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The role of attention on numerosity perception and number adaptation in adults, typical and atypical children.

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Abstract

There is considerable controversy as to how the brain extracts numerosity information from a visual scene and as to how much attention is needed for this process. Traditionally, it has been assumed that visual enumeration is subserved by two functionally distinct mechanisms: the fast and accurate apprehension of 1 to about 4 items, a process termed “subitizing”, and the slow and error-prone appraisal of larger numerosities referred to as “estimation”. Further to a functional dichotomy between these two mechanisms, an attentional dichotomy has been proposed. Subitizing has been thought of as a pre-attentive and parallel process, whereas estimation is supposed to require serial attention. In this thesis, the hypothesis of a parallel and pre-attentive subitizing mechanism was tested. In the first part of the thesis to this aim, the amount of attention that could be allocated to an Estimation task was experimentally manipulated. We shown that numerosity estimation is composed by different and separable, sub-systems. Results indicated that subitizing strongly depends on attentional resources, while estimation of larger quantities does not. Exactly the same results were found when the attentional resources dedicated to the visual numerical estimation task were limited on other sensory modalities: indeed visual, auditory and also haptic attentional load strongly and similarly impair visual subitizing but much less high numbers. We also demonstrated that visual adaptation to numerosity, absent in the subitizing range under normal condition, emerges under attentional load with a magnitude of the effect highly comparable to that measured for high numbers. Moreover we first demonstrate that the ability to accurately map numbers onto space also depends on attentional resources, showing that the assumption that performance on the ‘numberline task’ is the direct reflection of the internal numeric representation form could be misleading. In last part of the thesis we study how number adaptation affects number perception in two different population; high-functioning autistic and typically developing children. We demostrated that ASD children discriminated numerosity with the same precision as the typical children, but showed much less (about half) the levels of adaptation to number than the control group. These new results show that adaptation, processes, fundamental for efficient processing of variable sensory inputs, is diminished in autism.

General Introduction

Numbers are an integral part of our everyday life; we use them to label, rank, and quantify virtually everything that is imaginable. Symbolic number representations, using Arabic numerals and number words, are uniquely human cultural achievements that have enabled elaborate scientific developments and shaped our technologically advanced culture. For this reason, arithmetic was long thought to be an exclusively human faculty. Over the past decades, however, it has become clear that basic numerical competence does not depend on language and education, but is rooted in biological primitives that can be explored in innumerate indigenous cultures, infants, and even animals. Comparative psychologists have shown that animals can discriminate numerosities (i.e., the cardinality of a set, set size) (Brannon & Terrace, 1998; Davis & Pérusse, 1988), and field studies have convincingly demonstrated that animals use numerical information on a regular basis to make informed decisions (e.g, in foraging or in social interactions such as fights) (Hauser, Carey, & Hauser, 2000; McComb, Packer, & Pusey, 1994). These findings highlight the evolutionary significance of numerical competence; processing numerical information is important to guarantee an animal's survival. A breakthrough in developmental psychology was achieved when numerical cognition was demonstrated in human infants (Feigenson, Dehaene, & Spelke, 2004; Starkey & Cooper, 1980). Research has shown that infants of only a few months of age have the capacity to represent cardinality. Infants can also engage in rudimentary arithmetic, which was first demonstrated in experiments in which five-month-old infants were shown basic addition and subtraction operations on small sets of objects (Wynn, 1992). It means that we possess the ability to quickly and roughly estimate the numerosity of a group of elements even when the serial count is prevented (for example by a limited time exposure): an Approximate Number System (ANS). In humans, the signature of the ANS is reported surprisingly early, from the first hours of life: newborn babies habituated for some minutes to auditory sequences of a given number (e.g. six syllables), look longer at numerically matching visual sets (e.g. six dots) subsequently presented to them than to non-numerically matching sets (e.g. 18 dots) (Izard, Sann, Spelke, & Streri, 2009). Importantly, the babies fail to match numerosities that are more similar in their numerosity (with a ratio approximating a value of one). This highlight the main feaure of the Approximate Number System: it follow Weber's Law. Weber's law states that the just-noticeable difference (the threshold of discrimination) between two stimuli is proportional to the magnitude of the stimuli. Anthropological studies showed that even human adults who have been deprived of cultural transmission of number symbols, and thus cannot count, are still able to quantify objects (Gordon, 2004) . Indeed, while the representation of integers is exact, estimation of numerical quantities is approximate, with a certain degree of error associated with. Weber fraction here reflects the precision, with which two numerical quantities can been perceived as numerically different: an index of “number acuity”. Altogether, these behavioral studies underscore that a biological precursor system of elementary arithmetic exists in many species, not just humans. Moreover, this nonverbal quantification system seems to constitute the phylogenetic and ontogenetic foundation of all further, more elaborate numerical skills (Halberda, Mazzocco, & Feigenson, 2008). As previously mentioned, numerosity perception as almost all the visual proprieties follow Weber’s law (Ross, 2003). This has led to advance the idea that numerosity could reflect a primary visual properties of a scene. Indeed, as all the primary visual properties like color, orientation or motion, also numerosity has been demonstrate to be higlhy prone to adaptation: the prolonged exposure to a more numerous visual stimulus makes the current stimulus appear less numerous, and *vice versa* (Burr & Ross, 2008b; Thompson & Burr, 2009). This result strongly suggest that we possess “a *visual* sense of number”. However it has been argued that the perception of numerosity could derive from the perception of other visual cues, like the overall area or the texture density, defined as the number of elements per unit of area (Dakin, Tibber, Greenwood, Kingdom, & Morgan, 2011; Durgin, 1995, 2008; Tibber, Greenwood, & Dakin, 2012). According to these authors numerosity is not sensed independently, but it is derived from texture density. Nevertheless other psychophisical studies from Ross and Burr (2010) together with a hierarchical generative model of number perception (Stoianov & Zorzi, 2012) are demonstrating that selectivity to visual numerosity could develop naturally within visual neural structures, indipendently from texture perception (Ross and Burr 2012). Another particular aspect of numerical perception is the so-called subitizing: we never made estimation errors for numbers of items up to four. There has been a long-standing debate as to whether enumerating numbers in the subitizing range invokes different processes than for larger ranges of objects (estimation range). Although the nature of this phenomenon is still debated, one influential hypothesis propose that subitizing refer to a *pre-attentive* system (Trick & Pylyshyn, 1994a). Contrary to that, many recent studies has been demostrate that subitizing capacity is strongly dependent by the avaibility of attentional resources (Olivers & Watson, 2008;

