudes could be analysed separately and compared or integrated according to metrics unique to each comparison (a). Alternatively, the three magnitudes may be computed according to a common metric (b). The scheme in (b) represents the view proposed here.

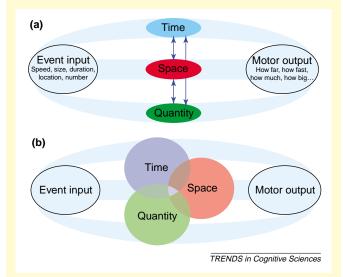


Figure I. Comparison of two schemas for processing time, space and quantity. The three magnitudes could be analysed separately and compared according to their own individual metrics (a), or, in a generalized magnitude system as suggested here, computed according to a common metric (b).

information-processing resources and behavioural goals. Thus, I will argue that:

- space, quantity and time are linked by a common metric for action.
- time and quantity estimation operate on similar and partly shared accumulation principles [1,2].
- the inferior parietal cortex is the locus of a common magnitude system.
- the apparent specializations for time, space and quantity develop from a single magnitude system operating from birth.
- hemispheric asymmetries in time, space and number have emerged as a consequence of the fact that advanced use of number for exact calculation requires access to language in a way that spatiotemporal co-ordinate maps do not.

Some behavioural evidence for a common magnitude system

Space and number

The case for a connexion between space and number has been made adequately in many places (e.g. [11]). The strongest behavioural evidence comes from the distance effect – the further apart two numbers are, the easier one

finds it to compare them. This led to the proposal of a mental 'number line' along which subjects make comparisons between the locations of numbers. The effect occurs even when the distance between numbers is constant, but the numbers vary in magnitude, and also when dots, words or mixtures of words and digits are presented rather than numbers alone. The distance effect is also seen in non-human species [2,11].

Time and quantity

The evidence linking time and number rests on dual-task experiments, many of which report that a secondary task impairs time estimation [12]. Time tasks are easily disrupted but are not themselves good disrupters, but one important exception provides evidence that time and number share resources [13]. Subjects were tested in three dual-task conditions: time and rotor tracking; time and visual detection; time and mental arithmetic. All secondary tasks disrupted performance on the temporal task, but only mental arithmetic was impaired by the temporal task. The explanation given by the author of that study is that mental arithmetic shares executive functions with time estimation. My alternative view is that it is unnecessary to invoke executive functions and that time and number draw upon common magnitude mechanisms, whereas the other two tasks make predominantly visual demands on the subject.

Time and space

Time and space are seldom considered together, but what little evidence exists suggests that spatial factors do affect the perception of time and other magnitudes. De Long [14], for example, asked subjects to carry out tasks in environments built to 1/6, 1/12 or 1/24 of actual size and to stop when thirty minutes had passed. The ratio of time passed to time estimated scaled according to environmental scale (see also [15]).

Neuropsychological and brain imaging evidence for a common magnitude system

Several fMRI [16], EEG [17] and neuropsychological [18] studies show that the right inferior parietal cortex (rIPC), is important for time perception. The occurrence of pure temporal deficits may be less salient (and certainly less sought) than spatial and visuomotor deficits following parietal lesions but, as Critchley noted [9], spatial and temporal deficits often coincide. Some recent neuropsychological work has returned to this co-occurence of spatial and temporal deficits [19]. A patient with left spatial neglect tested on short-duration estimation tasks (300 vs. 700 ms) consistently overestimated durations of stimuli presented in the neglected space and underestimated durations of stimuli presented in the good field.

The parietal cortex is activated in many studies that investigate aspects of temporal, spatial and number processes [16,20-23]. Spatial and temporal stimuli reliably activate the right inferior parietal cortex whereas number tasks may activate the parietal lobes bilaterally. Right parietal activation in number tasks is usually associated with comparison or estimation, rather than exact calculation, which relies on language [24,25]. Not all

