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Mapping numerical magnitudes into behaviour

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I, Vjaceslavs Karolis, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Abstract

The importance of spatial models for numerical representations and the functional relation between number and space in the parietal cortex are suggested by the evidence that numerical information may affect spatial processing. It has been hypothesized that number maps onto a unidimensional continuum, the mental number line, and that number and space share a common metric. An investigation of the metric for numerical magnitudes, whether it is shared with space, and how this relation is reflected in behaviour, represent the main topic of the thesis. The hypothesis of shared metric is evaluated by the experimental work in the context of two topics: a) the subjective scale for numerical representation and b) the origin of spatial numerical interactions in visuomotor behaviour. Chapter 2 addresses an issue whether number, similarly to some physical magnitudes, may be represented on the logarithmically scaled continuum. The method for differentiating between logarithmic and linear hypotheses about the scale for number is implemented using novel variants of the number-line task, with results supporting the linear scaling schema. In Chapter 3, the method of transcranial magnetic stimulation was used to investigate whether the parietal areas, known to process numerical distance and allegedly implementing the mental number line, are involved in ratio scale computations, which are not compatible with mental number line model. Chapter 4 proposes a structural similarity between scales for number and space as a criterion to support the common metric between number and space. The scale analysis of number mapping onto space demonstrated discrepancy between spatial and numerical metrics for the performance in the manual estimation. Chapter 5 was designed to differentiate between the effect of number on the automatic visuomotor adaptation and on the response selection. The results

show no evidence for the effect of number on the on-line motor corrections but reveal the signatures of non-sequential number mapping onto space at the stage of response selection. The findings in Chapter 5 are contrasted with the findings from Chapter 6, showing a pronounced effect of spatially non-specific expectations on the speed of the visuomotor coordination and spatial discrimination. The overall results do not support the hypothesis of the common metric for number and space and suggest that spatial models for number are deployed flexibly according to task demands.

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Chapter 1. General Introduction

1.1 The signatures of semantic number processing. Mental number line model

It is not unusual that a small range of highly replicable phenomena define a development of a whole scientific field. In the domain of the cognitive study of number, one could identify three phenomena of this sort. First, number processes are subject to the *distance effect*; that is, longer response times are required to distinguish between close magnitudes than distant ones. This effect was first demonstrated by Moyer and Landauer (1967) for number comparison. Second, number processes are also affected by the *size effect*; that is, it takes more time to distinguish between large magnitudes relative to small magnitudes when they are separated with the same numerical distance (Buckley & Gillman, 1974; Parkman, 1971; Parkman & Groen, 1971). Third, converging evidence suggests a specific compatibility between number magnitude and the side of space termed *spatial numerical association of response codes* (SNARC) effect. It was first demonstrated in the study by Dehaene, Bossini, and Giraux, 1993), where subjects had to perform a speeded parity judgement task by pressing the left (right) button if a number presented centrally is even (odd). Irrespective of parity, left-side responses were faster than right-side responses for small digits and, conversely, right-side responses were faster than left-side responses for the large ones.

A striking point about these three effects is that they suggest a close relation between spatial and numerical processes in the brain. The distance and size effects are equally characteristic of spatial magnitudes. It is much easier to tell the difference between two physical lines differing by 10 mm than by 1 mm (i.e., distance effect), and this difference will be easier to see if the shorter line were 10 mm long than if it were 100 mm long (size effect). The SNARC effect, meanwhile, shows that numerical process can directly interfere with spatial response. The similarity of processing signatures between number and space as well as the interference of number with spatial responses were interpreted to mean that subjective number representations have an implicit and unique spatial architecture (Hubbard, Piazza, Pinel & Dehaene, 2005; Izard & Dehaene, 2008). A unifying framework, accounting for the above phenomena, treats numerical magnitude as a random Gaussian variable (Izard & Dehaene, 2008; Nieder & Miller, 2004; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004) that maps in an increasing order from left to right onto a subjective continuum: the "mental number line" (Dehaene, 1992; Restle, 1970). To put it simpler, our representations of number are intrinsically noisy and, by default, spatially aligned from left to right. The distance effect, then, is the result of an increasing overlap between distributions for numbers with close magnitudes as compared with an overlap between distributions for far magnitudes.

Two hypotheses were proposed to account for the size effect. According to one, the scale of mental number line is logarithmically compressed (Dehaene, 2003; Izard & Dehaene, 2008). As a result of such compression, spacing between two neighboring numbers should decrease with an increase of their magnitudes, leading to a greater overlap of distributions. An alternative hypothesis proposes that the subjective scale is linear but the noisiness of mapping increases proportionally with number magnitude, also leading to a greater overlap (Gallistel & Gelman, 1992; Whalen, Gallistel, & Gelman, 1999). This property is also known by a term of a scalar variability (Izard & Dehaene, 2008).

Further evidence of an association between number and side of space as well as evidence for a common neural basis for spatial and numerical processing was demonstrated in the studies of neglect patients with a lesion in the right parietal cortex. Thus, Zorzi, Priftis and Umilta (2002, see also: Zorzi, Priftis, Meneghello, Marenzi & Umilta, 2006; Cappelletti, Freeman, & Cipolotti, 2007) showed that patients tend to overestimate the midpoint of a numerical interval, which is consistent with their left-side neglect of the physical space. Importantly, the neglect was shown to monotonically increase as the numerical interval increased. Analogous effect was observed for the length of the physical lines. By contrast, only the bias but not a monotonic increase was observed for alphabetic sequences (Zorzi, Priftis, Meneghello, Marenzi, & Umilta, 2006), suggesting that the spatial codes for letters, unlike for numbers, are rooted in a dichotomous categorical association rather than in a graded mapping. Rossetti et al. (2004) also showed that the neglect on the number task is susceptible to the therapeutic effect of the prism adaptation, known to improve subsequent performance in the line bisection task.

The hypothesis that the brain uses an implicit spatial model to access the meaning of numerical values should not be confused with the evidence for 'number forms', conscious and vivid synaesthetic images of numbers experienced by some individuals (Galton, 1880). These mental images appear to be obligatorily activated every time those individuals face numerical problems (Sagiv, Simner, Collins, Butterworth, & Ward, 2006). Subjects tend to over-rely on their number form representations, which may negatively affect performance in arithmetic tasks, such as multiplication and addition (Ward, Sagiv & Butterworth, 2009; see also Piazza, Pinel & Dehaene, 2006) for number comparison). Nevertheless, the relation of the number forms to number magnitude representations remains unclear, since there is a high inter-subject variability, i.e. oriented from left to right in one person, and in an other from right to left; or frequently being organized in two, or even three, dimensions rather than one.

1.2 Neural correlates of the distance effect

Converging evidence from functional imaging, patient and animal studies indicate the importance of the parietal regions for number processing (e.g. Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003; Kadosh, Kadosh, Kaas, Henik, & Goebel, 2007; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). In fMRI studies, among various methods, the experimental manipulations on numerical distance were particularly diagnostic for showing that parietal regions, specifically, bilateral intraparietal sulcus (IPS), implements semantic processing of magnitudes. It has been shown that manipulations with the distance evokes differential blood oxygenazation level dependent (BOLD) signal in the IPS (Pinel, Dehaene, Riviere, & LeBihan, 2001; Pinel LeBihan, Piazza, & Dehaene, 2004; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Ansari, Dhital, & Siong, 2006; but see Tang, Critchley, Glaser, Dolan, & Butterworth, 2006). The neural substrates for number processing apparently overlap with processing with those for physical magnitudes. For example, Pinel et al. (2004) observed that the modulation of the IPS activity by magnitude distance for both number and physical size. However, other studies showed that the overlap is not complete (e.g., Castelli, Glaser, & Butterworth, 2006) with distinct parietal regions involved in processing discrete and continuous quantities.

The casual relation, rather than just correlation, between IPS processes and the distance effect was documented in the transcranial magnetic stimulation (TMS) studies (e.g., Cappelletti, Barth, Fregni, Spelke, & Pascual-Leone, 2007; Cappelletti, Maggleton,

& Walsh, 2009; Kadosh, Muggleton, Silvanto, & Walsh, 2010). For example, Cappelletti et al. (2007) showed that repetitive TMS to the left IPS slows down performance in number comparison for both symbolic and non-symbolic notations, whereas the stimulation to the right IPS facilitates it as compared to sham. Critically, the stimulation to the left IPS slowed the comparison of close numbers more than that of far numbers. The effect of stimulation on the comparison of non-numerical stimuli (ellipses) showed the opposite lateralization; that is, the deterioration of performance (as well as the distance effect modulation) was found after the stimulation to the right IPS.

It has been argued, however, that increased activation in the IPS observed in fMRI studies and increased reaction time (RT) in TMS studies may be related to a more general component of a task such as the difficulty of response selection. Because differentiation between two close numbers behaviourally is more difficult than that between two far numbers, the modulation in the IPS by numerical distance may simply reflect an increase in the task demands. It has been shown that, when the numerical and non-numerical tasks are matched in difficulty, no specific area for number processing was found (Gobel, Johansen-Berg, Behrens, & Rushworth, 2004). In a more recent study (Cappelletti, Lee, Freeman, & Price, 2009), the activation in the left parietal cortex did not survive the contrast when RT was taken as a covariate. The activation in the right IPS was selective for number stimuli, but it was not exclusive to the magnitude computations (e.g., activated when the task was to judge whether numbers would represent a legitimate time in the calendar year).

The issue with the task difficulty can potentially be resolved by the use of the fMRI adaptation paradigm where no response is required from the subject (Grill-Spector &

Malach, 2001). The sequence of events in this paradigm is as follows: subjects are presented with a sequence of stimuli identical along a particular dimension; the repeated presentation leads to a decrease in the activation in the candidate area; after an adaptation period, a deviant stimulus is presented; the presentation of a deviant stimulus causes a disinhibition (increase) of the BOLD signal in the same area.

The results from this paradigm in the study of number are somewhat mixed. Thus, Shuman and Kanwisher (2004) presented subjects with repetitive stimuli but they failed to obtain the adaptation effect; that is, the brain activation in the IPS did not decrease as a function of the number of stimulus presentations. Piazza et al. (2004) used a different approach and measured not the adaptation effect but the dishabituation of the signal in response to a deviant numerosity following the repetitive presentation of a standard numerosity. They found a greater increase in the BOLD signal for more distant deviants, or to put differently, the strength of dishabituation positively correlated with the numerical distance. Meanwhile, the findings by Ansari, Dhital, and Siong (2006) were exactly opposite to that by Piazza et al, showing that the closer the deviant number to an adopted standard the greater the BOLD signal. The strength of dishabituation here reflected the difficulty of processing two close magnitudes as compared to two far magnitudes rather than the distance between habituated and deviant numbers. Although the differences in experimental designs might be responsible for this discrepancy between two studies (as suggested by Ansari et al.), it still remains an open issue what task-specific features could result in two different ways of implementing number metric.

1.3 Neural model for the number representations: Number-sensitive neurons.

A more refined description of the mechanism that implements encoding numerical magnitudes at the neuronal level is provided by neurophysiological studies in monkeys (Nieder & Miller, 2003; 2004; Sawamura, Shima, & Tanji, 2002). It has been shown (Nieder & Miller, 2003) that the individual neurons in parietal regions behave as numerically selective filters. They respond most actively for a preferred numerosity *n*, less actively for the numerosities *n*-1 and *n*+1, and so on, forming a Gaussian-like tuning curve. The range of such neurons can potentially be larger. The initial findings of the numerically selective neurons for a limited range of up to 5 numbers were further extended for the range of up to 30 (Nieder & Merten, 2007).

According to this framework, the refinement of the ability to discriminate between magnitudes, measured as a Weber fraction, is determined by the bandwidth of the neuronal filters. The neurons with narrower bandwidth are more selective and are able to encode numerical information with a greater precision. It should be noted that the neuronal model naturally predicts the distance and size effects. The Gaussians for neurons with close preferred magnitudes overlap, giving rise to the distance effect. The selectivity of the neurons also tends to decrease with magnitude accounting for the size effect.

The neural networks simulations also suggest that the encoding of a magnitude by numerically selective neurons should be preceded by additional processing layer which is numerically sensitive but not selective (Verguts & Fias, 2004; Stoianov & Zorzi, 2012). This is particularly important for processing non-symbolic magnitudes, e.g., numerosity of an array of a set of objects, and where numerical magnitude should be extracted from the physical dimension of a stimulus (Stoianov & Zorzi, 2012). The numerically-selective and numerically-sensitive layers are sometimes referred to as place and summation codings, respectively (Verguts & Fias, 2004). The difference between these two can be demonstrated using the same mental number line metaphor. If number line is composed of the aligned activation units, then the summation coding would activate the whole range of units from the beginning of the line up to the value of an encoded number (or, in general, up to value of its neural transform), whereas the place coding encodes a specific location on the line. One fMRI study (Santens, Roggeman, Fias, & Verguts, 2010) identifies the superior parietal lobe as an area, where the summation coding takes place. The behavioural evidence for two types of coding can be found in the study by Roggeman, Verguts, and Fias (2006). They used the magnitude naming task where target Arabic and dot numbers were primed with either Arabic numerals or dots. It has been shown that the dots primed responses in naming of only smaller or same magnitude numbers, whereas the priming effect of the Arabic numerals was a V-shaped – stronger facilitation for the same magnitude prime and target, decreasing with numerical distance between prime and target.

1.4 Common metric for number and space in the parietal cortex: a theory of magnitude.

A further step towards understanding relations between number and space became a theoretical hypothesis, generalizing both neuroscientific and behavioural evidence, proposed by Walsh (2003). According to this hypothesis, aka A Theory of Magnitude, (ATOM; Bueti & Walsh, 2010; Walsh, 2003), the neural circuitry in parietal cortex implements a common magnitude system for number, space and time, required to bring together magnitude information from different modalities in order to subsequently use it for visuomotor transformations. The functional relation between magnitudes is that by the common metric for action, and as Walsh (2003) put it, "the parietal cortex transformations, that are often assumed to compute '*where*' in the space, really answer the questions '*how far, how fast, how much, how long and how many'* in respect to action" (p.486). From ATOM perspective, the SNARC effect is just an instance of a more general SQUARC effect (spatial quantity association of response codes), i.e., the phenomenon of cross-domain priming between different sorts of the magnitudes. In other words, ATOM is not constrained with the spatial form of the numerical representations, presuming that any form of the spatial organization of number will be consistent with it.

The appeal of ATOM, as a theoretical framework, is that it attempts to provide an answer to three important questions: where (neural networks in parietal cortex), how (by a common metrics) and why (to enable transformations required to act) number and space are functionally related. ATOM also generates a number of predictions which can be experimentally tested. The first one is that the existence of common metrics implies similarity in subjective scales for numerical and spatial magnitudes. As spatial magnitudes obey Weber-Fechner Law, implying that their subjective scale is logarithmically compressed, the scaling schema for numerical representations is expected to be logarithmic. Second, because parietal networks are concerned with action metric and planning, one can predict that numerical processing may influence action execution by interfering with spatial parameters of movement.

1.5 Two problems considered in the present work

An investigation of the metric for numerical magnitudes, whether it is shared with space, and how this relation is reflected in behaviour, represents the main topic of the present thesis. In the remainder of the introduction, I will discuss both the findings that support the hypothesis of the common metric for number and space and the critique of this view. The problem of the metric for numbers can be considered in two contexts.

Problem 1. The quantitative nature of numbers justifies the use of psychophysical methods in the study of numerical cognition (e.g. Izard & Dehaene, 2008; Siegler & Opfer, 2003) and raises the question about the *internal (or subjective) scale* of numerical representations. I will describe the evidence for two proposed scaling schemas: one hypothesis holds that numerical magnitudes are represented on the linear scale, the other holds that numerical magnitudes are logarithmically compressed. Given that the processing of some spatial magnitudes obeys the Weber-Fechner law, the evidence of the logarithmic compression for numerical magnitudes would provide a strong evidence for a shared metric between number and space. I will argue, however, that the previous studies have not been able to differentiate between two hypotheses and that the reason for this is purely methodological.

Problem 2. One of the important sources of evidence for the shared metrics between number and space can be found in the studies of the effect of number on the visuomotor performance. I will discuss the literature on this topic, what information about spatial-numerical associations can be derived from it, and what is missing in those studies to support decisively an intrinsically spatial character of number representations.

1.6 Behavioural studies on the subjective scale

Because both linear and logarithmic hypotheses predict similar outcomes (Dehaene, 2003), distinguishing between them is a non-trivial empirical problem. An attempt to solve this problem has been made by studies exploiting the number-to-location mapping paradigm. For example, Siegler and Opfer (2003) presented subjects selected from four age groups (second, fourth, and sixth graders and adults) with a line labeled with “0” at one end and “100” or “1,000” at the other and asked them to mark on the line the magnitudes of numbers contained within those intervals. The study showed that the younger groups (second and fourth graders) exhibited responses that were best modeled by a logarithmic function, whereas older children and adults used linear mapping. The authors suggested that children initially possess a logarithmic subjective scale associated with a more primitive sense of numbers (Dehaene, 1997), and that the scale becomes linear at later stages of development through the use of counting series and language.

Other studies suggest that a logarithmic component persists in the subjective scale of adults if approximate estimation is required. Thus, Dehaene, Izard, Spelke, and Pica (2008) asked subjects to rate the magnitude of a non-symbolic numerosity (dots or tones) on the line bracketed with either 1 and 10 or 10 and 100 dots. They showed that small non-symbolic numerosities up to 10 items, which could be easily counted, were rated linearly. By contrast, rating large non-symbolic numerosities (10 – 100) exhibited a significant logarithmic component, suggesting that the scale for approximate estimation is not completely linearized.

The evidence for the logarithmic compression of non-symbolic magnitudes can also be found in dot enumeration. It has been shown (Izard & Dehaene, 2008; Krueger, 1982) that mapping from a number of dots to digits obeys Stevens power law (Stevens, 1957); that is, the relation between stimulus numerosity D and subjects’ response N is captured by a power function $N = \alpha D^{\beta}$, with exponent $\beta<1$. This form of mapping is consistent with the idea that both dependent and independent variables are the logarithmic interval scales (in other words, there is a linear relation between their logarithms, $\log N = \log \alpha + \beta \log D$; see Luce, 1959, Theorem 9). Given that two logarithmic scales are required for the power law to hold (if the magnitude encoded on the log subjective scale was mapped directly into behavior, the response function would be of the form $N = \beta \log D + \alpha$), Izard and Dehaene (2008) proposed the following mechanism. At the first stage, perceived numerosities are encoded on the log-scaled mental number line. At the second stage, the analogue representations on the mental number line are transformed into a response by means of a response grid. The latter is also log scaled, but it can be "calibrated" with respect to the mental number line with affine transformations (stretch or shrink and shift), allowing for the adjustment of response criteria as a result of a feedback, comparison to a standard, etc.

Longo and Lourenco (2007) also demonstrated the presence of a logarithmic component in the subjective scale in the estimation of symbolic magnitudes. The novelty of their approach was to vary the start of the interval and its length, making the task much more challenging for subjects when they needed to estimate the interval midpoint. Assuming homomorphism between physical and numerical magnitudes, the authors proposed that the bisection of numerical intervals should be affected by "pseudoneglect." This phenomenon is characterized by the tendency, found in healthy adults, to bisect physical lines to the left of the objective center (for review, see Jewell & McCourt, 2000). Provided that pseudoneglect represents an attentional bias of a constant strength, the authors argued that the error in the interval bisection task (i.e., the underestimation of an interval mean) should depend on the magnitude of this mean. Specifically, the authors predicted a greater underestimation for the interval mean of a larger magnitude, as the distance between large numbers on the logarithmic scale is smaller than between small numbers, meaning that an attentional bias of a constant strength should span a greater numerical distance. The results confirmed the predictions, showing that the underestimation of the interval mean increased with its magnitude. In another study, Lourenco and Longo (2009) administered a similar task, this time also asking subjects to retain in memory small or large numbers presented in the beginning of each trial. When subjects retained a small number, the modulation of the bias by number magnitude persisted; when subjects memorized a large number, no modulation was found. Following Banks and Coleman (1981), Lourenco and Longo (2009) proposed that the use of either logarithmic or linear scale may depend on the specifics of a numerical problem at stake.

1.7 Methodological issues in behavioural studies of subjective scale

Although the previous research provided evidence in favour of both linear and logarithmic hypotheses, there are reasons to believe that the methodology used in the study of subjective number scaling is problematic.

The most obvious problem is that the studies, such as one by Siegler and Opfer (2003), use numerical intervals that are standards for the decimal counting and metric systems. These intervals may be highly overtrained through education and life experience. The near 100% of variance explained by the linear fit in adult data suggests that the task was very easy, giving rise to a ceiling effect. Second, it is possible that the access to the magnitude of a number is not required for an adult to correctly perform in this task. In fact, the problem can be solved algorithmically on the basis of precise ordering provided by the counting system. For example, the interval can be roughly partitioned into parts hallmarked by the multiples of 10, and the required number between them can be found by interpolation.

A more critical problem, however, is that the presence or absence of a log-like non-linearity of the trend does not generally guarantee the presence or absence of a logarithmic component in the subjective scale. In the number line tasks (Barth & Paladino, 2011; Moeller, Pixner, Kaufmann, & Nuerk, 2009; Siegler & Opfer, 2003), this problem is reflected by an on-going discussion about the function that should be used to fit the data of young children. For example, Moeller et al. (2009) suggested that the non-linearity is better modeled by a segmented linear regression line. More recently, Barth and Paladino (2011) showed that the performance in the task can also be accounted for by Spence's power model of proportional judgements (Spence, 1990). The model predicts that the proportion P of some unit magnitude (e.g. length of a line or the length of numerical interval) will be overestimated if $P < .5$ and underestimated if $P > .5$. The predicted response function for the model is not linear, though, as the over- and underestimation starts converging monotonically to zero for extreme values of P (i.e. $P \to 0$ or $P \to 1$).

The same problem applies to the dot enumeration studies. There is no objective reason (see Luce, 1959, Theorem 1) for assuming the hypothesis of logarithmic interval scales (as in Izard & Dehaene, 2008) to interpret the data, given a basic principle underpinning the power law. According to the law, subjects use ratio scaling, where equal stimulus ratios tend to produce equal sensation ratios (Stevens, 1957). The log transformation of the power function does not have any functional significance here, but is motivated by presentational convenience: the slope of the line on the log-log plot is the exponent. Given that the exponent in dot enumeration tasks is less than 1, it means that each time the number of dots is doubled, an estimate increases less than twice.

Another problem is that the previous studies assumed that any trend observed in the responses follows solely from the idiosyncrasies of the subjective scale. However, this is not a valid assumption, as some systematic tendencies may result from response biases. One of these biases, the *central tendency effect*, was branded by Stevens (1971) as "one of the most obstinate" and "perhaps most important" (p. 428). It was first described by Hollingworth (1910), who found that judgments of physical magnitudes reveal a tendency to "gravitate toward a mean magnitude" (p. 461) of a series of presented stimuli, termed by him the *indifference point*. In other words, the stimuli of small magnitudes tended to be overestimated, and the stimuli of large magnitudes tended to be underestimated. The indifference point is not necessarily equal to a linear mean of the series. Helson (1947) argued that central tendency represents the pooled effect of all stimuli. Consequently, if the magnitudes of stimuli are represented on the compressive scale, the indifference point will be close to a geometric mean of the series; that is, its proportional magnitude to the range of series will be greater than that of an arithmetical mean.

The relevance of the central tendency issue for the study of number magnitude scaling is implied by two facts. First, the central tendency forces the response function to be less steeply increasing. For a cross-modal matching paradigm (e.g., dot enumeration), it means a smaller value for the exponent of power function. Because the "true" exponent is not available, the inference based solely on the analysis of exponent values (as is the case in Izard & Dehaene, 2008) may be inaccurate. Second, the central tendency may provide an alternative interpretation for compressive signatures found in the studies by Longo and

Lourenco (2007; Lourenco & Longo, 2009). It is not clear whether the change in the size of the bias with number magnitude, reported in those studies, resulted from logarithmic spacing between magnitudes on the underlying mental continuum or from a tendency to overestimate small numbers and underestimate large numbers. In other words, a weaker pseudoneglect, found for the small magnitude of an interval mean, could also occur if the underestimation due to pseudoneglect was counterbalanced by the response bias to overestimate small numbers; and conversely, a greater pseudoneglect for the large magnitude of the mean could be a sum of pseudoneglect and the response bias to underestimate large numbers.

1.8 Symmetry of the tuning curves

Some authors argued that the behavioural evidence may be insufficient to differentiate between two hypotheses but this can be done on the basis of the neurophysiological evidence (Merten & Nieder, 2009). An important characteristic of the tuning curves for the number-sensitive neurons, demonstrated experimentally (Nieder & Miller, 2003; Nieder & Merten, 2007; see also Piazza et al., 2004 for fMRI paradigm) and predicted from the neural network simulation (Verguts & Fias, 2004), is their positive skewness; that is, the Gaussian curve representing the firing rate of a neuron is shallower for numbers greater than its preferred numerosity. This feature was interpreted as an evidence for the log scale of the numerical representations, given that the log transform of the numerical magnitudes brings a positively skewed Gaussian into a symmetrical shape. It has been suggested that the symmetry of the distribution is a critical variable that allows dissociating between two scales (Merten & Nieder, 2009).

There are two problems with this view. First, the presumed advantage of the log scale schema from a computational point of view is that it does not require rescaling in order to make large magnitudes manageable. This is done by compressing the upper range of the scale. Nevertheless, Nieder & Merten (2007) showed, the representation of 30 numbers requires 30 types of neurons, that is as many as the representations of 30 numbers on a non-compressed scale. One could expect that less than 30 neurons would be required to 30 different numbers, if the representations were compressed.

Second, the relation between log scale and positive skewness is not necessary reciprocal. In other words, the log scale implies the skewed distribution, but it does not mean that the log scale is implied by a skewed distribution. An alternative hypothesis would hold that numerical magnitudes accord with the linear scale but the discrepancy detected by number neurons between an actually presented and preferred numerosity is represented relatively; that is, the distance function is determined not by the difference between magnitudes but by the ratio between them. It leads to similar predictions in respect to the skewness of the tuning curves. Specifically, the positive skewness in the distribution of the firing rates may occur when the process of the matching between preferred and actually presented magnitudes implements taking a ratio Preferred/Actual. The formal equivalence between two hypotheses is captured by the fact that $\log(A) - \log(B) = \log(A/B)$, implying that, when the difference between logs is mapped onto the linear scale, the relation between A and B is given as a ratio. It is also worth noting that the log function did not provide a better fit to the reported data than the power function (Nieder & Miller, 2003; Nieder & Merten, 2007), despite that the exponent for the fitting power function was chosen arbitrarily. In other words, the differentiation between linear ratio scale and logarithmic interval scale on the basis of the distribution symmetry only is not possible in principle unless there is a strong reason to believe that the distance function on the neuronal level is represented as a difference not as a ratio. So far, no evidence for this exists.

1.9 The origin of the spatial-numerical associations. Mental number line criticism

The critical point about the mental number line hypothesis is that mapping onto a mental number line is not a by-product of number semantic processing but *is* a semantic processing proper, in a sense that accessing numerical magnitude obligatorily relies on the use of an implicitly spatial representational model, the access to which is automatic and beyond cognitive control. Consequently, this framework treats the left-right association as a signature of the semantic processing in a same way as the distance and size effects. However, some authors questioned whether promoting left-right association to the status of a semantic factor is justified. First, there exists evidence that the SNARC-like effect is not unique in respect to numbers, as other ordinal sequences like letters and months may elicit similar behavioural patterns (Gevers, Reynvoet & Fias, 2003; Dodd, Van der Stigchel, Leghari, Fung, & Kingstone, 2008). This questions the basic premise of the mental number line hypothesis that spatial alignment reflects the access to a magnitude. Second, in patient studies, Doricchi et al (Aiello et al., 2012; Doricchi, Guariglia, Gasparini & Tomaiuolo, 2005) showed that the neglect for the physical line and for the number line can dissociate. They showed that the rightward bias in the number line bisection (cf. Zorzi et al., 2002) was found only in subjects with the lesions extending into the prefrontal areas. None of the patients without a prefrontal lesion showed the bias (see also the lesion sites in Rossetti et al., 2004). The authors suggested that the neglect on numerical intervals resulted from the disruption of the working memory structures. These findings contradict the claims made by Zorzi et al. (2006) about homomorphism of spatial and numerical representations as observed in neglect patients. Finally, the mental number line hypothesis presumes holistic magnitude representations. That is, it holds that symbolic numerical magnitudes are not being mentally decomposed into decades and units. This idea was questioned by Nuerk, Weger and Willmes (2001), who showed that, in the comparison of two-digit numbers, RTs in trials where a unit digit of a smaller number was smaller than that of a larger number (e.g. 42 vs. 57) were shorter than RTs in trials where a unit digit of a smaller number was greater than that of a larger number (e.g. 47 vs. 62), even though the numerical distance was matched.

An alternative interpretation for the number-space interaction was proposed by Proctor and Cho (2006) and Gevers and colleagues (Gevers et al., 2010), who argued that the interference may result from an association of the verbal concepts, such as ‘small’ and ‘left’ or ‘large’ and ‘right’. This association is brought about by polarity coding principle, which states that ‘people code the stimulus alternatives and the response alternatives as + polarity and – polarity, and response selection is faster when the polarities correspond than when they do not’ (Proctor & Cho, 2006, p. 418). Gevers et al. (2010) refer to this sort of coding as to verbal-spatial coding as opposed to visuospatial coding on the mental number line. Consistent with this, some evidence suggest that the SNARC effect originates at the response-selection stage (Keus & Schwarz, 2005; Keus, Jenks, & Schwarz, 2005). The verbal-spatial account for spatial numerical associations is also supported by the evidence that space is coded in two modalities: in coordinate system that is required to guide the movement and attention, and categorical system, associated with the linguistic concepts, such as above/below and small/large (Logan, 1995).

The categorical coding does not necessarily imply that spatial numerical associations cannot be graded. Gevers et al. (Gevers, Verguts, Reynovoet, Caessens, & Fias, 2006) proposed a computational model that accounts for the SNARC effect by assuming that numbers are associated with categories in a graded fashion. Experimental evidence for verbal-spatial mapping was provided in the studies by van Dijck, Gevers, and Fias (2009) and by Gevers et al. (2010). Van Dijck, Gevers, and Fias (2009) showed that the SNARC effect was eliminated if subjects memorized verbal sequences during the parity judgement task and spatial arrays in the magnitude comparison task. This double dissociation suggests that the numerical magnitudes can be associated with different task-dependent spatial codes. In the study by Gevers et al. (2010), the verbal-spatial and visuospatial mental number line codings were pitted against each other. Participants were asked to press the button on the touchscreen labelled as ‘left’ or as ‘right’ in response to the parity of the number. Those labels could be either congruent or incongruent with an actual location of the button (in the latter case, the button with label ‘left’ could be on the right), and varied randomly during experiment. It was shown that a regular SNARC effect occurs in the condition with labels congruent with side of space, whereas the reversed SNARC occurs in the condition with incongruent labels, consistent with verbal-spatial account. A similar result was obtained for the magnitude judgement task. In another experiment reported in the same article, Gevers et al. showed that verbal responding ‘left’ or ‘right’ to the parity of the numbers is sufficient to generate the SNARC effect, and the strength of the effect was comparable to that observed for manual responses.

1.10 Interference paradigms as a tool for the study of spatial numerical association

The study by Dehaene et al. (1990), showing the SNARC effect for the first time, as well as several other studies, cited above (e.g., Gevers et al., 2010), are prominent instances of a general framework which is often used in the study of relations between two cognitive dimensions. In this framework, subjects are instructed to perform a task, where one dimension of stimuli is task-relevant, i.e., subject should respond in accordance with the changes in the stimuli along this dimension. At the same time, stimuli can also be characterised along some other dimension, which is task-irrelevant, but systematically manipulated by the experimenter. The idea is that, if processing the task-relevant dimension utilizes some shared resources with the task-irrelevant dimension, then it may lead to interference, i.e., the task-irrelevant dimension may affect processing task-relevant dimension. For example, subjects may be asked to compare the size of the font between two written Arabic numbers (task-relevant dimension) and, at the same time, these two numbers can differ in their numerical magnitudes (task-irrelevant dimension). The basic finding is that if the size of the font of numerically greater number is also greater, the condition known as congruent, RT is generally quicker than when a number written in a greater font is smaller numerically (incongruent condition). Unsurprisingly, if the condition is neutral, that is, the magnitudes of number are equal, RT for the judgements of physical size of number falls somewhere between RT for congruent and incongruent conditions. This paradigm, showing an instance of spatial-numerical interference, is known as a numerical Stroop paradigm (Henik & Tzelgov, 1982; Tzelgov, Meyer, & Henik, 1992), to distinguish it from the Stroop paradigm proper, which, in its original form, is the task where subjects are instructed to name the colour of a word font when a word was the name of a colour. In general, the Stroop paradigm is able to demonstrate the autonomous access to the meaning of task-irrelevant dimension with differences in RT arising from the effort required to suppress its effect.

Using the logic of the interference paradigms, Fias, Lauwereyns, and Lammertyn (2001) were able to demonstrate evidence supporting the hypothesis of shared neural circuitry as an origin of SNARC. They showed that the SNARC effect occurs when subjects were required to make orientation judgements for the triangle or the line superimposed on the Arabic magnitude. In other words, subjects were quicker to respond to left orientation if the number was small and vice versa for responses to right orientation. In contrast, when the task was to judge the colour of the number stimulus or the shape of the superimposed figure, no effect was found.