Railo, Koivisto, Revonsuo, & Hannula, 2008; Vetter, Butterworth, & Bahrami, 2008, 2010). Attention is strongly linked with many aspects of numerosity and number processing. Attention acts as a filter to select and maintain relevant information while suppressing irrelevant distractors, improving the efficiency with which information arriving from the environment is acquired and processed, then memorized and learned (Posner & Rothbart, 2005). However, some evidence comes from studies on adult subjects, for example attention-training (through video-game playing) increases subitizing range (Green & Bavelier, 2003); merely looking at numbers causes a shift in covert attention to the left or right side, depending upon number magnitude (Fischer, Castel, Dodd, & Pratt, 2003). The recent literature that deals with people who have difficulty in learning math and/or reading is reporting that these subjects as well as having specific deficits in those capacities, also have deficit in attention (Ashkenazi & Henik, 2010; Askenazi & Henik, 2010). In line with this, dyscalculics children show impaired subitizing (Ashkenazi, Mark-Zigdon, & Henik, 2012; Koontz, 1996) and as mentioned above this is an attentional dependent enumeration capacity (Olivers & Watson, 2008; Railo et al., 2008; Vetter et al., 2010). The connection between attention and number processing also finds support from fMRI studies of neural correlates of visual enumeration under attentional load. Ansari, Lyons, van Eimeren, and Xu (2007) have shown that the temporal-parietal junction (rTPJ), an area thought to be involved in stimulus-driven attention (Corbetta & Shulman, 2002), is activated during a comparison task of quantities. The general picture that comes from the literature reveals a strong connection between the representations of numbers and attention. Using psychophysical paradigms and attentional manipulations, we investigated the relationship between attention and number perception. More specifically: we addressed the issue of the two possible separate mechanisms for the perception of low (<4, subitizing) and high numbers, and the effect of different attentional sensory modality on these two mechanisms, we dealt this using estimantion, numberline and number adaptation paradigm. In last part of the thesis we study how number adaptation affect number perception in two different population; high-functioning autistic and typically developing children.

1.1 Number Sense

Humans and other species have the ability to represent numbers (e.g., set of items) in an analog magnitude manner (Carey, 2009; Dehaene, 2011) .This nonverbal ability to represent magnitude in an approximate fashion is called the approximate number system (ANS) (Butterworth, 2010; Dehaene, 2011; Feigenson et al., 2004; Piazza et al., 2010) . This “number sense“ is at the heart of the preverbal ability to perceive and discriminate large numerosities (Feigenson et al., 2004) and relates to the intraparietal sulcus, a brain area which contains neurons tuned to approximate number in the macaque monkey and which is functionally active already at 3 months of age in humans (Izard, Dehaene-Lambertz, & Dehaene, 2008; Nieder & Miller, 2004b; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). Children discriminate numerosities long before language acquisition and formal education, as early as at 3 hours after birth (Izard et al., 2009). However, numerosity discrimination improves from a ratio of 1:2 to 2:3 before the year of age (Lipton & Spelke, 2003; Xu, Spelke, & Goddard, 2005) and undergoes progressive refinment throughout childhood (Halberda & Feigenson, 2008). The approximate number system is thought to encode numerosities as anolog magnitudes (Dehaene, Piazza, Pinel, & Cohen, 2003), that can be modeled as overlapping Gaussian distributions of activations on a logarithmically compressed internal continuum (Izard et al., 2008; Piazza et al., 2004). Logarithmic compression implies that the overlap between numbers increase with magnitude, which in turn decreases their discriminability (in obeyance of Weber’s Law). However, discriminability critically depends on the width of the Gaussian distributions. The width of the distribution, referred to as the “internal Weber fraction” (Izard et al., 2008; Piazza et al., 2004), measures the precision of the internal representation and is therefore a sensitive index of “number acuity”.

Studies from primate neurophysiology assess the neural foundation of the basic approximate numerical competence, showing that single neurons are able to encode the number of items in a visual display (Nieder, 2013; Nieder & Dehaene, 2009; Nieder, Freedman, & Miller, 2002; Nieder & Merten, 2007; Nieder & Miller, 2004a, 2004b). Recordings in monkeys trained to discriminate numerosities have revealed numerosity-selective neurons in the lateral prefrontal cortex (31% of all randomly selected cells), in the fundus of the intraparietal sulcus (18%) and a small proportion also in the anterior inferior temporal cortex (Nieder et al., 2002; Nieder & Miller, 2004b). These neurons showed a maximum activity to a particular quantity (which defined the neuron's preferred numerosity) and a progressive drop in response as the displayed numerosity changed from the preferred one. Interestingly these number-selective neurons are show a compressive logarithmic pattern of behavior with increasingly coarser encoding for high numerosities. This matches with the observation that as the numerosity increases, a larger difference between the two quantities is needed in order to maintain the same discrimination performance. This means that the number-selective neurons obey the Weber-Fechner law, a behavior that typically characterizes the representation of sensory magnitude. As a consequence it has been proposed that numerosity is a basic sensory visual dimension like colour, contrast, spatial frequency, orientation, size and speed. Supporting this idea it has been demonstrated that, as for the perception of these classical visual properties of the image, the perception of numerosity is susceptible to adaptation after effect (Burr & Ross, 2008a). Burr and Ross demonstrated that after 30 seconds of prolonged exposure to two patches differing in numerosity, two subsequent patches containing the same number of dots appear to be different in numerosity. They asked subjects to judge if a test stimulus (which they varied in numerosity) was more or less numerous than a probe stimulus (of a constant numerosity). The results showed that the apparent numerosity of the probe stimulus was decreased by adaptation to high numerosities and increased by the adaptation to low numerosities. The described number adaptation effect was found to be not dependent about variations in pixel density, orientation, shape or element size but instead coupled only with the number of elements. It was found that even changing contrast of the adapting stimulus had little effect on the magnitude of the adaptation effect. This result strongly suggests that we possess "a *visual* sense of number". Even if much physiological and psychophysical research suggests that we possiede a genuine "sense of number" several researchers have questioned whether number is sensed directly, suggesting instead that it can only be derived indirectly from other visual feautures as texture density (Dakin et al., 2011; Durgin, 2008).