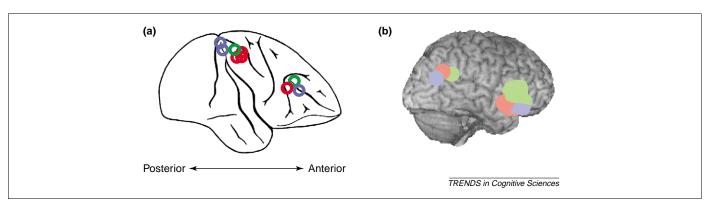


Figure 1. Comparative anatomy of anterior and posterior magnitude systems. There is evidence of what appear to be homologous magnitude systems in humans and monkeys (note that the two brains are not shown to scale). The posterior system, used for estimation of 'how much, how many, how far, how long, and how fast' for action is a feature of the posterior parietal cortex. (a) Responses on the basis of spatial (red circles; [42]), numerical (green circle; [39]) and temporal information (blue circles, [44,45]) have been recorded in macaque monkeys. (b) The homologous regions in humans: sites where the application of transcranial magnetic stimulation interferes with spatial (red circle; [33]), quantitative (green; [36]) and temporal (blue; [7]) processing. The anterior system, important for complex calculation, memory and longer term planning also contains neurons activated in the macaque by spatial (red circle; [43]), numerical (green circle; [40]) and temporal (blue circle; [44]) stimuli. In humans, functional imaging and neuropsychological studies implicate homologous and overlapping areas in the prefrontal cortex (red, green and blue indicate spatial, numerical and temporal processes, respectively). The view in (b) is of the right hemisphere of the human brain, which is accurate for the posterior system, but the anterior system is in fact dominated by left hemisphere processes [60].

studies have obtained a time-related activation of the right parietal cortex. This seems to be the case when other magnitude judgments (space, number, intensity) are used as control tasks, effectively subtracting out the right parietal time-related activity. One study that did obtain a time-related activation in rPPC, when a non-magnitude control was used, also showed that this activation disappeared when a magnitude control (intensity discrimination) was used [26]. Other studies have not obtained time-unique, right parietal activations when intensity discrimination is used as a control [27-29]. Tracy et al. [30] used mental arithmetic as a control and also did not see a right hemisphere activation that discriminated between number and time processing [30]. Others find a laterality difference between space and time but only when temporal and motor preparation factors are confounded [31]. Comparison of blood flow changes in temporal duration estimation and sound intensity discrimination shows 'a right hemispheric fronto-parietal network very similar to the one...observed for intensity discrimination' ([32], p.1956). In the context of ATOM it would be consistent to attribute this commonality to magnitude processing.

In addition to the overlapping brain regions associated with time, space and number in neuropsychological and brain imaging studies, several studies using transcranial magnetic stimulation (TMS) have shown that parietal cortex stimulation in human subjects can cause deficits in spatial tasks [33–35] and also in number comparison [36] and time discrimination [7]. Figure 1 compares some of the areas activated and disrupted with areas from which magnitude responses have been recorded in monkeys.

Hemispheric specialization

Cohen and Dehaene have suggested that the inferior parietal cortex in *both* hemispheres is essential for analogical quantity representation [25]. From the neuropsychological and brain activation findings discussed above it is clear that left IPC damage can selectively

disrupt number processes whereas right IPC is more critical for spatial and temporal processing. According to Dehaene [37], only the left hemisphere can use the verbal coding required in calculation. Therefore, a patient with left parietal damage might be able to make analogical number comparison, but this knowledge will be disconnected from left hemisphere language systems.

A similar question needs to be addressed with respect to time and space. Why is right hemisphere damage the dominant pathology and how do time and space become separately lateralized from number? The answer is analogous to the explanation for number and left hemisphere lesions. The use of time/space information and number information differ in their output: exact number processing requires verbal representations and output whereas time and space information are more important for co-ordinating action.

Taken together, then, evidence from the deficits following TMS or brain lesions, and activity in fMRI, PET and EEG studies consistently point to common mechanisms for space, time and quantity estimations in the right inferior parietal cortex of the human brain. If this is the case, there should be evidence of overlapping populations of magnitude neurons in the homologous regions of monkey cortex.

The neurophysiology of magnitude

Number selective neurons ('numerons') in non-human animals exist in the cat [38] and the monkey [39,40]. Sawamura et al. [39] recorded from the upper bank of the IPS and the superior parietal lobule in the macaque and reported neurons selective for numerical quantity (measured as a fixed number of movements). Similar neurons have been reported in the prefrontal cortex [40,41]. The locations of these numerons coincides with those that are spatially selective [42,43]. So space and quantity coincide in the monkey brain, but what of time?