Obviously, the response rule can be reversed and task-irrelevant condition becomes task-relevant and vice versa. In the case of numerical Stroop, the effect of number onto space is symmetrical to the effect of space onto number: numerical judgements are equally affected by the size of the font. However, this is not a general rule that, when processing one dimension interferes with processing the other, the reversed would also be true. The relation can be unidirectional, when one dimension affect the other but vice versa, or asymmetric, when the interference of one dimension with the other may be stronger than the interference in the reversed direction (Casananto & Boroditsky, 2008; Casananto, Fotakopoulou, & Boroditsky, 2010). For example, the earlier studies suggested that the SNARC effect is unidirectional, because lateralized stimulus presentation failed to produce any effect on number processing; that is, there was no advantage for small numbers when presented on the left and for large numbers when presented on the right (Keus & Schwarz, 2005; Mapelli, Rusconi, & Umilta, 2003). More recently, however, Stoianov, Kramer, Umilta and Zorzi (2008) argued that spatial information might decay or be inhibited before numerical information was processed, especially, in the situations when spatial location was task-irrelevant. To investigate this possibility, the authors used a positional cue paradigm (e.g. Posner, Snyder, & Davidson, 1980), where a left or right cue was presented before or after number for which subject had to do either number comparison ('Is a number bigger or less than 5?') or parity judgement tasks. According to the SNARC, the predictions were that the left cue should facilitate the processing of small numbers 1-4 (congruent condition) but inhibit performance for large numbers 6-9 (incongruent condition), and vice versa for the right cue. The findings were that a spatial cue presented after numerical stimuli elicited SNARC effect in both tasks, whereas the cue presented before a number did not have any affect on performance, confirming authors conjecture.

1.11 The effect of number on the visuomotor performance

Number in the grasping studies. One way to contest the possibility of the frontal working-memory verbal-spatial origin for the spatial numerical associations is to demonstrate that numerical information has the effect on the tasks where performance is expected to rely heavily on the parietal networks. One of the facts that motivated ATOM is that parietal cortex plays a critical role in the visuomotor control. Consequently, the effect of task-irrelevant numerical information could provide an important evidence for the common metric between number and space.

Most reliable evidence for the effect of number on visuomotor coordination was accumulated in the grasping tasks. In the first study of this kind, Andres, Davare, Pesenti, Olivier and Seron (2004) asked subjects to respond to a parity of a presented number by either opening or closing finger aperture. They showed that grip closure is initiated faster for small numbers than for large ones and vice versa for grip opening, irrespective of number parity. The difference in RTs between grip closure and opening showed a clear parametric pattern as a function of numerical magnitude. These findings were complemented by Moretto and di Pellegrino's study (2008), where subjects were required to make parity judgements by imitating a power/precision grip (i.e., without getting hold of an object). The precision grip was quickest for numbers 1 and 2, slower for 3 and 4, and even slower for 6 and 7 and 8 and 9. The pattern was opposite for the power grip.

The other two studies investigated the effect of number in actual grasping where reaching a target is a goal (as opposed to an imitation in two studies mentioned above). Lindeman, Abolafia, Girardi, and Bekkering (2007) asked subjects to reach either large or small target (power grip and precision grip conditions, respectively), depending on the parity of numerical magnitude. They showed that the power grip was executed faster for large magnitudes, whereas the precision grip was faster for small magnitudes. They also showed that the maximum grip aperture tended to be greater for large numbers than for small ones, irrespective of the type of grip. A similar approach was used in the study by Andres, Ostry, Nicol, and Paus (2008). They recorded the size of the hand aperture when subjects moved to grasp objects of different sizes and placed them forward or backward, depending on the parity of the number ('small' 1 an 2 and 'large' 8 and 9) printed on the objects. Andres et al. (2008) showed that the grasp aperture was greater, when number was also greater. A more prominent effect of number was found in the early stages of the movement, suggesting that control mechanisms counteract the number magnitude interference in later stages of movement execution to allow a precise scaling in accordance with actual object size.

Number in pointing tasks. Considering the voluminous literature on the SNARC effect showing association between number and location in space, the number of studies on the effect of numerical information on responses in rapid-pointing tasks remains rather limited. Four studies can be cited.

In the study by Fischer (2003), subjects were required to place their index finger at the centre of a touchscreen and respond by pointing to the left or to the right depending on the parity of a presented number. The critical measures were reaction and movement times, i.e. the time required to initiate the pointing response and the time required for transition of the limb from the starting point to the final location, respectively. Fischer argued that the effect that specifically modulates either reaction times or movement times should tap into a specific processing stage. Longer reaction times would be indicative of an increase in the planning demands, whereas longer movement times would be, by Fitts' law (Fitts, 1954), indicative of an increase in visuomotor demands for movement execution. It was found that movement times for responses to the left target was longer for large numbers 8 and 9 than for small numbers 1 and 2 and vice versa for responses to the right target. The interaction between side of response and number was less reliable for reaction time, as it was found only when the power of experiment was increased by a greater number of subjects (Experiment 3).

The limitation of the above study was that it exploited the categorical distinction between small and large numbers and could not establish the fact of a continuous mapping of number onto space. This issue was addressed in the study by Ishihara et al. (2006) who used a similar logic in respect to reaction and movement time measures. Subjects started from the bottom centre of the touchscreen, did not move if the number was even (NoGo trials) but responded by pointing to an odd number (Go trials 1 3 5 7 9). The target number could appear on the screen in one of the 5 (extreme left, left, centre, right, extreme right) possible locations. Contrary to the Fischer's findings, the movement times were unaffected and the differential pattern was found only for RT. The RT pattern revealed the graded spatial numerical association, consistent with left-to-right orientation of mental number line; that is, for small numbers 1 and 3 the reaction times increased from the extreme left to the extreme right location, and vice versa for large numbers 7 and 9. The reaction times for 5 could be described as a V-shaped function of the target location, with a decrease in reaction time for the central location and a monotonic increase for the eccentrical locations.

What is a possible explanation for the discrepancy between two studies? One way, as suggested by Ishihara et al., is to explain this discrepancy by the differences in the design that include greater amplitude of movement and categorical vs. continuous distinction between both numbers and pointing directions. This explanation is hardly satisfactory as it remains unclear why these differences should lead to these particular behavioural patterns. Meanwhile, a more fundamental problem with the above findings is that reaction and movement time measures can hardly be treated as markers of number interference at specific stages of visuomotor performance. First, longer RT for the incompatible side may simply signify longer magnitude processing times that has nothing to do with movement planning per se. As Stoianov et al. (2008) showed, the interference of spatial lateralization with numerical processing is possible if the spatial information is maintained active at the time of numerical decision. The requirement to move towards the target location could help to maintain the prominence of the spatial information for the length of the trial causing interference. Second, given that a simple pointing movement is executed ballistically (Flash & Hogan, 1985), the effect of number on motor preparation should not necessarily reveal itself only in RT differences. It may be the case that number magnitude elicits the generation of an ‘incorrect’ motor plan, with no differences in the time required to initiate the response. The initial error in the motor command should then be corrected at the stage of movement execution, leading to additional costs in timing. For this reason, movement times cannot be treated as a marker of interaction at the time of movement execution, since the implementation of the initial motor plan will affect the following motor execution and the consequences of the ‘incorrect’ motor plan will be felt later in the process.

An alternative approach to the study of the effect of number on performance in rapid pointing tasks was first taken by Song and Nakayama (2008). They argued that the spatial path of movement represents a natural marker of the spatial processing and it can better reveal the dynamic signatures of the unfolding cognitive processes (Song & Nakayama, 2009). In their experiment, subjects were presented with three squares horizontally aligned. The square in the centre contained a number between 1 and 9. Subjects were asked to execute a manual pointing to the left square if the number was less than 5, to the middle square if the number was 5 (standard condition) and to the right square if the number was more than 5. They observed that responses deviated more to the left or right as a function of numerical distance between presented and reference (i.e. 5) numbers, that is the deviation to the left was greater for 1 and 2 than for 3 and 4, whereas the deviation to the right was greater for 8 and 9 than for 6 and 7. The trajectory differences were found very early in the trajectory (5% of the length), suggesting that number does interfere with planning of the movement, and did not disappear until a very late part (95 %) of the trajectory length. This suggests an early occurrence of the number interference with spatial parameters of movement. However, it remains unclear whether the effect on the later stages is fully pre-determined by those early effects or it contains an independent component.

The findings of the study by Song and Nakayama (2008) were interpreted to support the hypothesis of mental number line mapping. However, the results are far from being conclusive. The source of the confusion is non-counterbalanced experimental design; that is, subjects responded to the left only if number was smaller than 5 and to the right otherwise. The reversed response rule (i.e., 'smaller than 5 –move to the right, larger than 5 – to the left') was not applied. Consequently, this allows for two equally probable interpretations. The first possibility is that the spatial numerical association reflects mental number line mapping proper. In this case, the laterality of the deviation for the reverse response rule would remain unchanged, that is the deviation to the right for 3 and 4 would be greater than for 1 and 2, whereas the deviation to the left for 6 and 7 would be greater than for 8 and 9. The other possibility is that differential pattern reflects the numerical distance. This particular mapping predicts that, for the reversed response rule the deviation would continue to increase with numerical distance between the standard and presented numbers, leading to the reversed laterality, that is - a greater deviation to the right for 1 and 2 than for 3 and 4, and greater deviation to the left for 8 and 9 than for 6 and 7. This kind of mapping was actually demonstrated in the reaction time study by Santens and Gevers (2008). In their experiment, subjects were required to indicate if a number presented was larger or smaller than 5 by pressing a button positioned closer to or further from the reference button depending on the response rule. It was found that numbers 1 and 4 were quicker to respond to by pressing the 'close' button than numbers 6 and 9, and the reverse was true for a 'far' button. Recently, using counterbalanced design, Santens, Goosens, and Verguts (2011) directly tested two hypotheses and showed that the deviations in the trajectories were due to the distance effect rather than mental number line mapping.

Despite the discrepancy in the results, the studies that used the rapid-pointing tasks agree in one important respect. All of them demonstrated mapping that is compatible with an apparently cross-cultural intuition (Dehaene et al., 2008) that numerical magnitudes are mapped onto space in a continuous way. However, they were largely unsuccessful in determining in what stage of the processing the interaction between time and space takes place.

1.12 Overview of the experimental chapters

In line with the two streams of evidence for a common metric for number and space, the experimental chapters of this thesis can be subdivided into two parts. The first part (Chapter 2 and 3) investigates the problems associated with a subjective scale for numerical representations; the second part (Chapters 4, 5 and complimentary Chapter 6) addresses the effects of the numerical information on the visuomotor performance.

Previous investigations on the subjective scale of numerical representations assumed that the scale type can be inferred directly from stimulus-response mapping. This is not a valid assumption because mapping from the subjective scale into behaviour may be non-linear and/or distorted by response bias. The aim of Chapter 2 was to present a method for differentiating between logarithmic and linear hypotheses that is robust to the effect of distorting processes. The method exploited the idea that a scale is defined not by the 'appearance' of response function but by transformational rules. According to Luce's Consistency Principle (1959), the scale is identified when some manipulations with independent variables are closed under admissible transformations for this particular scale. The method was implemented using novel variants of the number line task.

The criterion of admissible transformation is equally applicable to spatial models used to represent numerical information. For example, mental number line representations are not suitable for ratio scale computations. The aim of Chapter 3, using a variant of number line task, was to investigate whether the precision of the ratio scale calculations can be modulated by transcranial magnetic stimulations to the areas (left and right IPS), involved in processing numerical distance and thought to implement the mental number line.

The idea of the shared resources for number and space was supported by findings that numerical information may affect the explicitly spatial visuomotor behaviour. However, showing an interference is not sufficient to demonstrate that number and space share a common metric with respect to action. A more stringent criterion can be derived from a formal description of metrics, the scaling theory. One can propose that the critical test for the hypothesis is to show a structural similarity in the scales for number and space, at least as they can be inferred from the observations of behavioural outcomes. This issue has been investigated in Chapter 4 using the manual estimation task. Subject estimated the size of the stimuli, containing a task-irrelevant number, by scaling the distance between the index finger and the thumb. The primary interest was whether the scales for number and space demonstrate a structural similarity.

The previous pointing studies of number mapping onto space were unable to differentiate at what processing stage number interferes with motor performance. This issue has been addressed in Chapter 5, where the double-step structure of trials allows differentiating between the effect of number on the initial response selection and the effect on on-line visuomotor transformations per se. Here, subjects performed a parity judgement task that required pointing responses to the target containing an odd number. On a proportion of the trials, target could switch the location and subjects were required to adjust their movement trajectories in-flight.

Given that number parity judgement is not an (explicitly) spatial task, it is important to compare the effects of number on visuomotor adaptation with the effect of another type of quantity dissociable from space, but relevant to the behavioural goals. In Chapter 6, I investigated whether the spatially specific visuomotor performance is affected by the conditional expectations of a change in the environment, which, nevertheless, do not provide any information on the exact spatial localization of the change.

Chapter 2. The scale of numerical representations

Abstract

Previous investigations on the subjective scale of numerical representations assumed that the scale type can be inferred directly from stimulus-response mapping. This is not a valid assumption since mapping from the subjective scale into behaviour may be non-linear and/or distorted by response bias. Here I present a method for differentiating between logarithmic and linear hypotheses robust to the effect of distorting processes. The method exploits the idea that a scale is defined by transformational rules, and that combinatorial operations with stimulus magnitudes should be closed under admissible transformations on the subjective scale. The method was implemented using novel variants of the number line task. In the line-marking task, participants marked the position of an Arabic numeral within an interval defined by various starting numbers and lengths. In the line-construction task, participants constructed an interval given its part. Two alternative approaches to the data analysis, numerical and analytical, were used to evaluate the linear and log components. Our results are consistent with the linear hypothesis about the subjective scale with responses affected by a bias to overestimate small magnitudes and underestimate large magnitudes. I also observed that in the line-marking task participants tended to overestimate as the interval start increased, and in the line-construction task they tended to overconstruct as the interval length increased. This finding suggests that magnitudes were encoded differently in the two tasks: in terms of their absolute magnitudes in the line-marking task and in terms of numerical differences in the line-construction task.

2.1 The scale as a set of transformational rules

The mapping from the subjective scale into behavior may be affected by various distorting processes, such as the central tendency or any other form of response bias. Consequently, the type of subjective scale cannot be determined by simply asking people to estimate the stimulus magnitude (Gallistel & Gelman, 2005; Stevens, 1971). A method studying the subjective scale, has to dissociate those biases, which reflect the influence of the task context on the decision-making processes (Jazayeri & Shadlen, 2010), from mental representations. To develop such a method, it is necessary to consider which criteria are used to determine the type of scale. The theory of measurement holds that the type of scale is defined not by the appearance of the response function but by the transformational rules according to which a number gets its assignment (Luce, 1959; Stevens, 1951, 1968). That is, a magnitude N on a particular scale can be constructed by applying those transformational rules to an arbitrary set of other magnitudes. For example, the characteristic feature of the logarithmic scale is that $\log A + \log B = \log AB$, whereas for the linear scale that is not an *admissible* transformation (Luce, 1959), because $A + B = AB$ does not hold, unless $A = 0$ and $B = 0$.

Taking admissible transformations as a criterion defining the scale leads to the consistency principle formulated by Luce (1959): If the manipulations on stimulus magnitude are closed under a specific transformation, then the behavioral outcomes should also be closed under a specific transformation, though not necessarily the same one. That is, to determine whether the subjective scale is log or linear, one needs to determine whether behavioral outcomes in response to combinatorial operations with stimulus magnitudes are closed under the transformations admissible for the logarithmic scale. The critical point is that without combinatorial operations, it is not possible to tell whether the subjective scale is log or linear on the basis of the observed behavior in any mapping task. A log subjective scale could result in a linear mapping to a physical continuum by a log-to-linear transformation in the response generation process; similarly, a linear subjective scale could equally result in a log external mapping by a linear-to-log transformational process.

2.2 Combinatorial method

The main aim of the following study was to present a method for differentiating the hypotheses of linear and logarithmic mapping for numerical magnitudes while controlling for response bias. This method is applied to the data obtained using modified versions of the number-to-position paradigm. Subjects were required either to indicate the relative position of a number within a numerical interval by marking a physical line (the line-marking task, Experiment 1) or, given the segment of an interval, to extend the physical line to fit the length of the whole interval (the line construction task, Experiment 2). The numerical start and length of an interval were varied. Thus, in the line-marking task (see Figure 2.3), the problem subjects could face would be marking the location of the number 23 within an interval bracketed by 12 on one side and 45 on the other. A correct location would be, then, a third of the line from the end bracketed by 12. In the line construction task, the problem was somewhat different. Subjects would be presented with a physical line bracketed by 12 and 23, and they would be required to extend the physical line such that it would correspond to the length of the interval from 12 to 45. The intervals were presented in two orientations: left-to-right (L-R) and right-to-left (R-L). The hypothesis of an obligatory L-R mapping on the mental number line suggests that the performance for the R-L orientation could result in accuracy costs associated with remapping of a R-L interval on the L-R mental continuum. The change in the parameters of a response function is also a possibility.

In the current study three hypotheses were considered: (a) strong linear (i.e., the subjective scale is linear), (b) strong logarithmic (i.e., the subjective scale is logarithmic), and (c) weak logarithmic (i.e., the subjective scale is partly linearized but contains a significant logarithmic component). To make explicit the combinatorial operations underlying the method, let us define two numbers bracketing a numerical interval as Start and End and a number falling within this interval as Target. (The constraint that Target should lie between Start and End in its numerical value applies to the line-marking task only, but the predictions for the line construction task, where the Target magnitude falls outside that interval, are identical, with the only difference that the labels Target and End are swapped). Next, we express each stimulus magnitude as the arithmetical sum of two numbers. Taking *S* as a distance between Start and 0, and *L* and *T* are some arbitrary scalar magnitudes, such that $0 < T < L$, we define:

(1)
$$\begin{aligned} Start &= 0 + S = S \\ End &= L + S \\ Target &= T + S. \end{aligned}$$

The question we want to address now is, What is the form of the admissible transformations on the subjective scale that would account for the position of Target within the interval bracketed by Start and End, given the combinatorial operations with stimulus magnitudes, listed in Equation 1? First of all, the position of a Target magnitude within an interval is given as a relative distance between Target and Start to the length of the whole interval, that is,

(2)
$$Target_{[\text{Start-End}]} = \frac{f(Target) - f(Start)}{f(End) - f(Start)},$$

for some scaling function *f*. I will use the convention of adding the subscript to a variable to denote its relative position within an interval bounded by variables in the subscript brackets as opposed to the absolute value of that variable.

For the linear mapping function, $Target_{[\text{Start-End}]}$ becomes

(3)
$$\text{lin}\ Target_{[\text{Start-End}]} = \frac{T + S - S}{L + S - S} = \frac{T}{L},$$

i.e. lin $Target_{\text{[Start-End]}}$ does not depend on the start S of the interval, but only on the relative magnitude of T to the interval length L. In addition, lin $Target_{\text{[Start-End]}}$ is not affected by the length of the interval as long as the proportion between T and L is preserved.

For the strong logarithmic hypothesis, $\text{Target}_{\text{[Start-End]}}$ becomes

(4) $$\log Target_{\text{[Start-End]}} =$$

$$= \frac{\log(T+S) - \log(S)}{\log(L+S) - \log(S)} = \frac{\log\left(\frac{T+S}{S}\right)}{\log\left(\frac{L+S}{S}\right)} = \frac{\log\left(\frac{T}{S}+1\right)}{\log\left(\frac{L}{S}+1\right)}.$$

From the above expression, it can be seen that S does not cancel out; therefore, log $\text{Target}_{\text{[Start-End]}}$ depends on where the interval starts. In addition, the premultiplication of T and L by a common factor n does not imply that log $\text{Target}_{\text{[Start-End]}}$ remains the same. That is, log $\text{Target}_{\text{[Start-End]}}$ will depend on how wide the interval is, even though the linear proportionality between T and L is preserved.

Finally, the weak logarithmic hypothesis suggests that mapping is partially linearized but preserves a log component. A natural way to represent the magnitude of number on such a scale is that as a weighted sum of its linear and log components. Consequently, the relative distance is obtained by summing nominators and denominators of linear and log $\text{Targets}_{\text{[Start-End]}}$, that is,

(5) $$\text{linlog } Target_{\text{[Start-End]}} = \frac{w_1 T + w_2 \log\left(\frac{T}{S}+1\right)}{w_1 L + w_2 \log\left(\frac{L}{S}+1\right)},$$

where w_1 and w_2 are the weighting parameters for the linear and logarithmic components, respectively. In general, the term *linearization* of number representations implies that the size of the logarithmic component decreases as the size of the linear component increases. Consequently, all three hypotheses can be expressed by means of a single expression,

(6) $$Target_{\text{[Start-End]}} = \frac{wT + (1-w)\log\left(\frac{T}{S}+1\right)}{wL + (1-w)\log\left(\frac{L}{S}+1\right)},\ 0 \le w \le 1,$$

where linear and logarithmic components form a convex combination[1]. The weighting parameter w determines the identity of the scale, such that the strong linear hypothesis corresponds to $w = 1$; the strong logarithmic hypothesis corresponds to $w = 0$; and the weak log hypothesis, because $n << \log n$, corresponds to $w << 1$. The critical point is that Equation 6 represents a general case for admissible transformations on the subjective scale, under which the arithmetical operations with stimulus magnitude, listed in Equation 1, are closed. That is a direct implementation of Luce's consistency principle (Luce, 1959).

We assume that an estimate of a $\text{Target}_{\text{[Start-End]}}$ is subject to random Gaussian noise and is mapped into behaviour via some response function with coefficients $\mathbf{B}=\{\beta_i\}$. For the purposes of the current study, the response function is assumed to be linear, that is,

(7) $$Response = \beta_1 Target_{[Start\text{-}End]} + \beta_0 \quad .$$

In what follows, the model given by Equations 6 and 7 will be addressed as the full model, whereas the model given by Equations 3 and 7 as the linear model.

It is easy to see why the method is well posed for differentiating between the subjective scale and the response bias. For a particular value w, one can construct some

[1] An alternative formulation for the weak hypothesis as $Target_{\text{[Start-End]}} = w\ \text{lin}Target_{\text{[Start-End]}} + w\ \log Target_{\text{[Start-End]}}$ appears to be conceptually inappropriate. It would imply that the estimation of a Target position within an interval is performed twice, on the linear and log scale separately, and the result is then determined by mixing the results of two estimations proportionally to the weight w. In other words, this formulation would imply that two independent scales are used concurrently.

arbitrary $\text{Target}_{[\text{Start-End}]}$ in a multiple ways using two or more sets of values for *S*, *T*, and *L*. Every such set will generate a different $\text{Target}_{[\text{Start-End}]}$ for a different value of *w* (i.e., on a different scale). Owing to multiple assignments, the method does not confound magnitude information contained in $\text{Target}_{[\text{Start-End}]}$ with **B**. The latter provides the estimation for the size of response bias that, by definition, should be indifferent to the combinations of *S*, *T* and *L* as long as they produce the same magnitude of $\text{Target}_{[\text{Start-End}]}$. Obviously, manipulations with any two of the triplet *S*, *T* and *L*, while keeping a third one fixed, would suffice to generate an infinite number of a particular $\text{Target}_{[\text{Start-End}]}$ replications. This implies that orthogonal manipulations with any two variables (or, alternatively, with their sums, products, etc.) are both necessary and sufficient for discriminating between the linear and log hypotheses experimentally.

By contrast, the studies that used the standardized intervals (e.g. Dehaene et al., 2008; Siegler & Opfer, 2003) could not decouple the contributions of response bias and weights to the values of regression coefficients, since there was only one way to assign the magnitude of $\text{Target}_{[\text{Start-End}]}$. Longo and Lourenco (2007) apparently came closer than others to a realisation of the combinatorial method, when they manipulated the beginning and the length of the interval. However, they did not make use of the method, taking into consideration only one variable – the magnitude of the interval mean.

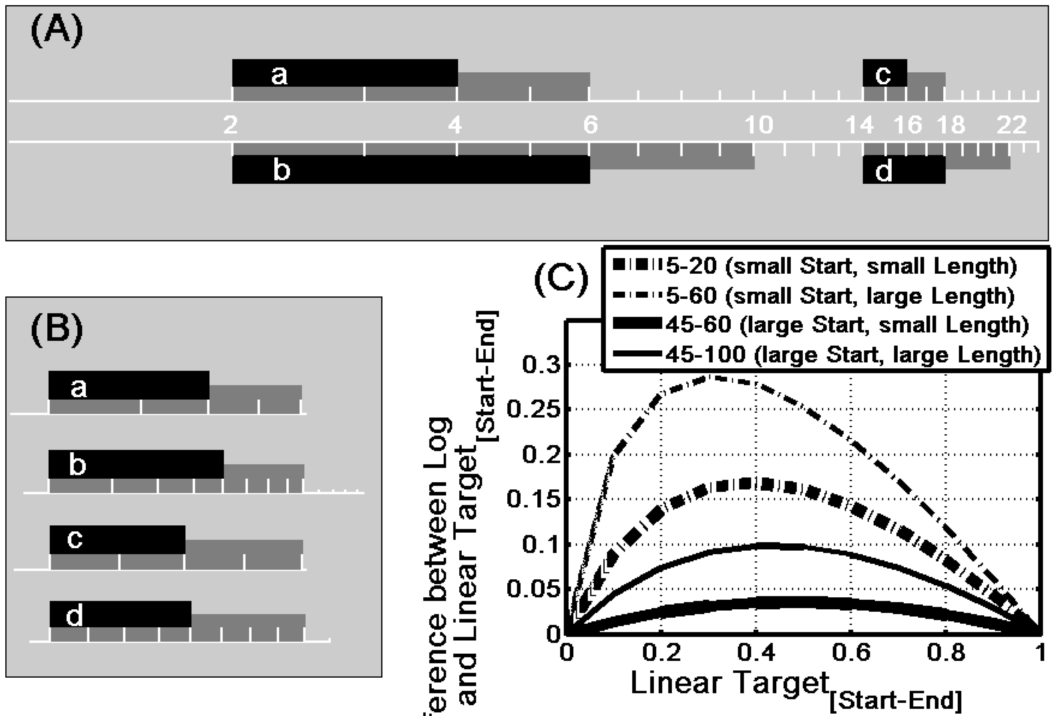

Figure 2.1. Placement on the logarithmic scale at different Starts and different interval Length. *(A). Bars represent numerical distances: black for from Start to Target, grey for from Start to End. The length of black bars relatively to the length of grey bars on the linear scale would always be .5. However, it is not the case for logarithmic scale as it can be seen in (B). The interval 'c' (greater Start and smaller Length) matches the linear proportion most closely. (C). The change in the difference between log and linear* $Target_{[Start\text{-}End]}$ *with the change in linear* $Target_{[Start\text{-}End]}$*, Start and Length. The scale of axes is normalized (both linear and log* $Target_{[Start\text{-}End]}$ *are proportional magnitudes.) In the legends, the first digit stands for Start (i.e. the beginning of an interval), the second digit stands for End (i.e. the end of an interval). Individual curves provide a 2 by 2 example of 4 different intervals, with 2 choices for Start, small (5) and large (45), and two choices for Length, small (20-5 = 15; 60-45 = 15) and large (60-15 = 55; 100-45 = 55). On average, the difference between log and linear* $Target_{[Start\text{-}End]}$ *is larger for linear* $Target_{[Start\text{-}End]}$ *between .1 and .6, for small Start (5) and for large Length (55).*

Evaluation of the linear and log components. The above formulation allows for two approaches to the data analysis. First, the contribution of the logarithmic component can be estimated directly by optimizing the model given by Equations 6 and 7. The second approach is analytical and provides with a broader picture about the factors affecting the performance. The geometric interpretation of this idea is given in Figure 2.1 A - B. I will drop the symbolic notation of Equation 6 and, instead, use the labels that define features of a numerical interval. The way *S*, *L* and *T* were defined implies that *S* stands for the magnitude of an interval Start, *L* stands for a linear Length of the interval, and *T/L* stands for a linear $\text{Target}_{[\text{Start-End}]}$. The primary concern here is how the difference between log and linear $\text{Target}_{[\text{Start-End}]}$ will change for different choices of Start, Length and linear $\text{Target}_{[\text{Start-End}]}$. The examples in Figure 2.1 C indicate that that the difference between log and linear $\text{Targets}_{[\text{Start-End}]}$ is greater: a). for the values of linear $\text{Target}_{[\text{Start-End}]}$ between .1 and .6, b). for the intervals with a smaller Start, and c) for the intervals with a greater Length. Furthermore, one can marginalize the effect of each variable by averaging across the other two.

Figure 2.2 A shows the marginalized difference between log and linear $\text{Targets}_{[\text{Start-End}]}$ for different values of linear $\text{Target}_{[\text{Start-End}]}$, and Figure 2.2 B shows that for different interval Starts and Lengths. All functions are non-linear, but their linear approximations have distinctive slopes. The predominantly decreasing trend for linear $\text{Target}_{[\text{Start-End}]}$ and the ever-decreasing trend for Start, can be approximated by a line with a negative slope, whereas the increasing trend for Length can be approximated by a line with a positive slope. Importantly, for mappings that are partially linearized, the sign of slopes for all variables remains unchanged, though the steepness of the trends will depend on the relative contribution of a logarithmic component. Moreover, the sign of slopes for Start and Length would remain unaffected by response bias (i.e. $\beta_0 \neq 0, \beta_1 \neq 1$). Consequently, a simple tool for testing both the weak and strong logarithmic hypotheses can be the following. Provided that linear Target$_{[Start-End]}$, Start and Length are uncorrelated or orthogonal, the deviations of the response from a correct value can be fitted using linear multiple regression. If numbers are represented on a (partially linearized) logarithmic scale, the regression coefficients for linear Target$_{[Start-End]}$ and Start are expected to be negative, whereas for Length they are expected to be positive.

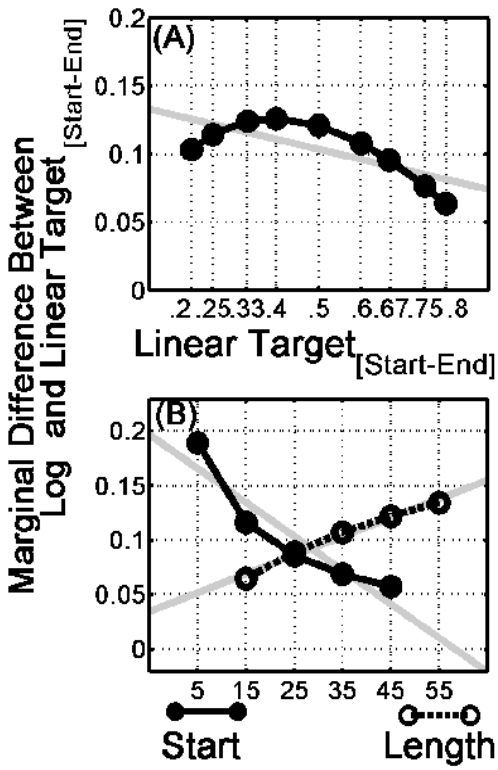

Figure 2.2. The predictions for logarithmic mapping.

(A). *The marginal difference between log and linear Target$_{[End-Start]}$ for 9 choices of linear Target$_{[End-Start]}$,* $\frac{1}{5}, \frac{1}{4}, \frac{1}{3}, \frac{2}{5}, \frac{1}{2}, \frac{3}{5}, \frac{2}{3}, \frac{3}{4}, \frac{4}{5}$, *averaged across 5 Starts (5,15,25,35,45) and 5 Lengths (15,25,35,45,55). The range of values approximates that used in the study (see Methods). Y axis is a normalized scale. The predicted trend is predominantly decreasing. The grey line shows the linear approximation to the trend.*

(B). *Marginal difference between log and linear Target$_{[End-Start]}$ as a function of Start and Length. The labels for X axis show numerical magnitudes for Start and Length, Y axis is a normalized scale. The choices for Start, Length and linear Target$_{[End-Start]}$ are as above in (A). For Start, the marginal difference is calculated by averaging across Length and linear Target$_{[End-Start]}$. For Length, the marginal difference is calculated by averaging across Start and linear Target$_{[End-Start]}$. Logarithmic mapping predicts a decreasing trend for Start and an increasing trend for Length. The grey lines show their linear approximations. For mapping, that is partially linearized or affected by the central tendency, the steepness of the trends for Start and Length will be smaller, but the directions remain unchanged.*

2.3 Experiment 1: Line-marking task

In the first experiment, the combinatorial method is implemented in a task that required mapping numbers to a location on the line. I systematically manipulated parameters *S*, *L* and *T/L* (experimental variables, Start, Length and linear $\text{Target}_{[\text{Start-End}]}$) and used both numerical and analytical approaches to the data analysis. In addition, using a Bayesian statistical approach, I compared the full model of Equations 6 and 7 with the simpler linear model of Equations 3 and 7.

2.3.1 Method

Participants. 20 healthy adults (10 male), 19-40 years old (mean age – 24.1; SD = 5.33) participated in the study. They all gave informed consent, had a normal or corrected-to-normal vision and declared themselves to be right-handed.

