

Chapter

PROCESSING MAGNITUDES WITHIN THE PARIETAL CORTEX

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ABSTRACT

Human beings constantly process numerosity, space and duration to regulate and adapt their behaviour to the external world. It has been suggested that these fundamental adaptive abilities rely on a common magnitude processing system hosted by the parietal cortex. In this chapter, we review the many recent behavioural, lesional and brain imaging studies demonstrating functional interactions, as well as the cerebral bases underlying magnitude processing in humans and, when relevant, in monkeys. The similarities and differences between numerical, temporal and spatial estimation processes are detailed to show that separate studies of each of these magnitudes, at the behavioural, neurophysiological and neuroanatomical level, have produced convergent results, pointing to the crucial role of the parietal cortex. We also show that the links between different magnitude estimation processes, as revealed by the behavioural interactions observed during multiple-magnitude processing, rely on common populations of neurons in areas around the left and right intraparietal sulci in monkeys and in humans. By integrating all these behavioural and neurofunctional findings, we make it clear that the areas around the intraparietal sulcus host both common and partially distinct and specific representations and mechanisms for numerosity, space and duration processing. We also show how these parietal areas may interact with frontal areas of the brain to achieve these functions.

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1. THEORETICAL MODELS OF NUMEROSITY, DURATION AND LENGTH PROCESSING

Number, space and time are fundamental dimensions of the environment, and are constantly used to regulate and adapt behaviour to the external world. The ability to discriminate these dimensions develops early in infancy and is shared by animals and human beings. In this section, we present two influential models: a functional model postulating a specific association between numerical and temporal estimation, and an anatomo-functional model postulating the existence of a generalised magnitude processing system situated in the parietal cortex.

1.1. The Accumulator Model

Inspired by studies in rats, the *accumulator model* was the first to suggest the existence of a functional mechanism capable of representing both numerical and temporal estimation on the same representational medium (Meck & Church, 1983). In a seminal experiment, rats were trained to discriminate series of sounds on the basis of their numerosity or on their total duration. Two series were used during the training phase: one included two sounds and lasted two seconds; the other included eight sounds and lasted eight seconds. Rats learned to respond to the series by pressing a left or a right lever and receiving a reward. Then, in the experimental phase, untrained sounds were presented in addition to the series used during training, while the reward situations were the same.

Unlike the trained series, for which temporal and numerical dimensions were confounded, the untrained sequences of sounds were built by keeping one of the two dimensions constant as the other dimension varied. In the numerosity discrimination condition, the number of sounds ranged from 2 to 8 while the total duration of the series was kept at 4 seconds. In the duration discrimination condition, the total duration of the series ranged from 2 to 8 seconds while the number of sounds was kept at 4. The rats generalised the learned associations and discriminated the series on the basis of their total duration or the number of sounds. For example, in the duration condition, a series of 2 seconds (4 sounds) was associated with the left lever, while a series of 8 seconds (4 sounds) was linked to the right lever. Interestingly, the psychophysical functions best describing the patterns of response for the discrimination of series on the basis of duration on the one hand, and of numerosity on the other hand, were superimposed.

In a second experiment, methamphetamine was administered to the rats, which produced a similar impairment of performance on both duration and numerosity discrimination conditions. Indeed, the psychophysical functions of responses of the two tasks were shifted 10% to the left. In other words, perceived durations and numerosities were overestimated with the same amplitude after the methamphetamine intake. Finally, in a third experiment, rats trained to discriminate the numerosity and the duration of series of sounds were able to transfer these abilities to the discrimination of skin-stimulation sequences. Based on these observations, Meck and Church argued that numerosity and duration estimation must have a common internal mechanism, corresponding to an accumulator allowing these two magnitudes to be represented in a similar manner through different operative modes.

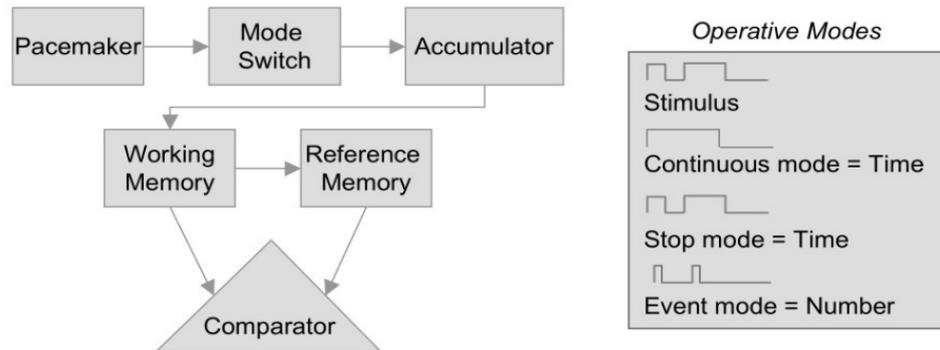
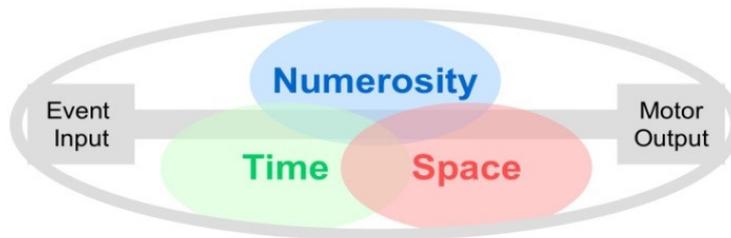
A. The Accumulator Model (Meck & Church, 1983)**B. A Theory of Generalised Magnitude (Walsh, 2003)**

Figure 1. Schematic representation of (A) the system for numerical and temporal processing according to Meck and Church's (1983) accumulator model, and (B) the generalised magnitude processing system (Walsh, 2003). The accumulator model is postulated to underlie the processing of numerosities and durations in animals using different operative modes and give them a common functioning mechanism. It is composed of three distinct stages: accumulation, maintenance in working memory, and decision making. The generalised magnitude processing model assumes that the processing of numerical quantities, space and time rely on the same metric system.

This accumulator model was inspired by the Gibbon's (1977) model of temporal information processing and extends it to the numerical domain. It relies on three successive steps (Figure 1A). During the first step, an internal generator, corresponding to a clock or a counter, sends pulses at regular intervals to an accumulator into which pulses are summed. The transmission of the pulses is also regulated by a switch, situated between the pulses generator and the accumulator, and operating through different modes (Figure 1A). When the switch is in *continuous mode*, the initial stimulus generates a pulse that continues until the end of the interval. When the switch is in *stop mode*, a pulse is released at each stimulation for a variable duration, corresponding to the stimulation duration. These two first modes allow the duration of temporal intervals to be represented.

A third mode, the *event mode*, is used for numerical estimation. In this case, each apparition of a stimulus triggers a pulse of fixed duration, regardless of the duration of the stimulus. According to the selected operative mode, the summed stimulations represent either the estimated duration or the estimated numerosity. In a second step, the pulses summed in the accumulator are stored for a short period in a working memory buffer before being

compared to previously memorised numerical or temporal references. Finally, a decision is taken on the basis of the comparison between the values of the accumulator, enabled temporarily in working memory, and those stored in reference memory. This model thus underlies numerical and temporal estimation processing in animals. Nevertheless, its functioning is not infallible and the precision with which the accumulator value is represented in working memory obeys Weber's law, that is, the accumulator's precision decreases as the magnitude to be judged increases. Finally, attentional resources can influence each of the processing steps and alter performance accuracy when estimating the temporal and numerical properties of a stimulus.

This model was able to account for a large part of the data pertaining to both animals and humans, by suggesting the existence of a unique accumulator which could process only one dimension at a time (i.e., either numerosity or duration). However, it had two major limitations. First, it cannot explain the possible presence of a dissociation between numerosity and duration processing, an impairment of the accumulator necessarily causing an equivalent impairment in both judgements. In addition, no behavioural interactions between the numerical and the temporal dimensions should be observed, as the two processes cannot take place simultaneously. However, as will be discussed in Section 3.3.1 below, a dissociation between numerosity and duration estimation processing was found in a brain-damaged patient with deficit in a duration task whereas his performance in numerical comparison was intact. Moreover, interference effects between these two magnitudes have been described several times in the literature (see Section 3.1). These findings are not compatible with the accumulator model.