Two non-human primate studies have addressed the cortical processing of duration [44,45]. Once *et al.* [44] trained monkeys to perform temporal discrimination tasks (longer vs. shorter duration) while being scanned using

PET. The two areas activated were dorsolateral prefrontal cortex (DLPFC) and the inferior parietal lobe – areas that have shown both number and spatial properties in single-unit studies. Once *et al.* also showed that bicuculline lesions of DLPFC impaired temporal discrimination, and suggested that DLPFC maintains the duration of the reference time whereas the parietal area 'may play a role in relaying information about the chronometric dimension of a stimulus'. The co-occurrence of space and time neurons has also been shown in a recent single-unit study in which neurons with spatial response fields show an association between spatial and temporal responses ([45], and see also [46]).

Thus, non-human primate studies show that two spatial processing areas contain neurons selective for numerical quantity and temporal duration. Once *et al.* concluded that 'temporal information in these regions may be coded in neurons with multiplex properties and/or in cell assemblies with overlapping connections in the same region'. Adding numerical quantity to this multiplex system follows from the findings of Nieder *et al.* [40] and Sawamura *et al.* [39], and is a prediction also made by Dehaene's group: 'an evolutionary precursor to number processing in primates, if it exists, might be found in the anterior part of the area LIP, the dorsal sections of 7a, 7b or the intermediate area PFG' ([20], p.484).

Having seen some evidence for phylogenetic precursors of the magnitude system, it is natural to look for ontogenetic pointers in the development of infant understanding of magnitudes.

One-bit babies?

In pursuing the possibility of a general magnitude system based around common action co-ordinates, one needs to speculate about the developmental origins of such a system. Piaget and Binet argued that children fail to discriminate between temporal and spatial order – that further in distance, in a child's mind, is equivalent to longer in time [47]. Perhaps the child is right. One might consider that an infant begins with a 'one bit' undifferentiated magnitude system, with which the infant responds motorically to changes in size, speed, distance and duration of external events, only learning to differentiate through interaction. As the child learns, it will do so according to the statistics of the environment [48], an environment in which the space, time, speed, size and quantity of events and objects are often highly correlated.

I cannot address in this article the interactions between the anterior and posterior magnitude systems but, as the number sense is built upon the magnitude system, and the magnitude representation appears to have a spatial basis, it is important to consider the extent to which the action-based magnitude system influences or even determines some features of the anterior system. As Bryant and Squires put it, 'There is good reason to pursue the strangely neglected possibility of a connection in children's development between their spatial and their mathematical understanding.' ([10], p.176). Given the utility of relational inferences on quantities and the power of a statistical picture of the physical world that would extract co-variance of time, space and quantity, it would perhaps

be as maladaptive for the infant brain *not* to use a common metric as it is difficult for an older child to unbind these three elements when learning mathematics. Gallistel and Gelman offered the argument 'that there is a non-verbal representation of numerosity by means of arithmetically processed noisy magnitudes in both non-verbal animals and human infants' ([1], p.62). I would suggest that statistical learning of associations between temporal and spatial features of the environment is the means by which this representation is learned.

The case for ATOM so far is based on the view that the main function, or at least the linking function, of the many capacities of the parietal cortex is the need to encode information about the magnitudes in the external world that are used in action. In other words, the parietal cortex transformations that are often assumed to compute 'where' in space, really answer the questions 'how far, how fast, how much, how long and how many' with respect to action. This view marks a departure from the view that the linking function of the parietal cortex is attention. Attention has too many incarnations, and explanations based on it too many degrees of freedom to be addressed in full here. However, it is worth looking at how attention has been used in at least one magnitude domain to illustrate its inadequacies.

Time to disengage from attention

In terms of ATOM, I want to suggest that attention is unlikely to add to the study of common mechanisms of magnitude and that some studies in which attention has been invoked as a post-hoc explanation of temporal processing may be reinterpreted with regard to common magnitude components in the tasks used. If one considers standard behavioural timing models, so far attention has been attributed to all possible levels of the temporal process: at the level of the pacemaker [12], the switch between the pacemaker and accumulator [49], the accumulator [50], the store or comparator and the planned time of movements [30]. Correspondingly, temporal attention mechanisms have been located in every brain region that has been associated with attention in general: the right and left parietal cortex [16,30], the right and left dorsolateral prefrontal cortex [51], the cingulate cortex [51] and the visual cortex [52].