1.2 Subitizing

Subitizing, which has puzzled researchers for many years, is the capacity to rapidly and accurately enumerate a small number of items (1-3 or 4). Subitizing (from the latin "subito" which means suddenly, first coined by Kaufman, Lord, Reese, & Volkmann, (Kaufman & Lord, 1949), is classically demonstrated when subjects are asked to enumerate visual sets of items, ranging for example from 1-7, as accurately and as fast as possible. In this case, responses times show a discontinuity between 3 and 4 (or 4 and 5), as there is very little increase in the 1-3 or 4 range (about 50ms/item) and much more for each additional item beyond this range (about 200-400ms/item) (Chi & Klahr, 1975; Mandler & Shebo, 1982; Trick & Pylyshyn, 1994b). Researchers have proposed that this reflects a distinction between two processes: the first, subitizing, would operate over the 1-3 or 4 range, whereas counting would be used for larger numerosities. The dissociation between the subitizing and counting ranges has also been shown with paradigms where presentation is brief, and sometimes also masked, leading to a discontinuity also in response accuracy, as estimation or faulty counting takes over outside the subitizing range (Green & Bavelier, 2003, 2006; Mandler & Shebo, 1982). Importantly, some studies have shown that subitizing occurs independently of ocular movements, as subjects are able to subitize even when presentation duration is too short to allow for saccades or when stimuli are presented as afterimages (Atkinson, Campbell, & Francis, 1976; Atkinson, Francis, & Campbell, 1976; Simon & Vaishnavi, 1996) in contrast, these modes of presentation affect performance in the counting range. Moreover, another manipulation of the stimuli presentation (cueing the area where items to be enumerated are going to appear) showed that subitizing did not require attentional focus, whereas counting does (Trick & Pylyshyn, 1993), so these researchers argue that counting and subitizing are phenomenologically distinct processes because subitizing reflects a preattentive, automatic process that proceeds via parallel processing whereas counting si a more attentionally demanding, conscious mechanism that implicates srial processing. These findings strengthen the idea that subitizing and counting are two dissociable processes. Recent research has challenged the notion os subitizing as a preattentive process (Egeth, Leonard, & Palomares, 2008; Olivers & Watson, 2008; Poiese, Spalek, & Di Lollo, 2008; Railo et al., 2008; Xu & Liu, 2008b). These studies have revealed that attentional demands increase with increasing numbers of to-be-enumerated stimuli, even in the subitizing range.

1.3 Numerical estimation

When one is presented with a large number of items, two processes can be used to determine how many there are: counting or estimation. Although counting can be exact, it is slow and becomes error-prone when there are a lot of items to be counted, especially if they are arranged randomly, rather than in a line for example. In contrast, estimation is approximate, and can be used more quickly than counting with large numerosities. When estimating a set of numerosities presented each several times, performance follows a particular pattern. Indeed, mean response may be quite close to the correct answer, although there is variability in response. Numerical estimation judgments become less precise as numerosity increases: the variability in responses increases proportionally to the increase in mean response, a characteristic which is referred to as *scalar variability*, a signature of estimation processes, whether non-verbal or verbal (e.g. giving a verbal estimate of a set of dots) (Cordes, Gelman, Gallistel, & Whalen, 2001b; Gallistel & Gelman, 1992; Whalen, Gallistel, & Gelman, 1999). This has been linked to Weber's law, which governs discrimination of numerosity, but also of other perceptual variables (weight, brightness, sound, etc.). Weber's law describes discrimination of two sets of numerosities becomes harder as the numerical distance between the sets decreases (*distance effect*). Also, at an equivalent numerical distance between the sets, increasing the numerosity of the sets also makes it more difficult (*size effect*). Discrimination of two quantities is thus proportional to their ratio. This is thought to reflect characteristics of the underlying representation of numerosity: representation of small numerosities would be more precise than larger ones: there would be an increase in overlap of numerosity representation as numerosity increases. This accounts for the distance and size effects: the larger the distance between the sets of numerosities to be compared, the less overlap, and the smaller the sets are, the less overlap. It also explains scalar variability: responses would become less precise as numerosity increases because there would be an increase in overlap of underlying representations. As mentioned before, scalar variability is reflected by a *proportional* increase in response variability, as presented numerosity (and mean response) increases: this yield a stable *variation coefficient* (standard deviation of mean response/mean response) across numerosities (Whalen et al., 1999). Mean variation coefficient across numerosities is thought to give an indication of the overall precision of the underlying representation.

Chapter 2 : Effect of spatial and temporal attention on subitizing and estimation

2.1 Abstract

The numerosity of small numbers of objects, up to about, four can be rapidly appraised without error, a phenomenon known as *subitizing*. Larger numbers can either be *counted*, accurately but slowly, or *estimated,* rapidly but with errors. There has been some debate as to whether subitizing uses the same or different mechanisms than those of higher numerical ranges, and whether it requires attentional resources. We measure subjects accuracy and precision in making rapid judgements of numerosity for target numbers spanning the subitizing and estimation range while manipulating the attentional load, both with a spatial dual-task and the "attentional blink" dual task paradigm. The results of both attentional manipulations were similar. In the high-load attentional condition, Weber fractions were similar in the subitizing (2-4) and estimation (5-7) range, (10-15%). In the low load and single task condition, Weber fractions substantially improved in the subitizing range, becoming nearly error-free, while the estimation range was relatively unaffected. The results show that the mechanisms operating over the subitizing and estimation ranges are not identical. We suggest that pre-attentive estimation mechanisms works at all ranges, but in the subitizing range attentive mechanisms also come into play.