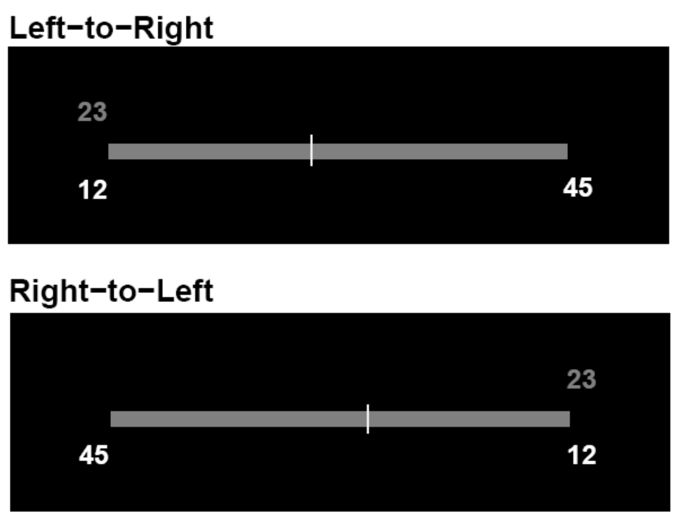

Figure 2.3. Stimuli in the line-marking task. *Subjects are required to mark the location of the GREY number (red in actual experimental settings) within the interval defined by the two WHITE numbers by sliding the cursor (vertical strip) along the line. At the beginning of each trial the cursor was presented at a random location on the line. Top). Left-to-right orientation; Bottom). Right-to-left orientation.*

Stimuli and apparatus. The line-marking task was administered by means of a custom-made Matlab program, and displayed using a 19-in LCD monitor (1440 by 900 pixels, pixel size .265 mm). All stimuli in the experiment were designed in terms of a pixel size. Subjects saw a grey 15-pixel-wide line presented against a black background in the middle of the screen along the vertical axis (Figure 2.3). Along the horizontal axis, the location of the line centre varied randomly within 50 pixels off the monitor centre in either direction. The length of the line varied randomly between 480 and 520 pixels, subject to constraints discussed below. A thin red vertical strip (1 pixel thick, 31 pixels long), functioning as a cursor, was presented simultaneously with the line. The cursor split the line into two parts and on presentation it could occupy any randomly selected location between the ends of the line. The cursor displacement, constrained to the horizontal dimension, was manipulated by a computer mouse. The trial was terminated by clicking the left button of the mouse. The location of the cursor at the time of the click was registered and used to calculate accuracy of the response. The resolution of the response was equal to the pixel size (.265 mm).

In each trial, subjects saw three numbers (font size – 20). Two of them (in white colour) were presented at the opposite ends of the line. A smaller number, *Start*, signified the beginning of an interval and a larger number, *End*, signified the end of the interval. A number to be marked, *Target* (in red colour), lay between Start and End in its numerical value. The orientation of the line could be either *left-to-right* (L-R) or *right-to-left* (R-L). In the L-R condition, a Start was presented at the left end of the line and an End at the right end. The layout was reversed for the R-L condition.

Three *numerical* factors were manipulated in the task: a) linear *Target*$_{|Start\text{-}End|}$, i.e. the relative distance between Start and Target to the length of the interval, b) *Start,* i.e. the origin of the interval and c) *Length*, i.e. the length of the interval. These variables corresponded directly to the values of *T/L*, *S* and *L*, respectively, used in the description of the combinatorial method. The choice of a Target magnitude was such that it divided the interval proportionally to one of 9 linear Target$_{|Start\text{-}End|}$ values: $\frac{1}{5}, \frac{1}{4}, \frac{1}{3}, \frac{2}{5}, \frac{1}{2}, \frac{3}{5}, \frac{2}{3}, \frac{3}{4}, \text{or} \frac{4}{5}$.

The experiment had a blocked design. In the *Start-controlled* block, the values for Start were drawn at random from one of the ‘bins’: 1-9, 11-19, 21-29, 31-39, and 41-49. A Start from each ‘bin’ was presented once with each linear Targets$_{|Start\text{-}End|}$. The assignment of Length was random in this block but was subject to two constraints. First, the value for Length was within the range between 10 and 60. Second, a numerical interval initially generated by the computer program was corrected to the nearest value divisible without remainder by the denominator of a linear Target$_{|Start\text{-}End|}$. The reason for using the latter constraint was to ensure that Target was always an integer.

In the *Length-controlled* block, a Length from each ‘bin’ was presented once with each linear Targets$_{|Start\text{-}End|}$. The ‘bins’ for Length were 11-20, 21-30, 31-40, 41-50, and 51-60. Again, the adjustments of Length magnitude were required to ensure that the value of Target is an integer. The assignment of Start was random in this block but its magnitude was contained in the range between 1 and 49 excluding the multiples of 10.

The final constraint in stimulus generation relates to the length of the presented line. Although the length for the line was drawn in the first instance from the uniform distribution to be between 480 and 520 pixels, the length of an actually presented line was adjusted to a nearest value, such that the line would contain a number of pixels divisible by the denominator of a given linear $\text{Target}_{|\text{Start-End}|}$ without remainder. This allowed for a precise marking of the line with respect to a required linear $\text{Target}_{|\text{Start-End}|}$.

Given the 2 x 2 design (L-R/R-L orientation by Start-controlled/Length-controlled block), the task consisted of 4 blocks of 45 trials (9 levels of $\text{Target}_{|\text{Start-End}|}$ times 5 levels of Start/Length) each. Both within- and between-block orders of presentation were randomized.

Procedure. Subjects were shown the stimulus material, explained the task, and instructed how to respond. They were asked to provide an approximate and unspeeded estimate of the position of the Target number on the line without performing exact arithmetical calculations. In order to respond, subjects were required to move the cursor along the line to an estimated location and mark the line by clicking on the left button of the mouse. Subjects were asked not to hurry or spend too much time on a trial. As guidance, the time interval of 5 to 10 seconds per trial was suggested. However, it was made clear that this time window was not obligatory. Subjects also underwent a training session to become familiar with the tasks. The training session involved a different set of linear $\text{Target}_{|\text{Start-End}|}$ values, namely, $\frac{1}{7},\frac{2}{7},\frac{5}{7}$ and $\frac{6}{7}$, and consisted of 2 – L-R and R-L – blocks, where each linear $\text{Target}_{|\text{Start-End}|}$ was presented twice within each block, giving 8 trials in the session. Both Start and Length were drawn randomly. Each block in the experimental session was preceded by a message on the screen specifying the orientation of the line.

Data analysis. The responses were normalized by calculating them as proportions of the line segment between the beginning of the line and the marked point divided by the length of the whole line. This transformation placed responses onto identical scale with linear $\text{Target}_{|\text{Start-End}|}$ and allowed for a straightforward calculation of the error as a difference between response and linear $\text{Target}_{|\text{Start-End}|}$. Three main issues were addressed in the analysis: a) the selection of a model for the data; b) the response bias; c) the marginal effects of linear $\text{Target}_{|\text{Start-End}|}$, Start and Length. Within each sub-section, the effect of orientation was also investigated.

Model selection. The parameters for the full model given in Eq's 6 and 7 were calculated for each subject and for each orientation separately. The magnitudes of Start, Length, and the difference between Start and Target were plugged into Eq 6 in place of *S*, *L*, and *T*, respectively. Values for β_0, β_1 and *w* were calculated according to the least-squares criterion, using an optimization algorithm (function *fmincon* in Matlab). The initial values for β_0, β_1 and *w* were set to 0, 1 and 0, respectively, corresponding to a null hypothesis that the subjects responded in accordance with the strong logarithmic hypothesis and a zero response bias. It should be stressed that a traceable logarithmic component would require a small value for the weight *w* (roughly, smaller than .1), given that log(n) << n.

In order to evaluate the performance of the full model, it was compared with the linear model, given by Equations 3 and 7, which is just a linear regression model with the linear $\text{Target}_{|\text{Start-End}|}$ as a predictor. To approximate the posterior distribution of the parameters β_0, β_1 and *w*, 10000 Markov Chain Monte Carlo (MCMC) parameter samples were drawn for each model, subject and orientation. The first 500 were dropped. The proposal distributions were assumed to be Gaussian. To correct for a small proportion of the interval between 0 and 1, for which parameter *w* implies a traceable contribution of the logarithmic component, an inverse arcsine transformation of the form $w = (\sin(w') - 1)^2$

was used, and *w'* was sampled instead of *w*. The value of the parameter *w'* was bound to be between 0 and π/2; the values that were sampled outside that interval were reflected back into the interval. Owing to the transformation, the proportion of the interval between 0 and π/2 that was compatible with the log hypothesis was roughly .5. For each model, I calculated the log of the marginal likelihood, *L(model)*, by transforming logarithmically the average likelihood over all MCMC samples. The differences in the logs of average likelihoods for two models*, L(linear) – L(full)*, (i.e. the logs of the individual Bayes factors between the models) was then tested against zero using nonparametric Wilcoxon sign-rank test. The values greater than 0 would support the hypothesis of the linear scaling and the values smaller than 0 would support the logarithmic hypothesis. The cross-subject log of the Bayes factor was calculated by summing the individual logs. Similarly, the effect of the line orientation was studied by looking at the Bayes factor between L-R and R-L conditions.

Analysis of bias. Two parameters were of interest in the analysis of response bias. The first was the slope β_1 of the full model (or of the linear model, if it performed better than the full one), which can be treated as a spread/compression index. For example, a value smaller than 1 would imply that the spread of the mean responses was smaller than it was required by the variance in $\text{Target}_{|\text{Start-End}|}$ of Equation 6, and therefore some values should be either overestimated, or underestimated, or both. The test of the slopes against 1 was complemented by the test suggested in Matthews and Stewart (2009). This requires testing the standard deviation of responses against the standard deviation of independent variable. In some respect, this test is more robust, as it takes into account the within-subject variability of responses.

The second parameter of interest was the value of the regression models at $Target_{[Start\text{-}End]} = .5$, i.e. the *regression mean*. This parameter provided information about the symmetry of the compression/stretch and can be interpreted as a marker of global under/overestimation. For regression slopes that were smaller than 1 (compressed responses), the regression mean below .5 would indicate that there was a tendency to underestimate in general and vice versa if the mean value was above .5.

The effect of linear $Target_{|Start\text{-}End|}$, Start and Length. The multiple regression analysis with Start, Length and linear $Target_{|Start\text{-}End|}$ as predictors was run to obtain the estimation of the marginal effect of each variable on the performance. The dependent variable of the analysis was the error, calculated as a difference between response and linear $Target_{|Start\text{-}End]}$. The betas for randomly generated variables, i.e. Start and Length in the Length-controlled and Start-controlled blocks, respectively, were disregarded. Consequently, I analysed two samples of beta values for Start (L-R and R-L in Start-controlled condition) and Length (L-R and R-L in Length-controlled condition), and four samples of betas for linear $Target_{|Start\text{-}End|}$ (L-R and R-L in both Start- and Length-controlled conditions). The significance of a trend was established by testing betas for each variable against zero using t-test statistics. In addition, betas for the L-R and R-L conditions were tested against each other, in order to see if manipulations with the line orientation had any effect on the data.

2.3.2 Results

Fifty-two trials (1.4 %) were excluded from analysis, either because RT was less than 200 ms (16 trials) or because the deviation from a correct response was more than .4 (36 trials).

Model selection. The estimated median weight *w* for the full model was equal to 1, all $w > .27$. The linear model provided a better account for the data than the full model, as the median log of the Bayes factor was significantly greater than zero (L-R: $z = 2.69$, $p < .01$; R-L: $z = 2.17$, $p = .03$). The results were supported by the analysis on the basis of Akaike information criterion (AIC), calculated for the numerically optimal models, *L-R* orientation: $z = 3.92$, $p < .001$; R-L orientation: $z = 3.88$, $p < .001$. The cross-subject log of the Bayes factor was equal to 4.95 and 3.78 for L-R and R-L orientations, respectively, implying very strong evidence in favour of the linear hypothesis. The effect of orientation was not significant ($z < 1$ for both the full and linear models, confirmed by AIC). The linear model accounted for 75 % of variance for *L-R* orientation and 76 % of variance for *R-L* orientation.

Analysis of bias. Because the linear model predicted the data better than the full model, I used this model for the analysis of response bias. The average response function was $Response_{(L\text{-}R)} = .816 * Target_{|Start\text{-}End|} + .106$ and $Response_{(R\text{-}L)} = .821 * Target_{|Start\text{-}End|} + .108$ for L-R and R-L orientations, respectively (Figure 2.4). The slopes of the regression models fitted to each subject data were significantly smaller than 1 ($t_{L\text{-}R}\ (19) = 5.15$, $p < .001$ and $t_{R\text{-}L}\ (19) = 5.02$, $p < .001$), indicating the presence of the central tendency bias in the data. The slopes for L-R and R-L orientations did not differ from each other ($t < 1$). The alternative test for the central tendency (Matthews & Stewart, 2009) showed that subjects' standard deviations of responses were significantly smaller than the standard deviations of linear $Target_{|Start\text{-}End|}$ values, $t_{L\text{-}R}\ (19) = 2.40$, $p = .027$ and $t_{R\text{-}L}\ (19) = 2.41$, $p = .026$.

The regression means were slightly greater than .5 (L-R: .51 and R-L: .52). Because of the small between-subject variability, the difference from .5 was statistically significant ($t_{L\text{-}R}$ (19) = 3.36, p < .005, $t_{R\text{-}L}$ (19) = 2.86, p = .01), which indicate some tendency to globally overestimate. There was no difference in regression means for L-R and R-L orientations.

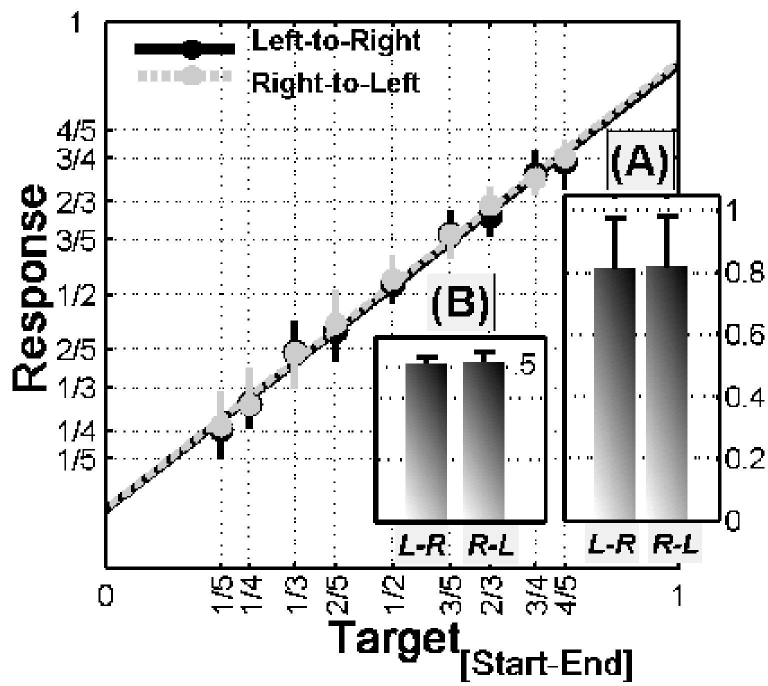

Figure 2.4. Line-marking task results. *The group means and their standard deviations of responses with the linear Target$_{[Start\text{-}End]}$ as a predictor. (A) shows that the slopes of linear regression models are significantly smaller than 1, indicating the presence of linear compression in the data, that is, a central tendency. (B) shows the bars for the regression means. The latter were slightly greater than the middle of the interval for both line orientations, suggesting a small overall overestimation.*

The effect of linear Target$_{|Start\text{-}End|}$, Start and Length. The marginal error in responses, calculated for each experimental variable by averaging across the others, is shown in Figure 2.5. The values for both Start and Length are arranged into 5 bins to enable averaging across subjects. The multiple regression analysis, meanwhile, was run on the actual numerical magnitudes for these variables.

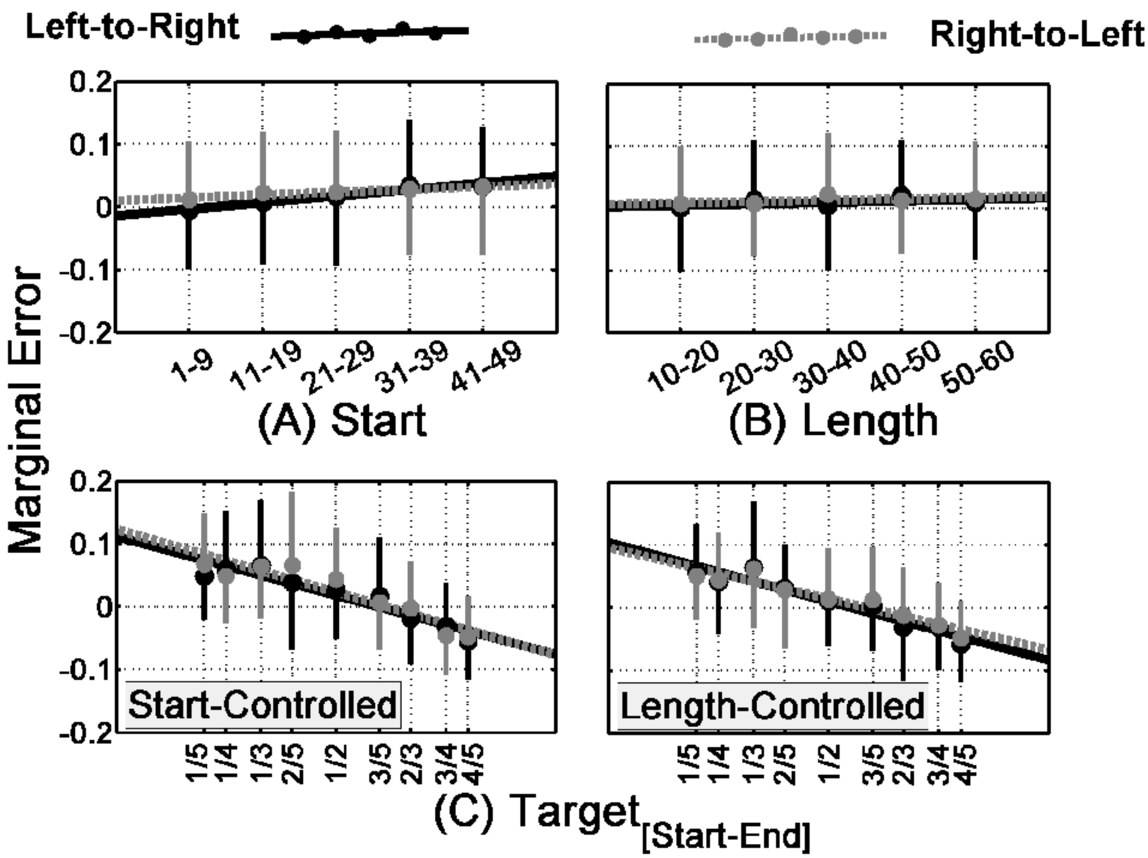

Figure 2.5. Line-marking task. *The marginal effect of interval Start, interval Length and linear Target$_{[Start\text{-}Target]}$ on the errors in responses. The error bars show the group mean standard deviations. The effect of Start was positive, whereas the effect for Length was completely flat, contrary to the predictions of the log-scale hypothesis. Neither of experimental variables showed a significant difference between left-to-right and right-to-left orientation.*

As would be expected from the fact that the slopes of linear models were considerably smaller than 1, there was a significant negative trend in errors as a function of linear $Target_{|Start-End|}$ (Start-controlled – L-R: t (19) = 4.81, p < .001, R^2 = .20[2]; Start-controlled – R-L: t (19) = 5.4, p < .001, R^2 = .18; Length-controlled – L-R: t (19) = 5.07, p < .001, R^2 = .18; Length-controlled – R-L: t (19) = 4.26, p < .001, R^2 = .16). The average sample slopes were $\beta_{L-R/Start} = -.190$, $\beta_{L-R/Length} = -.202$, $\beta_{R-L/Start} = -.187$ and $\beta_{R-L/Length} = -.160$. A repeated-measures 2 x 2 ANOVA on betas (Block: Start /Length; Orientation: L-R/R-L) showed no significant main effect or interaction (all F's < 1.6). There was a remarkable consistency in the beta values at a within-subject level, with correlational coefficients between betas for different blocks ranging from r = .62 to r = .81. In addition, there was a strong negative correlation between betas and R^2 estimated for the linear model (see the previous subsection), all $\tau > .52$, p < .001(non-parametric Kendall's test).

Testing the betas for Length against zero revealed no significant trend (t < 1 for both L-R and R-L), whereas the trend for Start was significant for both orientations (L-R: t (19) = 3.38, p < .01, R^2 = .06; R-L: t (19) = 2.64, p = .016, R^2 = .02). As Start increased, the error grew positively with the mean rate $\beta_{L-R} = .012$ and $\beta_{R-L} = .006$ per 10 number units. The positive value was found in 29 out of 40 cases (20 subjects by 2 line orientations). The magnitude of the effect was somewhat greater for L-R than for R-L, with a marginally significant difference between two orientations (t (19) = 1.97, p = .06). Despite this difference, there was a significant correlation between individual betas for L-R and R-L, r = .48, p = .032, suggesting that the effect (unlike the effect of Length, p = .19) was consistent at a within-subject level.

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[2] R^2 were calculated using linear models with each variable separately as a predictor to fit the data.

2.3.3 Discussion of Experiment 1

In the Experiment 1, the combinatorial method was applied to differentiate between subjective scale and response bias in a task where subjects marked the location of a numerical magnitude within numerical intervals in which Start and Length were varied systematically. The results unambiguously show that approximate estimation in this particular task is performed on a strictly linear scale. The linear regression model predicted the data better than the model that included the weight for the logarithmic component. This finding was supported by the analysis of the marginal effects of linear $\text{Target}_{|\text{Start-End}|}$, Start and Length on the error. For the logarithmic mapping, the regression slope for linear $\text{Target}_{|\text{Start-End}|}$ is expected to be negative and complemented with the negative slope for Start and the positive slope for Length. However, the results show an opposite trend for Start with no significant effect of Length.

The results showed that performance was affected by linear compression due to a response bias, known as the central tendency effect. In other words, the small values within a numerical interval were systematically overestimated and large numbers were systematically underestimated. The strength of the central tendency generally reflected subjects' ability to solve the task, such that the smaller central tendency was associated with higher proportion of the variance, explained by the regression models. The regression mean was close to, but statistically greater than, the middle of the numerical interval. This slight shift has a simple explanation in another factor that biased performance: the magnitude of Start. It can be noted that the intercepts of the least square lines for Start in Figure 2.5 A are approximately equal to zero. Consequently, each level of Start contributed to the magnitude of a responded ratio, causing, on average, a slight increase in the regression mean. It can also be confirmed by the fact that the regression means significantly correlated with the betas for Start at a within-subject level for either line orientation ($r = .61$, $p < .005$ and $r = .49$, $p = .03$, L-R and R-L, respectively).

Ascribing the biasing effect specifically to the magnitude of Start may be inappropriate, as the display of the task constitutes a rather complex composition of different numbers, where the magnitude of Start can strongly correlate with other magnitudes and their sums (but not with the differences between numbers). Consequently, the performance can be better accounted for by saying that subjects tended to provide a greater estimate for the magnitude of Target when they faced numerical problems of a greater numerical size. The question remains whether this bias, linear mapping and the central tendency effect generalize to a task involving a different set of constraints and response requirements. The following study aimed at extending the understanding of the processes that affect the mapping of the internal magnitude scale into behavior in a novel number-to-position task.

2.4 Experiment 2: Line construction task

To test the generality of the findings, a new task was designed in which subjects had to construct an interval. As before, they were presented with a line signifying the length of the numerical interval between Start and End. However, this numerical interval was deemed to be just a part of a whole interval. Given the length of the line and the numerical length of the part, subjects were asked to extend the line up to a magnitude of Target, which was always greater than End. For example, subjects could be presented with a line bracketed by 12 and 23. Given 45 as a Target number, subjects had to add an extension to the line, such that the length of the extension would correspond to the numerical distance between 23 and 45. In this particular example, the length of a correctly constructed extension would be twice as long the initially presented line segment. The differences in the task do not prevent us from using the same analytic apparatus for testing the linear and logarithmic hypotheses. To account for the fact that Target is larger than End, one can simply redefine Length as the distance between Start and Target and exchange Target and End in Equation 2 to get

$$(8) \qquad End_{[\text{Start-Target}]} = \frac{f(End) - f(Start)}{f(Target) - f(Start)}.$$

The result that follows is identical to Equation 6, except that $End_{[\text{Start-Target}]}$ substitutes for $Target_{[\text{Start-Target}]}$, T represents the distance between Start and End, and L - the distance between Start and Target. In this formulation, the predictions for the logarithmic hypothesis remain identical to the line-marking line, that is the slopes are expected to be negative for $End_{[\text{Start-Target}]}$ and Start, and positive for Length.

Apart from the differences in response requirements, it is also worth considering the differences in the constraints between two tasks. In the previous task, no cues, apart from numerical values, were available on where the line should be marked. On the other hand, the response was constrained to lie within a closed spatial interval, represented by the physical line. Given that the center of the line is easily identified, the tendency to overestimate or underestimate the magnitudes around the middle of a numerical interval could be artificially induced by the spatial format of the task.

In the context of the line construction task, the central tendency involves different processes and would manifest itself as the tendency to underconstruct a long addend to the part and overconstruct a short addend. In the current design, the length of a presented part provided a cue as to how long an added line should be. If an initially presented line was short, subjects could figure out fairly quickly that they need to construct a rather long addend to the line, and vice versa if an initially presented line was long. On the other hand, because the standard for the whole line was never shown to subjects, the presented segment did not clearly indicate how long the line should be and where the middle of an interval should lie. In this respect, the line construction task can be more sensitive for the study of the number magnitude scale than the line-marking task, as subjects were free to construct the size of representational space. If a logarithmic component was indeed present in the estimation, then subjects would systematically underconstruct the line (i.e., causing the shift of the regression mean toward a greater value).

2.4.1 Method

Participants. 20 subjects (12 female), 20-52 years old (mean age – 25.1, SD = 7.62) took paid participation in the study. They all gave informed consent, had a normal or corrected-to-normal vision and declared themselves to be right-handed.

Stimuli and apparatus. In this experiment, subjects saw a gray horizontal line that was deemed to be just a part of a longer whole line. The line width was identical to that used in Experiment 1. In the L-R condition, a Start and an End were presented in white below the line at its left and right ends, respectively. At the right end and above the line, a Target was presented in red. The location of the line's right end varied randomly between 60 and 140 pixels to the left of the monitor center. Moving the mouse to the right enabled subjects to extend the line by adding a white strip (extension) to the initially presented gray part. The extension continuously prolonged with the movement of the mouse, and it could also be reduced by moving the mouse backward. The spatial layout for R-L condition was reversed. The manipulations with the mouse had no effect on the length of the initially presented gray part. Any displacement of the mouse along the vertical axis was ignored, and the speed of the extension growth or shrink was identical to the speed of the cursor in Experiment 1.

Design and procedure. The experimental design and procedure of the line-construction task, with appropriate adjustments, mirrored those of the line-marking task in Experiment 1. By contrast to the line-marking task, the Target magnitude in the current task was always greater than End. Consequently, in order to make two tasks comparable, there were two changes in experimental variables. Firstly, linear $End_{[Start\text{-}Target]}$ substituted for linear $Target_{[Start\text{-}End]}$. That is, a relative distance between Start and End to the distance between Start and Target was manipulated instead of a relative distance between Start and Target to the distance between Start and End. Secondly, Length was defined as the distance between Start and Target (between Start and End in the line-marking task). The values for linear $End_{[Start\text{-}Target]}$, Start and Length were generated in the same way as described for the line-marking task.

The only difference in the experimental procedure was in the response requirements: Instead of marking a presented line, subjects had to construct the line as far as it was implied by the magnitude of Target, given a numerical distance between Start and End and the length of the gray line, representing the physical analogy of that numerical distance. The length of the presented line was such that a correct estimation would require a whole line to be between 460 and 540 pixels long. The value for the correct line length was drawn from a uniform distribution but subject to the same constraints as described for the line-marking task. I chose not to vary the length of the line to a greater extent, as it would make a comparison between the current and line-marking task problematic due to the differences in spatial parameters of the tasks.

In line with the change in the definition of experimental variables, the response was calculated as a relative magnitude of a gray part to the sum of the gray part and a constructed white segment.

2.4.2 Results

Eleven trials (<1%) were excluded from the analysis. For all of them the deviation from a correct response was more than .4.

Model selection. The median weight w for the full model given in Eq's 6 and 7 was equal to 1. Only for one subject the magnitude of the weight ($w = .065$) was sufficiently small to suggest the presence of the logarithmic component in the responses. The model comparison showed that the linear model predicted data better than the full model, L-R: $z = 3.25$, $p < .005$; R-L: $z = 2.24$, $p = .025$. The result was confirmed by the statistics on the basis of Akaike information criterion, $z = 3.67$, $p < .001$, for both orientations. The cross-subject log of Bayes factor was equal to 5.45 for L-R orientation and 4.11 for R-L orientation (very strong evidence in favour of the linear model). The linear model accounted for 87 % of the variance for the L-R condition and 85 % for the R-L condition. The effect of the line orientation was not significant, $z < 1$, for both models (confirmed by AIC).

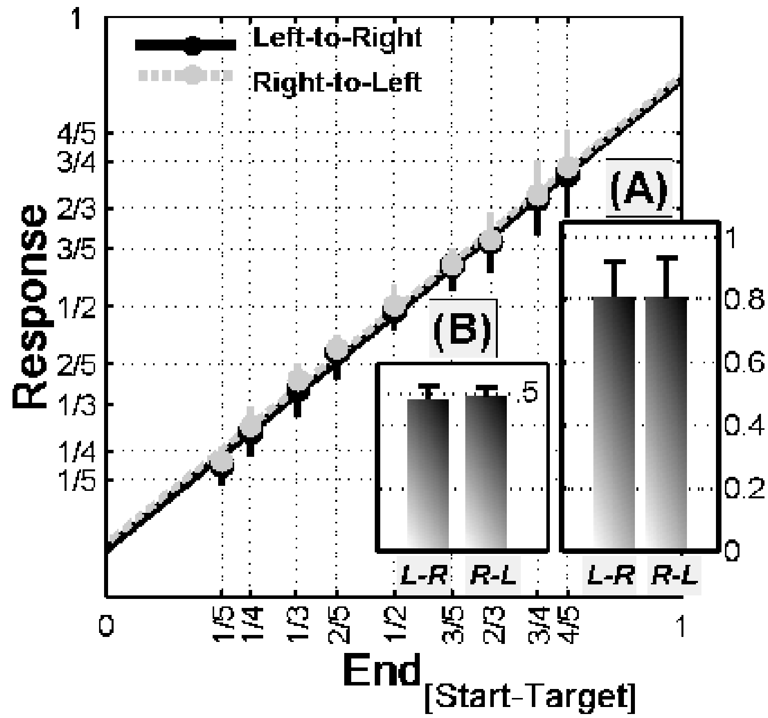

Figure 2.6. Line-construction task. *The group means and their standard deviations of responses with the linear End$_{[Start\text{-}Target]}$ as a predictor. (A) shows that the slopes of linear regression models, which are significantly smaller than 1, indicating the presence of linear compression in the data, that is, a central tendency. (B) shows the bars for the regression means. The latter were not statistically different from .5 implying that the cross-over from overestimation to underestimation took place at the middle of the interval for both line orientations.*

Analysis of bias. The mean equations of the linear regression model with the linear End$_{[Start\text{-}Target]}$ as a predictor were Response$_{(L\text{-}R)}$ = .811* End$_{[Start\text{-}Target]}$ + .081 and Response$_{(R\text{-}L)}$ = .808*End$_{[Start\text{-}Target]}$ + .092 (Figure 2.6).The slope of the linear regression line was significantly smaller than 1 ($t(19) = 7.61$, $p < .001$, and $t(19) = 6.95$, $p < .001$, L-R and R-L, respectively) and there was no difference between L-R and R-L orientations ($t < .1$). The alternative test for the central tendency showed that the standard deviation of responses were significantly smaller than the standard deviation of the linear End$_{[Start\text{-}Target]}$ values, $t_{L\text{-}R}(19) = 5.95$, $p < .001$ and $t_{R\text{-}L}(19) = 5.55$, $p < .001$). The regression means for

L-R and R-L were very close to and not statistically different from .5 (L-R: .49, $t < 1.5$ and R-L: .5, $t < 1$) and each other ($t = 1.63$, $p = .11$).