1.2. A generalised Magnitude Processing System

Since the introduction of the accumulator model, the question of the existence of distinct or common representations for different types of quantifiable dimensions has been a matter of keen concern. In line with the idea that all continuous and discrete magnitudes can be represented by similar mental magnitudes (Gallistel & Gelman, 2000), and given that in many cases several types of magnitudes are combined to guide important behavioural decisions, Walsh (2003) proposed the existence of a generalised magnitude processing system (A Theory Of Magnitude, ATOM). This system would underlie the representation of numerosity, space, and time from a common metric system (Figure 1B). Moreover, processing magnitudes would share a metric system oriented towards action. According to this model, processing magnitude would depend on a developmental algorithm for distinctions like “more than – less than”, distinctions applicable to any element of the external world. This algorithm would rely on areas of the parietal cortex and would develop in interaction with the environment, through the selection of sensory-motor actions (Figure 1B). Therefore, it is strongly linked to motor behaviours, which may explain its localisation on the dorsal pathway known to be involved in action processing and planning. Furthermore, the generalised magnitude processing system would be present at birth and would develop gradually. Finally, numerosity and duration estimation would rely on accumulation principles similar to those postulated in the accumulator model.

This theory is consistent with a vast majority of recent behavioural and neuroanatomical results (see Section 2). However, it reports data from the study of only one magnitude at a

time, and only defines the nature and extent of the magnitudes concerned in an approximate way. Moreover, it makes no clear prediction regarding the relationship between different magnitudes, and has few suggestions as to which mechanisms and cerebral correlates are specific to each magnitude and which are shared by several of them. In the light of recent studies exploring magnitude estimation processing, some predictions of this theory have now been completed and better specified (Bueti & Walsh, 2009). For example, the ontogenetic reasons for the specific development of this generalised system in the parietal cortex are highlighted. Children are expected to be endowed with a general system of magnitude apprehension situated within the parietal cortex, on the basis of which discrete numerical abilities develop later. The use of a common metric system is also justified without a context related to action. Finally, the parietal cortex is specified as one of the centres of magnitude processing, being a part of a larger network. The prefrontal cortex also seems to be involved in this network.

2. SIMILARITIES AND DIFFERENCES AMONG MAGNITUDE PROCESSING

The argument developed by the ATOM model is based on a broad review of behavioural, developmental, physiological, lesional and neuroanatomical data from three separate literatures on numerosity, duration and space processing. These data are synthesised and completed, with a particular focus on similarities and differences observed between the three magnitude-estimation processes. Studies addressing interactions, both functional and neuroanatomical, between different magnitudes are then described in detail. Finally, an integrated model of magnitude processing within the parietal cortex is proposed.

2.1. Behavioural Data

There are many parallels between the behavioural performances observed during discrimination tasks involving numerosities, lengths, and durations. First, all three perceptual discriminations obey Weber's law¹, according to which the increase in stimulus intensity required to produce a noticeable increase of sensation is a constant function of the intensity of this stimulus. Second, the behavioural signatures typically encountered in numerical judgements (Moyer & Landauer, 1967), that is the distance and size effects, are not only observed in the processing of this dimension, but also appear in comparisons of other magnitudes (Table 1). The distance effect refers to the observation that the ability to discriminate two numbers increases as the distance between them increases. The size effect reflects the fact that, at equal numerical distance, the discrimination of two numbers decreases as their numerical size increases. These effects are present in most judgements of quantifiable psychophysical dimensions such as line lengths (e.g., Dormal & Pesenti, 2007; Fias, Lammertyn, Reynvoet, Dupont & Orban, 2003; Henmon, 1906; Johnson, 1939), duration of sequences (e.g., Dormal, Seron & Pesenti, 2006; Droit-Volet, Turret & Wearden, 2004) or physical size of geometric forms (e.g., Fulbright, Manson, Skudlarski, Lacadie & Gore,

¹ Weber's law states that $\Delta I/I=k$, where I corresponds to the stimulus intensity and k is a constant.

2003), and of numerical symbols (e.g., Cohen Kadosh et al., 2005; Kaufmann et al., 2005; Pinel, Piazza, Le Bihan & Dehaene, 2004; Tang et al., 2006)².

Another similarity between these magnitudes lies in the progressive trajectory of the construction of these representations. The precise investigation of magnitude discrimination capacities in babies aged a few months old by using similar habituation paradigms converges to comparable results regardless of the dimension being studied. Thus, it appears that the performance pattern of these babies is identical for the discrimination of numerosities, surface areas and durations (see respectively, van Marle & Wynn, 2006; Brannon, Lutz & Cordes, 2006; Xu & Spelke, 2000; for a review, see Feigenson, 2007). In these studies, 6-month-old babies reacted to a change of numerosity, surface area or duration when the ratio between the two stimuli was 1:2 but failed to detect this change when the ratio was 2:3. Moreover, the progress of the children in their ability to discriminate durations and numerosities was similar: children aged 10 months were able to detect changes with stimuli in a 2:3 ratio (Brannon, Suanda & Libertus, 2007; Lipton & Spelke, 2003). Finally, in line with the results of these studies, the comparison of the developmental trajectory of the distance effect in symbolic and non-symbolic numerical, size and luminosity comparison tasks in young children showed a similar decrease, proportional to the increase in participants' ages, for all the comparisons tested (Holloway & Ansari, 2008).

However a few dissimilarities between the processing of these magnitudes have also been observed. These include the presence of a functional dissociation between discrete and continuous magnitudes depending on the operations that can be performed on them. Nine-month old babies can add numerosities (McCrink & Wynn, 2004; Wynn, 1992), while they are unable to carry out similar operations on continuous magnitudes such as volumes (Huntley-Fenner, Carey & Solimando, 2002).

Table 1.

Magnitudes	Stimuli	Effects	Studies
Numerosity	Dot collections	Distance & Size	Buckley & Gillman (1974)
Length & Size	Lines Geometrical shapes Arabic digits	Distance & Size	Birren & Botwinick (1955), Cohen Kadosh <i>et al.</i> (2005), Cohen Kadosh & Henik (2006), Fias <i>et al.</i> (2003), Fullbright <i>et al.</i> (2003), Henmon (1906), Johnson (1939), Kaufmann <i>et al.</i> (2005), Moyer & Bayer (1976), Paivio (1975), Pinel <i>et al.</i> (2004), Tang <i>et al.</i> (2006)
Duration	Duration of sequences	Distance	Droit-Volet <i>et al.</i> , (2004), Holyoak & Walter (1976)

²Note that a distance effect has also been observed in tonality (Henmon, 1906; Rusconi, Kwan, Giordano, Umilta & Butterworth, 2006) and luminosity (Cohen Kadosh et al., 2005; Cohen Kadosh & Henik, 2006; Pinel et al. 2004) judgement tasks, as well as in social status (Chiao, Bordeaux & Ambady, 2004), alphabet letters (Hamilton & Sanford, 1978; Lovelace & Snodgrass, 1971) and animal ferocity comparison tasks (Thioux, Pesenti, Costes, De Volder & Seron, 2005).

Together, these observations suggest the existence of a common mechanism for representing magnitudes. However, the presence of homologous behavioural effects during numerical and non-numerical magnitude processing and the presence of similarities in the acquisition of these abilities in the course of development do not necessarily imply the sharing of a single representation. Stimuli supporting similar response functions can, in theory, be processed, by distinct mechanisms (Rumelhart & McClelland, 1986). Thus, observing distance and size effects for different magnitudes does not necessarily imply a common representation, as these effects may emerge at the level of an intermediate step situated between the representation access and the decision-making stages (Cohen Kadosh, Tzelgov & Henik, 2008; Verguts, Fias & Stevens, 2005). The developmental results can also be the consequence of a comparison or processing mechanism shared by several distinct magnitudes. At this stage, additional evidence is necessary to establish a real distinction and to determine the level at which the convergence between magnitudes occurs. On the one hand, studies investigating mutual interference between the dimensions in several behavioural paradigms could provide more convincing evidence (see Section 3.1). On the other hand, more fundamentally, behavioural data alone appear insufficient to clearly determine the existence of separate or common representations. A complementary way of investigating this proposal consists of exploring the neuronal substrates underlying magnitude processing. These studies will be developed in the next section, neuronal recordings studies in monkeys being presented first, followed by neuropsychological and neuroanatomical studies in humans.

2.2. Neurophysiological Data in Monkeys

Compared to functional brain imaging in humans, animal cell recording is a technique with many advantages both in terms of temporal and spatial resolution and allowing brain activity to be analysed at the scale of neurons. Recent studies have thus greatly enriched our knowledge of the brain areas underlying the estimation of different magnitudes and how these magnitudes are represented at the level of neural coding in these areas.