2.2 Introduction

As mentionated before there has been a long-standing debate as to whether enumerating numbers in the subitizing range invokes different processes than for larger ranges of objects. For accurate denomination, or "counting," there is good evidence for the dichotomy: for items up to four, reaction times are quite constant, increasing by at most 40–100 ms per item; for larger numbers the cost of additional items is 250–350, leading to clear changes in curve slope (Atkinson, Campbell, et al., 1976; Mandler & Shebo, 1982). Evidence for the dichotomy has also been provided by a PET study (Sathian et al., 1999), but this was not replicated by a more recent, better controlled, functional magnetic resonance imaging study (Piazza, Mechelli, Butterworth, & Price, 2002). Some behavioral studies have also questioned the existence of two distinct processes. For example, Balakrishnan and Ashby (1992) found no evidence of a sharp discontinuity in reaction times between the subitizing and counting ranges: the "mental effort" for enumeration increases with each additional element in the display, both within and beyond the putative subitizing range, with no suggestion of two distinct processes. Even when subjects do not have the time or opportunity to count the number of objects in the field of view, they can *estimate* numerosity rapidly. Approximate *estimation* of number has been demonstrated in humans (Whalen et al., 1999), in infants (Xu & Spelke, 2000; Xu et al., 2005), in cultural groups with no word for numbers much above two (Dehaene, Izard, Spelke, & Pica, 2008; Gordon, 2004), in monkeys using a habituation–discrimination paradigm with auditory stimuli (Hauser, Tsao, Garcia, & Spelke, 2003; Sawamura, Shima, & Tanji, 2002), in birds (Pepperberg, 2006), and even in bees (Dacke & Srinivasan, 2008). After appropriate training, parrots can make a visual number estimation up to six items, and bees up to four. Both are able to generalize this to novel objects. Most recently, number discrimination has been demonstrated in newborns, with a cross-modal matching technique (Izard et al., 2009). The ability to estimate number correlates strongly with mathematics achievement (Halberda et al., 2008; Piazza et al., 2010), suggesting it is strongly linked to other number-based capacities. Estimation of numerosity is rapid and effortless but not errorless. As Jevons (1871) first showed, error increases in direct proportion to the number of items to be estimated, a property known as *Weber's law*. The *Weber fraction*, defined as the just noticeable difference or precision threshold divided by the mean, is usually found to be quite constant over a large range of base numerosities. For example, in a recent study, using rigorous two-alternative forced choice techniques, Ross (2003) reported Weber fractions for adult subjects to be about 0.25 over a wide range of base values (8–60). The value of 0.25—1 in 4—lead Ross to suggest that the precision for estimation may explain the subitizing limit: the quantal leap from the limit 4 to the nearest neighbor is 1, corresponding to the Weber fraction precision limit. Thus, subitizing may be nothing special, merely a consequence of the resolution of estimation mechanisms and the quantal separation at low numbers. Similar ideas have been advanced by Dehaene and Changeux (1993) and Gallistel and Gelman (1992). Although this idea is appealing, it has not received experimental support. Revkin, Piazza, Izard, Cohen, and Dehaene (2008) explicitly tested the idea by measuring estimation precision for numbers ranging from 1 to 8 (grain of 1) and 10 to 80 (grain of 10). If the same mechanism determined precision over the entire range, Weber fractions for the 1–8 range should be like those of the 10–80 range: but they were not, they were three times lower. Subitizing tends to be resistant to attempts to disrupt it, and this has lead many to assume that subitizing is *pre-attentive*, or at least makes use of pre-attentive information (Trick & Pylyshyn, 1994a). However, a few recent studies suggest that subitizing is in fact vulnerable to manipulations of attentive load. About 200 ms after performing an attentive task, attentive mechanisms are at a low ebb, a phenomenon referred to as the "attentional blink" (Raymond, Shapiro, & Arnell, 1992). During this period, subitizing is highly compromised (Egeth et al., 2008; Juan, Walsh, & McLeod, 2000; Railo et al., 2008). Other studies have shown that during dual tasks, when spatial attention is diverted from the estimation task, subitizing suffers (Railo et al., 2008; Vetter et al., 2008). In this study, we take advantage of the fact that manipulations of attention in both space and time can affect subitizing and examine whether it has the same effect on estimation at larger number ranges. The results show that both spatial and temporal attention affects number estimation for low but not high numbers. Furthermore, under conditions of high attentional load, the precision in the subitizing range is reduced to be similar to the estimation range. This suggests that pre-attentive estimation mechanisms can operate over both high and low number ranges: but small numbers, within the subitizing range, can call on an additional attentive mechanism that operates—when attentional resources permit—over a range of up to four items.

2.3 Methods

The stimuli were presented in a dimly lit room on a 15-inch Macintosh monitor with 1440 × 900 resolution at a refresh rate of 60 Hz and mean luminance of 60 cd/m^2. Subjects viewed the stimuli binocularly at a distance of 57 cm from the screen. Stimuli were generated and presented under Matlab 7.6 using PsychToolbox routines (Brainard, 1997).

Attentional blink

Three subjects (2 males, 1 female: mean age 25) with normal or corrected-to-normal vision participated in this study. The technique was to present a stream of 12 white letters in rapid serial visual presentation (RSVP), followed by a cloud of dots, then a random-noise mask. The letters were chosen randomly from the set "A B C D E F G H M N O P", presented on a gray background (see Figure 1). Each letter was presented within a (5° × 5°) matrix for 83 ms (5 frames) with a 33-ms (2-frame) blank gap between consecutive letters. The first target was one of these letters, chosen randomly in each trial and presented in a yellow instead of white, in a position selected to create a specific lag between it and the next target, the dot pattern to be estimated. At the end of the stream, a cloud of dots (T2), varying in number from one to eight, was presented for 130 ms (8 frames) followed immediately by a binary pixel noise mask of 600 × 600 pixels, randomly black or white, presented for 150 ms. Dots in the target were half-white and half-black so luminance was not a cue to number. Each dot was 0.4° in diameter, with position chosen at random within a matrix of 14° diameter (Figure 1A). The task of the subjects was to report first the target letter, then estimate the number of dots that appeared, by mouse-clicking two virtual keyboards that appeared after each trial, the first contained all possible letters, the second the range of numbers from 1 to 8. The important variable was the time lag between the yellow letter and dot stimulus, set at random to be 110, 220, 330, or 880 ms. In separate sessions, subjects were either instructed to ignore the letters and respond only to the number (single-task control); or to respond to both, as mentioned above (experimental attentional blink condition). The response to the number task was considered only if that to the first task was correct (about 90% of trials, constant across lag). In total, we measured 8 levels of numerosity, 4 lags and two response conditions (8 × 4 × 2 = 64 conditions in all). A total of 2764 trials were run for the control condition (number only) and 3496 for the experimental condition (number plus letter). When plotting the results, the extremes of the range (1 and 8) were discarded, as the subjects were aware of the range, and therefore tended to make fewer errors in the extremes.

Spatial attention

Four subjects (mean age: 24, 1 female, 3 males, different from those of Experiment I) with normal or corrected-to-normal vision participated. The experiment employed a dual-task paradigm (Figure 1B). The stimulus for the primary task was made up of 4 centrally positioned colored squares, each subtending 3° of visual angle. The squares could take up eight color combinations, which determined whether the stimulus was a target or not. In the low attentional load condition, the stimulus was a *target* if it contained red squares, irrespective of the spatial arrangement of colors. Under high attentional load conditions, the stimulus was a target if a specific conjunction of color and spatial arrangement was satisfied: two green squares along the right diagonal *or* two yellow squares along the left diagonal. In the no-load condition, the primary stimuli appeared, but subjects could ignore it. The stimulus for the secondary task was a cloud of dots (like those of the other experiment), displayed in random position within an eccentric annulus of 6° inner diameter and 18° of diameter, displayed simultaneously with the primary stimulus. Subjects were required to estimate number of dots in the cloud (which could vary from 1 to 8). On each trial, the fixation point was presented for 1 s, then the primary and secondary stimuli for 200 ms, followed by the binary pixel noise mask (600 × 600 pixels). Subjects responded with mouse press on a virtual keypad, first to the primary then to the secondary task. Responses to the secondary task were recorded only if those to the primary task were correct. In total, there were three attentional load conditions and 8 numerosities, resulting in 24 conditions per subject. Forty trials were run for each condition, yielding a total of 4000 trials for 4 subjects (Figure 1B).