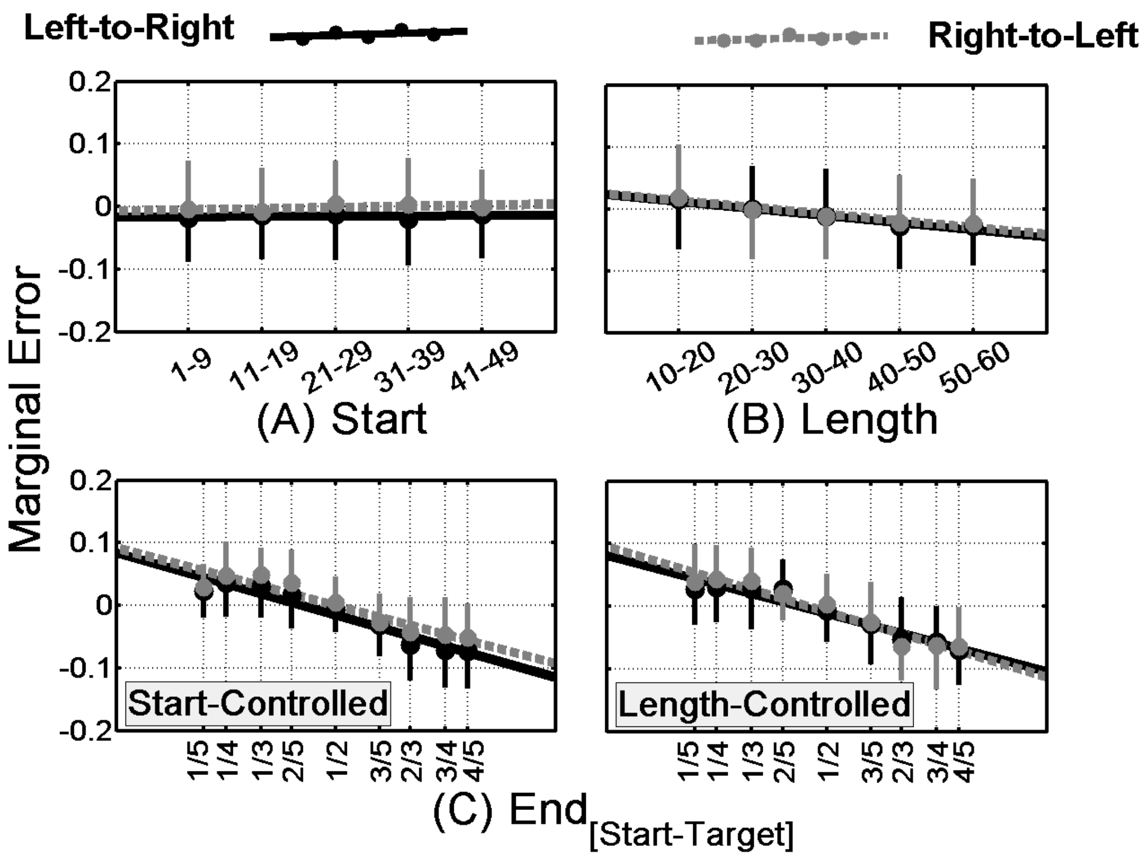

Figure 2.7. Line-construction task results. *The marginal effect of interval Start, interval Length and linear End$_{[Start-Target]}$ on the errors in responses. The error bars show the mean standard deviations. The effect of Start was no longer positive, whereas the effect for Length was consistently negative, contrary to the predictions for the log-scale hypothesis. Neither of experimental variables showed a significant difference between left-to-right and right-to-left orientation.*

The effect of linear End$_{[Start-Target]}$, Start and Length on error. The results for linear End$_{[Start-Target]}$, Start and Length are shown in Figure 2.7. There was a significant negative trend as a function of linear End$_{[Start-Target]}$ (Start-controlled – L-R: $t(19) = 7.50$, $p < .001$, $R^2 = .34$; Start-controlled – R-L: $t(19) = 5.31$ $p < .001$, $R^2 = .29$; Length-controlled – L-R: $t(19) = 6.52$, $p < .001$, $R^2 = .27$; Length-controlled – R-L: $t(19) = 7.52$ $p < .001$, $R^2 = .34$). A repeated-measures 2 x 2 ANOVA on slopes (Block: Start /Length;

Orientation: L-R/R-L) showed that neither main effects were significant nor their interaction (all F's < 1.2). The mean slopes were $\beta_{L\text{-}R/Start} = -.191$, $\beta_{L\text{-}R/Length} = -.181$, $\beta_{R\text{-}L/Start} = -.183$ and $\beta_{R\text{-}L/Length} = -.20$. The beta values for linear $End_{[Start\text{-}Target]}$ were very consistent at a within-subject level, with the correlation between them for different experimental blocks ranging from r = .71 to r = .8, all p < .001. In addition, there was a strong negative correlation between betas and R^2 of the linear models, all $\tau > .43$, $p < .01$. A t-test on the regression slopes for Start showed that they did not statistically differed from zero and there was no difference between L-R and R-L (all t's < 1.46, p > .16). The distribution for betas of Length visibly deviated from normality, approximating the form of a non-symmetrical one-tailed Gaussian. Therefore, Wilcoxon sign-rank test was used instead of t-test. The beta values for two line orientations were significantly smaller than zero (L-R: z = 3.81, p < .001, R^2 = .07; R-L: z = 3.88, p < .001, R^2 = .06) and were not different from each other (z < 1). The betas for Length were negative in 37 cases out of 40 (median $\beta = -.007$ per 10 number units for both L-R and R-L). Non-parametric correlation analysis showed that the correlation between the betas of Length for L-R and R-L was very close to significance, Kendall's $\tau = .32$, p = .055, suggesting that the effect was moderately consistent at a within-subject level.

One of the possibilities why no significant effect of Start was found is that there was a non-zero correlation between pairs of independent variables. In the Start-controlled blocks, the values for Length were generated randomly, but were not orthogonal to Start by design. Although the group mean correlation between Length and Start in the Start-controlled blocks was close to zero, it ranged from r = –.24 to .32 for individual subjects. Consequently, one can ask whether the positive trend for Start did not show up because it was counterbalanced by a stronger and more consistent effect of Length in this task. There is an indirect way of inquiring into this issue. It can be expected that the counterbalancing would reveal itself as a negative correlation between individual beta values for Start and the strength of the correlation between Length and Start for each subject. Testing this hypothesis, however, did not support that the counterbalancing took place, as the strength of the correlation was found to be negligible, $p > .67$ for either line orientation.

2.4.3 Discussion of Experiment 2

The results of Experiment 2 demonstrated that the approximate estimation of symbolic numerical magnitudes was performed on the linear scale. I showed that the linear regression model predicted the data better than the full model with a weight for a logarithmic component. The analytical method, decoupling the effects of linear $End_{[Start-Target]}$, Start and Length, provided a further support for the strong linear hypothesis. The logarithmic hypothesis predicts a negative trend for linear $End_{[Start-Target]}$, complemented by the negative trend for Start and the positive trend for Length. However, the effect of Start was non-significant, whereas the negative trend for Length was very consistent at a between-subject level and moderately consistent at a within-subject level. The results suggest that the negative trend for linear $End_{[Start-Target]}$ was due to the central tendency bias. The regression means were statistically indistinguishable from .5, implying that the switch from overestimation to underestimation was in the middle of a numerical interval. Once again, the strength of the central tendency was a marker of randomness in performance, such that the stronger effect was accompanied with lower variances explained by the regression models.

The effect of Length essentially implies that subjects tended to construct longer extensions to the line as the numerical difference between Target and Start increased, resulting in an increasing underestimation of $End_{[Start\text{-}Target]}$. The findings of this effect with the null effect for Start are in a striking contrast to the results of the line-marking task, where subjects were biased by the magnitude of Start, not Length. Taking into account that the effect cannot be ascribed exclusively to Length (i.e. the difference between Start and Target), as the latter should correlate with the difference between other stimulus magnitudes, one can interpret the results as showing that subjects' decisions in the line-construction task were biased by the magnitude of numerical differences between numbers rather than the individual absolute magnitudes of the latter.

2.5 Discussion

The investigation of the subjective scale for magnitude representations cannot take for granted the notion that the type of the scale can be inferred directly from the stimulus–response mapping. The aim of our study was to describe and exploit a method that addresses the theoretically motivated problem of differentiating between the linear and logarithmic scaling hypotheses for numerical magnitudes, while controlling for the bias in the decision making. The method exploits the idea that a scale is defined not by its appearance but by the transformational rules according to which magnitudes get assigned (Luce, 1959; Stevens, 1968). The method was implemented in a modified version of the number-to-position paradigm, where subjects were required either to mark the position of an Arabic numeral within an interval of varying length and start or to complete such interval by constructing the line of an appropriate length. The modification also allowed us to avoid the shortcomings of the previous studies, where a digit number was positioned within standardized intervals. This sort of interval is easy to deal with for adult subjects, and hence, the null result does not provide convincing evidence for the linearization of the numerical scale.

The results of model selection showed that responses were derived from a linear subjective scale irrespective of whether subjects were required to mark or construct the line. I used two complementary approaches to the data analysis, those of model fitting and analytical decomposition, and none of them revealed signatures of a logarithmic trend in responses. Instead, the presence of the central tendency was found: a form of linear compression where small numbers in an interval are overestimated and large numbers are underestimated. This effect has been observed in diverse experimental settings (e.g., Huttenlocher, Hedges, & Duncan, 1991; Matthews & Stewart, 2009; Nakamura, 1987; Preston & Baratta, 1948; Sheth & Shimojo, 2001) and is likely to represent a general response bias under uncertainty. This view is supported by the findings in our study, showing that the responses were more randomly distributed for the subjects with a stronger central tendency.

One of the possible reasons why the performance in our tasks revealed a perfectly linear mapping is that the magnitudes presented as Arabic numerals are more susceptible to algorithmic computations than those presented non-symbolically. For example, the judgments could be partially based on the analyses of the decade differences. That might impose a roughly linear structure on the estimation, even though the latter remained approximate. Consequently, a generalization of our findings to the other formats for numerical magnitudes (i.e., dots or the number of tones) should be treated with caution.

However, the combinatorial method, when applied to numerosities presented non-symbolically, provides an opportunity to resolve the issue.

Prior to further discussion, a separate note is required regarding the value of the model for the transformational rules, presented in the beginning of this chapter. In many applications, the model selection is often just a problem of describing the data in a concise way. Little emphasis may be given to the processes that make the data be organized in a particular way. In the present study, the selection of the model for a set of transformational rules goes beyond that. Effectively, the problem of model selection here is concerned with the question 'How is a numerical magnitude computed?' and, for this reason, it closely relates to the problem of cognitive model for number representations. The set of transformational rules determines abstract properties of a cognitive model. If a cognitive model is unable to implement the set of transformational rule that account for the behaviour, then it should be discarded or treated as providing only a partial explanation for the data.

The mental number line hypothesis plays an important role in our understanding of the processes underlying the representations of number. The hypothesis can be characterized by two statements. First, the mental number line is held to represent magnitudes in one orientation only, left to right in our alphabetic cultures (Shaki & Fischer, 2008). Second, the mental number line is held to be the representation of numerical magnitudes automatically and obligatorily activated in all numerical tasks. This implies that the performance in the right-to-left condition would require some sort of mental rotation, which could have the effect of producing more internal noise, and hence more responses variability. Despite the fact that a number line analogy was explicitly used in the design of the study, the results did not show any accuracy differences between L-R and R-L conditions in either task. However, as most evidence for an oriented representational continuum is derived from reaction time data, it is possible that the accuracy measures in the absence of a limit on reaction times may be insufficiently sensitive to detect the costs.

Our results also demonstrate that the performance was affected by task-specific effects. In the line-marking task, subjects tended to overestimate target magnitude when the start of an interval increased, whereas in the line construction task they overestimated when the length of the interval increased. These particular trends are not compatible with the logarithmic mapping that predicts a greater overestimation for smaller starts in the line-marking task and for smaller lengths in the line construction task. Meanwhile, the finding that subjects were biased in different ways clearly indicates that marking magnitude and constructing magnitude emphasized different numerical relations and that, other factors being equal, the way subjects manipulate and combine the quantities can have a specific effect on an estimation outcome. If the task required an assignment of a discrete magnitude to a *location* on the physical line, then the relations between numbers were represented in terms of their absolute magnitudes. If the task was to complete an *interval*, that is, something that extends from *A* to *B*, then those relations were represented in terms of differences between numbers.

Alternatively, two possible mechanisms predicting the overestimation of a target number can be envisaged in terms of the mental number line hypothesis. The first possibility is that the bias can be a result of an attentional shift, evoked by the canonical L-R orientation of the line. As proposed by Lourenco and Longo (2009), the amount of compression in the mental number line may depend on whether some part of the number line is in a focus of attention. The segment of mental number line becomes decompressed when it is in the focus; otherwise it returns to a default compressed state. For example, in our line-marking task, subjects may tend to fixate on the interval between Start and Target more than on the interval between Target and End, as the position of Target should be marked at some distance from the interval Start. As a result, the unattended part may become represented compressively, resulting in the overestimation. This idea seems to account for the findings that the overestimation was somewhat smaller for the non-canonical orientation. Here the magnitude of interval End was presented in the location of Start for a canonically oriented interval and therefore could have a greater saliency than in the non-canonical condition.

The second possibility is that the target overestimation may be closely related to so-called operational momentum bias, reported for the operations of addition and subtraction (Knops, Viarouge, & Dehaene, 2009; McCrink, Dehaene, & Dehaene-Lambertz, 2007). The phenomenon is characterized by subjects' tendency to increasingly overestimate for addition and underestimate for subtraction as the true sum or the true difference increase. It is thought that the effect arises from dynamic representations of symbolic operations on the mental number line and can be described with a physical analogy: Before a moving body stops under the effect of counteracting forces, it travels some distance, which is greater for heavier bodies. In this analogy the body is a number, the mass is its magnitude, and the path along which the body moves is the mental number line. Given that, from a mental number line perspective, finding a location of a number within an interval could require moving along the mental continuum from left to right, the process of mapping numbers and performing addition appear to be operationally similar to each other and can cause similar behavioral outcomes.

The main reason why both possibilities provide at best a partial interpretation for our results is that an obligatory mapping that is automatic and beyond cognitive control, as required by the mental number line hypothesis, presumes a unique mode for representing the relation between magnitudes. The contrast of the numerical factors biasing performance in our tasks clearly shows that it was not the case. In keeping with the physical analogy, the performance in the line construction task would require a different sort of dynamics, as compared with the line-marking task: Here the overestimation was caused not by the mass of the body (i.e., number absolute magnitude) but by the differences between two masses (i.e., numerical difference). If the mental number line allows for such flexibility, then it represents an adaptive strategy used to operate with abstract quantities: convenient and conventional but not obligatory.

The question remains what these task-specific and number-related effects tell us about magnitude representation and processing. First, the presence of a consistent bias per se suggests that there is a capacity limit that constrains representing the relations between two pairs of numbers simultaneously. If the difference between Start and Target versus the difference between Start and End could be optimally contrasted, then subjects would not consistently weight the difference between one pair of numbers more than the other. Second, our findings suggest that the choice of the format for representing numerical relations on the numerical scale depends on the particular task requirements. In one task, the response bias was triggered by the absolute magnitudes of the numbers, with no effect of differences between numbers, and vice versa for the other task. As this contrast suggests, the relations between magnitudes would be encoded as either the difference between two magnitudes or the magnitude of their difference. From the point of view of formal arithmetical rules, the distinction is meaningless because the statements are numerically equivalent. However, from the point of view of the mental operations with magnitudes, each way of encoding may be better suited than the other for a numerical problem at stake.

In summary, the results imply that the subjective scale of numerical magnitudes in adults is linear. Mapping from the subjective scale into behavior is affected by response biases and can be deployed flexibly according to task demands.

Chapter 3. Ratio scale in the parietal cortex. A TMS study

Abstract

The metric for numerical representations is defined by the distance function, which determines the distance for any two magnitudes. The mental number line hypothesis is restrictive with respect to how the distance between numbers may be computed - as the difference between numerical magnitudes. However, the ratio scale computations allow for another type of the distance function representations, namely, by taking their ratio. This type of computations is not compatible with mapping number on the uniform number line continuum, but is compatible with an alternative type of spatial models for number representations, one that is called here a 'stripe' model. The present task combines the theta-burst TMS protocol and the line-construction task, where subjects compute proportionate magnitudes of numerical intervals, in order to demonstrate the reliance of this sort of computations on the parietal cortex usually argued to implement the mental number line representations.

3.1 Introduction

The numerical distance has apparently been the most important experimental variable in the cognitive study of number. The manipulations with numerical distance elicit the distance effect, which is generally agreed to be a marker of the semantic processing of magnitudes (Pinel et al., 2001). These manipulations helped not only to understand better number processing (e.g. Tang et al., 2006), but also to identify the brain regions critical for implementing metrics for numbers (e.g. Piazza et al, 2004; Pinel et al., 2001; 2004). They have also been instrumental in TMS studies providing the evidence for a causal link between IPS regions in the brain and number processing (e.g. Cappelletti et al., 2007).

Meanwhile, the question that is rarely asked is 'What is the numerical distance per se and how is it computed?' In a broader sense, the question regards the form of *the distance function* that defines the set of operations required to compute numerical distance. The tacit consensus seems to be that the numerical distance is equivalent to the numerical difference. This equivalence especially pronounced in the framework provided by the mental number line hypothesis, where two concepts are indistinguishable. The distance between two magnitudes here is determined by a number of steps, or order values, separating those two numbers. Since the distance function uniquely determines the metric for numerical representations, that is, the distance between any pair of numerical magnitudes on the subjective scale, number line hypothesis proposes a specific metric for numerical representations which is compatible with its spatial form.

However, the statement about the equivalence between numerical difference and numerical distance is not true. An alternative way to compute the distance, which is not compatible with the mental number line hypothesis, is by taking the ratio between magnitudes. In other words, the distance may indicate not *how far* one number from the other on the number line, but *by how much* greater it is. This would require a different form of spatial representations, obtained by decomposing a uniform representational continuum, akin to the mental number line, into 'stripes'.

The problem of what determines the distance function and the spatial model compatible with that closely relates to the dichotomy in the concept of numerical magnitude. One way to conceptualize it, embraced by the advocates of the MNL hypothesis, holds that numerical magnitude is given by position in a sequence, an ordinal value (Izard & Dehaene, 2008). The other alternative is to characterize number as a collection of items in a set, a numerosity (Butterworth, 2005). In the cognitive study of number processing this dichotomy is reflected by a distinction between place and summation coding (Verguts & Fias, 2004), whereas in the language of classical psychophysics (Stevens, 1951; 1957) the dichotomy implies that numerical continuum is both methathetic (having to do with *where*, represented on the interval scale, where zero is just a convention) and prothetic (having to do with *how much*, represented on the ratio scale, where zero is absolute, the absence of 'stuff'). The important point is that these two alternatives differ in respect to possible distance functions for numerical magnitudes. Number as a set allows for two distance functions. One is that the distance function is determined by the numerical difference. Set A can be made equal to set B by adding/subtracting that many items, which is equivalent to the shift of a position in a sequence by that many ordinal values. The other way to define the distance function is in terms of the ratio between set A and set B, such that the numerical distance will be given by estimating how many items are contained in set A for any given item in set B.

3.2 Present study

The possibility that IPS may implement alternative spatial models and associated with them computations was considered in the present study. Here I used the theta-burst TMS protocol to disrupt performance in a numerical task following stimulation of the IPS. The main problem I address in this study was not whether IPS is important for number processing. Previous literature provides ample evidence for this (Pinel et al., 2001; 2004; Piazza et al., 2004). The concern of this study is whether IPS implements a specific type of computations, namely, those admissible for the ratio scale. In order to select the task, which would reveal the signatures of the ratio scale computations and would also utilize explicit spatial representations for numerical relations, the following discussion is required.

The 'number line' and 'stripe' models in the number-line tasks. It is argued sometimes that the number line tasks test directly the visuospatial intuition about number representations and the process of marking the line in accordance with number magnitude mirrors the process of placing magnitude on the mental number line, a sequential mapping (Dehaene et al., 2008; Opfer, Siegler, & Young, in press). However, this may be correct only to a point. The results from the previous chapter show very clearly that the format for representing numerical relations is dependent on the layout of the task. A systematic pattern was observed that provides an insight on the computations used to perform in the task. In the line-marking task, subjects tended to overestimate when the magnitudes of numbers bracketing the interval increased, whereas, in the line-construction task (Figure 3.1), the results showed a highly consistent and highly replicable bias by the length of the numerical intervals. An example with concrete numbers can be drawn for the line-construction task. Given a part of the line bracketed with 12 and 33 and requiring to be extended up to the value 45 (i.e., the interval length is equal to 33), subjects would tend to construct a longer extension as compared to a line bracketed with 59 and 62 and with the target magnitude of 68 (i.e., the interval length is equal to 9). In both cases the correct response would require the construction of a line two times longer than the presented one. Importantly, the responses would not be biased by the fact that the magnitude of 68 is greater than 45, as this sort of the bias would be more characteristic of the line-marking task. In other words, the performance in the line-marking task was biased not by the position of number on the number line, but by an extent of a numerical interval.

This bias is a clear indication the performance in the line-construction task utilizes the ratio scale computations. In other words, subjects mentally manipulate with finite intervals, not with a number line continuum, and construct physical representations of numerical intervals by taking into account their proportionate lengths. This kind of manipulation can be called a 'stripe' model, as opposed to 'number line' model, for representing numerical relations. The possibility that number-line tasks may require ratio judgements was pointed out recently by Barth and Paladino (2011). The results of the previous chapter suggest that it is unlikely to be the case for the line-marking task, as the bias by the absolute magnitude suggests that subjects use sequential mapping, compatible with 'number line' model. The reason why the line-construction task protocol elicits this sort of calculation apparently lies in the rules of the task. Unlike the line-marking task, where subjects had to assign number to a location on the line, the line-construction task explicitly required to produce the length of an interval by the actual construction of the length of a physical line. That is, the task explicitly required manipulations on prothetic continua – both numerical and physical.

3.2.1 Method

Participants. 12 right-handed healthy adults (6 male), 19-35 years old (mean age – 26.4; SD = 5.97) participated in the study. They all gave informed consent, had a normal or corrected-to-normal vision and were screened to be TMS compatible. The study was approved by the UCL Ethical Committee.

Stimuli and apparatus. The stimulus and apparatus was identical to those described for the line-construction task in the previous chapter. The only difference was that the length of a 'part' was such that a correct estimation of the 'whole' would require constructing a line between 480 and 520 pixels long, not between 460 and 520 pixels long.

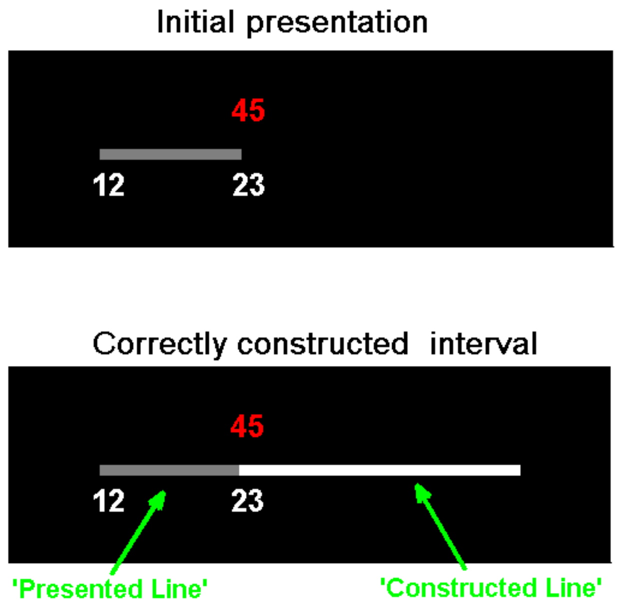

Figure 3.1. The line-construction task. *Subjects are required to extend the line (by moving the computer mouse) such that the ratio between the length of an initially presented line segment to the length a constructed segment would correspond to the ratio between two numerical intervals: one, Standard, defined by two WHITE numbers (i.e. 12 and 23) and the other, Addend, defined by a greater WHITE number (i.e. 23) and RED number (i.e. 45). In this particular case Addend is twice as large as Standard, therefore, the length of a correctly constructed white line has to be two times greater than the length of an initially presented grey line.*

Design. Subjects were presented with a line bracketed below with two numerical magnitudes, Start and End (Figure 3.1). The extent of the physical line signified the numerical distance between the bracketing numbers. Given the length of the presented line and the length of the numerical distance between Start and End, subjects were required to construct the line extension such that its length would correspond to the length of the numerical distance between End and another numerical magnitude, Target (Target > End), presented above the right end of the line. In what follows, the relative magnitude of the numerical interval between Start and End to the sum of the intervals between Start and End and between End and Target (i.e. the interval between Start and Target) will be referred to as *Standard*. Its counterpart, equal to 1 – Standard, i.e. the relative magnitude of the interval between End and Target, will be referred to as *Addend*. Three numerical factors were manipulated orthogonally in the task: a) Addend, b) *Length*, i.e. the numerical distance between Start and Target, and c) *Start*. The choice of a Target magnitude was such that 8 Addends would be $\frac{1}{6}, \frac{1}{4}, \frac{1}{3}, \frac{2}{5}, \frac{3}{5}, \frac{2}{3}, \frac{3}{4}$, or $\frac{5}{6}$ of combined numerical length of Addend and Standard. For the purposes of analyzing the data, Addend magnitudes were arranged into Small (<.5) and Large (>.5) groups (see below for rationale). The values for Length were drawn at random from one of the 4 'bins': 11-20, 21-30, 31-40 and 41-50. A Length from each 'bin' was presented once with each Ratio and with a Start from each 'bin'. The 'bins' for Start were 1-9, 11-19, 21-29, 31-39. The stimulus values were generated in the same way as described in the previous chapter. Each experimental session consisted of 128 trials (8 Ratios x 4 Lengths x 4 Starts). Due to the time limits and no effect of orientation on the performance shown in the previous study, the task was presented only in the left-to-right orientation.

TMS protocol. Subjects attended 3 sessions – one for each of the three stimulated *Sites*: the left intraparietal sulcus (LIPS), the right intraparietal sulcus (RIPS) and the vertex (VRT) as a control site. The order of the session was counterbalanced. The coordinates for parietal stimulation (LIPS: -40, -44, 36; RIPS: 44, -56, 48; in the x-y-z order) were taken from an fMRI study of number comparison by Pinel et al. (2001). These coordinates corresponded to the areas showing the differential effect to numerical distance. Locations on the scalp were determined using Brainsight TMS-MRI coregistration system (Rogue Research, Montreal, Canada), that enables mapping the stereotaxic coordinates, via the use of the subject's normalized brain image, onto the real brain. For each session, subjects underwent coregistration procedure between the pre- and post- TMS blocks. Subjects wore a swimming cap, on which the site for stimulation determined in the coregistration procedure was marked. Stimulation was administered by means of a Magstim Super Rapid stimulator with 4 external boosters with maximum output of 2 T (MagStim, Whitland, UK). A figure-of-eight coil, held orthogonally to the scalp, was used for stimulation with the centre positioned over the marked site. A theta-burst stimulation was used with the parameters of 3 pulses at 50 ms, repeated at intervals of 200 ms for 30 seconds (totalling 450 pulses). The output strength was equal to 40 % of maximum output strength of the stimulator. The stimulation parameters were chosen to cause a reduced cortical excitability for at least 30 minutes. Previous studies (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005) showed that for a period of up to 5 minutes after stimulation, the excitability in the cortex increases. Consequently, subjects were instructed to perform the task only after a 5-minute break following the stimulation.

Procedure. Subjects were shown the stimulus material, explained the task, and instructed how to respond. In the very beginning of each session they underwent the training session with a different set of Standards. Each task was administered twice – before and after TMS. Subjects were asked to provide an approximate and unspeeded estimate of the position of the Target number without performing exact arithmetical calculations. In order to respond, subjects had to construct the line as far as it was implied by the magnitude of Target, given a numerical distance between Start and End and the length of the gray line, representing the physical analogy of the latter numerical distance. Subjects were asked not to hurry or to spend too much time on a trial. For guidance, the time interval of 5 to 10 seconds per trial was suggested. However, it was made clear that this time window was not obligatory. Before the post-TMS block, subjects were asked to keep the rate of responding similar to that in the pre-TMS block.

Data analysis.

Model for Addend. It should be noted that the notation and metrics used in the previous chapter reflected the need to contrast the performance in two different number line tasks and some of them are not suitable for the purposes of the current study. This also refers to the model used to fit the data, which has to be redefined in order to account for ratio scale computations.

According to these computations, the estimates of the proportional relations between magnitudes of Addend and Standard intervals are given by the ratio between lengths of the constructed (*CL*) and initially presented lines (*PL*). Taking into consideration that, the central tendency can affect the generation of the responses, the model would be of the form:

$$(1) \qquad Estimate = \frac{CL}{PL} = \frac{\beta_1 Addend + \beta_0}{Standard} + error,$$

or, if to reshuffle the above expression,

$$(2) \qquad Estimate = \frac{CL \times Standard}{PL} = \beta_1 Addend + \beta_0 + error.$$

In order to obtain the best-fit estimates for the magnitude of the Addend interval, one can note that responding in the task should have the Weber-like variability structure: the construction of a representation for a greater Addend (that is, a construction of a greater physical line) would be subject to a greater variability. Consequently, the model fitting the data should reflect this relation. The realistic model for the variability is given by the generalized Weber Law (Getty, 1975):

(3) $$\text{std}(Estimate) = \alpha_1 Addend + \alpha_0 .$$

Consequently, the best fit estimates for the magnitude of Addend were obtained by maximizing the likelihood in the following expression:

(4) $$L(Estimate \mid Addend) = \\ = \prod_i \frac{1}{\sqrt{2\pi}\,\alpha_1 Addend_i + \alpha_0} \exp\left(-\frac{1}{2} \left(\frac{Estimate_i - (\beta_1 Addend + \beta_0)}{\alpha_1 Addend_i + \alpha_0} \right)^2 \right),$$

with four free parameters β_1 (slope), β_0 (intercept), α_1 (Weber-fraction slope) and α_0 (Weber-fraction intercept). The model was fitted to the data for each subject and condition (3 Sites by 2 TMS conditions).

Bandwidths of the tuning curves for the preferred magnitudes (ratio distance formulation). In the context of the current work, the best fit to the magnitude of Addend, will be treated as a preferred magnitude in response to a particular Standard. Assuming that subjects compute the ratios in this task, the bandwidth for the tuning curves around the preferred magnitude with the ratio distance function will be given by the standard deviation of the distribution for the ratio $\frac{Estimate}{BestFit}$, transformed logarithmically in order to linearize the scale (i.e., $\log\left(\frac{Estimate}{BestFit}\right) = \log(Estimate) - \log(BestFit)$). Note that the log transformation does not imply the logarithmic scale as the normalized magnitudes of Standard and Addend were obtained using linear operations.

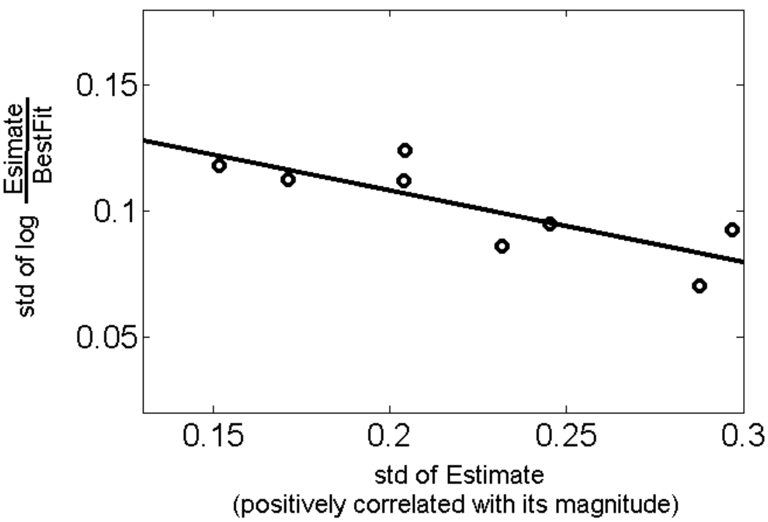

Figure 3.2. The variability structure in the line-construction task. *The variability in response generation, x- axis, which increases with the increase of Addend, is negatively correlated with the variability of the log of the ratio between best fit value and the actual estimate, y-axis. The data presented are group averages for pre-TMS/VRT condition.*

The distributions have an important and useful property, that allows one to use the metric instrumentally, i.e., to increase the sensitivity of the task and, hence, to maximize the statistical power. In practice, it turns out that the bandwidth of the tuning curves for $\log\left(\frac{Estimate}{BestFit}\right)$ monotonically increases as Addend magnitude decreases, i.e., the variability in the construction of physical line to represent Addend magnitude and variability of $\log\left(\frac{Estimate}{BestFit}\right)$ are negatively correlated (Figure 3.2). This property follows from the fact ratio error is inversely related to the length of an interval: if an interval is large, then the increase in the error by *N* units will be relatively small than when the interval is small[3]. Consequently, if the effect of TMS will result in a small additive affect on the precision of Addend estimation, this is more likely to be pronounced in the variability of the tuning curves around small Addend rather than for large Addend. To account for this possibility, the variability data were analysed in two different groups, Small (<.5) and Large (>.5) Addends. The full Anova design consisted of 2 x 3 x 2 factors (Addend: Small and Large; Site: LIPS, RIPS and VRT; TMS: pre- and post-TMS).

3.2.2 Results

Timing data. There were considerable individual differences in the durations of the experimental run. On average, subjects spent 18.7 min to do the task, with minimum and maximum durations of 10 and 34 min. The repeated-measures Anova, with Site (LIPS, RIPS and VRT) and TMS (pre-TMS and post-TMS) as within-subject factors, showed no significant effect. No significant effect was found for mean RTs of the individual trials ($F < 1$).

Exclusion criterion. Four trials were excluded for which no extension was constructed. In order to identify the outliers, the model for Addend (Equation 4) was fitted to the data. The deviation from the values predicted by the fitted models by more than .48 was taken as a cut-off criterion for the non-representative trials, due to inattention or just an error in making a response. The use of a fixed criterion was preferred to the procedure of excluding responses falling beyond several standard deviations from the subject mean because in the present study standard deviations were a critical measure on their own. The magnitude of the cut-off criterion was chosen on the basis of the empirical observations.

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[3] As an example, consider the magnitude of the error equal to *N* units, and the magnitude of two intervals A and A+B, both A and B greater than 0. The magnitude of the error for the ratio distances will be given then as N/A and N/(A+B), and obviously, N/A > N/(A+B).

Figure 3.3 shows the exclusion rate as function of the error magnitude. It can be seen that, staring from the mark '.48', the rate of exclusion increases and never drops back to zero. To obtain an accurate identification of the outliers according to the criterion, the model was fitted iteratively. The trials falling outside the criterion were dropped after each iteration. The first iteration used a larger cut-off criterion (.55), given that the obvious outliers may have a considerable leverage on the best-fit function. Two iterations were required before no trial was dropped after fitting (32 and 26 trials for the first and the second iteration, respectively). Altogether, 55 trials out of 9216 (.67%) were excluded.