Numerosity-sensitive neurons were originally recorded in parietal areas of the cat brain (Thompson, Mayers, Robertson & Patterson, 1970). More recently, cell recording in the primate brain helped identify neurons in parietal and prefrontal areas during sensori-motor tasks (Sawamura, Shima & Tanji, 2002) or during visually-presented collections-of-dots matching tasks (Nieder, Freedman & Miller, 2002; Nieder & Miller, 2004; Roitman, Brannon & Pratt, 2007). Neurons responding selectively to numerosity are abundant in the dorsolateral prefrontal cortex and in a deep part of the intraparietal sulcus (IPS), the ventral intraparietal area (VIP) (Colby, Duhamel & Goldberg, 1993). These neurons respond to specific numerical values independently of the non-numeric attributes of the stimuli. They discharge at high levels for a preferred numerosity but also for near numerical values, the activity decreasing as the numerical distance with the preferred numerosity increases. Moreover, the profiles of these neurons activity correlate with the behavioural performance of the monkeys and correspond to Weber's law (that is, the precision of the numerical representation decreases linearly with the increase of the preferential numerosity) (Nieder & Miller, 2003). Other neurons recorded in a more lateral and posterior intraparietal area (LIP) also respond specifically to numerosity but discharge in a monotonic way (i.e., by increasing or decreasing

with the logarithm of the numerosity presented, without being bound to a particular numerosity) and have limited receptive fields, responding only to the numerosity of the subset of items presented in a delimited retinotopic region (Roitman et al., 2007).

These two types of numerosity neural coding (linked to or proportional to numerosity) may reflect the two distinct stages of numerosity extraction proposed by computational neuronal models of numerical representation (Dehaene & Changeux, 1993; Verguts & Fias, 2004). The monotonous coding of magnitude sustained by neurons from the LIP area would correspond to the numerosity sensitive coding stage (or accumulation stage) and would be transformed into a cardinal representation of the total numerosity (or selective coding of numerosity stage) by neurons from the VIP area (Roitman et al., 2007)³. Moreover, the comparison of response latencies for numerosity-selective neurons in these prefrontal and parietal areas indicates an earlier differentiation of the numerosities for the activity profile of the SIP neurons than to the profile of the dorsolateral prefrontal neurons. These results suggest the involvement of a fronto-parietal network in numerosity processing in which the numerical information is initially extracted in the parietal cortex and then transmitted to the frontal areas for subsequent processing.

Moreover, several studies of the estimation of duration in monkeys have revealed the presence of neurons sensitive to this dimension in the parietal cortex (Janssen & Shadlen, 2005; Leon & Shadlen, 2003), in the prefrontal cortex (Genovesio, Tsujimoto & Wise, 2006; Oshio, Chiba & Inase, 2006; 2008; Sakurai, Takahashi & Inoue, 2004) and in the striatum (Chiba, Oshio & Inase, 2008). The way in which temporal information is represented at the neuronal level varies depending on the brain area from which these neurons come and the type of task during which they are recorded. In the LIP as well as in the striatum, time-sensitive neurons appear to encode temporal information in a quantitatively and approximate way, whereas neurons from the dorsolateral prefrontal cortex represent this information in a binary or categorical way.

Finally, cytoarchitectonic, connectivity and physiological data exploring spatial processing in monkeys has highlighted a functional segregation of the IPS into several sub-regions, according to a postero-anterior axis. They appear to code space as a function of a reference level ranging through the head (VIP) from the eyes (LIP) to the hand (AIP) (see Hubbard, Piazza, Pinel & Dehaene, 2005 for a review). Two studies of spatial estimation, investigated the modulation of cellular activity during the comparison of length lines (Tudusciuc & Nieder, 2007; 2009). Neurons responding selectively to the length dimensions were recorded in the prefrontal and parietal cortex, specifically in the depth of the IPS. The activity profile of these neurons showed a progressive decline in the firing rate for the lengths further away from the preferred length. It is important to note that these studies use the same protocols for the estimation of numerosity to identify the common neural coding of continuous (i.e., length) and discrete (i.e., the numerosity) quantity processing. The results of this direct comparison will be developed later in this chapter (see Section 3.2).

In summary, whatever the specific dimension (numerosity, length or duration), the results converge towards the systematic involvement of two cerebral areas in monkeys, the parietal cortex (more precisely the IPS) and the dorsolateral prefrontal cortex. However, this

³ The cerebral substrate underlying these two successive stages has recently been explored in humans (Santens, Roggemans, Fias & Verguts, 2010). It appears that the intermediate stage of numerosity sensitive coding that converts the visual data into a selective code takes place in the posterior part of the superior parietal cortex, whereas the selective coding step takes place in the anterior part of the IPS.

conclusion is based on a variety of different studies, using specific experimental paradigms, and recording neuronal activity of different monkeys. So great care is needed in formulating any hypotheses about links between magnitudes. Paradigms coupling the exploration of several magnitude dimensions may be necessary to support the existence of direct links (see Section 3.2). It is worth noting that, although this cell-recording technique in monkeys has improved our knowledge of the cerebral localisation of processing various magnitudes, it has significant limitations as far as the understanding of the same functions in the human brain is concerned. One possible limit of neurophysiological studies, as well as most of the studies conducted with animals, lies in the fact that the monkeys are submitted to massive training periods before the experimental testing phase, which may lead to changes in their neuronal tissue during this period (e.g., Pascual-Leone, Amedi, Fregni & Merabet, 2005; Poldrack, 2000). In addition, although proposals for homologies between some monkey and human cerebral areas exist, a close anatomical comparison reveals not only differences in the complex cortical areas but also in early sensory areas (Sereno, 1998; Tootell et al., 1997). Therefore, it seems essential to resort to data from neuropsychological or neuroimaging studies to understand exactly how magnitudes are represented at the cerebral level in humans.

2.3. Neuroanatomical Data in Humans

2.3.1. Neuropsychological Studies

The role of the parietal cortex in symbolic number processing has been shown in many neuropsychological studies of brain-damaged patients (e.g., Dehaene & Cohen, 1997; Henschen, 1919; Takayama, Sugishita, Akigushi & Kimura, 1994). Yet, studies investigating numerosity processing are scarce. An impairment of the ability to estimate dot collections was observed in patients with right hemispheric parietal lesions (Warrington & James, 1967), and more recently, in MC, a patient suffering from a focal lesion in the left parietal cortex, between the supramarginal and the postcentral gyrus (Polk, Reed, Keenan, Hogarth & Anderson, 2001). MC presented a clear dissociation between severely altered capacities in tasks involving symbolic number processing and totally preserved capacities in numerical tasks using non-symbolic materials such as comparing dot collections or estimating the frequency of occurrence of events. This suggests a predominance of the right parietal cortex in non-symbolic numerosity processing.

Several other studies have indicated that a left parietal lesion is often at the origin of a massive numerical deficit, during both symbolic and non-symbolic numerical processing (Ashkenazi, Henik, Ifergane & Shelef, 2008; Cipollotti, Butterworth & Denes, 1991; Lemer, Dehaene, Spelke & Cohen, 2003). A disruption of the estimation of dot collections, for example, was highlighted in a patient with focal damage in the left IPS (Lemer et al., 2003). Parietal areas are thus involved bilaterally in non-symbolic numerosity estimation, while a unilateral impairment may alter this quantification processing (Dehaene & Cohen, 1995). Note that the assessment of non-symbolic numerical estimation capacities in patients is rather rare and, when present in the testing, the selected tasks often used small collections of dots, or collections presented or a long enough period of time to allow the patients to use counting strategies.

Table 2.

Magnitudes	Studies	Frontal areas	Coordinates		Frontal areas	Coordinates	
			Left	Right		Left	Right
Numerosity	1. Ansari & Dhital (2006)	L inf Frontal Gyrus	-34 17 19		L & R IPS	-62 -50 44	32 -49 46
	2. Castelli <i>et al.</i> (2006)				L & R IPS	-24 -48 48	33 -57 51
	3. Piazza <i>et al.</i> (2006)	R middle Frontal Gyrus		48 42 14	R IPS		52 -48 50
Time	1. Belin <i>et al.</i> (2002)	R middle Frontal Gyrus		40 30 24	R inf Par Lobule		54 -50 50
	2. Coull <i>et al.</i> (2004)	R DLPFC		21 36 33	L & R IPS	-51 -48 33	48 -45 33
	3. Ferrandez <i>et al.</i> (2003)	L & R inf Frontal Gyrus	-39 9 30	45 9 36	L & R inf Parietal Lobule	-42 -36 42	39 -45 42
	4. Pouthas <i>et al.</i> (2005)	R DLPFC		39 33 15	R IPS		39 -42 39
	5. Rao <i>et al.</i> (2001)	R DLPFC		34 23 25	R IPS		38 -40 41
Length	1. Fias <i>et al.</i> (2003)				L IPS	-36 -68 58	
	2. Fink <i>et al.</i> (2000)				R inf Parietal Lobule		44 -32 52
	3. Fink <i>et al.</i> (2001)	R DLPFC		50 20 20	L & R inf Parietal Lobule	-38 -42 40	40 -40 42
	4. Pinel <i>et al.</i> (2004)				L & R IPS	-36 -52 52	40 -40 44
	Mean coordinate		-37 12 25	40 28 24		-37 -49 45	52 -44 45
	Standard Deviation		3,5 5,7 7,8	9,9 11,1 8,4		8,3 9,9 8,2	7,1 6,7 5,9