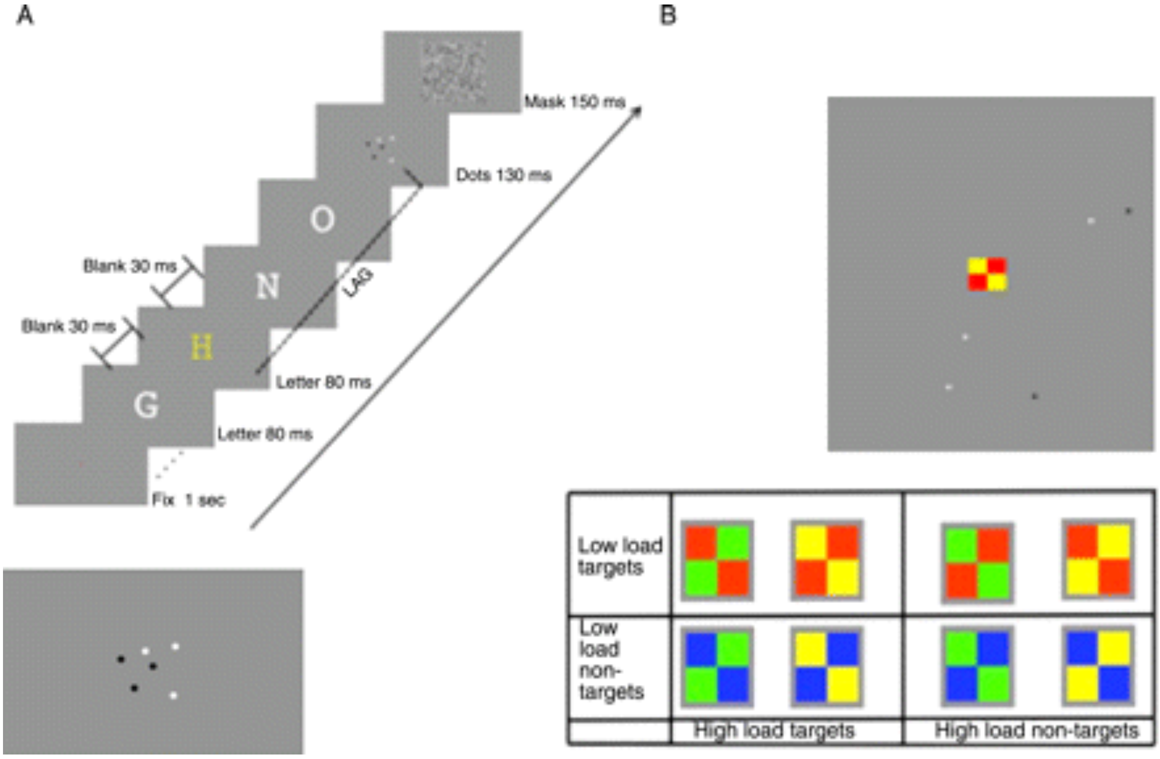

Figure 1. (A) Attentional blink paradigm. The letter stimuli were presented in RSVP. Each trial began with a fixation point presented for 1 s, followed by an RSVP stream (12 letters), each letter displayed for 80 ms with a 30-ms blank gap. The dot array was displayed for 130 ms and from 110 ms to 880 ms after the target letter (yellow) and was followed by a binary pixel noise mask (150 ms). (B) Spatial attention paradigm. The presentation began with a fixation point for 1 s. Stimuli (dots and colored square) were presented simultaneously for 200 ms, followed by a binary pixel mask (200 ms).

Data analysis

Data were analyzed separately for each subject. For each subject, the responses were pooled for each condition and numerosity, from which two parameters were estimated: the mean and standard deviation. The standard deviation is the main parameter, providing an estimate of response precision, which, normalized by the number of items in that condition, provides an estimate of the *Weber fraction*, the standard parameter of precision performance that is often independent of magnitude. The mean estimates systematic biases in judgments, or accuracy, plotted in Figure 6.

2.4 Results

Attentional blink

As detailed above, the “attentional blink” is a double-task paradigm where subjects first identify the odd-colored letter in an RSVP stream, then estimate the number of dots in a cloud. Examples of number estimation are shown in Figure 2A, for numerosities 3 and 6, under control conditions (when the letter was presented but ignored: red symbols), and during the peak of the attentional blink (lag 220 ms: black symbols). The distributions of the estimates were well described by a Gaussian, from which the Weber fraction is readily calculated from the standard deviation of the fit. When subjects were not required to perform the dual task, the curves for 3 and 6 were quite different: for numerosity 3 there were no errors (hence a delta function), while for numerosity 6 there were many errors resulting in a distribution with standard deviation of 0.66 (Weber fraction of 0.11).

Spatial dual task

Here subjects performed a double-task paradigm, but for stimuli simultaneously presented. While estimating numerosity of the dot cloud, subjects also performed a central task, reporting either the presence of a red square (low load), or a conjunction of color and orientation (high load). Figure 2B shows sample distributions of number estimation for target numbers 3 and 6 in high-load and single-task (no-load) conditions. The distributions are very similar to those of Figure 2A. Estimation of three dots was error-free with the single task, while at 6 the estimates formed a clear Gaussian distribution, whose standard deviation yielded a Weber fraction of 0.9. Under high attentional load, this distribution changed little, while that for 3 elements became as broad as that for 6.