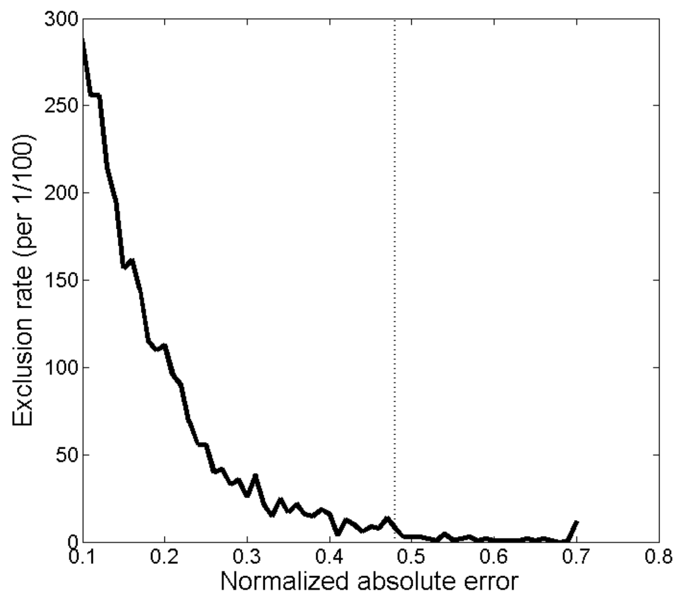

Figure 3.3. Exclusion rate *(the number of the trials falling inside an interval between NAE (normalized absolute error, X axis) and NAE+.01. Dotted vertical line shows the cut-off criterion for non-representative trials*

Model fit. The mean linear function fitting the means was $.82 Addend + .10$, (std (β_1) = .22, std (β_0)=.11), showing the presence of the central tendency in responses. No experimental factor affected the slopes (parameter β_1) and the intercepts (parameter β_0), Site by TMS interaction: $F(2, 22) = 3.08$, $p = .072$. The magnitude of Length fitted to the residuals of the fitted model showed that subjects tended to overestimate as the magnitude of Length increased in 67 cases out of 72, confirming the previous results. No effect of Start was found. The analysis of the Weber-fraction slopes and intercepts showed that they reliably differed from zero, all p's < .05 (corrected), justifying the choice of the model for the response variability.

The bandwidth of the tuning curves. The data for each condition are shown in Figure 3.4 A. The analysis using the full Anova design showed the significance of only one factor. That was a significant effect of the Addend magnitude, $F(2,22) = 9.36$, $p = .011$, effectively confirming that the variability of the distributions for Small Addend was greater for the ratio-distance metric. The effect of the TMS, Site by TMS and triple interactions were not significant, $F(2,22) = 3.45$, $p = .09$, $F < 1$, and $F(2,22) = 2.18$, $p = .16$, respectively. However, the conclusiveness of this result can be questioned. It can be noted that the group standard deviation of the mean bandwidths tended to be greater for RIPS/post-TMS/Big (z-scores = 2.2), creating the problem of unequal variance. Similarly, for the difference between the TMS conditions the group standard deviation for RIPS – Big was nearly twice as great as compared to VRT and 1.5 as great as compared to LIPS. The presence of unequal variance was confirmed by Mauchly test both for the raw data and for the differences between pre- and post-TMS conditions, $p = .02$. When the analysis was re-run only for LIPS and VRT, the effect of Addend magnitude, as previously, was significant, $F(1, 11) = 11.31$, $p = .006$. In addition, two other significant effects were observed. First, there was a significant main effect of the TMS condition, $F(1,11) = 7.67$, $p = .018$, showing a smaller variability for post-TMS condition. Second, the triple interaction Site by TMS by Addend magnitude was also significant, $F(1,11) = 11.76$, $p = .006$.

The t-test of the difference between pre- and post-TMS conditions against zero showed that VRT/Small tended to be smaller than zero, $t(11) = 2.90$, $p = .014$ (uncorrected), implying that the performance improved after TMS stimulation (Figure 3.4 B). No difference for the other Sites and Addend magnitude was different from zero. The planned contrasts between control VRT/Small and (RIPS+LIPS)/Small showed a significant effect of the group, $t(3, 33) = 2.70$, $p = .011$. There was nothing to separate the performance between Sites for Big Addend.

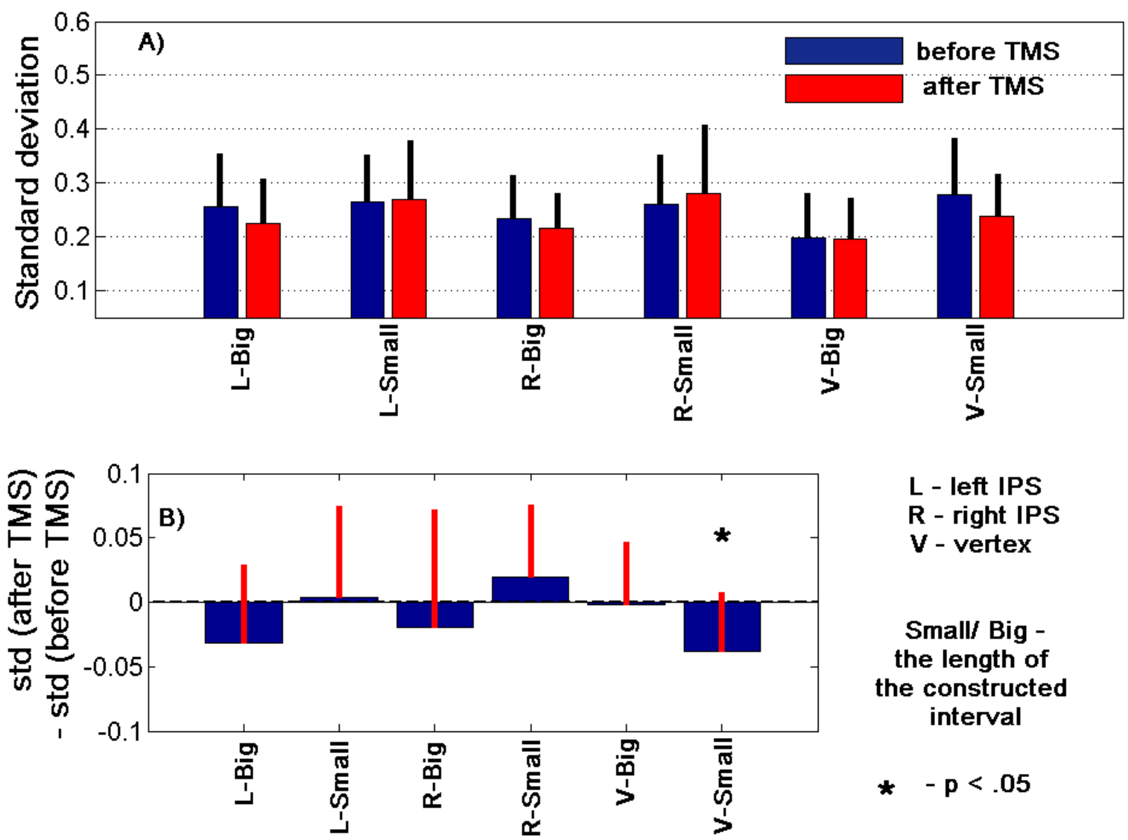

Figure 3.4. The means and group variability of the error. *Vertical lines represent the group standard deviation in the bandwidths of the tuning curves. (A) The raw standard deviations. (B) The difference in the individual standard deviations.*

Correlational structure for the bandwidths. The correlational analysis of within- and between-session performance showed that the accuracy at the within-subject level of performance tended to change from one day session to the other. Meanwhile, within the day session, the bandwidths for pre- and post-TMS conditions and for Small and Big Addend, with one exception, tended to co-vary. There was a reliable correlation for both Big and Small in pre- and post-TMS conditions, all $p < .05$ (corrected for 6 comparisons) and between Small and Big for both pre- and post-TMS condition, $p<.06$ (corrected). Small and Big across TMS conditions also tended to correlate, but less systematically. The exception in this correlational pattern was Small/ post-TMS for RIPS. The bandwidths for this condition correlated with neither Big/post-TMS nor Small/pre-TMS.

In summary, the correlational analysis shows that the individual levels of performance, with the exclusion of the performance after stimulation to the right IPS, showed a within-session consistency, but no between-session consistency was observed for any condition. This suggests that the between-Sites differences for either pre- or post-TMS condition are not informative per se, as the individual level of performance could change from session to session, and so could the group means do.

3.3 Discussion

The purpose of the present study was to investigate, using the line-construction task, whether transcranial magnetic stimulation to the parietal areas, associated with processing numerical distance (Pinel et al., 2001) and allegedly implementing mental number line (Dehaene, Piazza, Pinel, & Cohen, 2003), would interfere with computations on the ratio scale. The ratio scale, as opposed to the interval scale, presumes an alternative way to determine the distance function as a ratio between two magnitudes. Because mental number line representation for numbers is not compatible with this type of computations, showing that the IPS is involved in these computations amounts to showing that mental number line is only one of the available spatial models used to represent numerical relations, but by no means an obligatory one.

The effect of stimulation was assessed by analyzing the variability of responses, which I referred to, following the terminology used in neurophysiological and imaging studies (Nieder & Miller, 2003; Piazza et al., 2004), as the tuning curves around preferred magnitudes. The metric used to calculate responses and error, apart from explicating the ratio computations, possessed a property that could be used instrumentally in the analysis. It presumed a slightly greater bandwidth for the small constructed intervals than for large constructed intervals, despite that the variability of responding per se grew in an opposite direction. This implied that the systematic changes in the variability would be easier to detect when constructed interval was relatively small as compared to the presented one.

The TMS effects are usually reflected in the decrease of the speed or accuracy of the cognitive processes. The advantage of using the unspeeded response paradigm is that it rules out an explanation that stimulation could interfere not with numerical computations per se but with the response selection (Gobel et al., 2004). Meanwhile, the analysis did not show that the precision in the performance deteriorate after stimulation of the number-related areas, the left or right IPS. In this view, the results do not provide strong evidence for interference with the ratio scale computations. In addition, the analysis was complicated by the finding of an abnormal between-subject variability in the bandwidth of the tuning curves following the right IPS stimulation. Characteristically, for each day session, the performance tended to correlate at a within-subject level, and only the performance for small constructed intervals following the right IPS stimulation showed no such correlation. Meanwhile, when the analysis was re-run for the left IPS and vertex only, there was a significant interaction between TMS condition, site of stimulation and the magnitude of the constructed interval.

The further analysis showed a significant difference between pre- and post TMS condition for the small constructed intervals for the vertex only. Here, the performance was more accurate after stimulation than before stimulation. It does not imply that TMS of the vertex caused the improvement in the performance. This finding should rather be interpreted in the context of an effect non-specific to the site of stimulation. A small but significant difference between pre- and post-TMS performance was found, showing that there was a tendency to perform more accurately following the TMS. This suggests that there was a global learning effect of a prolonged exposure to the task within a day session. Consequently, the effect of TMS appears to be responsible for the lack of the improvement in the performance in the LIPS and RIPS conditions.

The study was not able to clearly differentiate between functional significance of each side of IPS for the performance, and a part of the analysis simply demonstrates the difference between control site, vertex, and the average effect of parietal stimulation (see planned contrasts for the difference between pre-and post-TMS condition). There are some indications, however, that the effect was stronger after stimulation of right IPS. First, as mentioned above, the variability after RIPS stimulation violated the correlational pattern for within-session performance. Second, when the differences between pre- and post-TMS conditions were compared between sites of stimulation directly, only the difference between right and vertex reached the significance level, $p < .05$ (uncorrected), whereas for the difference between left IPS a vertex there was only a trend towards significance, p = 13. Combined with the previous results, showing the importance of right IPS processing both numerical and non-numerical magnitudes (Pinel et al., 2004), these data may suggest that right IPS can be involved in linking numerical magnitudes to a spatial model used to represent the relations between them.

The importance of the problem what computations are implemented in the IPS bears not only on the proposals that the parietal areas, associated with the numerical distance processing, effectively implement the 'number line' model (Dehaene, 2009; Dehaene, Piazza, Pinel, & Cohen, 2003; Pinel et al., 2001). Another prominent claim that should go under scrutiny is that the positive skewness of the tuning-curves for number-sensitive neurons represents a critical variable that allows differentiating between linear and log scales (Merten & Nieder, 2009). However, if the numerical distance can be represented by a ratio between preferred and actual magnitude, similar predictions can be made about the skewness, therefore, making difficult to defend this claim. A more careful scaling analysis in future research is required to establish, which interpretation is more accurate.

Chapter 4. Scale analysis of number mapping onto space: manual estimation study

Abstract

Different sources of evidence suggest that number and space share a common metric with respect to action. A part of this evidence comes from the studies showing that task-irrelevant numerical information interferes with spatial parameters of visuomotor performance. Here I propose that the demonstration of the structural similarity between scales for number and space would be a more stringent test for the shared metrics than a mere fact of interference. The scale of number mapping onto space was investigated in a manual estimation task, where the physical size of target stimuli and task-irrelevant numerical magnitudes were parametrically manipulated in the context of the Titchener illusion. Whereas estimates in response to changes in stimulus physical size showed a gradual increase, the effect of number was categorical with the largest number (9) showing greater manual estimate than the other numbers (1, 3, and 7). Possible interpretations that are not necessarily incompatible with the hypothesis of shared metrics with respect to action are proposed. However, the present results show that, without a meticulous scale analysis as a starting point of inquiry, the nature of number-space interaction remains indeterminable

4.1 Introduction.

It has been proposed that the representations of number, space and time utilize a common magnitude system required to bring together magnitude information from different modalities in order to subsequently use it for visuomotor transformations (Bueti & Walsh, 2009; Walsh, 2003). This hypothesis is supported by two lines of evidence. The first can be found in neuroimaging and neurophysiological studies showing that number, spatial, and motor representations partially overlap in the parietal cortex (Pinel et al., 2004; Sawamura, Shima, & Tanji, 2002; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002; review: Hubbard, Piazza, Pinel, & Dehaene, 2005). The second is represented by the studies of visuomotor tasks, showing that task-irrelevant numerical information may interact with the spatial parameters of motor response, e.g., the spatial path of reaching (Song & Nakayama, 2008) or the magnitude of grip aperture (Lindeman, Abolafia, Girardi, & Bekkering, 2007; Andres, Ostry, Nicol, & Paus, 2008). These findings suggest that different magnitudes are related by the common metric for action, and "the parietal cortex transformations, that are often assumed to compute '*where*' in the space, really answer the questions '*how far, how fast, how much, how long and how many'* in respect to action" (Walsh, 2003, p.486, original italics).

Although an interference of number with spatial parameters of movement may seem to support strongly the hypothesis of common metric with respect to action, it can be noted that spatial representations may occur in at least two complementary forms (Kosslyn, 1987; Logan, 1995). One is a categorical form of representations that reflects human cognitive ability to conceptualize experience. The categories like 'extreme left', 'rightwards', 'centre', 'top', as markers of a general direction, may play an important role for movement planning, but they are not sufficient to bring the limb in a precise location in space in order to, for example, grasp an object (cf. Glover, 2004). To do so, motor system requires fine-grained representations of space. Whereas the studies of the effect of number in visuomotor tasks tend to interpret their results as the evidence of the interference with a second type of representations, the categorical mapping of number onto space may also be a possibility and is a well documented fact outside the visuomotor domain (Tzelgov, Meyer, & Henik, 1992; Gevers et al., 2006) The situation in the visuomotor studies of number has not been helped by a frequent use of categorical experimental designs with extreme numerical magnitudes grouped as large and small (e.g.

1 and 2 vs. 8 and 9; e.g., Andres et al., 2008; Fischer, 2003; Lindeman et al., 2007). Such approach is hardly diagnostic for the type of number mapping onto space.

In order to establish whether number and space share a common metric with respect to action, a criterion is required that is more stringent than the mere fact of the interference. This criterion can be derived from a formal description of metrics, for example, the scaling theory (Stevens, 1951). One can propose that the critical test for the hypothesis is to show a structural similarity in the scales for number and space, at least as they can be inferred from the observations of behavioural outcomes. For example, in grasping tasks, the gradual increase in the size of an object leads to the gradual increase of aperture (Marteniuk, Leavitt, MacKenzie, & Athenes, 1990). Consequently, if number and space share a fine-grained metric with respect to action, one can also expect a parametric effect of number on the parameters of movement. That is to say that some value, proportional to task-irrelevant number magnitude, is expected to add up to a computed size of an object, resulting in a gradual increase of the grasp aperture with task-irrelevant numerical magnitude. The critical point is that without a demonstration of the structural similarity between scales for number and space, one cannot tell whether the effect of number on visuomotor performance is determined by the common metric with respect to action or whether it just represents a contextual bias similar to that shown for words with implicit magnitude semantics (e.g., Gentilucci & Gangitano, 2000; Glover, Rosenbaum, Graham, & Dixon, 2004).

The parametric effects were observed in two grasping studies where subjects were required to select between two types of motor response in the parity judgement task (opening/closing finger aperture – Andres, Davare, Pesenti, Olivier, & Seron, 2004;

power/precision grip - Moretto & di Pelligrino, 2008). However, these studies do not provide a direct spatial measure for the effect of number and show a gradual effect on the latencies in the two-alternative forced choice of a response type. The interpretation of the interference with the selection between two response alternatives is not straightforward per se. Several authors argued that the interference of number with spatial processing occurs here from the competition between spatial and numerical codes at the response selection stage (Keus & Schwarz, 2005; Keus, Jenks, & Schwarz, 2005). Such competition may originate from an associations of the verbal concepts applied to number and space, also known as polarity coding (e.g. small/left vs. large/right; e,g. Gevers et al., 2010; Proctor & Cho, 2006).

Consequently, a better test would be to show that the parametric effect occurs within one type of motor behaviour. Although there is limited evidence for parametric effect of number on spatial path of the movement showing an association between number and location (Song & Nakayama, 2008; but see Santens, Goessens, & Verguts, 2011), the evidence of the parametric effect of number on parameters of grasping, that could indicate an association between number and spatial magnitude, does not always conform the metrics-for-action hypothesis. For example, Andres et al. (2008) showed that the effect of number on the grasp aperture is greater, when subjects reach for a larger object. By contrast, the maximum grip aperture has been shown to be a linear function of an object's size with a slope <1 (Marteniuk et al., 1990). In other words, the effect of the spatial magnitude on the aperture is additive, whereas the effect of number is multiplicative, or exponential-like, providing the evidence for structural dissimilarity of the scales for number and space.

4.2 Present study

Here, the scale of numerical mapping onto space was investigated using a manual estimation task, where subjects are required to provide a report about perceived stimulus magnitude by scaling the distance between the index finger and the thumb, also known as aperture (Haffenden & Goodale, 1998; Amazeen & DaSilva, 2005). Under normal circumstances, manual estimation is not restricted by a time window and its proximal consequences may be later corrected to a desired precision using proprioceptive or/and visual feedback. This allows one to test the hypothesis that the effect of numerical information on the spatial parameters of movement is short-lived. For example, Andres et al. (2008) found that number interferes at the early stage of movement, suggesting that control mechanisms counteract the number magnitude interference in later stages of movement execution to allow a precise scaling in accordance with actual object size (also see Glover et al., 2004).

In the present study, manual estimates were provided in the context of the Titchener illusion. The display for this illusion contains a target circle, surrounded by an array of either small or large circles. A circle surrounded by an array of large circles is generally perceived as being smaller than an identical circle surrounded by an array of small circle. Four levels of numerical magnitudes (1, 3, 7, 9) presented inside target circle were used. The trials with no number presented were also included to discourage subjects from thinking that presentation of a number may somehow relate to the purpose of the study.

Given that the study was concerned with fine-grained parametric effects, the critical issue was whether manual estimates could veridically differentiate between relatively fine-grained differences in the stimuli. Previous studies of manual estimation do not report how the estimates change with small parametric increases in stimulus magnitude. It may be the case that responding to the difference is categorical with roughly big estimates if stimulus is perceived as big and roughly small estimates otherwise. To obtain a reliable evidence for fine-grained estimations, 5 levels of target size with 1 mm step between two adjacent levels was used. The study comprised two experiments in two independent groups of subjects with the only difference that in Experiment 1 subjects responded without seeing their hand (*OL* (open-loop) condition), whereas in Experiment 2 the visual feedback was available (*CL* (closed-loop) condition). This manipulation was used since motor responses may be less affected by contextual information in the presence of the sensory feedback (Bruno & Franz, 2009; Glover, 2004), and consequently, a significant effect in one feedback condition may not necessary generalize to the other.

4.2.1 Method

Subjects. Healthy adult subjects were remunerated for their participation in the study. All reported to be right-handed and with normal or corrected-to-normal vision. They were recruited via UCL Subject pool and gave informed consent to participate. 20 subjects were tested in each experiment (open-loop experiment: 9 male, mean – 25.4, SD – 4.9; closed-loop experiment: 10 male, mean – 22.7, SD – 5.1).

Apparatus. The experiment was run in a darkened room. The head movements of subjects were restricted by a chinrest located 570 mm in front of the 20.1’ LCD monitor (1600 x 1200, pixel size 0.255 mm). The midline of the eyesight approximately coincided with the centre of the monitor. In one of the feedback conditions (open-loop, see below Stimuli and Design), subjects kept their right hand in an opaque box (200x200x150 mm). A motion tracking Fastrak 3Space system (Polhemus Inc.) with sampling rate 120 Hz and spatial static accuracy 0.8 mm was used to collect kinematic data. Two sensors were taped on the top of the most distal phalanges of the index finger and the thumb (Figure 1).

Stimuli and design. The experiment was administered in two independent groups. In OL (open-loop) group, subjects kept their right hand in an opaque box and were unable to monitor their responses visually. In *CL* (closed-loop) condition, subjects held their hand in front of their body, so that they could see the gap between the fingers without turning their head.

The stimulus display showed a target circle surrounded by an array of non-overlapping white circles (Figure 4.1), presented against a grey background. The circles in the surrounding array were evenly distributed around the target circle with their centres equidistant from it. The angle for the centres of the circles in the array was varied pseudorandomly. The radius of the target circle was manipulated parametrically in steps of 1.02 mm (4 pixels). There were *5 Sizes* for the target circle with a minimum diameter of 30.6 mm and a maximum of 34.68 mm. The second experimental variable was the type of the surrounding circles, or *Array*. In the *Big Array*, there were 5 circles surrounding the target circle with their radii *twice as long* as that of the target circle. In the *Small Array*, there were 10 circles surrounding the target circle with their radii *half as long* as that of the target circle. The distance between the rims of the middle circle and the circles in the array was fixed at 21.2 mm, and was chosen to minimize variation in the distances between the rims of the circles in the surrounding array as they were changing as a function of the target size.

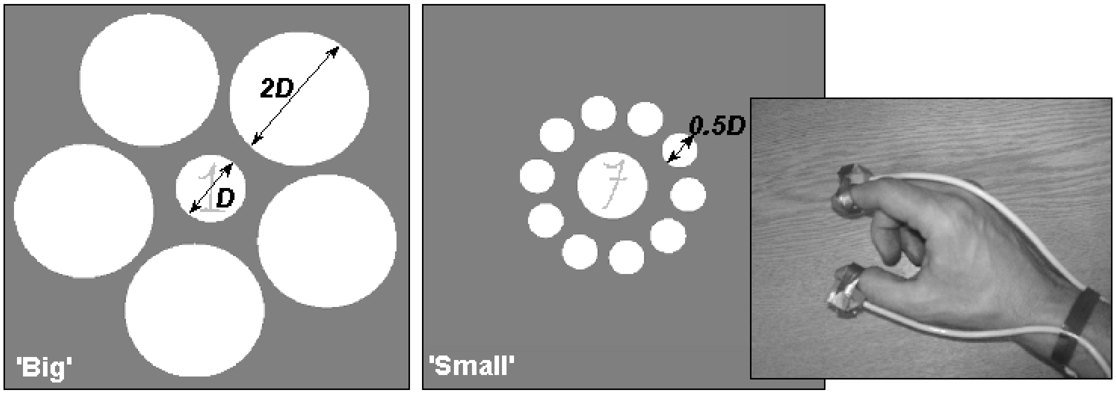

Figure 4.1. Stimulus material (left and centre picture) and response (right picture). *Letter 'D' stands for a diameter of the target circle. Five sizes of D at 1.02 mm steps, starting from 30.6, were used. The diameters for circles in Big (on the left) and Small arrays (in the centre) were 2D and 0.5D, respectively. Numerical symbols – 1, 3, 7 or 9 - in the middle of the target circle contained the same number of pixels for each size of the target. The responses were collected using motion tracking device. The sensors were taped to the distal phalanges of the index finger and thumb. The trial always started with fingers pinched together (zero-distance aperture). In the open-loop condition, the hand was placed in a non-transparent box, preventing the sight of the hand.*

The third experimental variable was the *Number* presented inside the target circle. The colour of a Number was half-saturated grey. A Number was one of four Arabic numerals - 1, 3, 7 and 9, created on the basis of Bradley Hand ITC font. Numerical symbols were approximately equal in size (the height was equal to radius of the target circle divided by 2, the width - the radius divided by 4, at the highest and the widest points, respectively) and were composed of the same number of pixels for every size of the target circle (minimum - 1800 pixels, maximum - 2178 pixels, the difference in pixels for numbers presented in the circles of two adjacent sizes being 126 -/+ 4 pixels). In addition, the *No-Number* condition, in which Target did not contain any number, was also presented. Its functional role was to prevent subjects from thinking that the experiment is 'all about numbers'. The data for this condition were excluded from the analysis.

The design of 2 (*Array*: *Big* and *Small*) x 5 (*Size* of the target circle) x 5 (*Number*: 1, 3, 7, 9 plus *No-Number* condition) factors rendered 50 combinations of variables. There were 8 blocks in the experiment 50 trials each, each condition being presented once within each block.

Procedure. The procedure was self-paced with stimulus presentation controlled by the experimenter. The design, stimuli, apparatus and procedure were identical in both experiments. The lighting conditions were also identical. The only source of light was the ambient light of the monitor, which was sufficiently bright to see the hand in the CL condition. The alignment of the aperture with the stimulus in order to make a direct comparison was not permitted in the CL condition. Here either the hand or the stimulus could be in the foveal field but not both.

At the beginning of a trial, subjects saw an empty grey screen. A vocal instruction 'Pinch together' given by the experimenter immediately followed. On hearing it, subjects were required to close the gap between the index finger and the thumb. They were asked to do it in a natural and consistent way without squeezing the fingers against each other. The purpose of closing finger aperture was twofold. First, a reading from the sensors was made just before a stimulus presentation, determining a zero distance between fingers. Second, it provided for a similarity in the initial state for each particular trial, relating magnitude of the response to the amplitude of movement. Once subjects pinched fingers together, a stimulus was displayed on the screen. At that stage, subjects were required to open up the gap between the index finger and the thumb and scale it accordingly to the size of the target circle. Once subjects decided that aperture is appropriately scaled, they were required to give a vocal signal that they are ready. The vocal signal was either naming the identity of a number in case it was contained in a stimulus or saying 'None' in case it was No-Number condition. On hearing the signal, experimenter pressed the button and a white mask covered the screen for 800 msec. Subjects were required to keep finger aperture 'frozen' as long as the duration of the mask. After the white mask disappeared, the screen turned grey again and a following trial began. Subjects were allowed to rest between experimental blocks.

Performance measures and exclusion criteria. The readings were collected for the first 420 ms of the white mask, giving 25 readings for each of two sensors taken in every trial. The response for a single trial was calculated by computing the distances between pairs of readings and subtracting from them the distance between sensors collected when fingers were pinched together prior to stimulus presentation. The mean and standard deviation of the obtained values then was computed. The mean distance was used as a measure of aperture for that particular trial. A large value for the standard deviation was taken as a signature of subjects not complying with requirements to keep aperture 'frozen'. Usually, it could happen when subjects closed the gap between fingers before the white mask disappeared from the screen. Those trials, where the variability lay beyond 2 standard deviations from subject variability mean, were excluded from analysis. In addition, those trials where response was smaller than 5 mm were also excluded. This exclusion criterion targeted those trials where subjects failed to pinch their fingers together prior to stimulus presentation.

Visual appearance of numerical symbols. There is a possibility that the differential effects of numerical stimuli will be driven by some latent visual features. Consequently, it would be useful to obtain a measure of similarity for visual appearance of stimuli. Here a locally linear embedding algorithm (Roweis & Saul, 2000) was used, which reveals the latent structural similarity of objects via their projection onto a manifold of a lower dimensionality while preserving non-linear relations of the original manifold. The relative separation between projections would indicate similarity/dissimilarity between items. In order to ensure that the original manifold is well sampled, the vectors encoding the images of numerical symbols were complemented with randomly generated vectors. These random vectors were obtained from the original images by random perturbation of each pixel's position. Because numerical symbols were of 5 sizes, the number of grey pixels, used to draw numerical shape differed for original images. To account for this, 5 groups of 200 random vectors were generated, 1000 vectors altogether.

The two-dimensional projection, accounting for most variance, onto the new manifold is shown in Figure 4.2. The analysis shows a relative similarity between 3 and 9 as opposed to 1 and 7.

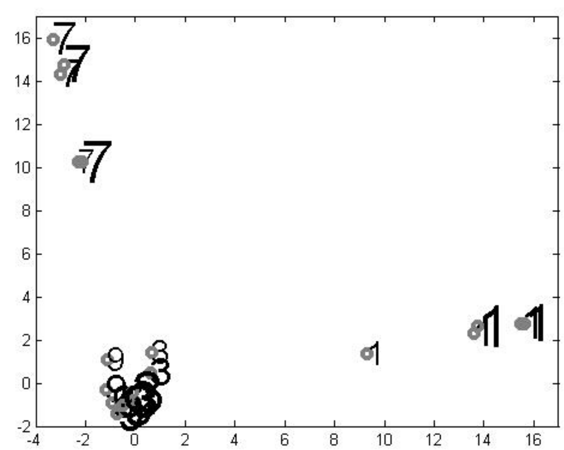

Figure 4.2. 2-d projection of numerical magnitudes onto a manifold of a lower dimensionality using LLE algorithm. *The distance between data points indicates their structural similarity: the closer the data points the more similar they are. The sizes of the font for numerical symbols indicate the levels of Size.*

Data analysis. The analysis of the data was performed in two steps. In the first step, the Anova was used as a filter in order to separate factors and interactions that significantly affected performance from the non-significant ones. The Anova analysis was run on the subjects' means, calculated for each condition, with Array, Size and Number as within-subject factors and Feedback (OL vs. CL) as a between-subject factor. In the second step, significant factors and interactions from Anova results entered as predictors in a more detailed regression analysis of parametric effects. Linear regression models were fitted to the data for each subject independently. A subject-by-subject regression analysis arguably provides a more accurate estimate for the parametric effects than the group level trend analysis, because, due to averaging artifacts, the group-level trend may be non-representative of the individual functions that map from experimentally controlled variables into behaviour (Estes, 1956). The obtained samples of beta-values for each predictor were tested against zero. A visual inspection of the beta-values distributions indicated regular deviations from normality; therefore, a more robust Wilcoxon sign-rank test was adapted to determine whether a beta-values sample comes from a distribution with median equal to zero at the significance level of $p = .05$. The continuity of the response change between different levels of a variable of interest was evaluated using a paired t-test on the subject means for those levels obtained after collapsing data across other experimental factors.

Because the influence of task-irrelevant numerical magnitude on aperture scaling is of a primary interest for this study, the regression analysis of Number-related effects was run separately from the analysis of other factors. In addition to the above-described routines, the t-test analysis of the data partitioned into small (1 and 3) and large (7 and 9) magnitude groups was also run. Given that a significant difference between two groups creates an impression of pseudoparametric mapping (e.g. Fischer, 2003; Lindeman et al., 2007), the findings of this sort have previously been used to argue for the common metric between number and space.

4.2.2 Results

Outliers. On the basis of the exclusion criteria defined above, 113 trials out of 6400 (1.8 %) were excluded in the open-loop condition and 71 trials out of 6400 (1.1 %) in the closed-loop condition.

Non-independence of estimates. Prior to statistical analysis of the effects of experimental factors, the issue of non-independence of responses should be addressed. Motor memory appears to play an important role in movement planning. Converging evidence suggest that the motor system tends to recycle the memory traces of previous responses, resulting in a systematic fluctuation in the variability (Diedrichsen, White, Newman, & Lally, 2010; Johansson & Westling, 1988; Slifkin & Newell, 1999). The present data also showed a considerable degree of the autocorrelation in responses for neighbouring trials, which gradually decreased as the lag between trials increased. The mean Pearson correlation for adjacent trials was .51 for OL condition and .34 for CL condition ($p < .001$). To partial out the influence of the preceding trial, responses in the current trial were regressed on the response in the preceding trial. The first trials in the block, for which there was no preceding trial, were excluded from the analysis. In order to preserve between-subject variability for the following analyses, predicted variance was subtracted without centering the data, i.e., the grand mean of subject responses after subtraction was equal to the grand mean of the original data.

Full Anova analysis. The Anova analysis showed that all three within-subject main effects were reliably significant, Array: $F (1, 38) = 73.70$, $p < .001$, Size: $F (4, 152) = 129.96$, $p < .001$; Number: $F (3, 114) = 13.91$, $p < .001$. Among interactions, that of Array and Size reached significance level, $F (4, 152) = 4.63$, $p = .005$, showing that estimates for Small Array tended to grow quicker with the size of the target circle, as well as the interaction of all experimental factors, $F (12, 456) = 2.60$, $p <.01$. Given these results, the effects of Array, Size, their interaction and the effect of Number were analysed further using linear regression technique.