It is an additional problem that attention models do not make a priori predictions about attention and time. Temporal processing deficits due to decreased attention have variously explained the lengthening [19] or shortening [50] of experiential time; attention is sometimes preferred for long intervals [53] and at other times for short intervals [54], and is said to be important because time demands sustained [51] or rapid switching of attention between a short or long interval [30]. There is also little differentiation about the precise role of attention: it can be the mediating influence - 'attention conditions time processing' ([51], p.482); or the mediated - 'the gate mediates the affect of attention' ([12], p.196); or attention can use time in the 'modulation of target-related neural activity' [54]. Finally, attentional explanations can also loosely refer to attention *to* time, refocusing attention in time or to temporal order [30,54,55].

Questions for Future Research

- How do an infant's perception and behaviour of the time, space and quantity interact?
- How do the key brain areas (PFC, PPC, basal ganglia, cerebellum) implicated in time, space and quantity processing interact?
- Is there a perception—action distinction for time as there is for space?
- Have we underestimated the co-occurrence of magnitude deficits in patients with damage to the brain areas involved in magnitude processing?
- Are there interference or priming effects between the magnitudes?
- Does the spatial numerical association of response codes generalize to other magnitudes?

The flexibility of attention is unrestrained: an equivalent span of explanatory freedom in the spatial domain would encompass everything from hyperacuity to a sense of place. Given the psychophysical elegance of models of time perception and timing behaviour [1,2,8,56–58], attention is too non-specific and malleable a parameter to add any light.

Conclusions and predictions

Atoms can be smashed of course, and some of the suggestions in this article will be revised or rejected as empirical data accumulate. Some strong predictions can be made from ATOM: the SNARC effect (spatial numerical association of response codes), in which small number judgments are associated with response codes in left space and large numbers with response codes in right space, should prove to be a SQUARC effect (spatial quantity association of response codes) in which any spatially or action-coded magnitude will yield a relationship between magnitude and space. Correspondingly, experiments in which responses are made to two or more magnitudes on successive trials should show cross-domain, withinmagnitude priming. It is also important to extend ATOM to considerations of how the parietal cortex interacts with other structures involved in temporal processing, particularly the cerebellum and the prefrontal cortex [57–59] (see also Questions for Future Research). Brain regions not considered essential to date might also prove to be important, especially those involved in other aspects of spatial processing (V3, V3a) and those with neurons responsive to motion (V5/MT).

Acknowledgements

V.W. is supported by The Royal Society. Some of the work reported here is supported by the Wellcome Trust, The Medical Research Council and The Dr Hadwen Research Trust. The author is grateful to Lauren Stewart for comments on previous drafts, to Andrew Bremner for references and to Fulvia Castelli for discussing the ideas from her forthcoming paper, which also addresses a common magnitude system. The author is also grateful to the anonymous reviewers and the editor for several important comments and suggestions.