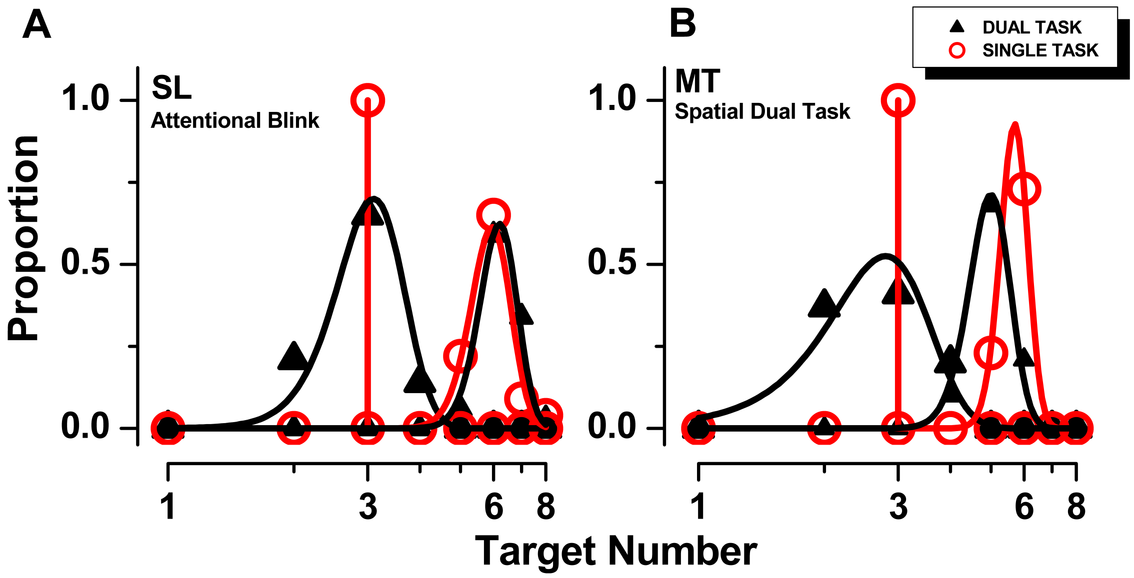

Figure 2. Example of mean probability distribution in the two ranges of numerosity for the two experimental conditions (single task and dual task) in the (A) attentional blink and (B) spatial attention paradigms; N = 3 (subitizing) and N = 6 (estimation). The increase of the attentional load lead to a considerable increase in the response variability in the subitizing range, while that in the estimation range remained virtually unchanged.

Effect of attention on subitizing and estimation

Figure 3 brings the effect of attention out more clearly, plotting Weber fractions (obtained from the standard deviation of the Gaussian fits) against numerosity, for various levels of attentional loads. The results are similar for both paradigms: in the high number range all conditions lead to a similar estimate of Weber fraction around 15%; in the subitizing range, however, the results clearly depend on attentional load, with perfect (or near-perfect) performance at 2 and 3 in the no-load conditions of both experiments.

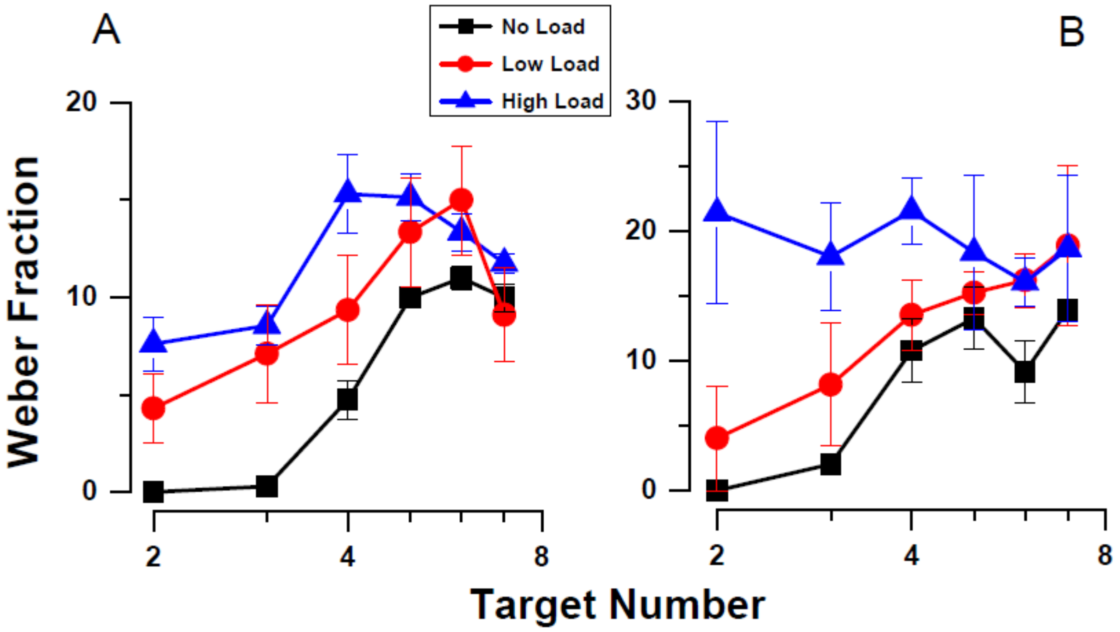

Figure 3. Plot of mean Weber fraction against target number for various attentional loads (see legend) against target number for the (A) attentional blink paradigm and (B) spatially divided attention. For attentional blink paradigm, "No Load" refers to the average of 880-ms lag and all conditions without the double-task; "Low Load" is 110-ms lag; and "High Load" is the average of 330- and 220-ms lags. For both spatial and temporal paradigms, the curves become much flatter at high attentional load.

Figure 4 plots the results another way, separately for the six different numerosities: for the attentional blink experiment, they are plotted as a function of the lag between the two stimuli, for the spatial attention experiment as a function of task complexity. The effect of attentional load is clearly different for different numerosities. At the higher numerosities (5–7), the curves were fairly flat, sitting around 15%, independent of load. However, performance at low numerosities (2–3) clearly depended on task load, reaching near-perfect performance at low and no-load conditions. Performance at 4 was somewhat in between, sitting with the higher number range in the spatial task and lower range in the temporal task. Note that in the subitizing range (<4) the curves in Figure 3° follow the classical attentional blink result, peaking around 200–300 ms, returning to baseline for separations of 900 ms.