Turning to duration processing, further to altered performance observed during temporal estimation in patients with Parkinson's disease, neuropsychological research suggests the involvement of the basal ganglia and the cerebellum (Artieda, Pastor, Lacruz & Obeso, 1992; Harrington, Haaland & Hermanowicz, 1998; Malapani et al., 1998; Malapani, Deweer & Gibbon, 2002; Merchant, Luciana, Hooper, Majestic & Tuite, 2008; Pouthas & Perbal, 2004) and in cerebellar patients (Casini & Ivry, 1999; Ivry, Keele & Diener, 1988; Mangels, Ivry & Shimizu, 1998; Nichelli, Alway & Grafman, 1996; Spencer, Zelaznik, Diedrichsen & Ivry, 2003). In addition to this double subcortical involvement, a lesional study exploring a broad panel of brain-damaged patients has shown that frontal and parietal areas lateralised in the right hemisphere may be involved in temporal discrimination (Harrington, Haaland & Knight, 1998). Indeed, only patients with right hemispheric damage showed a deficit in an auditory temporal discrimination task. The analysis of the localisation of the lesions in this sub-group of patients revealed anterior and posterior lesions (corresponding to the prefrontal and inferior parietal cortex, respectively), suggesting that a right fronto-parietal network plays a role in duration estimation. Other neuropsychological studies later confirmed the involvement of these areas (e.g., Koch, Oliveri, Carlesimo & Caltagirone, 2002; for a review, see Battelli, Pascual-Leone & Cavanagh, 2007; Battelli, Walsh, Pascual-Leone & Cavanagh, 2008).

Finally, studies exploring the visuo-spatial performance of patients with right parietal lesions have detected contralateral spatial neglect (i.e., an inability to detect, to move to, or to respond to stimuli presented in the contralesional hemi-space) (Heilman, 1979), and impairments in both line bisection (Bisiach & Luzziatti, 1978; Harvey, Milner & Roberts, 1995; Marshall & Halligan, 1989), and line-length comparison tasks (Irving-Bell, Small & Cowey, 1999; Milner & Harvey, 1995). Neglect patients presented a rightward bias when they were required to indicate the middle of a line, and systematically underestimated the length of lines presented in their contralateral hemispace during length comparison tasks (which reflects a left-sided neglect of the line).

To sum up, like cell-recording studies in monkeys, neuropsychological studies in humans have indicated the involvement of the parietal cortex in processing different magnitudes. The neuropsychological studies exploring estimation impairments in patients seem to converge towards the existence of a common neuroanatomical substrate for all magnitudes. However, it is worth noting that patients often have large lesions, not strictly limited to the parietal cortex, therefore making it difficult to draw final and firm conclusions (Buetti & Walsh, 2009). Few studies have investigated the estimation of various dimensions in the same population of patients, so little information is available on the presence of either associations or dissociations of deficits (see Section 3.3.1).

2.3.2. Brain imaging Studies

Parallel to the evolution of brain-imaging technology and the development of new experimental paradigms, the last twenty years have seen a considerable increase of the number of studies investigating the cerebral substrate of numerical, spatial and temporal processing. In this section, only the studies specifically exploring the estimation processing of numerosity, duration and length will be discussed (Table 2).

While the involvement of parietal areas in numerical processing is well established (for a review, see Dehaene, Piazza, Pinel & Cohen, 2003), a few functional brain-imaging studies have recently been devoted to the estimation of non-symbolic numerosity (e.g., visual collections of dots). The results of these studies demonstrate the key role of the parietal

cortices, and more specifically the areas around the IPS (Figure 2). The activation of both the left and the right IPS was reported in response to a deviant numerosity when participants were passively exposed to collections of dots in habituation paradigms (Cantlon, Brannon, Carter & Pelphey, 2006; Piazza, Izard, Pinel, Le Bihan & Dehaene, 2004; Piazza, Pinel, Le Bihan & Dehaene, 2007). The bilateral involvement of the IPS was also observed during the comparison of visual and/or auditory collections of elements presented sequentially or simultaneously (Ansari & Dhital, 2006; Castelli, Glaser & Butterworth, 2006; Piazza, Mechelli, Price & Butterworth, 2006), during the enumeration of dots (Fink et al., 2001; Piazza, Mechelli, Butterworth & Price, 2002; Piazza, Giacomini, Le Bihan & Dehaene, 2003; Sathian et al., 1999), and during a simple addition task with non-symbolic materials (Venkatraman, Ansari & Chee, 2005). Some of these studies revealed additional activations in the frontal cortex, suggesting the involvement of a fronto-parietal network in numerosity processing (Ansari & Dhital, 2006; Piazza et al., 2006). The activity of these areas was found to be modulated by the distance effect (Ansari & Dhital, 2006; Piazza et al., 2004), this modulation being highly similar to the distance effect observed at the neural level in monkeys (Nieder & Miller, 2004).

The studies investigating temporal estimation in the range of a few hundred milliseconds revealed the activation of a wide cerebral network including the basal ganglia, the premotor areas, the supplemental motor area and the cerebellum, and also a fronto-parietal network with a right hemispheric dominance (Belin et al., 2002; Coull, Vidal, Nazarian & Macar, 2004; Ferrandez et al., 2003; Pouthas et al., 2005; Rao, Mayer & Harrington, 2001; for a review see Lewis & Miall, 2003a; Macar et al., 2002) (see Figure 2). However, the exact role and the specificity of these areas in relation to the different stages of temporal information processing is still a matter of debate. A study examining more specifically the time course of activations during a duration-estimation task assigned the role of internal clock to the basal ganglia, which was associated with a system of attentional resource allocation underpinned by the right inferior parietal cortex (Rao et al., 2001). On this model, premotor areas were involved in the temporary maintenance of temporal information in working memory, whereas the right dorsolateral prefrontal cortex controlled later steps related to the manipulation of the duration information required to compare and make decisions on intervals.

The parietal cortex, mainly in the right hemisphere, plus the cerebellum and the prefrontal cortex, are the cerebral substrate underlying length estimation. This was revealed during line bisection (Fink et al., 2000; Fink, Marshall, Weiss & Zilles, 2001), size judgement (Pinel et al., 2004), and the comparison of line lengths (Fias et al., 2003) (Figure 2). It should however be noted that neither of the two latter studies directly aimed to investigate length or size estimation per se, this task constituting only one condition among many others intended to reveal activations common to several magnitudes. The results of these studies therefore focused on common activations and little information is available on direct contrasts between magnitudes.

As shown in Figure 2, the bilateral involvement of posterior parietal areas reported systematically during numerosity estimation also seems to be observed during length and duration discrimination. However, within-subject data are needed to assess identical brain activations across several tasks. Exploring several estimation processes with the same paradigm therefore appears essential to establish precisely the possible overlap between these areas of activation.

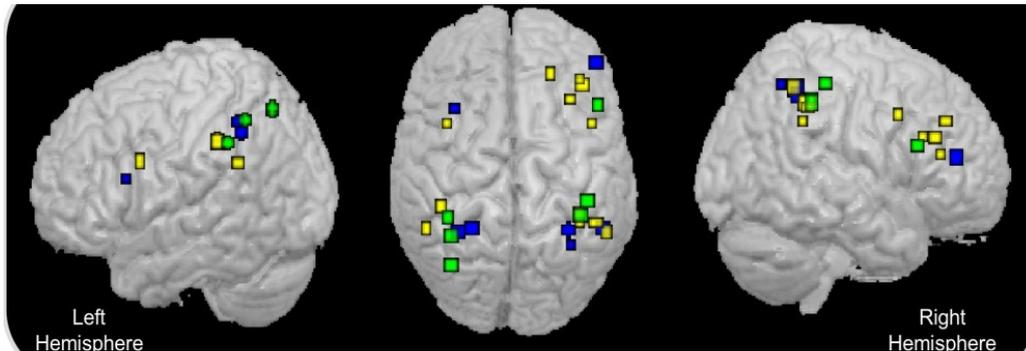


Figure 2. Activation peaks observed in the frontal and parietal cortices during the estimation of numerosity (blue; Ansari & Dhital, 2006; Castelli et al., 2006; Piazza et al., 2006), duration (yellow; Belin et al., 2002; Coull et al., 2004; Ferrandez et al., 2003; Pouthas et al., 2005; Rao et al., 2001) and length (green; Fias et al., 2003; Fink et al., 2000, 2001; Pinel et al., 2004). The coordinates of the activation peaks, reported in Table 2, are represented on a 3D standard brain reconstruction.