References

- 1 Gallistell, R.C. and Gellman, R. (2000) Non-verbal numerical cognition: from reals to integers. *Trends Cogn. Sci.* 4, 59–65
- 2 Brannon, E.M. and Roitman, J.D. (2003) Nonverbal representations of time and number in animals and human infants. In *Functional and Neural Mechanisms of Interval Timing* (Meck, W.H., ed.), pp. 143–182, CRC Press
- 3 Rossetti, Y. and Pisella, L. (2002) Several 'vision for action' systems: a geode to dissociating and integrating dorsal and ventral functions. In *Attention & Performance XIX: Common Mechanisms in Perception and Action* (Prinz, W. and Hommel, B., eds), pp. 375–396, Oxford University Press
- 4 Cajal, S.R. (1898/1999) Advice for a Young Investigator (Transl. Swanson, N. and Swanson, L.W.), MIT Press
- 5 Freund, H.J. (2001) The parietal lobe as a sensorimotor interface: a perspective from clinical and neuroimaging data. *Neuroimage* 14, 142-146
- 6 Pisella, L. et al. (2000) An 'automatic pilot' for the hand in the human posterior parietal cortex: toward reinterpreting optic ataxia. Nat. Neurosci. 3, 729-736
- 7 Walsh, V. and Pasual-Leone, A. (2003) Transcranial Magnetic Stimulation: A Neurochronometrics of Mind, MIT Press
- 8 Church, R.M. and Meck, W.H. (1984) The numerical attribute of stimuli. In *Animal Cognition* (Roitblat, H.L., Beaver, T.G. and Terrace, H.S., eds), pp. 445–464, Erlbaum
- 9 Critchley, M. (1953) The Parietal Lobes, Hafner Press
- 10 Bryant, P. and Squire, S. (2001) Children's mathematics: lost and found in space. In *Spatial Schemas and Abstract Thought* (Gattis, M., ed.), pp. 175–201, MIT Press
- 11 Dehaene, S. et al. (1998) Abstract representations of numbers in the animal and human brain. Trends Neurosci. 21, 355–361
- 12 Casini, L. and Macar, F. (1997) Effects of attention manipulation on perceived duration and intensity in the visual modality. Mem. Cogn. 25, 812–818
- 13 Brown, S.W. (1997) Attentional resources in timing: interference effects in concurrent temporal and non-temporal working memory tasks. *Percept. Psychophys.* 59, 1118–1140
- 14 De Long, A.J. (1981) Phenomenological space-time: towards an experiential relativity. $Science~213,\,681-683$
- 15 Mitchell, C.T. and Davis, R. (1987) The perception of time in scale model environments. *Perception* 16, 5–16
- 16 Rao, S.M. et al. (2001) The evolution of brain activation during temporal processing. Nat. Neurosci. 4, 317–323
- 17 Mohl, W. and Pfurtscheller, G. (1991) The role of the right parietal region in a movement time estimation task. *Neuroreport* 2, 309–312
- 18 Harrington, D.L. and Haaland, K.Y. (1999) Neural underpinnings of temporal processing: a review of focal lesion, pharmacological and functional imaging research. Rev. Neurosci. 10, 91–116
- 19 Basso, G. et al. (1996) Time perception in a neglected space. Neuroreport 7, 2111–2114
- 20 Simon, O. et al. (2002) Topographical layout of hand, eye, calculation and language-related areas in the human parietal lobe. Neuron 33, 475–487
- 21 Piazza, M. et al. (2002) Are subitizing and counting implemented as separate or fucntionally overlapping processes? Neuroimage 15, 435–446
- 22 Dehaene, S. et al. (1999) Sources of mathematical thinking: behavioral and brain imaging evidence. Science 284, 970–974
- 23 Cochon, F. et al. (1999) Differential contributions of the left and right inferior parietal lobules to number processing. J. Cogn. Neurosci. 11, 617–630
- 24 Seymour, S.E. $et\ al.\ (1994)$ The disconnection syndrome: basic findings reaffirmed. $Brain\ 117,\ 105-115$
- 25 Cohen, L. and Dehaene, S. (1996) Cerebral networks for number processing: evidence from a case of posterior callosal lesion. Neurocase 2, 155-174
- 26 Maquet, P. et al. (1996) Brain activation induced by estimation of duration: a PET study. Neuroimage 3, 119–126
- 27 Pouthas, V. et al. (2000) ERPs and TEP analysis of time perception: spatial and temporal brain mapping during visual discrimination tasks. Hum. Brain Mapp. 10, 49-60
- 28 Macar, F. et al. (1999) The supplementary motor area in motor and

- sensory timing: evidence from slow brain potential changes. Exp. $Brain\ Res.\ 125,\ 271-280$
- 29 Fias, W. et al. (2003) Parietal representation of symbolic and non-symbolic magnitude. J. Cogn. Neurosci. 15, 47-56
- 30 Tracy, J.I. et al. (2000) Functional localization of a 'time keeper' function separate from attentional resources and task strategy. Neuroimage 11, 228–242
- 31 Coull, J. and Nobre, A.C. (1998) Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. J. Neurosci. 18, 7426–7435
- 32 Bellin, P. et al. (2002) The neuroanatomical substrate of sound duration discrimination. Neuropsychologia 40, 1956–1964
- 33 Bjoertomt, O. et al. (2002) Spatial neglect in near and far space investigated by repetitive transcranial magnetic stimulation. Brain 125, 2012–2022
- 34 Ashbridge, E. et al. (1997) Temporal aspects of visual search studied by transcranial magnetic stimulation. Neuropsychologia 35, 1121–1131
- 35 Rushworth, M.F.S. *et al.* (2001) Complementary localization and lateralization of orienting and motor attention. *Nat. Neurosci.* 4, 656–661
- 36 Gőbel, S. $\it et\,al.\,(2001)$ The mental number line and the human angular gyrus. $\it Neuroimage\,14,\,1278-1289$
- $37\,$ Dehaene, S. (1992) Varieties of numerical abilities. Cognition 44,1–42
- 38 Thompson, R.F. et al. (1970) Number coding in association cortex of the cat. Science 168, 271–273
- 39 Sawamura, H. et al. (2002) Numerical representation for action in the parietal cortex of the monkey. Nature 415, 918–922
- 40 Nieder, A. et al. (2002) Representation of the quantity of visual items in the primate prefrontal cortex. Science 297, 1708–1711
- 41 Walsh, V. (2003) Numerate neurons. Curr. Biol. 13, R447-R448
- 42 Stein, J. (1989) The representation of egocentric space in the posterior parietal cortex. Q. J. Exp. Physiol. 74, 583–606
- 43 Wilson, F.A.W. et al. (1993) Dissociation of object and spatial processing domains in primate prefrontal cortex. Science 260, 1955–1958
- 44 Onoe, H. et al. (2001) Cortical networks recruited for time perception: a monkey positron emission tomography (PET) study. Neuroimage 13, 27, 45
- 45 Leon, M.I. and Shadlen, M.N. (2003) Representation of time by neurons in the posterior parietal cortex of the macaque. *Neuron* 38, 317–327