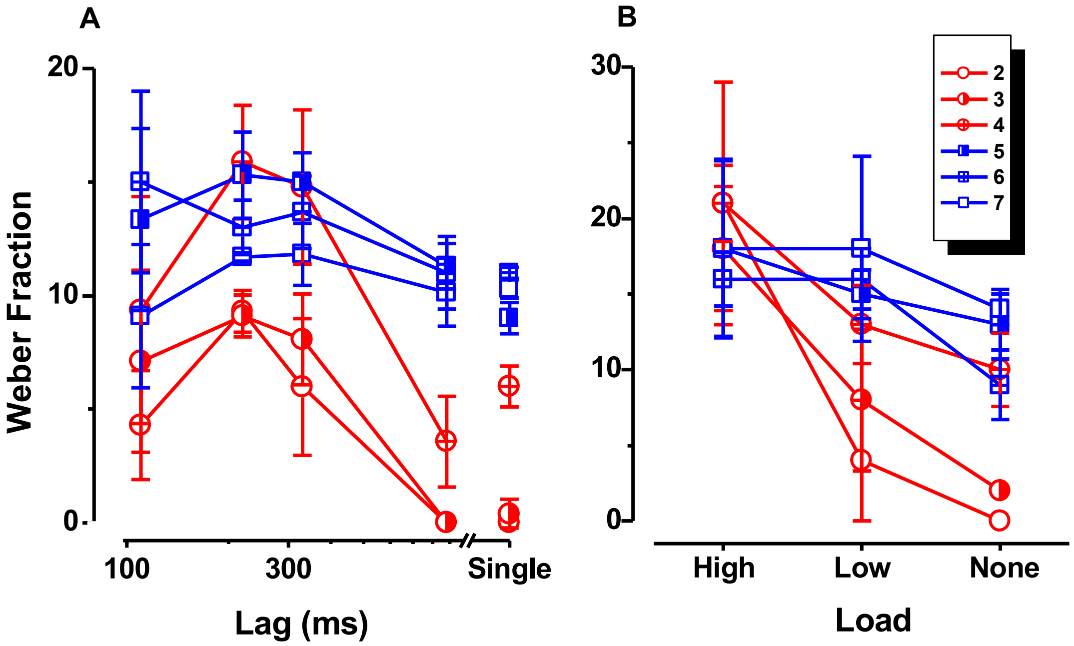

Figure 4. Weber fraction against attentional load, separately for all numbers, in the (A) attentional blink and (B) spatial attention conditions. Large number (5–7) are largely unaffected while small numbers (2–4) show a large effect of attention

Figure 5 shows individual results for the three subjects in the attentional blink experiment (Figure 5A) and four in the spatial dual task Figure 5B, plotting Weber fractions in the high-load conditions against those in the low-load conditions, separately for the subitizing (2–4) and estimation (5–7) ranges. For the attentional blink, the high load is the average of 220- and 330-ms lag and no load is the average of single task at all lags. The results were very similar for all subjects and both tasks: performance in the higher estimation range was largely independent of load, while in the subitizing range it was strongly dependent on load. The ordinates of all points were very similar for high load, but at low load form two non-overlapping clusters, with near perfect for the subitizing range.

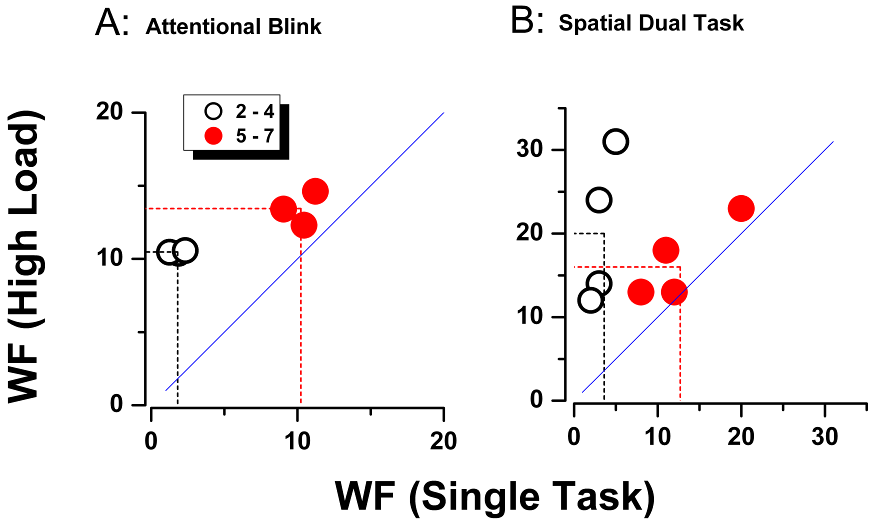

Figure 5. Scatter plot of Weber fractions in high-load against low-load conditions for all subjects in both (A) attentional blink and (B) spatial dual-task conditions, separately for low numbers (2–4) and high numbers (5–7). For the attentional blink, high load was the average of 220 and 330 ms, single task was the average of all delays with no primary task. For all subjects, attentional load affected Weber fraction much more in the subitizing than estimation range

As mentioned in the Methods section, the numerosity estimation trend is well described by a Gaussian probability distribution, defined by two numbers: the standard deviation, the estimate of response precision, that leads to the Weber fraction when normalized by the target number; and the mean, which estimates the response *accuracy* (a bias away from veridical behavior). Figures 6A and 6C plot the perceived numerosity obtained from the means of the Gaussian fit, averaged over subjects for the two attentional conditions. In general, the perceived numerosity was quite accurate (little bias), tending to follow the actual target number (dashed diagonal). The only systematic deviation from veridicality was in the high-load spatial dual-task condition, where there tended to be an underestimation at the higher numbers. Finally, Figures 6B and 6D plot "error rate" as a function of target number, to help relate the present results to previous reports, that often express results as error rate. There are two problems with this approach; one is that it confuses bias and precision, as both lead to errors, but are quite different attributes; the other is that the magnitude of the error is lost. When expressed in this way, the effect of attentional load appears to be larger for higher numerosities, but this is in fact quite misleading.