2.3.3. Transcranial Magnetic Stimulation Studies

Neuroimaging studies have demonstrated the presence of a local transient change in parietal activity during various magnitude judgements, but they do not reveal the existence of a direct causal link between these changes in brain activity and their respective behavioural consequences (Sack, 2010). Transcranial Magnetic Stimulation (TMS)⁴ is a non-invasive technique investigating the extent to which a brain area necessarily contributes to a specific cognitive process by causing a temporary and reversible impairment of this process (Hallett, 2000; Walsh & Cowey, 2000). In recent years, this opportunity to interfere actively with cerebral processes during behavioural performance has been used to investigate the higher cognitive functions, including magnitude estimation processing.

Several TMS studies investigated the role of the parietal cortices in various numerical tasks with symbolic materials (i.e., Arabic digits; for a review, see Sandrini & Rusconi, 2009), but, to the best of our knowledge, only one study provides new evidence of the IPS contribution to the representation of numerosities (Cappelletti, Barth, Fregni, Spelke & Pascual-Leone, 2007). In this study, a low-frequency train of stimulations (15min, 1Hz) was applied to four separate sites (left and right IPS, left and right angular gyri). After each period of stimulation, the participants had to perform a standard comparison task (standard = 65) either with Arabic numerals (between 31 and 99) or with a non-symbolic material (collections of dots between 31 and 99). Compared to the control condition (the sham stimulation⁵), performance in Arabic numerals and dots comparison was impaired only after left IPS stimulation, suggesting the predominant role of this cerebral area in numerical processing, irrespective of whether the notation was symbolic or non-symbolic.

Several studies using TMS and exploring the discrimination of durations of a few hundred milliseconds demonstrated the involvement of the cerebellum (Koch, Oliveri, Salerno, Lo Gerfo & Caltagirone, 2007; Lee et al., 2007), the right dorsolateral prefrontal cortex (Jones, Rosenkranz, Rothwell & Jahanshahi, 2004; Koch, Oliveri, Torriero &

⁴ This technique is based on the induction of an electromagnetic field in a specific point on the surface of the scalp. Through the scalp and skull, this field stimulates the underlying neural tissue and temporarily causes a functional alteration of the neuronal tissue being stimulated.

⁵ That is, a stimulation reproducing auditory sensations of a real TMS without actually applying a magnetic field.

Caltagirone, 2003), and the right temporal cortex (Buetti, van Dongen & Walsh, 2008; for a review, see Koch, Oliveri & Caltagirone, 2009). In addition, an involvement of the right inferior parietal cortex was observed when the participants had to carry out a temporal generalisation task on sounds of varying duration (i.e., 1200 ms \pm 60, 120, 180 or 240 ms) before and after a train of low-frequency stimulations (10 min, 1 Hz) was applied to the left and right inferior parietal lobules or the vertex (Alexander, Cowey & Walsh, 2005). Compared to the vertex stimulation, only the right parietal cortex stimulation impaired performance by increasing response latencies. Similarly, stimulation of this area generated an increase in performance variability during a temporal generalisation task on sounds of slightly briefer durations (i.e., sounds between 435 and 765 ms; Buetti, Barhami & Walsh, 2008). As suggested by functional neuroimaging studies, a large cortical network with a right hemispheric dominance seems to be involved specifically in duration estimation, whereas no impairment was observed during control tasks using tone discrimination (Alexander et al., 2005). Moreover, the stimulation of the cerebellum appears to interfere with the estimation of durations of less than a second (i.e., \pm 500 ms), while dorsolateral prefrontal cortex stimulation alters performance during processing of slightly longer intervals (i.e., \pm 2 sec) (Koch et al., 2007). These results were recently confirmed by a meta-analysis of fMRI studies (Wiener, Turkeltaub & Coslett, 2010).

The exploration of length processing during line-bisection tasks was also completed with TMS, right parietal cortex stimulation reproducing the specific deficit observed in brain-damaged patients with spatial neglect (e.g., Bjoertomt, Cowey & Walsh, 2002; Fierro et al., 2000; Fierro, Brighina, Piazza, Oliveri & Bisiach, 2001). This rightward bias is observed when stimulation is applied early after the stimulus presentation (i.e., 50 ms) (Pourtois, Vandermeeren, Olivier & Gelder, 2001) and only appears when the stimulus is presented in peri-personal space (Bjoertomt et al., 2002; Bjoertomt, Cowey & Walsh, 2009). Apart from those using line-bisection tasks, no TMS study has, until now, investigated the explicit comparison of lengths.

TMS has thus demonstrated the preponderant and decisive role of the parietal cortex in the processing of various magnitudes. However, not all these studies show the same degree of precision concerning the definition of stimulation sites. The methods used to gather data vary from the conventional benchmarks of the international 10-20 EEG location system to a neuro-navigation system guided by anatomical or functional cerebral data. As the 10-20 EEG system localises electrodes on the scalp by using standard benchmark of the skull (Jaspers, 1958), deformities and asymmetries of the skull and the brain can be responsible for significant inaccuracies in the determination of stimulation sites. The most recent techniques of neuro-navigated coregistration use structural or functional data from MRI to localise cerebral areas on the brain of each participant. This method appears to provide sufficient localisation accuracy, eliminating problems associated with inter-subject structural and/or functional brain anatomy variability. Given the variability of coregistration methods used in the different studies described above, it is difficult to affirm that the stimulated areas were exactly the same from one study to the other, and it is therefore impossible to draw firm conclusions from them about the involvement of common cerebral areas. Again, investigating several dimensions in a single study using a reliable neuro-navigation system constitutes a possible solution to circumventing these limitations.

These studies addressing the processing of different magnitudes separately have identified many similarities; in particular, the parietal cortex appears recurrently as the

common cerebral substrate underlying magnitude estimation. However further studies investigating the direct functional and anatomical relationships that may exist between magnitudes are necessary to draw firm conclusions on this common parietal involvement. They will be described below.

3. LINKS BETWEEN MAGNITUDE ESTIMATION PROCESSES

3.1. Behavioural Data

Several studies have investigated the behavioural interactions between various magnitude estimation processes, primarily, by using interference paradigms to explore the influence of an irrelevant magnitude on the judgement of another magnitude (for a review, see Dormal & Pesenti, in press).

First, a robust interference effect of numerical dimensions, both in symbolic and non-symbolic form, was consistently observed during duration comparison tasks (Brown, 1997; Dormal, Seron & Pesenti, 2006; Oliveri et al., 2008; Roitman, Brannon, Andrews & Platt, 2007; Vicario et al., 2008; Xuan, Zhang, He & Chen, 2007) (see Figure 3A for an example of paradigm). For example, although not relevant for the task, the numerical magnitude of Arabic digits interferes with duration judgements: participants underestimate the duration of presentation of small, and overestimate the duration of large, Arabic digits (Oliveri et al., 2008; Vicario et al., 2008; Xuan et al., 2007). Moreover, the numerosity of dot collections presented sequentially (Dormal et al., 2006) (see Figure 3D) or simultaneously (Xuan et al., 2007) interacts with duration comparison: numerical cues facilitate duration judgement when they are congruent, and interfere with it when they are incongruent. The reverse influence of duration on numerosity has been much less frequently explored and is only reported in one study (Brown, 1997). Similar results have been observed in 5- and 8-year-old children in numerical and temporal sequence bisection tasks, a unilateral interference effect of numerosity cues on temporal performance being reported (Droit-Volet, Clément & Fayol, 2003).

Next, time and space are naturally related through the concept of speed, and they have been investigated in several studies exploring the effect of spatial cues on duration discrimination (see Figure 3B for an example). These studies have showed that the spatial dimension has a strong influence on duration processing, congruent and incongruent cues causing respectively facilitation (i.e., a decrease in response latencies and/or the percentage of errors committed) and interference (i.e., an increase in response latencies and/or the percentage of errors) effects. The size of geometric shapes (Xuan et al., 2007), the length of dot arrays (Casasanto & Boroditsky, 2008), and the side of space in which the stimuli are presented (Vicario et al., 2008) were all found to affect the duration judgement: the duration of presentation of small shapes, short sequences and left hemifield-presented dots were underestimated, whereas the duration of presentation was over-estimated for large shapes, large sequences or a dot presented in the right hemifield. This spatial interaction with duration processing has also been detected in children. For example, the judgement of the speed of a train was influenced by its size (Stavy & Tirosh, 2000): at constant speed, they estimated that a large train was going faster than a smaller one. The estimate of presentation duration of a

light signal has also been shown to depend on its size and brightness (Levin, 1977; 1979; 1982).