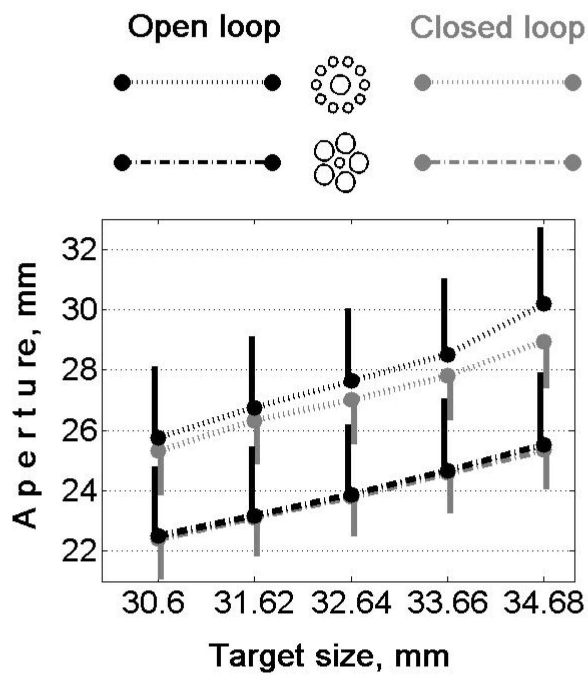

***Figure 4.3. Manual estimates** as a function of the array of surrounding circles and the size of the target circle size. Bars represent the standard error of subjects' mean responses.*

The effect of stimulus size and illusion. The mean responses for Size and Array are shown in Figure 4.3. The regression model with Array, Size and their interaction term as predictors together explained 21 % of variance in open-loop condition and 28 % in the closed condition, suggesting considerable variability in individual responses. Although the median intercepts of the fitting models were slightly greater than zero (OL: 3.7 mm, CL: 4.38 mm), the analysis did not show that the difference was reliable, $p > .10$.

The betas for Array were significantly greater than zero for both Feedback conditions (both $p<.001$, z-score approximation > 3.92). In other words, subjects provided smaller estimates when the target circle was surrounded by large circles than when it was surrounded with large circles. This replicates previous findings showing that the manual estimates are affected by Titchener illusion. The estimated median size of illusion was 2.7 (OL) and 3.2 (CL) mm.

The betas for Size also deviated from zero significantly for each Feedback condition ($z = 3.92$, $p < .001$) showing that, despite great response variability, estimates monotonically increased with the size of target circle. The median increase in estimate for an increase of 1 mm in Size was .81 (OL) and .77 (CL) mm. The paired t-test on the means for different levels of Size collapsed across other conditions showed that each level differed significantly from any other level, even an adjacent one, all $p < .005$ (Bonferroni-corrected for 10 comparisons). It should be noted that the grand average of standard deviations calculated for each condition and subject separately was 3.75 mm for OL and 2.8 mm for CL. If one is to take these values as a measure of discriminability for manual estimates, then it means that subjects demonstrated monotonic increase in the estimates that is well below the discrimination threshold.

There was a significant or near-significant correlation between betas for Size and Array at the within-subject level for OL (Spearman rank correlation: $r = .63$, $p = .003$) and CL ($r = .43$, $p = .058$) condition, respectively, showing that the gain in response to the change in one of the stimulus parameters was proportional to the gain in response to the change in the other.

The interaction between Array and Size was significant only in the open-loop condition (OL: $z = 2.58$, $p = .01$, CL: $z = 1.61$, $p = .11$). For the OL loop, the gain rate for Small array was approximately .4 mm greater then for Big array, that is 1.08 and .65 mm, respectively (for CL, .86 and .75). None of the comparisons between betas for two Feedback conditions, including that for betas of the interaction term (rank-sum test for independent groups) was significant, suggesting that under two different feedback policies subject exploited similar metrics.

Analysis of the effect of Number. Prior to the regression analysis of the effect of Number, the variances explained by Array, Size and their interaction were removed from the data. The mean results are shown in Figure 4.4. The residuals were then fitted with magnitude of Number. Even though the beta-values significantly deviated from zero (OL: $p < .005$, median $\beta = .064$ (+/- .024) mm per unit magnitude; CL: $p < .01$, $\beta = .042$ (+/- .057)), the obtained R^2 were very small (less than $\leq .003$). The inclusion of squared and cubic terms (these terms were either significant or near significant at for the group-level trend analysis) improved the predictive power of the models, $R^2 = .008$ and .016 for OL and CL conditions, respectively. However, the improvement of the fit was at the expense of the significance of the linear term in both OL and CL conditions, $p > .12$.

The paired t-test on the means for numbers collapsed across other conditions showed that the effect of Number was predominantly driven by larger aperture in responses for 9 as compared to other numbers (all p-values < .05, corrected for 6 comparisons for both OL and CL condition, other comparisons – NS (uncorrected)). Following the common practice (e.g. Fischer, 2003), the t-test analysis was repeated for the data partitioned into small (1 and 3) and large (7 and 9) magnitude groups. The t-test showed that the difference between two groups was statistically significant (OL condition: $t(19) = 4.07$, $p < .002$; CL condition: $t(19) = 2.90$, $p < .01$), suggesting that this sort of grouping does not expose the real differences between magnitudes.

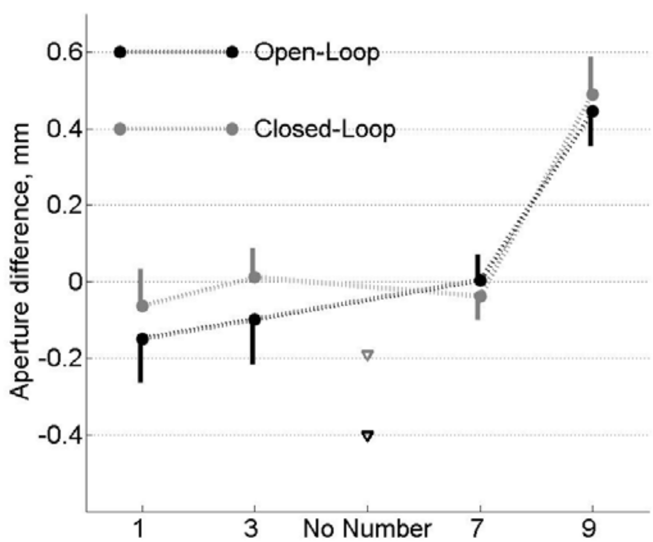

Figure 4.4. The means of aperture differences for each number*, obtained after subtraction of variance predicted by Size and Array. Inverted triangles show the data for No-Number condition. The bars show the standard error of the subjects mean.*

4.3 Discussion

The hypothesis that number and space share a common metric with respect to action predicts the structural similarity of the scales between two magnitudes. This prediction was tested using manual estimation paradigm. The estimates were provided in the context of Titchener illusion. Subjects were required to scale the aperture between the index finger and the thumb in accordance with the size of presented stimuli either with or without visual feedback. The study replicated the findings from the previous reports showing that manual estimates reflect changes in the physical size of the target circle and are affected by the illusionary context (Amazeen & DaSilva, 2005; Haffenden & Goodale, 1998). Responses were more accurate for the closed-loop condition than for the open-loop condition, reflecting the fact that the availability of the visual feedback allows for a better correction of the error (Woodworth, 1899).

The novelty of the present results relates to two critical manipulations with the stimuli. First, manual estimation was found to reflect fine-grained changes in target stimuli. Despite the considerable variability of responding, average estimates showed monotonic increase comparable with the objective increase in the stimulus size. These findings were supplementary to a more critical finding of a small but statistically reliable effect of task-irrelevant numerical magnitude, presented inside the target circle. The effect occurred irrespective of the feedback policy, open- or closed-loop. Subjects tended to provide a greater estimate if numerical magnitude was large. However, unlike the effect of the size of target stimulus, the effect of number was non-parametric. It was largely driven by a categorical distinction between the largest number in the range (9) and the rest, whereas the other ‘large’ number (7) did not differ from ‘small’ numbers even for uncorrected comparisons. This is unlikely to be explained by a relatively minor effect size for number in the presence of high variability. First, the differences between two adjacent sizes of target were also considerably smaller than the average standard deviation of the estimates. This fact did not prevent the estimates for the size from showing, on average, a reliable parametric increase. Second, the paired t-test of number effect was run on the residuals obtained by subtracting effect of all other factors, including the differences in individual grand means. Consequently, the variability in the data was substantially reduced, making it easier to detect subtle effects. Meanwhile, the considerable variability in responses may explain why the presence of visual feedback did not eliminate the effect of the contextual information as it could be expected on the basis of existing literature (Andres et al., 2008; Bruno & Franz, 2009; Glover, 2004). Given that the variability of responses marks a limit for control efficiency, the effects that are well below this threshold may be insensitive to the control mechanisms.

A separate analysis also showed that categorical experimental designs, that group numbers as either large or small (e.g. Fischer, 2003; Lindeman et al., 2007), may not be informative about the relations between number and space. Whereas the significant difference between two groups may create an impression of parametric mapping, the regression analysis and the number-by-number paired comparison suggest that this sort of grouping may obscure the real differences between magnitudes and is insufficient to demonstrate a common scale.

An analysis was performed in order to establish whether the effect of number could be driven by some latent factors originating in the visual appearance of numerical symbol. Local linear embedding algorithm (Roweis & Saul, 2000) was used to project numerical symbols onto a manifold of a lower dimensionality. A close distance on the projected manifold indicates the visual similarity between items across different dimensions. This analysis is of a particular importance given the findings from a pointing study (Ishihara et al., 2006) showing that the number 7 does not gradually map onto space. Because the effect of this number was similar to the effect of 1, Ishihara et al. argued that this may be due to the visual similarity between 1 and 7. The analysis of the visual features indicated a relatively small similarity between these two numbers in the present study. It turned out that the average distance between 9 and 3 was considerably smaller than the distance between them and other numbers. If the visual properties of numerical symbols were a critical factor, then one would expect that responses for 3, given its visual similarity to 9, would also be greater than responses for 1 and 7. However, this clearly was not the case.

The question remains why task-irrelevant numerical information affects motor performance even though the scales for number and space dissociate. One possibility is that they dissociate because the effects of number and size are constrained in different ways. Manual representations of variable target size may be strictly determined by the perceived size of the stimuli, whereas numerical magnitudes might create imaginary context (De Hevia, Girelli, Bricolo, & Vallar, 2008) directly affecting movement execution. Whereas this may be the case, one can note that manual estimation is not just a report of the perceived stimulus size. Amazeen and DaSilva (2005) were the first who argued that this view would be too simplistic. They showed the illusionary effects are stronger for manual estimation than for perceptual reports. Their analysis also showed that percepts used for the perceptual reports and for manual estimation are at least in part independent, despite the fact that both are affected by illusion. The present results identify additional points of the deviation of the manual estimate from being a simple report of the perceived size. These deviations seem to occur at the stage of mapping a percept into a motor response. First, responses showed a relatively high degree of autocorrelation. This suggests that the response in manual estimation is coded in two complementary reference frames: one is determined by the actual size of the stimulus, the other is determined by the memory traces of previous motor commands. A considerably weaker autocorrelation in the closed-loop condition also suggests that the functional role of the visual feedback is not simply monitoring performance to decrease variability, but also to transform routinely repeating behaviours, based on prior motor memories, into an object-oriented performance. Second, there was a correlation between beta values for Array and Size at the within-subject level, or in other words, the gain in response to the change in surrounding array was proportional to the gain in response to change in the target circle. Here again the correlation was weaker for the closed-loop condition. Given that the open- and closed-loop conditions were identical in respect to the perceptual processing of stimuli, this modulation of the relations between gains suggests a non-perceptual origin for the latter.

An alternative explanation for the effect of number on manual estimates is that the number magnitude interacted with categorical representations of space. This type of representations can provide contextual cues for movement planning (Glover, 2004), but does not represent the proper metric for action. This view would relate the effect of number to the effects of the other types of symbolic stimuli that bear implicit magnitude semantics. Current theories of motor control describe mechanism that can enable such interaction. According to these theories, sensorimotor processes are formally equivalent to a decision under uncertainty (Trommershauser, Maloney, & Landy, 2008), because motor system constantly faces a selection from an unlimited number of options while executing a single movement. It is believed now that motor system utilizes contextual and memory-based information (priors) in order to constrain the decision space and simultaneously counteract the inherent noise in sensory and motor signals (Kording & Wolpert, 2006). This is consistent with the idea that, according to Tzelgov et al. (1992), the origin of categorical representations of numbers is an everyday experience in which subjects consistently classify numbers as small and large. The retrieval of categorical values is relatively effortless and therefore they can be relied on as long as a task does not require a fine-grained scale to address the problem.

The present findings support the view that representational models for numbers may assume different forms, not necessarily continuous. Despite earlier claims that there is a unique format for number representations, aka the mental number line (Dehaene, 2003), more recent findings started challenging this view (Gevers et al., 2010; Van Dijck, Gevers, & Fias, 2009). The representational multiplicity is supported by the evidence presented in Chapter 2, showing that the representational models for numbers appear to adapt easily to the requirements of the task (also Van Dijck, Gevers, & Fias, 2009). A switch from continuous mapping onto space to a categorical one may be elicited by asking subjects to perform magnitude comparison task instead of parity judgements (Gevers et al., 2006).

What are the principles for categorization of numbers into small and large? It has been argued that number 5 has a special role as a natural borderline between sets of small and large numbers for the range 1 - 9 (Link, 1990; Tzelgov et al., 1992). This categorization, however, has been discussed in connection with the magnitude comparison paradigm and may be triggered by specific features of the task. It is often elicited by the explicit instructions like ‘Press left key if number is < 5 and the right key if the number is > .5’, or, when the comparison is between any two numbers rather than between a number and a standard, such categorization may have behavioural relevance if speeded judgements are required. As Link (1990) suggests, magnitude judgements may be analysed in probabilistic terms: the probabilities of responding smaller are not equal between numbers. It is more likely to respond ‘smaller’ for numbers 1- 4 than for numbers 5-9 with the point of equal objective probability for responding ‘smaller’ and ‘larger’ centered on 5. Consequently, the model that categorizes number in this way optimizes behaviour and increases chances to respond correctly at a rapid rate.

Such categorical model does not automatically generalize to other tasks. For example, under different experimental settings, when subjects are required to enumerate items after a brief exposure, number 4 may be considered as a borderline between small and large numbers - the small set is also known as a subitizing range (Trick & Pylyshyn, 1994). The task presented in this study did not have time constraints nor required a selection between alternatives and, therefore, the categorization of numbers could be principally different from any of the above examples. The results suggest that subjects implicitly categorized 9 as large number and all smaller numbers as small. Even the presence of a gap in the stimulus range through omitting number 5 did not prompt subject to use the categorization with respect to 5. The question is whether the observed categorization of 9 as large number and the rest as small can be psychologically relevant. A tentative answer may be as follows. One of the most widely known results in the cognitive science is that the ability to represent differences between items along unidimensional continuum is limited to approximately 7 items (Miller, 1956). This fact has been related to a limited cognitive capacity to transmit information. As long as the measurement theory is concerned (Stevens, 1968), this is equivalent to the limited capacity of assigning a number to a stimulus magnitude. Consequently, these limits may suggest a naturalistic model for a categorization into small and large sets, with 7 rather than 5 completing the set of small numbers. One could speculate that the present results represent the first albeit limited evidence for such categorization.

In conclusion, it could be noted that it is of a particular importance for the hypothesis of the shared metrics that numerical magnitudes may interact differentially with the spatial parameters of different types of movement. Previous research on the effect of number seems to underestimate the fact that different types of motor behaviour may rely on different computations (but see Andres et al., 2008). For example, the type of movement investigated in the present study is a non-rapid and imitated movement, rather than one that aims at getting in contact with an object (see also Andres et al., 2004, and Moretto & di Pellegrino, 2008). Therefore, it may be not surprising that the parametric effect here was lacking, as imitated and actual motor responses may rely on the different neural computations and different representations of space (Carey, Dijerkman, Murphy, Goodale, & Milner, 2006). Consequently, the present finding of the categorical effect of number on the non-rapid motor responses does not in itself refute the hypothesis of shared metrics for number and space. However, these findings stress the point that the attribution of observed effects of number on motor performance does not in itself entail a shared metric or a shared mechanism. They suggest that without a meticulous scale analysis as a starting point of inquiry, the nature of number-space interaction remains indeterminable.

Chapter 5. Levels of spatial numerical association

Abstract

The present study investigated the mechanisms affected by numerical magnitudes in pointing task. Previous studies made a distinction between effects of number on motor planning and motor execution but they lacked methodological tools to draw clear-cut boundaries between them. Here, a novel paradigm is presented enabling to study the effect of number on planning and execution in separation. In a variant of the double-step task, subjects were required to make pointing responses to a target if the latter contained an odd number and to correct trajectory in-flight in case target switched location after movement initiation. The results showed that numerical magnitudes affected the initial direction of the movement, with no effect found for in-flight visuomotor corrections following location switch. The pattern of trajectory deviations suggests a non-sequential mapping of number onto space, with extreme values (1 and 9) associated with the left side and medial values (3 and 7) associated with the right side.

5.1 Introduction

5.1.1 Rationale

The very first investigation of the effect of number on reaching performance (Fischer, 2003) stated the distinction between the effects on motor planning and on motor execution. However, that and the following studies (Ishihara et al., 2006; Song & Nakayama, 2008) lacked methodological tools to draw clear-cut boundaries between those two processes. The main purpose of the current study was to investigate which of them, motor planning or motor execution, is affected by the interaction of number with spatial processing.

To this end, I used a modified version of a well-established experimental framework, known as a double-step paradigm. The structure of the task presumes that the initial goals affecting response selection may differ from the goals that define the final outcome of the movement. This allows investigating the effect of number on the processes of motor planning and execution in separation. Some discussion is required regarding specifics of this visuomotor task.

5.1.2 Double-step paradigm

A characteristic feature of this paradigm is an instantaneous change in a stimulus location *at the very moment* when the speeded response (a saccade or a hand movement) is initiated towards a target. It has repeatedly been demonstrated that that the success or failure to perform in this task are largely independent of the frontal executive functions and that the visuomotor adjustments of a reaching movement towards a new target location could be observed before or even without subjective awareness of the location change. Thus, Pelisson et al. (Pelisson, Prablanc, Goodale, & Jeannerod, 1986) asked subjects to make rapid pointing movements toward a visual target without vision of the hand. A minor displacement of the target was synchronized with saccade and, hence, it could not be perceived due to saccadic suppression. It was shown that hand movements were corrected toward the final position, whereas subjects' verbal reports consistently revealed the absence of any conscious experience of the target shift. Later, Desmurget et al. (Desmurget, Epstein, Turner, Prablanc, Alexander, Grafton, 1999) exploited this design in a TMS study and found that stimulation of the posterior parietal cortex interfered with the corrections of hand trajectory. Although the attempts to replicate the TMS effects have largely failed (e.g., Johnson & Haggard, 2005), a recent study by Reichenbach et al. (2011), by using an fMRI localizer task to neuronavigate the TMS stimulation, showed delayed corrections after stimulation of the anterior parts of the posterior parietal cortex: anterior intraparietal sulcus (aIPS) and anterior supramarginal gyrus. In addition, the involvement of the posterior parietal cortex for on-flight adaptation was supported by a study of a patient with bilateral posterior lesion who showed slow and deliberate motor corrections to target perturbation (Pisella et al., 2000). This finding represents a double dissociation with the findings from the patients with the frontal lesions who often demonstrate an abnormal behavioural automatism (Perret, 1974; Lhermitte, 1986).

In another double-step experiment (Castiello, Paulignan, & Jeannerod, 1991), the target perturbation was synchronized with the initiation of hand movement. Although the displacement was clearly visible to subjects, Castiello et al. found that perceptual awareness of the perturbation occurred with 300 ms delay comparing to adjustments in hand kinematics. They observed that a peak acceleration was achieved at different times for perturbed (when the target switches the location) and unperturbed (when the target remains in the initial location) trials, 105 and 120 ms after initiation of hand movement, respectively, whereas the vocal signal times, which were the measure of the time when the conscious perception occurred, were around 400msec after the onset of movement. Furthermore, several studies showed that the adaptation to the target perturbation may be difficult to suppress even though subjects were instructed to do so; at least partial adaptation to the perturbation occurs when the task instruction require to stop the movement (Pisella et al., 2000) or to point in an opposite direction (Day & Lyon, 2000). On the basis of these findings, the parietal processes guiding the hand movements towards the target were characterized by the metaphor of an ‘automatic pilot’ (Pisella et al., 2000).

5.2 Present study

The current protocol of the double-step task was similar to that used in the study by Castiello et al. (1991) but included a number of modifications that were required to adapt the task for the purposes of studying the effect of number on the visuomotor behaviour. In the present task, a presented circular target contained an Arabic numeral. The Go/Nogo procedure was used to ensure that subjects attend to the magnitude of the number. The subjects were required to respond by executing a pointing response if the number was odd and not to move if the number was even. In Go condition, the target remained stationary in one third of the trials, or would switch to the left or to the right in the remaining ones (each 1/3 of the trials). The signatures of spatial-numerical association were expected to reveal themselves in the differential deviations of spatial paths and/or timing. If a particular number is associated with a side of space then one could expect that the trajectory would deviate to that side, irrespective whether second-step stimulus switches to the right or to the left, or, as an alternative, the point of transition from the initial direction to a new target location could occur earlier in time and space if the perturbation is compatible with the space-number association. For the deviation compatible with mental number line mapping, trajectories for small numbers are expected to deviate to the left, whereas for large numbers trajectories are expected to deviate to the right. For timing measures, meanwhile, the side by number interaction, not the main effect of number, is predicted, since the association of number with a side of space is expected to facilitate the pointing response to this side and inhibit the execution to the opposite side. Two measures, discussed in the next section, were chosen to hallmark the early stages of the response selection and the later visuomotor on-line adaptation.

5.2.1 Method

Participants. 12 subjects (8 female and 4 male, aged 19-28, mean 23.1) participated in this experiment. All gave an informed consent, reported to be right-handed and to have normal dexterity and a normal or corrected-to-normal vision.

Apparatus and stimuli. Subjects sat at a shorter end of a table (surface size: 60x112 cm). A projector (Epson EMP-X5, refresh rate 60 Hz) vertically mounted 143 cm above the table was used to present stimuli - white circles of 40 mm in diameter containing a black number inside. The background for stimuli presentation was black. The Arabic numerals were created on the basis of Bradley Hand ITC font as to be approximately equal in size (35.4 mm high, 17. 7 mm wide at the highest and the widest points, respectively) and be composed of the same number of pixels (1586 pixels, actual pixel resolution .57 mm). A motion tracking Fastrak 3Space system (Polhemus Inc.) with sampling rate 120 Hz and spatial static accuracy 0.8 mm was used to collect kinematic data. A custom-made Matlab code was written to control operations of the device and save data for the off-line analysis. The stimuli were administered by means of Cogent toolbox. A sensor was taped to the top of subjects' index finger within 10 mm of the tip. An easily palpable 'bump' (7 x 7 mm) was attached to the table 25 cm from and right in the middle along a shorter end of the table and served as a 'starting point' of movements. All computer procedures were triggered by pressing and releasing a button of a computer mouse which was firmly taped to the table behind the 'bump' and individually adjusted for each subject in order to be conveniently pressed and held down with muscular inflation situated at the base of a thumb, otherwise known as a thenar eminence.

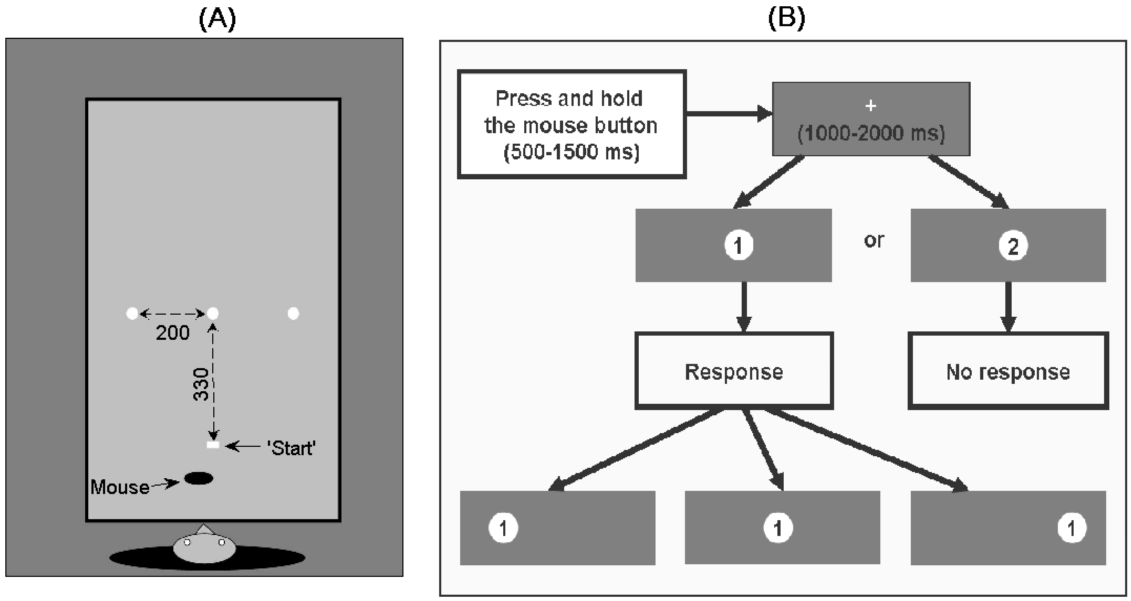

Figure 5.1. Materials and procedure.

(A) *Workspace layout. The index finger was positioned at the 'Start' location. All procedures were triggered by pressing the mouse button by the back of the palm. The white circles indicate the three possible locations for the target stimulus. The first-step stimulus was always presented centrally. After pointing response is initiated, the target could remain in the same location or instantaneously switch to the left or to the right after 67(± 9) ms from response initiation.* ***(B)*** *Flow diagram of the experimental trials. More than one arrow directed outwards from a box indicate various outcomes.*

Procedure. In the beginning of each trial, subjects were required to place the tip of their index finger on the 'bump' (Figure 5.1A: Experimental layout) and press and hold down the button of the computer mouse. If pressing the button had not been interrupted, a fixation cross appeared at the central location at some random time within an interval of 500-1500 ms and then was followed by a target stimulus at the same location after another randomly selected interval lasting from 1000 to 2000 ms (see Figure 5.1B for a flow diagram). The target stimulus was a white circle, 40 mm in diameter, and remained in that location until a response was made. The response rule was as follows. If a number presented in a target circle was odd (1, 3, 7 or 9 - Odd/Go rule, 3/4 of the trials), subjects were required to respond by moving their right hand towards the target and touching it. Alternatively, if a presented number was even (2, 4, 6 or 8 - Even/No-Go rule, 1/4 of the trials), subjects were required not to respond and carry on holding the mouse button down. No data were collected for trials under this response rule. If subjects did not manage to respond for an odd number within 1 sec from a stimulus onset or if they did not followed the rule and responded for an even number, the error messages ‘Too long!!!’ and ‘Number is even!!!’ were displayed, respectively, and the trial was discarded.

Once a response toward a target was initiated in the Odd/Go condition, the target could remain stationary (Unperturbed trials, 1/3 of the Go trials) or instantaneously switch the location to either left or right (Perturbed trials, each side is 1/3 of the Go trials). In the latter case, subjects needed to adjust hand trajectory on-flight towards a new location. The latency between response initiation (i.e. a release of the mouse button) and location switch was 34 $\pm$ 9 ms, and comprised 25 ms in terms of programming code, 0-17 ms due to the projector refresh rate period. The target remained at its location for 1000 ms.

Four numerals of each parity and three possible locations of a target under the Odd/Go rule made up 4 x 3 + 4 = 16 conditions. The main experimental session consisted of 400 trials divided into 5 blocks of 80 trials each. Each condition was repeated 5 times in a block. The order of presentation was pseudorandom.

A training session was administered before main experimental blocks and differed from the latter only in number of trials and numerical magnitudes of digits used as stimuli. For the odd/go and even/no-go conditions, numbers 5 and 0 were used, respectively. There were 20 trials in the training session – 5 odd/right, 5 odd/left, 5 odd/unperturbed and 5 even/no-go.

Instructions. Three points were particularly stressed in instructions to subjects: a) the importance of keeping the index finger's tip on the 'bump' in the beginning of each trial, b) the importance to respond both quickly and accurately, c) the importance of starting to move the hand *towards* the target as soon as the decision to respond was taken and to adjust trajectory on-flight if a target perturbation occurred.

Data pre-processing. The position of the sensor taped to the index finger was taken for the location of the hand. The collection of the data started immediately after a stimulus was presented for the first time in the trial and stopped 1000ms after the movement initiation. The data were smoothed using second-order Butterworth filter with a cut-off frequency of 10Hz. The frame of coordinates was transposed as to align each coordinate axis with principal directions of the pointing movement: X axis - with lateral deviation, Y axis – with forward distanced and Z axis -with the elevation above the table. In order to do this, the coordinates of three points on the table were collected before a subject performed the task. Two points were on the line joining the centres of the target at any two locations. The coordinates of the third point was taken 300 mm from the centre target on the line joining the centres of the target and the 'bump'. Using this coordinates and the method of principal components, the angles of rotation were calculated. Only X and Y coordinates were used in analysis of spatial paths and kinematics of movement.

The first reading of the sensor in a trial was taken for the starting point of the trajectory. It was aligned with zero coordinates. Before that, in order to ensure that the alignment did not reveal any bias, the mean position in all trials for each subject separately was calculated and subtracted from the data. The transformed starting positions for perturbed trials were submitted to repeated measures 2 x 4 ANOVA with Side (i.e. left/right perturbation) and Number (1, 3, 7 and 9) as the main factors. No statistical difference was found between conditions for either X or Y coordinates. The ends of trajectories were calculated using a tangential velocity threshold: the velocities had to drop below .1 m/sec and remain below this mark for at least 33 ms (time required to obtain 4 readings from the sensor). Spline interpolation (Matlab command *interp1*) was used to find the critical points on trajectory (see below: Performance measures). The timing of trajectory events was inferred from the sampling rate of the device. The interpolation was used to obtain trajectory data points for each millisecond of movement from the raw data of the device. The time of the mouse button release was taken as a time of the movement initiation. I compared this measure to the estimations based on the time when hand passed the velocity threshold of 6 cm/sec. The correlation between two measures was very high, r = .98, sd = .01, despite that the releases of the mouse button was made by the wrist movement, whereas the velocity profiles refer to the movement of the index finger (it is known that fingers tend to start moving earlier than the wrist, see Castiello et al., 1991).

Performance measures. The Unperturbed trials were discarded. Two time measures, the time of the movement initiation (reaction time - RT) and movement time (MT), were used to characterize the duration of the preparatory and executional stages of the motor response, respectively. RT was calculated as a time between the presentation of the target in the central location and the release of the computer mouse button. MT was calculated as a time between the release of the computer mouse and the completion of the movement.

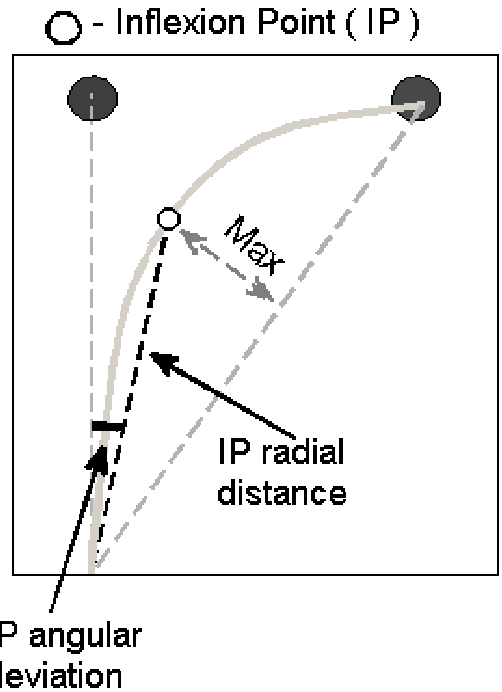

Figure 5.2. The definition of Inflexion Point *as point where trajectory (light grey solid curve) deviates maximally from the line connecting the start and end points. The dark grey circles indicate the position of centrally presented and perturbed-to-the-right targets*

Two spatial measures were used, one for the early processes in motor planning, the other one for visuomotor adaptation to the target perturbation. As a measure of the early processes, I took the location of the hand after 50 mm from the trajectory start and refer to this as to an Initial Thrust (IT). The parameters of interest associated with IT were its time and lateral deviation. The latter was defined as an angle between vector pointing at the forward direction and a line connecting start of trajectory and the location of the hand. As a measure of visuomotor adaptation, I used the point of maximal deviation of the trajectory from a straight line joining the start and end points. In what follows, this point will be referred to as *Inflexion Point (IP* –see Figure 5.2*)*. Given that the adaptation to a consciously perceived perturbation produces composite trajectories resulting from superposition of initial and corrective movements (Flash & Henis, 1991; Desmurget, Problanc, Jordan, & Jeannerod, 2006), IP appears to be a natural marker for an on-going adaptation, since it represents a point of transition from a movement with a principal direction towards unperturbed target to a movement directed to a perturbed target. IP also closely relates to the measure proposed as a path curvature index (PCI – Atkeson & Hollerbach, 1985; Desmurget et al., 1999). PCI represents the ratio $l = a/b,$ where a is a maximal distance between the movement path and the straight line joining the start and end points, and b is this straight line. However, for the purposes of the current study, the magnitude of curvature itself was not important. The critical characteristics were the location of this point in space and its timing. To this end, three parameters associated with IP were analyzed: the radial distance from the start point, the angular deviation from the line joining the start point and the centre of an unperturbed target, and the IP time.

A 2 (*Side*: left - right) by 4 (*Number*: 1-3-7-9) repeated measures ANOVA (within-subject design) was run to evaluate statistical differences. The degrees of freedom for Side 1 and its error were 1 and 11 respectively. Number and the Side by Number interaction had 3 degrees of freedom and their errors had 33. P-values were subjected to Greenhouse-Geisser correction.

5.2.2 Results

Exclusion criteria. The number of discarded trials where subjects did not respond within 1000 ms after stimulus presentation was negligible (16 trials). There were four criteria for the exclusion of the perturbed trials. First, a trial was excluded if the onset of movement was less than 200 ms after the 1-step stimulus presentation (3 trials). Second, a trial was excluded if the subject failed to adapt to a new location and movement was terminated more than 50 mm from the target (3). Third, a trial was excluded if subjects did not follow the instructions and failed to move their hand rapidly towards a target after the movement was initiated. To identify these trials, I calculated each subject's mean and standard deviation of the time required to cover 100 mm in a forward direction for all trials, including the unperturbed ones. Those trials, where the time was longer than 1.75 standard deviations from the subject mean, were excluded (121). Finally, the trials with gross misplacement of the sensor from the mean starting position (beyond 10 mm either along X or Y axes) were also dropped (12).