- 46 Walsh, V. (2003) Time: the back-door of perception. *Trends Cogn. Sci.* 7, 335–338
- 47 Fraisse, P. (1964) The Psychology of Time (Trans, Leith, J. ed.), Eyre & Spottiswood
- 48 Kirkham, N.Z. et al. (2002) Visual statistical learning in infancy: evidence for a domain general learning mechanism. Cognition 83, B35–B42
- 49 Zackay, D. and Block, R.A. (1995) An attentional gate model of prospective time estimation. In *Time and the Dynamic Control of Behaviour* (Richelle, M. et al., eds), pp. 167–178, University of Liege Press
- 50 Burle, B. and Casini, L. (2001) Dissocation between activation and attention effects in time estimation: implications for internal clock models. J. Exp. Psychol. Hum. Percept. Perform. 27, 195–205
- 51 Macar, F. et al. (2002) Activation of the supplementary motor area and of attentional networks during temporal processing. Exp. Brain Res. 142, 475–485
- 52 Ghose, G.M. and Maunsell, J.H.R. (2002) Attentional modulation in visual cortex depends on task timing. *Nature* 419, 616–620
- 53 Fortin, C. and Breton, R. (1995) Temporal interval production and processing in working memory. *Percept. Psychophys.* 57, 203–215
- 54 Minniussi, C. et al. (1999) Orienting attention in time: modulation of brain potentials. Brain 122, 1507–1518
- 55 Shapiro, K. et al. (2002) Control of visuotemporal attention by inferior parietal and superior temporal cortex. Curr. Biol. 12, 1320–1325
- 56 Wearden, J.H. (1999) 'Beyond the fields we know...' exploring and developing scalar timing theory. *Behav. Processes* 45, 3–21
- 57 Ivry, R.B. (1996) The representation of temporal information in perception and motor control. *Curr. Opin. Neurobiol.* 6, 851–857
- 58 Gibbon, J. et al. (1997) Toward a neurobiology of temporal cognition: advances and challenges. Curr. Opin. Neurobiol. 7, 170–184
- 59 Hazeltine, E. et al. (1997) Neural mechanisms of timing. Trends Cogn. Sci. 1, 163–169
- 60 Gruber, O. et al. (2001) Dissociating neural correlates of cognitive components in mental calculation. Cereb. Cortex 11, 350–359
- 61 Stevens, S.S. Psychophysics, John Wiley
- 62 Rossetti, Y. et al. Is action the link between number and space representation? Visuo-manual adaptation improves number bisection in unilateral neglect. Psychol. Sci. (in press)
- 63 Fischer, M.H. (2003) Spatial representations in number processing evidence from a pointing task. Vis. Cogn. 10, 493–508

Searching TiCS online

Tends in Cognitive Sciences is fully archived and searchable online, on BioMedNet, at: http://journals.bmn.com/browse/subjects/search?jcode=tics&subject_code=

You can use your personal subscription to search the journal using keywords, author names or subjects, and browse all issues back to 1998 Vol. 1.

If you are a BioMedNet member, you automatically have full-text access to all articles, in addition to:

- High quality printouts (from PDF files)
- Links to other articles, other journals and cited software and databases
- Articles in press, published online ahead of print

Use your subscription to search and read the latest in TiCS today!!