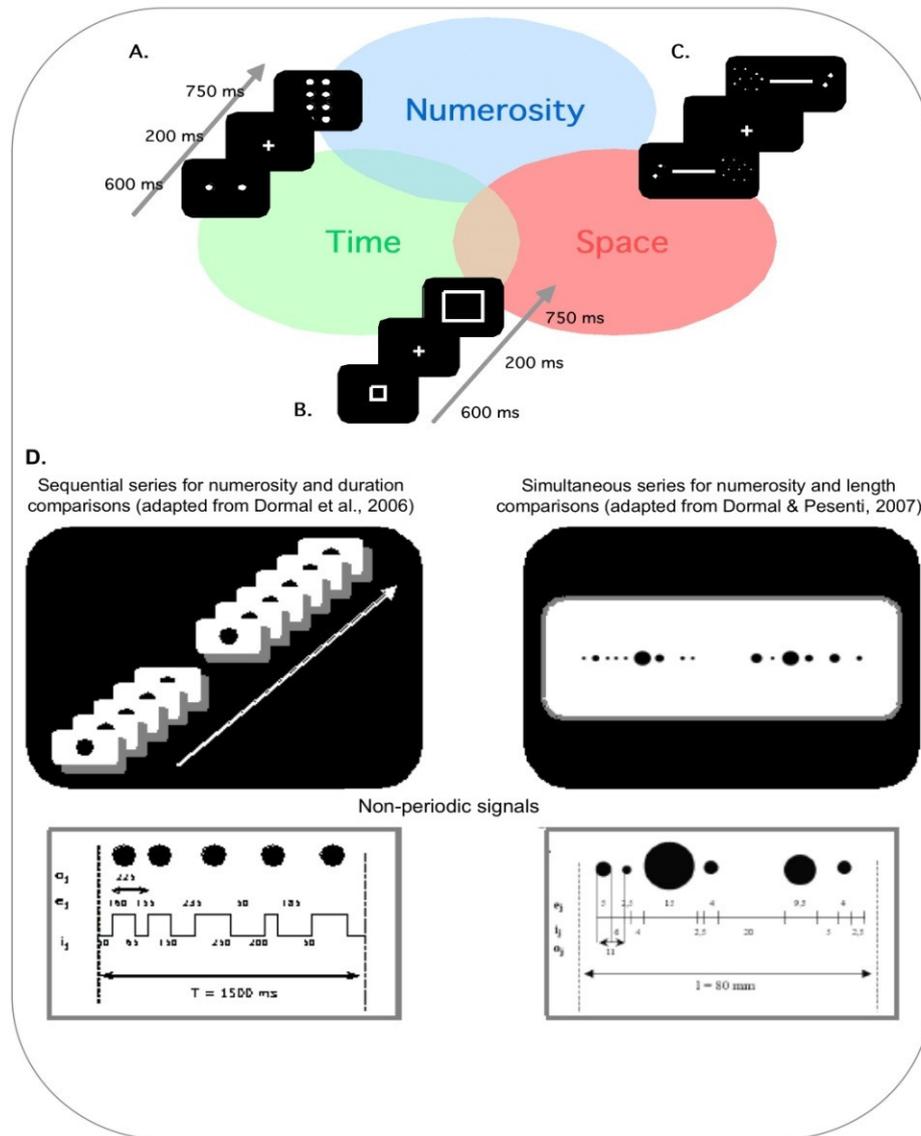


Figure 3. Examples of experimental paradigms to investigate the interference between magnitudes: (A) a duration comparison task where the numerosity represented by collections of dots interferes with the judgement of presentation duration of these collections (adapted from Xuan et al., 2007); (B) a duration comparison task where the size of the geometric shapes interferes with the judgement of presentation duration of these forms (adapted from Xuan et al., 2007); (C) a line bisection task where the numerosity of collections of dots interferes with the bisection of horizontal lines (adapted from de Hevia et al., 2009); (D) Examples of non-periodic stimuli (i.e., stimuli controlled for the regularity and rhythm of presentation) used in the study of Dormal et al. (2006) (left part) and of Dormal & Pesenti (2007) (right part).

Finally, the existence of an association between numerosity and space has been widely demonstrated. Obviously space covers a wide variety of motor and cognitive processes; only experiments addressing the spatial dimension in the strict form of the discrimination of length determined by two bounds will be described here. Reciprocal and mutual interferences have been reported during line bisection tasks (de Hevia & Spelke, 2009; Fischer, 2001) (Figure 3C), reproduction of lengths (de Hevia, Girelli, Bricolo & Vallar, 2008), comparison of linear arrays of dots (Dormal & Pesenti, 2007) (Figure 3D), and comparisons of the physical and numerical size of Arabic digits (e.g., Henik & Tzelgov, 1982). For example, a systematic bias towards the largest magnitude is usually observed in the bisection of horizontal lines flanked by two Arabic numerals (Fischer, 2001) or two collections of dots (de Hevia & Spelke, 2009). Similarly, when participants are asked to compare the numerosity or the length of arrays of dots, for which the two dimensions are manipulated independently, the spatial cues have been shown to strongly interfere with the processing of numerosity, whereas the numerical cues only moderately interfere with the processing of length (Dormal & Pesenti, 2007).

This pattern of results suggests a difference in terms of automaticity for numerosity and length processing. During comparisons of the physical and numerical size of Arabic digits, interference between spatial cues and numerical comparisons and vice versa has been detected (Henik & Tzelgov, 1982). Spatial interference with numerical judgements is also frequently observed in children. When two rows with the same number of elements have different lengths, children erroneously decide that the longer row contains the larger number of objects (Gelman, 1972; Piaget & Szeminska, 1941; Pufall & Shaw, 1972), suggesting a visuo-spatial bias (correct in the majority of cases) automatically linking number and length as covariates (Houdé, 1997). Among adults, the correct comparison of such conflicting materials requires inhibiting this visuo-spatial bias, which translates into longer reaction times (Dempster, 1995; Dixon, 1978; Houdé & Guichart, 2001; Pascual-Leone, 1988). Moreover, a mutual interference between numerical and perceptual information was observed in children from the age of 3 (Rousselle & Noel, 2008). The numerical comparison of collections of dots or vertical rectangles was influenced by the occupied surface and vice versa, demonstrating the early automatic processing of spatial and numerical dimensions respectively.

Currently, only two studies have brought these three quantifiable dimensions together in the same experiment. First, the influence of numerical and spatial cues on the perception of duration of intervals was explored (Vicario et al., 2008). In this study, the participants had to determine the duration of presentation of Arabic digits presented in the left or right part of the visual field. In addition to the presence of an interference effect of spatial and numerical cues on the performance of duration estimation (see above), a joint effect was observed when these two dimensions were manipulated simultaneously: the duration of presentation of a small Arabic numeral (i.e., 1) was more underestimated when it was presented in the left hemispace, and conversely, the duration of presentation of a large digit (i.e., 9) was more overestimated when it was presented in the right hemispace. Secondly, mutual and bidirectional interactions between numerosity, length and duration were examined within the same experimental paradigm (Dormal & Pesenti, in press). Participants had to compare the numerosity, the length or the duration of two successive linear arrays of sequentially flashed dots. The results showed that numerosity and length both affected duration processing both separately and cumulatively, whereas temporal cues did not influence judgements of either numerosity or length. Moreover, numerosity and length influenced each other, with numerical cues having a stronger influence on length processing than vice versa. These findings support

the hypothesis that, in sequentially presented stimuli, numerosity, length and duration are processed with different levels of automaticity, with numerosity showing the highest levels of automaticity and duration the lowest.

3.2. Neurophysiological Data in Monkeys

Two recent electrophysiological studies have investigated the neural coding of several magnitudes in the same monkeys to test if the neurons known to be sensitive to numerosities were also sensitive to other continuous variables, such as length (Tudusciuc & Nieder, 2007; 2009). The response characteristics of neurons situated in the VIP and in the prefrontal cortex of rhesus monkeys were analysed as the monkeys carried out numerosity and length discrimination. The results showed that while certain neurons responded selectively to numerosity or to length, others responded to both dimensions equally, suggesting the existence of three distinct, if partly overlapping, neuronal populations. Finally, the role of the IPS in numerosity perception was investigated specifically when presented sequentially and simultaneously (corresponding respectively to presentations recorded in time and in space) (Nieder, Diester & Tudusciuc, 2006). Again, three numerosity-sensitive populations of neurons were identified: the first two contained neurons whose activity was dependent on the mode of presentation (i.e., one population responded specifically to sequential numerosities and the other to the simultaneously-presented numerosities), while the third population only discharged during the period of retention, independent of the presentation mode.