Altogether 139 perturbed trials out of 3584 were excluded (3.9 %).

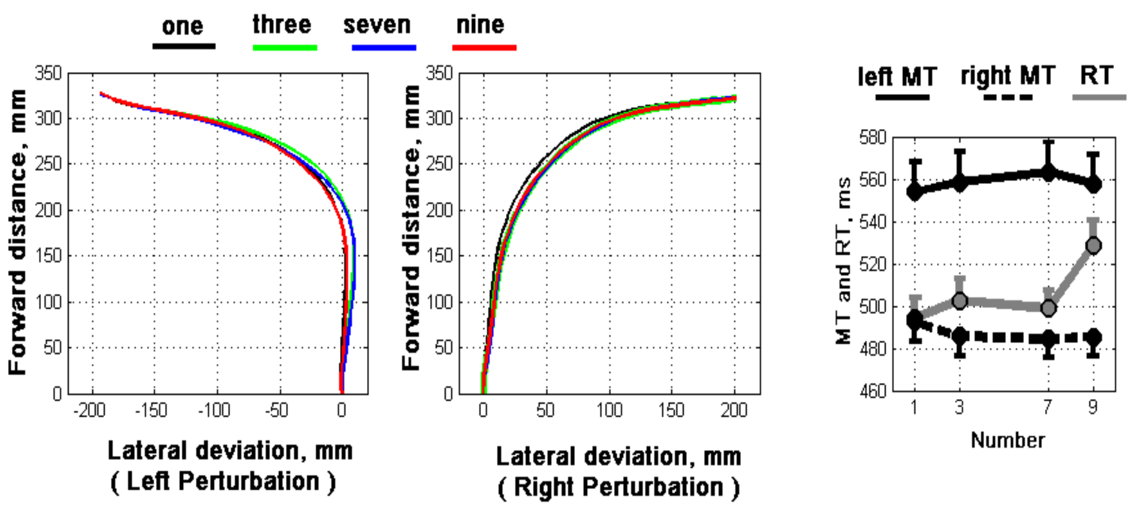

Figure 5.3. Spatial paths, reaction and movement times.

Left and middle graphs: *Trajectory profiles, plotted separately for the left and right perturbation. For averaging purposes, the individual trajectories were stretched/shrunk to have 380 mm distance between start and end points.*

Right graph: *Reaction and movement times. The effect of Number was significant for RT, as 9 took longer to initiate the response than the other numerals. For MT, there was a significant Side by Number interaction.*

Trajectory end points, reaction and movement times. The trajectory profiles and reaction and movement times are shown in Figure 5.3. To estimate whether there was any difference for trajectory ends, the deviations from the subject mean end point were calculated for left and right trajectories separately. The analysis of these deviations showed no significant effect.

The reaction times were analysed using one-way repeated measures Anova with Number as a factor. The results showed a significant effect, $F = 9.98$, $p < .005$. The paired t-test showed (Bonferroni-corrected for 6 comparisons) showed that 9 significantly differed from 1 and 7 ($p < .05$ and $p < .005$, respectively), and nearly so from 3 ($p = .055$). The difference between the remaining Numbers did not even pass uncorrected comparisons.

For movement times, the main effect of Side was highly significant, $F = 41.23$, $p < .001$ (77 % of variance in subject means), with right responses being quicker than left ones. The effect of Number was negligible, $F < 1.2$. However, there was a significant Side by Number interaction, $F = 7.40$, $p < .005$. Both linear and quadratic components were significant, $F = 9.10$, $p = .012$, and $F = 9.54$, $p = .01$, but given a high variance due to Side, etas squared were negligible. When variances due to Side were removed from the data, the partial eta^2 was .12 and .15 for linear and quadratic component, respectively. Overall, the quadratic component in MT data shows that the hand movement to the left perturbation was accomplished quicker for 1 and 9 than for 3 and 7 and vice versa for the right perturbation, whereas the significant linear trend is compatible with the SNARC effect: the hand movement to the left tended to be delayed if the number was large and vice versa for the hand movement to the left.

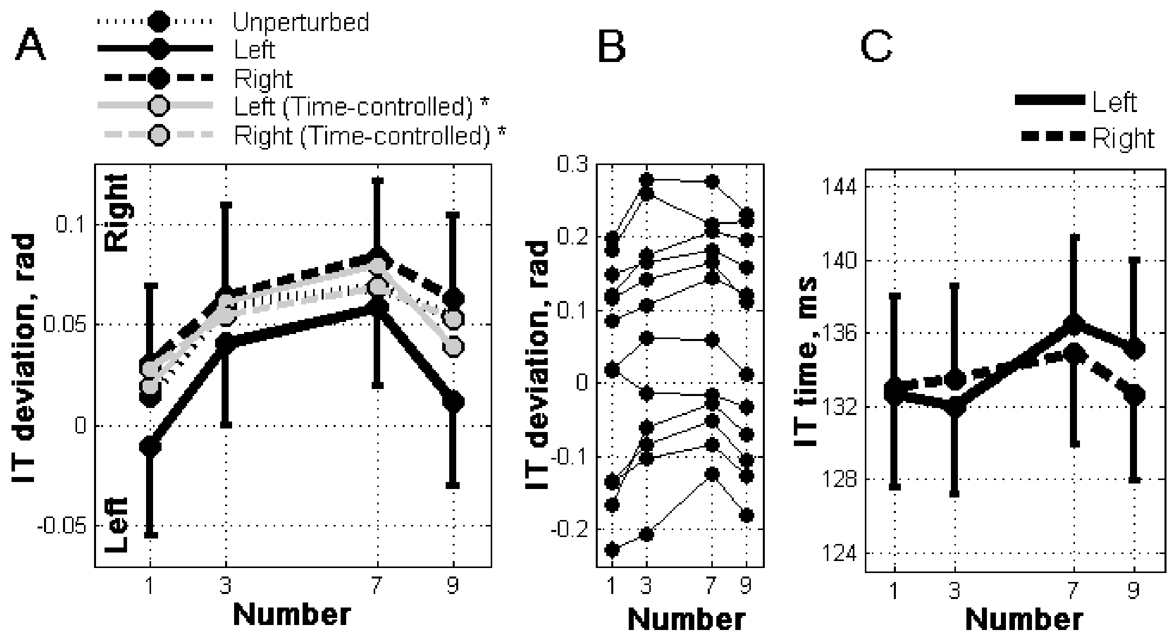

Figure 5.4. Statistics for the Initial Thrust (IT).

(A) *Deviation of IT from the forward direction. The data show a significant quadratic trend, such that the IT deviation to the left tended to be greater for the 'extreme' magnitudes 1 and 9, and vice versa for the 'medial' 3 and 7. The pattern did not depend on the timing of IT (see grey lines). Unperturbed trials (not analysed statistically) are also plotted and exhibit a similar trend.*

** - variances due to time of IT and its interaction with Side removed.*

(B) *Individual IT deviations (12 subjects), averaged across Side. The quadratic trend, found at the group level, is also characteristic for individual means of most subjects.*

(C) *Time of IT. The large magnitudes 7 and 9 required more time to reach the point at which the Initial Thrust was measured.*

Initial Thrust. The statistics for Initial Thrust is shown in Figure 5.4. Both the effect of Side and Number were significant, $F = 13.16$, $p < .005$, and $F = 14.16$, $p < .001$, respectively, but not their interaction, $F < 1$. Side accounted for 17 % in variance of the subject means. The polynomial contrasts for the effect of Number showed that the linear component was significant $F(1, 11) = 6.54$, $p = .026$, 7 % of variance, showing some tendency for a trajectory to deviate to the right as the magnitude of a presented number increased. The contribution of a quadratic term was even more substantial, $F(1,11) = 40.16$, $p < .001$, explaining 19 % of variance in the subject means. The trend indicates that the trajectories for 1 and 9 tended to the left, whereas the trajectories for 3 and 7 tended to the right. The timing of Initial Thrust was also affected by the numerical magnitude, $F = 4.33$, $p = .016$, effectively showing that the speed of the movement tended to be slower for large numbers 7 and 9. This categorical difference between small and large group of magnitudes was shown by the presence of both linear and cubic significant components, $F = 7.73$, $p = .018$, $eta^2 = .05$ and $F = 6.29$, $p = .029$, $eta^2 = .08$, respectively. The Side by Number interaction failed to reached the significance level, $F = 2.79$, $p = .077$, whereas the effect of Side was negligible, $F<1$.

In order to control for the effect that the timing of IT can have on the IT deviation, the variance predicted by the timing and its interaction with Side[4] were removed from the IT deviation data, and re-submitted to the Anova test. After variance removal the effect of Side was eliminated, $F = 2.70$, NS, suggesting that the differential effect for IT deviation was driven by the trials when subjects tended to move slowly at the start. The significance of the effect of Number somewhat diminished, $F = 7.77$, $p < .005$, but the removal of variance predominantly affected the significance of the linear component of the trend, $F = 4.22$, $p = .064$, $eta^2 = .07$, whereas the quadratic component remained reliable, $F = 15.56$, $p < .005$, $eta^2 = .19$.

Inflexion Point. The statistics for timing of Inflexion Point failed to reach the significance level (Side: $F = 1.86$, $p = .2$; Number: $F = 2.83$, $p = .065$; Side by Number

[4] The interaction term in the regression is needed because if time affected the magnitude of the deviation, then the trajectory would tend to deviate to the left for the left perturbation and to the right for the right perturbation.

interaction: F = 2.64, p = .092). For the deviation of inflection point, both main factors and their interaction were significant (Figure 5.5), Side: F = 279.06, p < .001, Number: F = 9.88, p < .005, Side x Number: F = 6.59, p < .005. All factors produced a much weaker affect on the IP radial distance. The effect of Side was significant, F = 9.14, p = .02, whereas the main effect of Number, when corrected for unequal variance (Greenhouse-Geisser procedure) was only marginally significant, F = 3.41, p = .052. The interaction between Side and Number was not significant.

In order to compare the variability of IP between conditions, the 95 % confidence ellipses for spatial distribution of the IP points were calculated for each subject separately. Their principal components (long and short axes of the ellipse) were submitted to the Anova analysis. The results showed no significant difference for Number and its interaction with Side for both components. The factor of Side affected the variability along short principal component, p < .001, which was greater for the movements to the left.

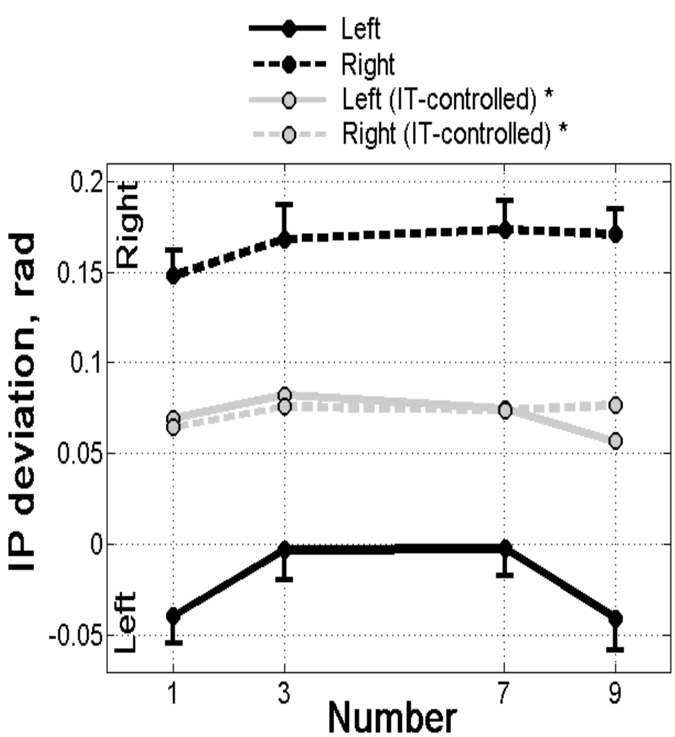

Figure 5.5. IP angular deviation. *The raw data showed a significant effect of Number and Side by Number interaction. However, when the deviations of trajectories for Initial Thrust are taken into account, the effect of Number disappears, and only its interaction with Side remains significant (grey lines).*

** - variance due to the deviation of Initial Thrust and its interaction with Side removed.*

To identify the proportion of variance due to the effect of Number on the on-flight corrections as opposed to those due to the initially taken direction of the trajectory, the linear regression with the Initial Thrust deviation and its interaction with Side as predictors was used to fit IP deviations for each subject separately. The variance predicted by the regression models was removed from the data and the transformed data were re-submitted to the ANOVA analysis. Despite being substantially reduced, the effect of Side by Number interaction remained significant, $F = 4.33$, $p = .016$. However, it was exclusively due to the difference between the left and right Side for 9 that was greater than the difference for other Numbers (for uncorrected comparisons, all $p < .05$; no difference between the remaining Numbers), effectively meaning that number 9 was the easiest to adapt to, irrespective of Side. The effect of Number, meanwhile, was no longer significant, $F = 2.16$, $p = .14$.

5.3 Discussion

The current study investigated the effect of number on the visuomotor performance in the double-step pointing task. The design of the task enables one to differentiate between the effect of number on motor planning and that on subsequent automatic adaptation to target perturbation. It has been hypothesized that association between number and space would reveal itself in the trajectory differences and timing for two critical points on the trajectories. One point characterized the direction of the movement soon after response initiation, the other characterized in-flight corrections after the target switch location. The results showed that the interference of number can be seen early in spatial path of the hand in both perturbed and unperturbed trials. This suggests that the numerical information affects the planning of motor response. A rather unexpected association between extreme values in the experimental range (1 and 9) and the left side and between medial values (3 and 7) and the right side was found. This association appeared to have an overall impact on movement execution as longer times were required to complete responses to the left for numbers 3 or 7 than for numbers 1 and 9, and vice versa for responses to the right. Meanwhile, the contribution of numerical information to the subsequent visuomotor adaptation was minimal. When deviation pattern for in-flight corrections was controlled for motor decisions at the stage of motor planning, only a significant interaction for lateral deviation between side and number survived, showing that the difference in deviation for the left and right perturbations was greater for 9 only. Provided that this finding is not an artifact, its interpretation is problematic, because this effect implies that number was the easiest to adapt to, whatever the side of perturbation. One of the possibilities is that this effect was somehow related to the longer RT times for this number, i.e. it required more time to initiate the movement. Importantly, no effect of number was found on time or radial distance covered by the hand at the inflexion point, which would indicate the delay or facilitation for in-flight corrections.

The results pose certain challenges for the present views on the sources for the interaction of number and space with respect to action. First, the hypothesis of the functional relation between number and space would receive a strong support if numerical information were shown to affect the automatic visuomotor transformation, processed by parietal cortex. The data present no evidence for this. Second, an important point about the space-number association observed in this task is that it was not sequential, i.e., it did not follow the orderly position of the number on the number line. Such result is difficult to reconcile with a view that spatial numerical associations arises from the semantic representation of number on the mental number line. On the other hand, the findings seem to be compatible with the hypothesis of verbal-spatial coding. The principle of polarity remains preserved here, despite that the grouping of the magnitudes differs from the spatial numerical mapping reported in the literature. Given that three other effects have already been reported (SNARC, MARC and Far-Close) in the literature, it is likely that with an introduction of new paradigms, the other forms of number-space interaction may emerge. Consequently, the problem what mapping of number onto space characterizes better the spatial architecture of numerical representations may be secondary to the problem what experimental factors and peculiarities of an experimental procedure drive one or another form of spatial numerical association. The knowledge of the factors would potentially allow for better understanding of the functional significance of these associations.

One possible explanation why number failed to influence the visuomotor coordination proper is that the performance in the double-step task may be robust to the influence of the quantities that are not explicitly spatial However, as the next chapter shows, in-flight corrections can be affected by the quantities that are dissociable from space but relevant for behaviour. Moreover, the implementation of this quantities is automatized and beyond cognitive control.

Chapter 6. The effect of spatially non-specific cues on visuomotor adaptation and spatial discrimination

Abstract

Current theories often address perceptual processing as an act of statistical inference whereby observations of dynamically changing and ambiguous environment are combined with prior expectations. The present study investigates changes in expectations in rapid spatial decision-making using manipulations on spatially non-specific expectations. In the first experiment, subjects made rapid pointing movements towards a centrally presented target and adapted trajectories in-flight if the target was perturbed, i.e., switched the location after movement initiation. The cue presented with the target indicated that the target either would switch to a new location with probability 1 ('switch' cue) or was likely to remain in the same location, but occasionally might switch ('stay' cue). Even though the cue was completely uninformative regarding the side of location switch, automatic in-flight corrections were slower for the 'stay' cue. More critically, the results showed that a switch delay of 100 ms inhibited performance for the 'stay' cue even more strongly, consistent with a change of expectations conditioned on time as opposed to expectations elicited by the cue. This interaction between cue and the latency was further replicated in the spatial discrimination task, where subject pressed a response key compatible with the side of perturbation. The observed interactive pattern indicated sub-optimal processing. The findings suggest that the evolution of internal models can be on an extremely rapid time scale and is supported by autonomous processes, whereby subjects behave in a rational, but not optimal, way.

6.1 Introduction

Current theories often address perceptual and sensorimotor processes as acts of statistical inference. In particular, Bayesian theory of perceptual decision-making holds that in order to work out a solution brain combines available evidence for a hypothesis with prior expectations in a statistically optimal way (Kording, 2007). Such computations seem to be embedded into neural functioning and arguably differ from explicit decision-making (Chater, Tenenbaum, & Yuille, 2006), where the deviation from optimality is often observed (e.g., de Gardelle & Summerfield, 2011; Tversky & Kahneman, 1971;

Summerfield, Behrens, & Koechlin, 2011) and where people often use simpler heuristics (Gigerenzer & Goldstein, 1996).The decision-theoretic approach has been shown to account for the performance in sensorimotor tasks (Kording & Wolpert, 2004), object recognition (Kersten, Mamassian, & Yuille, 2004) and other information-processing routines (e.g. Jazayeri & Shadlen, 2010; Stocker & Simoncelli, 2006). In line with this, the neurophysiological studies find the evidence for probabilistic computations in the brain of non-human species, lacking ability of the conscious control over behaviour (Janssen & Shadlen, 2005; Platt & Glimcher, 1999; Roitman & Shadlen, 2002; Rorie, Gao, McClelland, & Newsome, 2010).

The role of prior expectations in this process can be conceived as providing initial conditions for a decision-making act. The evolution of prior expectations is extrinsic to unfolding decision-making process at a (notional) within-trial level. Accordingly, prior expectations have been modeled as a starting point of evidence acquisition (Summerfield & Koechlin, 2010) or as a factor affecting the decision criterion for accepting the hypotheses (Jepma, Wagenmakers, & Nieuwenhuis, 2012). Owing to their relative stability, prior expectations can be utilized to guide decisions in an ambiguous and rapidly changing environment.

It is not clear, however, whether the above picture is accurate, as little is known about the actual time scale that constrains the changes in perceptual expectations. An alternative view could be that the changes are rapid - to a degree, that they might be supported by autonomous processes. Some insights on relatively rapid changes in expectations are provided by variable foreperiod tasks, where subjects respond with a single key press to a target stimulus presented after a variable interval from a warning signal (for review see: Niemi & Naatanen, 1981). The performance here is affected by a range of factors, three of which are worth mentioning here. First, the reaction time was found to diminish for longer foreperiod interval (Klemmer, 1956; Drazin, 1961), suggesting that subjects learn to use an objective increase in the probability of stimulus occurrence with the flow of time (Elithorn & Lawrence, 1955). Second, the performance is affected by the probability of stimulus occurrence, such that reaction time is generally slower for an unexpected stimulus (Drazin, 1961; Gordon, 1967; Naatanen, 1972). Third, the more relevant (but usually unattended) evidence is that the effects of probability of occurrence and foreperiod length tend to interact such that difference between more certain and less certain stimuli increases for longer foreperiods (Drazin, 1961).

In order to see the relevance of this interactive effect, one could estimate the change in probabilities of target occurrence conditioned on time for a simple case with two forperiods. From a perspective of an ideal observer, if the target is due to occur with certainty, then the probability that it will occur at either time point is .5 at the start of a trial. However, if the earlier time point has been passed, the probability of target occurrence at the later time point is doubled, i.e., equal to 1. Same is true for a target with smaller probability to occur, for example, for one that is expected to occur with probability .4. The initial probability of occurrence at any time point is .2, but it should as well double for the later time point once the earlier point has been passed. The critical point here is that the difference between initial probabilities (i.e., .5 and .2 in the above example), is smaller than the difference between their doubles (1 and .4). This difference, given that all other factors remain constant, is apparently reflected in the interactive effect on RT.

One caveat that remains, however, is that the above findings are not diagnostic in supporting the conjecture of autonomous processing. It has been argued that performance in foreperiod task reflects non-specific preparation under cognitive control supported by the frontal regions of the brain (e.g., Stuss et al., 2005; Vallesi, Shallice, & Walsh, 2007). Consistent with this, the interactive effects are shown for relatively large differences in foreperiods, in a range of seconds, and appear to decrease as the foreperiod range decreases (Drazin, 1961).

The present study attempts to provide a robust test for autonomous processing of prior expectations on a minute time scale and to investigate. The study is concerned with the effect of perceptual expectations that can be characterized as spatially non-specific. These expectations are elicited by a cue, which informs participants that a target is likely/unlikely to switch location, whereas there is no available information about the new location and when it may happen. Meanwhile, responses required from subjects were spatially specific – either pressing the left or right response key or adjusting reaching movement to the left or to the right.

Such paradigm presents certain advantages for the analysis of decision-making in spatial behaviour. In particular, it allows one to differentiate between decision-making processes and a range of other factors affecting performance and to analyze decision-making routines in a purer form. First, it allows dissociating the decision-making process from selective attention (cf. Summerfield & Egner, 2009). For example, these two factors are confounded in Posner's paradigm (Posner, Snyder, & Davidson, 1980) where attentional factors are held responsible for quicker performance for a validly pre-cued location than for an invalidly pre-cued location, even though is not clear how much of the behavioural effect here is due to attention, and how much is due to expectations. Second, by asking for spatially specific responses the paradigm can dissociate decision-making processes from the preparation of a specific response prior to target stimulus occurrence. The spatial non-specificity of the cue implies that neither response alternative can be preferred before stimulus switches its location. This allows one to control for the response bias and response pre-selection. The importance of the motor preparation of a particular response for efficient processing was previously identified in EEG and TMS studies of foreperiod task (Davranche et al., 2007; Tandonnet, Burle, Vidal, & Hasbroucq, 2006) and this factor can be considered as a confound.

The present study utilizes the double-step task protocol (Castiello et al, 1991; Day, & Lyon, 2000; Desmurget et al., 1999; Johnson, Van Beers, Haggard, 2002; Pelisson, Prablanc, Goodale, & Jeannerod, 1986; Pisella et al., 2000) and comprises two experiments, one involving sensorimotor coordination, the other – spatial discrimination. A characteristic feature of this paradigm is an instantaneous change (aka kinematic perturbation) in a stimulus location after a speeded response (most commonly, reaching movement) is initiated. It has repeatedly been demonstrated that the success or failure to perform in this task are largely independent of the frontal executive functions and that the visuomotor adjustments of a reaching movement towards a new target location could be observed before or even without subjective awareness of the location change (Castiello et al., 1991; Pelisson et al., 1986). On the basis of these findings, the parietal processes guiding the hand movements towards the target were characterized by the metaphor of an 'automatic pilot' (Pisella et al., 2000), suggesting that the double-step pointing task is a good choice if a 'proof of a concept' is required in the domain of autonomous behaviour.

The experimental protocol used in the first experiment was similar to that of Castiello et al. (1991). Subjects were required to make rapid, visually-guided movements towards a centrally presented target and adapt trajectories in-flight in case the target switched to the left or to the right after movement initiation. A novel feature of the task was combined manipulations on the probability of target perturbation using probabilistic cues and on the latency of perturbation unknown to subjects and not pre-cued. The cue was completely uninformative regarding the side of the location switch. An interaction between probability and the latency of perturbation would indicate (a) the implicit changes in prior expectations on a very rapid time scale and (b) the autonomous implementations of these statistics into a sensorimotor behaviour.

It has been argued that motor planning is formally equivalent to the decision-making under uncertainty, given that reaching a target may be executed in a numerous ways (Trommershauser, Maloney, & Landy, 2008). The pointing task may be particularly susceptible to experimentally-imposed manipulations on probabilities that will not generalize to other domains. The second, spatial discrimination, task allows one to investigate whether processing implicit changes in the prior expectation is specific for visuomotor behaviour or it is a more generic, amodular, mechanism. The design of the task was very similar to that in the visuomotor task but, instead of pointing to the target, subjects were required to press a response key compatible with the side of location switch. In addition, the task allowed one to investigate whether the priors are implemented in a statistically optimal way. To do so, one has to estimate a within-cue gain between short and long latencies. One would expect that performance should be facilitated for long latency, even though the facilitation should be less pronounced for a cue predicting location switch with a smaller probability. The estimation of the within-cue gain is possible in the spatial discrimination task but is problematic in the pointing task, because the states of motor system differ between latencies of perturbation.

6.2 Experiment 1: Pointing task

6.2.1 Method

Participants. 11 subjects (9 female and 2 male, aged 19-28, mean 23.1) participated in this experiment. All reported to be right-handed and to have a normal or corrected-to-normal vision. One male subject was excluded for the reasons explained below (Results: exclusion criteria).

Apparatus. Subjects sat at the shorter end of the table, surface size: 60x112 cm. A projector (Epson EMP-X5, refresh rate 60 Hz) vertically mounted above the table was used to present stimuli. A motion tracking Fastrak 3Space system (Polhemus Inc.) with sampling rate 120 Hz and spatial static accuracy 0.8 mm was used to collect kinematic data. A sensor was taped to the top of subjects' index finger within 10 mm of the tip. A custom-made Matlab (Mathworks Inc.) program presented stimuli, controlled operations of the device, and saved data for the off-line analysis. The design and presentation of stimuli were aided by Cogent toolbox. The background for stimuli was black. An easily palpable 7 x 7 mm 'bump' was attached to the table and served as a 'starting point' of movements. All computer procedures were triggered by pressing and releasing the button of a computer mouse which was firmly taped to the table behind the 'bump' and individually adjusted for each subject in order to be conveniently pressed and held down with the muscular inflation situated at the base of the thumb, otherwise known as the thenar eminence.

Stimuli and procedure. The flow diagram of the pointing task is shown in Figure 6.1A. In the beginning of each trial, subjects were required to place the tip of their index finger on the 'bump' and press and hold down the button of the computer mouse with the same hand. If pressing the button had not been interrupted, a fixation cross occurred at the central location (330 mm from the 'bump') at some random time within an interval of 500-1500 ms. The fixation cross was followed by a target stimulus presented at the same location after another randomly selected interval lasting from 1000 to 2000 ms. The target stimulus was a white circles of 40 mm in diameter and remained in that location until a response was initiated. After 17 ms of the target presentation, the letter 'U' or 'H' (Arial font) was presented for 100 ms inside the target and then disappeared. Subjects were required to respond as soon as they could by making the pointing movement towards the target with their right hand. If subjects did not respond within 1 sec from the stimulus onset, the error message 'Too long!!! Release the button' was displayed. This trial was moved to a random location in the order of the remaining trials.

Once a response towards a target was initiated, the target could remain stationary (Unperturbed trials) or instantaneously move 200mm to either left or right (Perturbed trials). In the latter case, subjects needed to adjust hand trajectory in-flight towards a new location. The target remained at that location for 1000 ms.

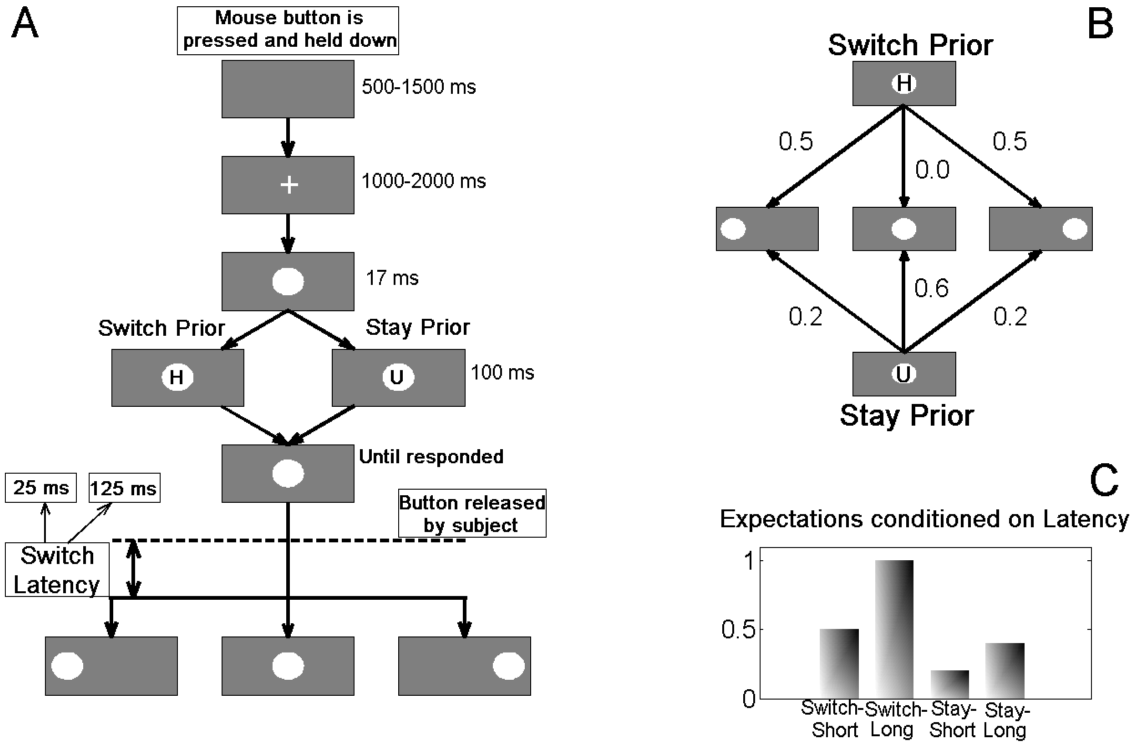

Figure 6.1. Experimental Design. *(A) Flow diagram for an experimental trial. The boxes represent stages of the trial. The bold black lines connect each stage of the trial to a following one. More then one line pointing outward from a box shows optional outcomes. (B) Contingencies of the location switch associated with each Prior. (C) Expectations conditioned on perturbation latency.*

Design. There were 3 variables in the experiment: the type of a perturbation, the latency of perturbation and the prior expectation of perturbation. The type of perturbation comprised 3 conditions: 1) no perturbation, i.e., the target remained in the central location for the whole length of the trial; 2) left perturbation, i.e., the target switched to the left following movement initiation; 3) right perturbation, i.e., the target switched to the right.

The prior expectations (see Figure 6.1B) were manipulated by presenting letters ‘H’ and ‘U’. ‘H’ (the Switch prior) signified that the target is going to be perturbed to either left or right with a probability equal to 1, p (switch | ‘H’) = 1. Left and right perturbations were equiprobable (*p* (left switch | 'H') = *p* (right switch | 'H') = .5). 'U' (the Stay prior) signified that the target is more likely to remain unperturbed. The actual contingency of perturbation was *p* (switch | 'U') = .4, with left and right perturbations being equiprobable, *p* (left switch | 'U') = *p* (right switch | 'U') = .2.

There were two perturbation latencies in the experiment, defined as intervals between movement initiation (i.e., the release of the mouse button), and target perturbation. In terms of the programming code, the latency could be either 25 ms or 125 ms. The actual latency depended on two additional factors. First, the projector refresh rate period of ~17 ms implied a variation between 25 and 42 ms (+100 ms for the longer latency). Second, there was a minor fluctuation as a result of the mouse mechanical latency. Both sources of variability were random.

In what follows, the terminology that makes the description of details more concise was adopted. The term *Side* was used as a short name for type of perturbation. Because of the exclusion of unperturbed trials from statistical analysis due to their non-informativeness, the number of levels for *Side* was reduced to two: *Left* and *Right*. The prior expectations were referred to as *Prior*, with *Switch* and *Stay* levels. Finally, the time of perturbation after the movement was initiated was termed *Latency*, with *Short* and *Long* levels.

The above-described explicitly manipulated expectations can be distinguished from expectations conditional on perturbation latency (see Figure 6.1C). From a perspective of an ideal observer, the initial probabilities of target perturbation at each Latency were .5 and .2 for Switch and Stay prior, respectively. If the perturbation did not occur after 25 ms after movement initiation (i.e. at Long Latency), then expectations that it would occur at 125 ms time should double. Correspondingly, the conditional expectations of target perturbation for Short and Long Latencies are, respectively, .5 and 1 for Switch Prior, and .2 and .4 for Stay Prior.

The main experimental session consisted of 420 trials divided into 6 blocks of 70 trials each. The order of trials was pseudorandom. There were 30 Unperturbed trials in each block. The remaining 40 Perturbed trials were partitioned according to a balanced 2 (Left/Right) x 2 (Switch/Stay) x 2 (Short/Long) design, 5 trials for each condition. Before the main experimental session, subjects completed the training session of 28 trials (12 unperturbed).

Instructions. Subjects were made clear the meaning of the letters presented with the target. They were told that the presentation of the letters indicates a simple rule: if U is presented, then the target is more likely to stay in the same location, whereas if H is presented, then the target is 100% going to 'jump'. Subjects were also clearly explained that the letters do not provide any information on the direction of target jump. Subjects were not informed that there were two latencies for target perturbation.