These results are consistent with the presence of neural populations involved in the perception of numerosity and other magnitudes, partially overlapping in the IPS in human adults. Note that no study of neuronal recording has, until now, investigated duration and numerosity processing simultaneously.

3.3. Neuroanatomical Data in Humans

3.3.1. Neuropsychological Studies

A few studies have attempted to assess the presence of associations or dissociations of deficits in the estimation of several magnitudes, mainly in patients with lesions in the parietal cortex. For example, in neglect patients known to have difficulty with line-bisection tasks (Irving-Bell et al., 1999; Marshall & Halligan, 1989), similar deficits were observed in the bisection of numerical (Cappelletti, Freeman & Cipolotti, 2007; Hoeckner et al., 2008; Zorzi, Priftis & Umiltà, 2002; Zorzi, Priftis, Meneghello, Marenzi & Umiltà, 2006) and of temporal (Basso, Nichelli, Frassinetti & di Pellegrino, 1996; Calabria et al., 2011; Danckert et al., 2007) intervals. Studies of patients with right-hemispheric brain injury presenting persistent left-spatial neglect have shown that these patients misplaced the central value of the numerical interval during bisection tasks (e.g., they might designate 5 as the centre of the interval 2-6). This deficit seems otherwise dependent of the orientation of the mental line (Cappelletti et al., 2007), this bias being absent when the bisection operated on a vertical representation. On the other hand, the study of the comparison and production of temporal intervals inferior to the second in a left-neglect patient has highlighted a systematic overestimation of the stimuli duration presented in the neglected hemifield (Basso et al., 1996). Similarly, spatial neglect

seems to distort time representation, as suggested by the overestimation of durations observed in a time discrimination task (Calabria et al., 2011). However, when asked to estimate intervals of many seconds, neglect patients with right-hemispheric lesions widely underestimated the durations (Danckert et al., 2007). All these data suggest the existence of an association of disorders in the estimation of numerosity, length and duration in neglect patients.

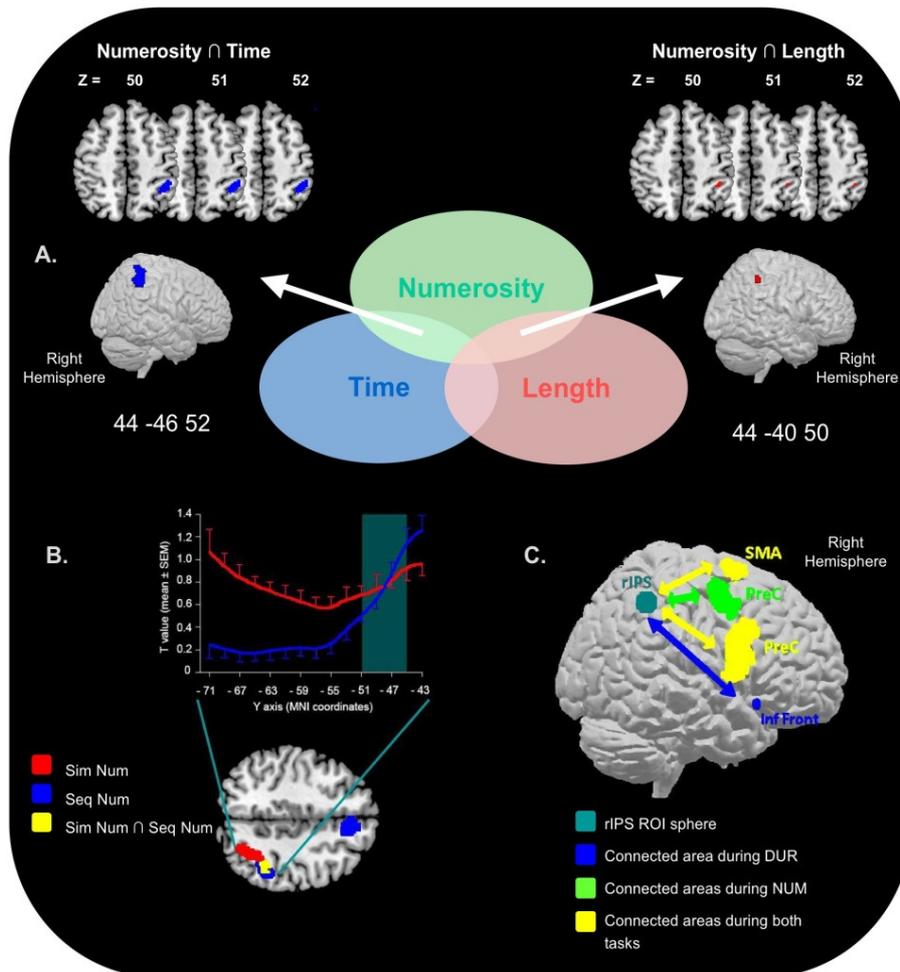


Figure 4. (A) Common activation areas in the right IPS for numerosity and duration estimation (in blue, left panel) and for numerosity and length estimation (in red, right panel). Axial sections and reconstruction in three dimensions are shown on a standard brain. (B) Brain regions activated specifically and jointly in sequentially- and simultaneously-presented numerosity comparison tasks (Dormal et al., 2010; Seq Num = Sequential Numerosity; Sim Num = Simultaneous Numerosity). The plot represents an anterior-to-posterior index (i.e., averaged contrast weighted t -values) within the range of -43 to -71 on the y axis in stereotactic space for Seq Num (blue) and Sim Num (red) respectively. (C) Psychophysiological interaction (PPI) of the right intraparietal sulcus (IPS) showing task-specific coupling rendered on a canonical brain surface (Dormal et al., 2011). Areas linked to the right IPS during the numerosity task are shown in green, those linked during the duration task in blue, and their overlap in yellow (PreC = precentral gyrus; rIPS = right intraparietal sulcus; SMA = supplementary motor area; Inf Front = inferior frontal gyrus).

Importantly, by exploring for the first time three distinct magnitude judgements (i.e., number, time and space) in brain-damaged patients, a double dissociation was found in two patients with left (JT) and right (CB) parietal lesions and selective impairment of number and time processing respectively (Cappelletti, Freeman & Cipolotti, 2009; 2011). Whereas spatial processing was preserved in both patients, JT was selectively impaired in processing numbers, as indicated by poor performance in arithmetic tasks and in numerosity estimation. By contrast, CB had difficulty estimating and compare duration intervals. Moreover, their performance in Stroop-like tasks (i.e., comparison of a relevant dimension while an irrelevant dimension was manipulated) reflected the unilateral interference classically observed in healthy participants (see point 3.1): numerical magnitude interfered with duration processing but temporal cues did not interfere with numerosity estimation. The numerosity–duration dissociation seems to involve distinct processing mechanisms, but the presence of an asymmetric interference between numerosity and duration does not support the idea of fully independent magnitudes. Altogether, these results are better accounted for by a partly-shared magnitude system. This suggestion is supported by recent neuroimaging and electrophysiological studies, described below.

3.3.2. Neuroimaging Studies

Some studies have investigated more specifically the common cerebral substrates underlying several magnitude representations, by examining whether the cerebral areas involved in numerical processing are also enabled when other continuous dimensions (such as size, brightness, amplitude and length) are processed (Cohen Kadosh et al., 2005; Fias et al., 2003; Pinel et al., 2004). While some results showed convergent activity within the left IPS for line length, angular amplitudes and pairs of numbers comparisons (Fias et al., 2003), activations associated specifically with physical or numerical size were identified as distributing along the IPS, and only partially overlapping (Pinel et al., 2004). Together, these results suggest that the neuronal population coding numerosity is highly distributed within the IPS. This is in accord with recent observations in monkeys.

It is however important to note that all these studies used symbolic numerical materials (i.e., numbers of one or two Arabic digits), which are known to preferentially activate the hemisphere dominant for language. To date, only a few studies have examined directly (i.e., in a within-subject design) whether some parietal areas are involved in judgements of two-or-more different magnitudes. First, an fMRI study compared the cerebral substrate of discrete and continuous quantities processing using exclusively non-symbolic materials (Castelli et al., 2006). These quantities were collections of green and blue geometrical forms changing either in a steep (i.e., discrete) or in a progressive (i.e., continuous) way and this, either in time (i.e., sequential presentation of green and blue squares) or in space (i.e., simultaneous presentation of green and blue rectangles). All the stimuli were composed of 20 elements (blue and green) in total and the participants had to carry out a colour judgement task to decide whether each stimulus contained more green or more blue. Greater activation of the IPS was observed during discrete quantity processing, suggesting a specific representation of quantifiable dimensions within this region.