Apart from giving the description of the experimental procedure, three points were particularly stressed in the instructions: a) the importance of keeping the index finger's tip on the 'bump' in the beginning of each trial, b) the importance to respond both quickly and accurately, c) the importance of starting to move the hand *towards* the target as soon as the decision to respond was taken and to adjust trajectory in-flight if a target perturbation occurred.

Data pre-processing. The position of the sensor taped to the index finger was taken for the location of the hand. The collection of the data started immediately after a stimulus was presented for the first time in the trial and stopped 1000ms after the movement initiation. The data were smoothed using a second-order Butterworth filter with a cut-off frequency of 10Hz. The frame of coordinates was transposed as to align each coordinate axis with principal directions of the pointing movement: X axis - with lateral deviation, Y axis – with forward distanced and Z axis -with the elevation above the table. In order to do this, the coordinates of three points on the table were collected before a subject performed the task. Two points were on the line joining the centres of the target left and right locations. The coordinates of the third point was taken 300 mm from the central target on the line joining the centres of the central target and the 'bump'. Using these coordinates and the method of principal components, the angles of rotation were calculated. Only X and Y coordinates were used to derive relevant measures (see below). The ends of trajectories were calculated using a tangential velocity threshold: the velocities had to drop below .1 m/sec and remain below this mark for at least 33 ms (time required to obtain 4 readings from the sensor). The timing of trajectory events was inferred from the sampling rate of the device. Spline interpolation (Matlab command *interp1*) was used to obtain trajectory data points for each millisecond of movement from the raw data samples. The time of the mouse button release was taken for the time of the movement initiation.

Performance measures. The way the data were collected and pre-processed as well as performance measures was identical to that described in the previous chapter. Given that Inflexion Peak represents a peak in the ongoing adaptation rather than its earliest stage, it would also be useful to consider earlier markers. It is a well-established fact that velocity profiles have invariant characteristics: bell-shaped in unperturbed trials and having a second smaller peak in perturbed trials (Flash & Henis, 1991). The positional characteristics of velocity peaks were previously used to investigate processes related to processing sensory feedback (Smith & Shadmehr, 2005). A similar approach was used in the present study. The measure, referred to as peak velocity (PV) distance, was calculated as a one-dimensional distance in the direction of hand movement towards 1-step stimulus between starting position of the hand and the first velocity peak.

As a main tool of the analysis, a 2 x 2 x 2 repeated measures Anova was used with factors Side (Left/Right), Prior (Switch/Stay) and Latency (Short/Long). The cells of Anova contained the mean statistics for each subject. Consequently, for all F-statistics, including interaction terms, there were 1 degree of freedom for the effect and 9 for the error (taking into account an excluded subject).

6.2.2 Results

Exclusion criteria. There were two criteria for the exclusion of perturbed trials. First, a trial was excluded if the subject failed to adapt to a new location and movement was terminated more than 30 mm from the target centre. One subject systematically failed to adapt to perturbation, in particular, for the Late Latency condition. The data for this subject were excluded from the analysis. For the remaining 10 subjects, the number of excluded trials according to the criterion was 51 (out of 2400). Second, a trial was excluded if subjects did not follow the instructions and failed to move their hand rapidly towards a target after the movement was initiated. To identify these trials, each subject's mean and standard deviation of the time required to cover 100 mm in a forward direction was calculated for all trials, including the unperturbed ones. Those trials, where the time was longer than 1.75 standard deviations from the subject mean, were excluded (122). The perturbed trials that were within 1.75 standard deviations were subjected to the fullfactorial Anova analysis. The Anova analysis showed no difference between conditions with respect to the time when this point was passed. Altogether, 173 perturbed trials out of 2400 were excluded (7.2 %).

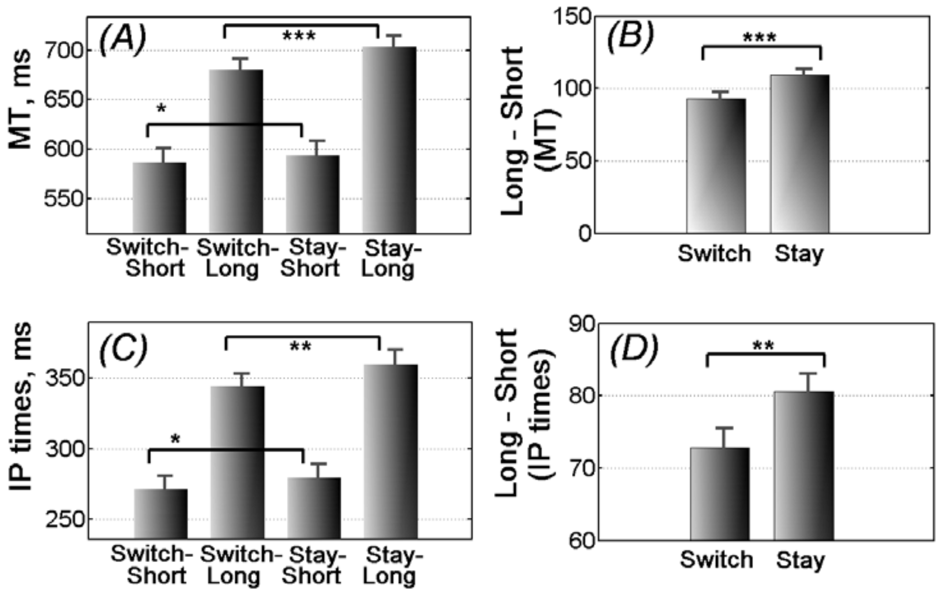

Figure 6.2. The effect of Prior and Prior by Latency interaction. *All data are collapsed across Sides. Switch and Stay stand for Switch and Stay Priors. Short and Long are the perturbation Latencies. Error bars represent group standard error of the mean.*

(A) *Movement times in ms (MT). The effect of Prior was highly significant for Long Latency, whereas for Short period the tendency failed to reach significance level.*

(B) *The difference in the movement times for Long and Short Latencies. The costs of Long Latency are greater for Stay Prior.*

(C) *Inflexion point (IP) times. The time of the adaptation to a new location, measured by IP, was significantly affected by Prior for both Long and Short Latencies.*

(D) *The difference in IP times for Long and Short Latencies. The results mirror the interaction pattern for MT.*

* - $p<.05$. .... ** - $p<.01$. *** - $p<.001$

Movement times. In the analysis of movement times (MT), both the effects of Side and Latency were highly significant, $F(1,9) = 29.00$ and $F(1, 9) = 567.51$, respectively, p

$< .001$. The effect of Prior was also significant $F(1, 9) = 27.17$, $p < .005$ (Figure 6.2A), showing that the responses were completed faster for Switch Prior. T-test for MT collapsed across Side showed a highly significant effect for Long Latency, $t(9) = 6.07$, $p<.001$, and a less pronounced effect for Short Latency, $t(9) = 2.74$, $p = .023$. There was also a significant Prior by Latency interaction, $F(1, 9) = 52.35$., $p < .001$, showing that the difference between Long and Short Latencies was greater for Stay Prior than for Switch Prior (Figure 6.2B). The mean end points, calculated for each subject separately after subtracting the subject's grand mean for each side did not differ either along Y (forward distance) or X axis (lateral deviation), suggesting that this factor was not responsible for MT differences.

Inflexion Point (IP) time. The effect of Latency, as it could be expected, was highly significant, $F(1, 9) = 1044.27$, $p <.001$, whereas the effect of Side was not, $F < 1$. The mean and its standard error for the time of IP, averaged across Side, are shown in **Figure 6.2**C. The main effect of Prior was significant, $F(1, 9) = 15.02$, $p < .005$, showing a faster adaptation in the Switch Prior condition. The post-hoc t-test showed that the difference in IP timing for two Priors was significant for both Short and Long Latencies ($t_{Short}(9) = 2.67$, $p = .026$; $t_{Long}(9) = 4.62$, $p < .005$, respectively). There was also a significant Prior by Latency interaction $F(1, 9) = 18.29$, $p < .005$, as the difference between Long and Short Latencies was significantly greater for Stay Prior (**Figure 6.2**D).

Peak Velocity (PV) distance. The most important variable modulating PV distance was Side, as it not only showed a significant main effect ($F(1, 9) =10.19$, $p =.011$) but also tended to interact with all other experimental factors (with Latency $F(1, 9) =10.76$, $p =.011$; with Prior: $F(1, 9) = 4.91$, $p = .054$; triple interaction Side x Prior x Latency: F (1,

9) = 6.20, p = .034). What is more important for the aim of the present study is that there was a small but statistically significant interaction between Latency and Prior, F (1, 9) =10.30, p =.011. This interactive pattern (Figure 6.3) shows that, for Switch Prior, the peak velocity in the late Latency condition tended to occur earlier in space than in the Short Latency condition, and vice versa for Stay Prior. The effect of Prior was not significant, F <1. On average, the PV was reached ~205 ms after movement initiation. Despite it smallness in the absolute terms, the interactive effect on PV distance is unlikely to be spurious, given that there was a one-to-one correspondence in the results from the analyses of PV distance and PV time. Two data sets showed very similar levels of significance for the experimental factors, with Prior by Latency interaction for PV time: F (1, 9) =16.3, p < .005.

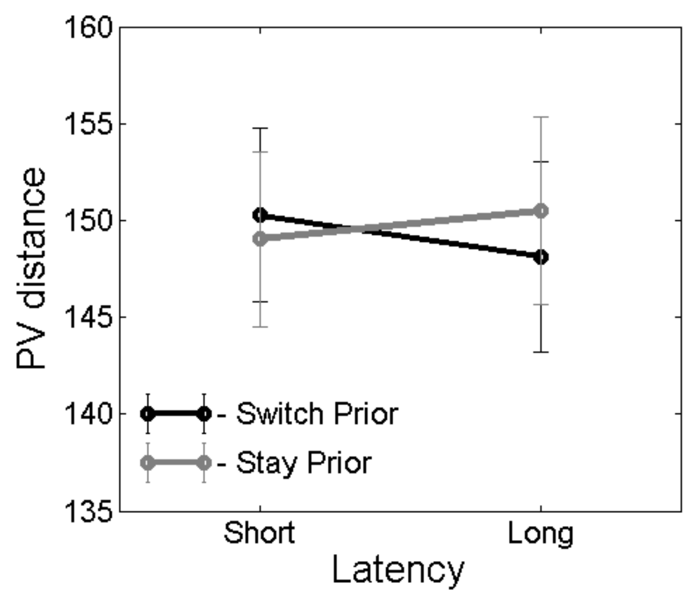

Figure 6.3. Peak Velocity times.

6.2.3 Discussion of the pointing task

In the first experiment, subjects were instructed to make pointing movements to the target and adjust trajectories in-flight if the target switches location after response initiation (i.e., gets perturbed). A spatially non-specific cue was presented in the beginning of the trial indicating whether the target would switch location or is unlikely to do so. Unknown to subjects, the target could switch location after 25 or 125 ms. Manipulations with cues and the latency of perturbation defined two types of prior expectations. One type of expectations was explicitly manipulated by presenting a cue in the beginning of the trial, the other one, implicitly manipulated, depended both on the cue and the latency of location switch.

The analysis showed a clear effect of expectations elicited by the cue only. Subjects were quicker to adapt if they knew for certain that the target was about to switch the location, even though the cue did not provide any information on the direction of the perturbation. The facilitation was found for both movement time and the time needed to reach the inflexion point (IP), i.e., the point where trajectory deviated maximally from the line joining the start and end points of movement.

The primary interest of the present study were manipulations with expectations conditioned on perturbation latency. The critical statistical effect was the interaction between Prior and Latency. The interaction is predicted by the fact that the objective probability of the location switch for Switch and Stay conditions changes between Short and Long Latencies at an unequal rate. Given a very tight time scale, both processing and adapting to this changes would require the work of autonomous mechanisms. The analysis showed that the changes in conditional expectations affected a range of performance measures. Their effect was statistically significant both for the times required to complete the whole movement and the times of the inflexion point. It was also significant for the time and distance of peak velocity.

Although an investigation of what motor mechanisms have been affected in each particular case is beyond the scope of this study, it should be noted that the interactive effects on peak velocity data could not be related to the interactive effects on IP and MT data in a simple way. The strength of correlation of PV time and distance with IP times and MT depended on the side of perturbation (greater for left) and latency (greater for short). This consideration is important with respect to how one has to interpret the direction of the changes in PV distance, in particular, whether earlier peaks can be taken as the marker of response facilitation and vice versa for later peaks. However, even though the behavioural consequences of the peak velocity differences are not unequivocal, this fact does not conceal the significance of these differences, namely, that one can see the observable consequences of implicit manipulations on prior expectations as early as PV time.

With respect to the question whether processing of prior expectation was statistically optimal, the predictions are that performance should be facilitated for Late Latency for both Switch and Stay Priors, but not in equal measure: facilitation for Switch Prior should be greater. However, the present data cannot establish the fact of facilitation per se given that the location switch in the pointing task occurs when the response is already initiated and, therefore, one finds the motor system in different states for different latencies of perturbation. In order to determine an absolute gain or loss caused by the latency when it interacts with the prior and proceed with the question about statistical optimality of processing spatially non-specific expectations, a task with a simpler response modality could be utilized. The following spatial discrimination task was better suited for the purpose, since the initial states of the motor system here were identical for two latencies.

6.3 Experiment 2: Spatial discrimination task

In a spatial discrimination experiment, instead of making a pointing movement, subjects pressed with the index finger of their *right* hand on the left key of the keyboard or with their middle finger on the right key, depending on the side of the perturbation. No key press was required if the target remained stationary. In the first half of the experiment, the discrimination task mirrored closely the sequence of events of the pointing task. The target perturbation followed the release of the mouse button with the *left* hand. In the second part, the control over time for the location switch was withdrawn from subjects, as they passively waited for the perturbation to respond. The second part was introduced in order to control for possible issues related to a) the effects of preparatory activity prior to the release button, given that procedure in pointing task and the first part of the present task provided subjects with means to control over perturbation time; b) a hypothetically possible refractory period effects, given that in the first part of the task subjects needed to respond to perturbation soon after they release the button with their left hand.

6.3.1 Method

Participants. 10 subjects (6 female and 4 male, aged 22-32, mean 25.4, sd = 3.6) participated in this experiment. All reported to be right-handed and to have a normal or corrected-to-normal vision.

Apparatus. A 1280 by 1024 pixels LED monitor was used for stimulus presentation. The computer keyboard was used to log responses.

Design and procedure. The 1-step stimuli, 20 mm in diameter, were presented in the centre of the monitor. On perturbed trials, stimuli switched 100 mm to the left or to the right. The set of experimental variables were identical to that in Experiment 1. Arial font, size 60, was used to present cues for Priors. There were 2 tasks in the experiment. The 'active' discrimination task emulated as closely as possible the sequence of events in the pointing task. The trial in this task started when subjects pressed and hold down the right button of the computer mouse with their *left* hand. They had to release the button as quickly as possible once a stimulus was presented. If the mouse button was not released within 1 sec following target presentation, a message 'Too long' was presented. This trial was moved then to a random location in the order of remaining trials. A perturbation occurred after the release of the mouse button with the same latencies as in the pointing task. If the target was perturbed, subject responded by pressing either '←' or '→' button on the keyboard with their index or middle fingers, respectively, depending on the outcome of perturbation. No key press was required if the target did not switch the location. The error message 'False alarm!' was presented if a key press was made for an unperturbed target. The discrimination time (DT), calculated as a time interval between a target perturbation and a response on the keyboard, was used as a critical measure for performance. DT should be distinguished from the reaction time (RT) defined as the time between the first-step stimulus occurrence and the release of the mouse button.

The 'active' task was followed by the 'passive' task. Here subjects no longer needed to press and release the mouse button to, respectively, start the trial and initiate a possible perturbation. Instead, they passively waited for a target perturbation, in which case they responded in a same way as they did in the ‘active’ task. As this task did not have an analogue of RT of the ‘active’ part, the time for perturbation was chosen to be the sum of either Short or Long Latencies and a ‘virtual RT’. The latter was a number randomly drawn from a Gaussian distribution with the mean and standard deviation corresponding to the grand mean and standard deviation of a subject’s RT in the first, ‘active’, part. Consequently, the times between the initial target presentation and the occurrence of a target perturbation were approximately matched between the ‘active’ and ‘passive’ tasks. To indicate the end of the ‘virtual’ RT, the target disappeared for one refresh rate interval (16.7 ms), and reappeared in the same location for the same duration, unless the trial wan unperturbed (in the latter case, it remained there for the whole duration of the trial).

The procedure comprised 6 blocks of trials (3 blocks for ‘active’ and 3 blocks for ‘passive’ tasks, altogether 420 trials). The stimulus content in a block was identical to that in the pointing task.

6.3.2 Results

Errors. There were 4 % and 2.75 % trials where the side of key press did not correspond to the side of perturbation in the ‘active’ and ‘passive’ tasks, respectively. Because of a small prevalence, the erroneous responses were not analysed. However, this type of responses was more characteristic for the Switch Prior condition, 66 trials vs. 15 trials in the Stay Prior condition, suggesting the factor of a speed-accuracy trade-off**.**

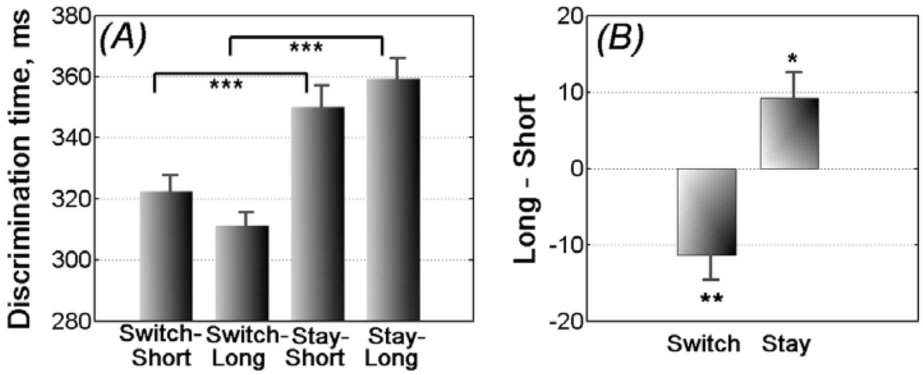

Figure 6.4. Discrimination times averaged across 2 tasks.

(A) *The effect of Prior was highly significant for both Short and Long Latencies.*

(B) *The difference in the discrimination times for Long and Short Latencies. The significance levels are given for the test against zero. For Switch Prior, there was significant response facilitation for Long Latency as compared to Short Latency. For Stay Prior, the effect of Long Latency tended to be inhibitory as compared to Short Latency.*

** - p < .05 ** - p < .01. *** - p < .001.*

Discrimination times. The analysis was run on the discrimination times, measured from the moment of perturbation to the response on the keyboard. In addition to error trials, the trials with DT from the range 120-800 ms were excluded (8, < 1 %). The 2 x 2 x 2 x 2 repeated measures Anova (Task: ‘active’/ ‘passive’, Side: Left/Right, Prior: Switch/Stay, Latency: Short/Long) was used for the analysis. The main effect of Prior and its interaction with Latency were highly significant, $F(1, 9) = 109.29$, $p < .001$ and $F(1, 9) = 31.79$, $p = .001$, respectively. No other main effect or interaction was significant. The post-hoc test showed that the responses for Switch Prior, collapsed across Task and Side, were significantly quicker than the responses for Stay Prior for both Short and Long Latencies, both $p < .001$ (**Figure 6.4**A) Regarding Prior by Latency interaction effect (**Figure 6.4**B), the test of the difference between Short and Long Latencies showed that the difference was significantly below zero for Switch Prior, $t(9) = 3.50$, $p < .01$, whereas for Stay Prior the difference was significantly larger than zero, $t(9) = 2.65$, $p = .027$, indicating that response in Long Latency condition were facilitated for Switch Prior and delayed for Stay Prior.

6.3.3 Discussion of the spatial discrimination task

The results from the spatial discrimination task showed that both the effect of prior expectations and the interaction of these expectations with perturbation latencies were highly significant. There was a greater number of the incorrect responses for Switch prior. This suggests that subjects tended to anticipate the perturbation in this condition and that the gain in speed of responding could have resulted from a compromise on the accuracy. On the other hand, the tendency to anticipate cannot explain the interaction between prior information and the latency, as the latency of perturbation could not be inferred from a cue by design.

After the subtraction of the main effect of the prior, the interaction revealed a cross-over property. The greater latency for a target perturbation was facilitatory for performance when subjects were certain that the target is going to switch the location, and detrimental for performance otherwise. This finding is not compliant with the idea that subjects would follow objective probabilities of perturbation. From a perspective of the ideal observer, the conditional expectation that the perturbation would occur at time of the Long Latency given that it did not occur at Short Latency is higher than the expectations that the perturbation will occur at Short Latency. Consequently, the performance for Long Latency is expected to be facilitated for either Prior. Meanwhile, the data showed that performance for Stay Prior in the Long Latency condition slows down as compared to that in the Short Latency condition.

6.4 Discussion

In the current study, the kinematic perturbation paradigm was used to investigate the effect of spatially non-specific cues that predict the change in the environment with different probabilities without providing information on a specific location of this change. The spatially non-specific property of prior expectations allows one to differentiate their effect from the factors of selective attention and response pre-selection and investigate the decision-making routines in a purer form. Manipulations on prior expectations were combined with manipulations on the latency of target perturbation, unknown to subjects and un-cued. The combination of these two factors allowed for distinguishing two types of expectations. The explicit manipulations on prior expectations using cues were contrasted with implicit manipulations that reflected the objective changes in expectations associated with the cues with the flow of time. The latter implicit manipulations were the primary interest of the study. Specifically, one could expect an interaction between the value of prior expectations, signaled by a cue, and the latency of target perturbation, because the expectations for switch and stay priors changed disproportionally between shorter and longer latency of target perturbation.

The results from both pointing and spatial discrimination tasks showed reliable interactive effects. The observed pattern revealed that the disadvantage of the stay prior as compared to the switch prior was greater for the longer perturbation latency. Given an extremely tight time scale, finding an interactive effect suggests that the processing of implicit changes in expectations is supported by fast and autonomous processes.

The second goal was to analyze whether obtained interactive pattern could be characterized as reflecting statistically optimal processing. One can expect a response facilitation in the long latency condition for either cue, even though for the stay prior this facilitation should be moderate (or, alternatively, not significant if the power of experiment was low). The spatial discrimination task allows one to measure this facilitation. Contrary to the predictions, the interaction in this task revealed a cross-over property: a comparison of the longer perturbation latency with the shorter one showed that responses were facilitated for the switch prior, but inhibited for the stay prior. This suggests that participants failed to be ideal observers and seemingly preferred the following heuristics: the longer time elapsed the more likely that an event that should happen by all means (as it is the case with the switch prior) would happen any time soon; and, conversely, for an initially low expectation for an event to happen (as it is the case with the stay prior), the possibility that it will happen fades away as the time passes by. In other words, the flow of time appear to boost the initial expectations: positive expectations of a change became more positive, and negative expectations became more negative.

It can be noted that processing the value of expectations should be distinguished from implementing this value into behaviour. The relation between two processes may take different forms. First, the process of estimating the value of expectation may be associated with a specific response. This is unlikely possibility, as the cross-task replication of interactive effect indicates independence of this process from the response modality. Second, processing the value of expectation may rely on a generic mechanisms but the output of this system could differ for different types of response. For example, the performance could be sub-optimal in the discrimination task but optimal in the pointing task. Within this study, it is quite problematic to distinguish this possibility from a possibility of a third type of relation when the system processing the value of expectations provides a common output irrespective of the type of behaviour. One fact, however, is appealing to the third possibility. The positional and temporal characteristic of velocity peak in pointing task showed that, for the switch prior, the peaks tended to be reached earlier for the late perturbations than for the early perturbation, and vice versa for the stay prior. This pattern is in partial agreement with the DT measures in spatial discrimination task, where cross-over interaction is obtained after subtraction of the main effect of the prior. However, this evidence should be treated with caution, given that change in velocity peak timing and position, unlike inflexion point and movement times, were not directly related to the speed of response completion and it remains somewhat ambiguous whether earlier peaks in velocity are the sign of a quicker adaptation.

The results from both pointing and spatial discrimination tasks showed strong effects of explicitly manipulated expectations. Subjects responded to perturbation earlier if they knew that perturbation should certainly happen, even though the cue was spatially non-specific and the direction of perturbation was unknown. In pointing task, the effect could be observed for a range of collected measures: the time required to complete movement and time of inflexion point, i.e., the time when hand trajectory switches its principle direction towards a new target location. The effect of explicit manipulations could be predicted on the basis of existing literature (cf: manipulation with probabilities of occurrence in the foreperiod paradigm – Gordon, 1967), even though previous studies demonstrated it only for reaction time data. In this respect, one point is worth mentioning. Previous results presume the presence of the conscious monitoring and control (Stuss et al., 2005), whereas the processes guiding the visuomotor adaptation in perturbation tasks are widely considered as being resilient to them (Castiello et al, 1991; Pisella et al., 2000). Consequently, the present findings present a certain dilemma: either certain degree of automaticity in implementation of pre-cued expectations should be allowed for, or the processes involved in the perturbation task are not totally independent from conscious monitoring. Similarly, it could also be asked whether the main effect of prior expectations in the spatial discrimination task was exclusively due to the subjects' tendency to anticipate a perturbation. One observation suggests that this may be an open issue. Given that the time of perturbation in the 'active' part of the discrimination task was linked to subject's own responding (i.e. release of the mouse button with the left hand), one could expect that this should help a subject to maintain the appropriate level of alertness for a specific time window, leading to a greater effect of the prior. However, no significant interaction was found between the prior and the task, suggesting that the effect of the prior was of a comparable strength in the 'active' and 'passive' parts of the task.

What do these findings suggest if put in the context of now prevalent Bayesian models of perceptual and motor behaviour? Two assumptions are of importance for these models. The first assumption is that perceptual and motor processes require relatively stable internal models that guide noisy decision process in the correct direction. The second assumption, which is implied but rarely investigated, is that prior expectations themselves evolve optimally. It is evident that the current results suggest a somewhat different picture. They question the notion of priors as the islands of the relative stability, showing that they can change on an extremely quick time scale. Second, the evolution of the priors is not optimal per se, meaning that they direct decisions to a sub-optimal solution.

This interpretation of results can apparently be challenged in several ways. One possibility to explain the form of interactive pattern is that RT differences reflected changes in a utility function, i.e., expectations multiplied by expected reward (costs), rather than just changes in expectations only. The observed pattern might then occur if the costs of responding for the stay prior after longer latency increase at a greater rate than the expectations of perturbation. This may potentially apply to the pointing task but even here not in a full measure. Indeed, the motor system has been shown to take into account that the costs of correcting positional error increase when the hand approaches a target,as there is less time remaining for new corrections if the current ones went wrong (Lui & Todorov, 2007). This suggests that, given that adaptation is generally delayed in the stay prior condition, the costs can also be greater. However, the above logic applies to the data for inflexion point but not to the data for peak velocity. What is even more evident is that it is quite difficult to find a plausible explanation why the costs should differentially increase for key press responses in spatial discrimination task.

It could also be argued that, even though the data do not satisfy strong predictions for statistically optimal performance, they satisfy weak predictions. In other words, despite the fact that the interactive pattern does not demonstrate optimal evolution of prior expectations, the mere fact of significant interaction, that is, that the changes in conditional expectations were reflected in behaviour, suggests an optimal-like performance, or *subjective* optimality (Beierholm, Quartz, & Shams, 2009). Whereas it may be a legitimate argument, the downside of such weakly-constrained perspective was recently highlighted by Bowers and Davis (2012) who argued that without strict constrains (including those imposed by a comparison with alternative fits), Bayesian models may be too flexible to account for almost everything (also see Mamassian & Landy, 2010). One relevant example, in this respect, is the application of hazard rate models to account for the performance in the foreperiod task (Janssen and Shadlen (2005) in an animal study, and later Bueti, Bahrami, Walsh & Rees (2010) in a human fMRI study). The results of the studies show an RT pattern roughly mirroring changes in hazard rate, i.e., the probability of target occurrence given that the target has not occurred yet. The value of this model, however, is compromised by a prediction it generates. The prediction is that the strength of the foreperiod effect should be particularly strong for a late target presentation, because the predicted expectations of a forthcoming signal are rapidly increasing when the latency approaches maximum. There is no empirical evidence that it is the case, at least, for human subjects; conversely, the overwhelming number of studies show that RT decrease for longer foreperiods becomes shallower (Niemi & Naataten, 1981), presumably, as a consequence of scalar variability of time interval representations (Getty, 1975).

To summarize, the present findings invite a somewhat unorthodox perspective on prior expectations that are usually seen as islands of stability in ever-changing and ambiguous environment, with their function to help resolving this ambiguity. The present data show that the estimated value of expectations can change on an extremely narrow time scale and its processing and implementation can only be supported by autonomously functioning mechanisms. In addition, the present findings suggest that the evolution of prior expectations in rapid spatial decision-making is more compliant with (sub-optimal) common sense than with objective utility. The latter evidence presents a certain challenge for the statistical theory of perceptual decision-making, given that the criterion of statistical optimality for low-level autonomous behaviour is quite important for the theory that strives to provide a normative account of the fundamental principles governing neural computations.

Chapter 7. Conclusions

The present thesis was concerned with the problem whether numerical and spatial representations share a common metric. Several streams of evidence were considered from theoretical perspective and subsequently tested experimentally. To re-iterate, this is the evidence a) that number representations are subject to logarithmic compression b) that subjects utilize an obligatory spatial representation for numbers - the mental number line - while solving numerical tasks, and c) that functional relation between number and space explains the observed effects of number on the visuomotor performance.

In Chapter 2 I presented the robust method for differentiating between linear and log hypothesis for the subjective scale of numerical representations, and showed that adult people use the linear scale when they perform an approximate estimation. In the chapter 3 I elaborate on the evidence obtained in Chapter 2, showing that, in order to solve a numerical task, people may utilize different spatial models. The choice of the model determines the metric used to compute magnitudes – the distance function. The TMS protocol was used to interfere with a particular type of computations – ratio scale computations, which are not compatible with computations enabled by the representations of number on the mental number line continuum. Although I was unable to disrupt the precision of the responses in a variant of the number line task, the statistical comparison between control condition and the performance following stimulation of the IPS showed a significant difference. This provides partial evidence that IPS may implement, if required by task demands, an alternative spatial model to that of mental number line. Chapter 4 investigated whether numerical information may bias responses in the manual estimation study. The effect turned out to be non-parametric, which is not compatible with the idea of gradual mapping number onto space. In addition, the evidence, that task-irrelevant information may affect not only rapid visuomotor transformations, relying on the parietal networks, but also the unspeeded motor responses, suggest that the effect of number can not be attributed to the work of all and the same mechanisms. In Chapter 5, I addressed the issue of the differentiation between the effects of number on the response selection and the visuomotor coordination proper. The double-step paradigm allows differentiating between initial motor planning and subsequent visuomotor adaptation through the introduction of the rapid perturbation in target location after the hand movement was initiated. The results showed that the number magnitude affected the choice of the initial direction of the hand movement, with no reliable evidence that there was an effect on the subsequent automatic adaptation to target perturbation. The pattern of associations revealed non-sequential mapping, where extreme numbers (1 and 9) were more associated with the left side of space, and intermediate magnitudes (3 and 7) with the right side. This result was interpreted as compatible with the polarity coding hypothesis. As the results in Chapter 6 demonstrated, the absence of the numerical effect on the automatic visuomotor adaptation can not be explained by the fact that number is not an explicitly spatial decision variable. The study shows that responses can be affected with spatially non-specific information, provided it is relevant for the behaviour.

To sum up, the present data suggest that the numerical and spatial magnitudes are processed as independent dimensions, at least as it demonstrated by the independence of their metric.

Design issues. Some notes regarding the designs of tasks can also be added.

Chapter 2. The limitations of the study have already been mentioned in the discussion of Chapter 2. To re-iterate, it is not possible to generalize the findings to processing non-symbolic magnitudes. The decimal structure of the Arabic numerals does not completely eliminate possibility of the algorithmic computations. If a non-linear pattern were observed for non-symbolic magnitudes, it could provide a strong support to the idea that the linear structure is imposed on the subjective scale as a result of training and education (Dehaene et al., 2008; Siegler & Opfer, 2003).

The choice of the variables is another issue in the line-marking and line-construction tasks. For example, there is no specific requirement to use the set of elementary ratios, such as 1/3, 1/5 etc. For the study of approximate estimation it may be even more appropriate if the ratio could not be reduced to the form with the single-digit numerator and denominator. A separate comment is required regarding the line-construction task, which represents a novel variant of the number line task. The contrast between performance in the standard line-marking task and the line-construction tasks showed the different sort of transformation, a different type of scales. In the current thesis, no attempts has been made to identify specific factors that force subject to use this or that way of representing numerical relations. It remains unclear whether these differences in computations is rigidly related to the requirements in the response generation, or just to a specific form of the current task, where the construction of the interval construction should have to be started from zero length. The task could be made more similar to the line-marking if the responses required the adjustment of the line to a required length, not its construction from zero.

Chapter 3. The main shortcoming of the study presented in this chapter is the absence of no-stimulation condition. As the results did not show the increase in the variability after the stimulation of the IPS as compared to the stimulation of vertex, the study did not provide strong support for the ratio scale computation. Instead, I found that the performance after IPS stimulation does not improve, as it was the case for the performance after vertex stimulation. Given that this improvement was concomitant with a non-specific improvement in the post-TMS sessions, this result can be interpreted as the evidence that the TMS effects prevented this improvement. Certain changes in the design could be made in order to elaborate the design. The possibility of using non-elementary ratios and non-symbolic magnitudes was mentioned above. In the discussion of the experiment I also mentioned the problems associated with the lenient policy on the timing. Another possibility is to provide subjects with a sufficient training to stabilize the performance between and within sessions and, by doing this, reduce variance in group results.

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