Similarly, but with smaller numerosities, a recent study explored the cerebral network of numerosity processing presented in space (i.e., simultaneous presentation of linear arrays of dots) or in time (i.e., sequential presentation of flashed dot sequences) (Dormal, Andres, Dormal & Pesenti, 2010). Processing simultaneous numerosities induced activations

bilaterally in several areas along the IPS, whereas processing sequential numerosities produced activations restricted to the right hemisphere. A conjunction analysis showed that only the right IPS and the precentral gyrus displayed overlapping activations during the judgement of sequential and simultaneous stimuli. Voxelwise correlations confirmed the highly similar pattern of activation found in these regions during the two tasks. Finally, a closer look at the right IPS revealed an anterior-to-posterior gradient of activation with selective activation for sequential and simultaneous stimuli in the anterior and posterior areas respectively, and overlapping activations in between (Figure 4B). This study provides the first direct evidence that, in humans, the right IPS contains representations of numerosity both dependent on and independent of the mode of presentation.

Secondly, the precise anatomical overlap between numerosity and duration estimation processing has been explored using fMRI (Dormal, Dormal, Joassin & Pesenti, 2011). Participants were asked to categorise the numerosity of flashed dot sequences or the duration of single-dot displays. The results revealed a large right-lateralised fronto-parietal network, including the IPS and areas in the precentral, middle and superior frontal gyri, that was activated by both numerosity and duration processing. Complementary psychophysiological interaction (PPI) analyses showed functional connectivity between the right IPS and the frontal areas in both tasks, whereas the right IPS was connected to the left IPS and the right precentral area in the numerosity categorisation task only (Figure 4C). These findings suggest that the right IPS underlies a common magnitude processing system for both numerosity and duration, possibly corresponding to the encoding and accumulation stages of the accumulator model, whereas the frontal areas are involved in subsequent working-memory storage and decision-making processes.

Finally, a third study used fMRI to localise the cerebral network involved in processing both numerosity and length (Dormal & Pesenti, 2009). Blood oxygenation level-dependent signal changes were measured while healthy volunteers were making numerosity comparisons of linear arrays of dots, and length comparisons on discrete linear arrays of dots and continuous rectangles. The results showed the bilateral involvement of parietal areas around the IPS in explicit and implicit processing of numerosity, and a right lateralised occipitoparietal network activation in length processing; numerosity and length processing both activate the right IPS and the precentral gyrus. Together, the results demonstrate for the first time in a within-participant design the involvement of an area along the right IPS in the processing all three of numerosity, duration and length (Figure 4).

3.3.3. Transcranial Magnetic Stimulation Studies

The causal role of the IPS area which recent fMRI studies have been found to be most jointly activated during magnitude processing (Dormal et al., 2009; 2011) was assessed with TMS. First, a possible dissociation of numerosity and duration processing was tested in an off-line repetitive TMS design (Dormal, Andres & Pesenti, 2008). Participants were asked to compare the numerosity of flashed dot sequences or the duration of single dot displays before and after 15 min of 1 Hz rTMS over one of three sites (the left or right IPS, or the vertex chosen as a control site). Performance was only slowed down, compared to the control site, for the numerosity comparison task after the left IPS stimulation, whereas it was not affected for the duration comparison task for any of the parietal sites. These results suggest that the parietal area critically involved in numerosity processing is not involved in duration

processing, revealing at least one cerebral site where duration and numerosity comparison processes dissociate.

In a second study, the critical involvement of the left and right IPS in numerosity and length processing was tested with neuro-navigated rTMS (Dormal, Andres & Pesenti, 2011). Participants had to categorise linear arrays of dots as containing “few” or “many” dots, and filled rectangles as “short” or “long”. The stimulation sites were determined for each individual participant by identifying the IPS areas showing peak activity during a number comparison task in earlier fMRI studies (Dormal et al., 2009; 2011). Compared to the stimulation of the vertex chosen as a control site, rTMS over the right IPS increased the error rate in both tasks. This result indicates that the integrity of the right IPS is a necessary condition, not only for discriminating numerosities but also for performing accurate judgements of lengths, suggesting that these two processes rely on a common representation and/or mechanism in the right IPS.

4. TOWARDS AN INTEGRATED MODEL OF MAGNITUDE PROCESSING IN THE PARIETAL CORTEX

All the studies presented in this chapter have helped us to explain the importance of numerosity, duration and length estimation processing, present at an early age in young children and shared by other animal species.

At a behavioural level, a few classical effects (e.g., distance, size effects) are observed in various judgements of the three magnitudes, and show similar developmental trajectories. The exploration of interactions between these magnitudes, through Stroop-like paradigms and with carefully controlled materials, has highlighted the existence of a continuum of automaticity. Numerosity processing takes place more or less automatically, followed by length processing and finally duration processing (Dormal & Pesenti, 2007; in press). Future investigation of the time course of these facilitation and interference effects, using for example ERPs, will identify the stage at which the differences between the dimensions emerge and will establish whether or not accessing a common representation is necessary.

At a neuroanatomical level, several studies converge towards the common involvement of a specific brain area located along the right IPS when processing different magnitudes (Dormal et al., 2009; 2011). This common activation focus therefore underlies a mechanism and/or a representation system of generalised magnitude, as postulated by Walsh (2003). The parietal cortex, a sensory convergence region, is the ideal candidate for the role of the “magnitude primary cortex” (Buetti & Walsh, 2009; Walsh, 2003). Indeed, this area contains, from birth, a system dedicated to action and able to undertake general dichotomous processing associated with quantities such as “more than – less than”, “quicker – slower”, “closer – further”, “larger – smaller”, a system on and from which the abilities of numerical discretisation can be developed. In addition, with the leading role of the parietal cortex in sensory-motor transformations related to action, it seems natural that spatial processing and temporal processing, recognised as essential in the metric of action, share brain areas close to the parietal area. However, as pointed out by Walsh (2003), if the parietal cortex is a central area, it is not the only cerebral area underlying magnitude processing. Thus, for example, the involvement of the prefrontal cortex in different magnitudes judgements has been highlighted

in recent studies both in monkeys (Diester & Nieder, 2008; Nieder & Miller, 2003; Tudusciuc & Nieder, 2009) and in humans (e.g., Dormal et al., 2011a; 2011b; Lewis & Miall, 2003b; Rao et al., 2001; Rusconi, Buetti, Walsh & Butterworth, 2011). Neurophysiological data in monkeys suggest that the activation of the parietal cortex is different and earlier than that in the prefrontal cortex (Nieder & Miller, 2003; Tudusciuc & Nieder, 2009), but little information is currently available on the similar or distinct contributions of these areas during magnitude processing, because to date the studies have focused primarily on the role of the parietal cortex.

Importantly, the existence of this common representation allows us to account, firstly, for the behavioural interference effects observed between several magnitudes (for a review, see Dormal & Pesenti, in press), and, secondly, for the common impairments observed in the processing of length and numerosity after the stimulation of the right IPS in a TMS study (Dormal, Andres & Pesenti, 2011). However, if a common representation exists, the IPS also appears to host partially distinct representations. Both neurophysiological studies in monkeys (Tudusciuc & Nieder, 2007; 2009; Nieder et al., 2006) and the double dissociation observed in two brain-damaged patients presenting specific deficits in either numerical or duration processing (Cappelletti et al., 2009; 2011) indicate the existence of common and distinct representations. Similarly, the presence of some unilateral interactions between magnitudes in behavioural studies (e.g., Dormal et al., 2006; Droit-Volet et al., 2003), the disruption of numerosity processing after TMS over the left IPS (whereas no effect was observed on duration judgement (Dormal et al., 2008)), and the distribution of activation along the IPS during sequential and simultaneous numerosity comparisons (Dormal et al., 2010) all support this hypothesis. In future, the combination of behavioural, neuropsychological, neurophysiological and neuroimaging studies will establish the exact role of these different representations and will shed light on the possible involvement of other brain areas which may constitute a magnitude representational network.

To sum up, both behavioural and neuroimaging results suggest the coexistence in the IPS of specific (i.e., concerned with the processing of a single dimension) and shared (i.e., common to several magnitudes) magnitude representations and/or processing mechanisms. A magnitude system partly-shared among dimensions implies that, in addition to sharing a general magnitude system, numerosity, length and duration are also implemented by dimension-specific processes (e.g., Cantlon et al., 2009; Cappelletti et al. 2009; 2011; Walsh, 2003).

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