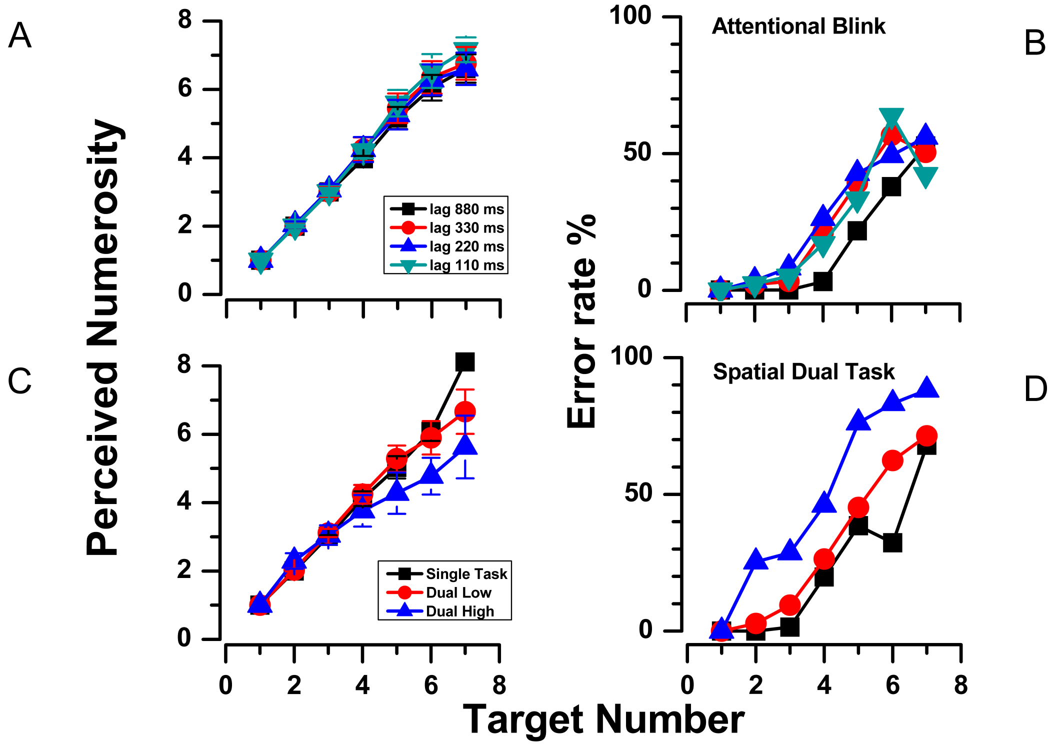

Figure 6. Plot of (A, C) perceived numerosity and (B, D) error rate in the (A, B) attentional blink paradigm and (C, D) dual-task spatial attention. Attentional load had little effect on perceived numerosity. Error rate, as always, is difficult to interpret because it contains errors both in accuracy and precision and does not weight for the amplitude of the error.

2.5 Discussion

Using two complementary techniques, this study shows that subitizing depends strongly on attentional resources, while estimation of larger quantities depends far less on attentional load. Under conditions of high attentional demand, both during the attentional blink (200–300 ms after recognition of a target letter) or during an attentionally demanding simultaneous task (detection of a color-orientation conjunction), performance in estimating the number of dots in a cloud remained remarkably constant, around 15% for target numbers ranging from 2 to 8. It would be difficult to account for these results within the framework of a single mechanism covering the whole range. If this mechanism were attention-dependent at low numbers, it should also be attention-dependent at high numbers. It appears far more plausible that two mechanisms are at work. One possibility is that "density estimation" comes into play in the higher number range. Although we did not control specifically for this possibility, as our previous study (Ross & Burr, 2010) showed that for adult humans density and numerosity activate different processes, it seems likely that the two mechanisms revealed by this study are both involved in number judgment, not density. However, these mechanisms need not be completely separate. A parsimonious explanation could be that estimation mechanisms operate over the entire range, with similar normalized resolution capacity (Weber fraction), but at low numerosities these mechanisms are supplemented by attentional mechanisms, mechanisms that identify and enumerate very precisely, but have a very low capacity, around four items. A capacity of four items would be consistent, for example, with the capacity to track moving stimuli (Pylyshyn & Storm, 1988), which is heavily dependent on visual attentive mechanisms (Arrighi, Lunardi, & Burr, 2011). This explanation also finds support from recent fMRI studies of neural correlates of visual enumeration under different attentional loads. Ansari, Lyons, van Eimeren, and Xu (2007) have shown that the temporal-parietal junction (rTPJ), an area thought to be involved in stimulus-driven attention (Corbetta & Shulman, 2002), is activated during a comparison task of quantities, but only for small numbers of items, up to 3 or 4. More recently Vetter, Butterworth, and Bahrami (2010) showed that this area responds to small numbers only in conditions of low attentional load. All these studies suggest that this area could be the neural substrate for the attention-assisted boost in performance of estimation in the subitizing range. Our current results suggest that when this attention-based system is unavailable because of competing demands, the estimation system still functions, providing numerosity estimates for small numbers, but with greatly reduced precision. That the estimation range also spans small numbers is consistent with the single unit physiology (Nieder et al., 2002) and behavioral data (Nieder & Miller, 2004a) of macaque monkeys, and also fMRI studies that suggest that the same mechanisms are active for small and large numerosities (Piazza et al., 2002). Subitizing is often considered to be a pre-attentive process or at least to have access to pre-attentive processes (Trick & Pylyshyn, 1994a), while enumeration of larger numbers is considered to require attention. This study shows, at least as far as estimation (rather than counting) is concerned, that this distinction is not true. Subitizing was heavily dependent on attentive resources, as previous studies have shown (Egeth et al., 2008; Juan et al., 2000; Olivers & Watson, 2008; Railo et al., 2008; Vetter et al., 2008, 2010; Xu & Liu, 2008a), while thresholds for numbers outside the subitizing range were completely unaffected by attentional manipulations. Interestingly, the limit of the subitizing range is very similar to that of other attention-related phenomena, such as transfer of information across saccades (Melcher, 2009). It is interesting that both spatial and temporal manipulations of attention produced similar results, suggesting that the dependence of subitizing on attention is general, not specific to a particular type. It would be interesting to examine the effect of dual attentional tasks in other modalities, such as sound, on visual subitizing (and *vice versa*), as previous studies have shown that vision and audition tap separate attentional resources (Alais, Morrone, & Burr, 2006). Broadly speaking, our results fit well with other studies of the effects of attention on enumeration. For example, Vetter et al. (Vetter et al., 2008) showed, with a paradigm very similar to our spatial dual task, that attentional load affected enumeration. They claimed that attention affected equally the subitizing and estimation ranges. However, inspection of their data (their Figure 3D) suggests that although statistically significant, the effects of attentional load were far less in the estimation than the subitizing range. In our hands, the effect of attention in the estimation range (5–7) was very small, and not statistically significant (for both paradigms $p > 0.05$), while the effect of attentional load is strong in subitizing range and is statistically significant (for both paradigms $p < 0.0002$). They also agree in principle with studies showing that the attentional blink and attentional spatial task affects subitizing (Egeth et al., 2008; Juan et al., 2000; Olivers & Watson, 2008; Xu & Liu, 2008a). However, it is difficult to see in those studies whether the effect also occurs in the estimation range, as they report error rate rather than precision, that does not estimate performance well. In our experiments, attentional load caused very little bias in perceived numerosity: *precision* was impaired in dual-task conditions in the subitizing range, but there was very little effect on average perceived numerosity (*accuracy*). Only in the high-load spatial dual task was there a systematic under estimation of numerosity, and there only in the estimation range (where Weber fractions were unaffected by attentional load). Most studies on numerosity tend to concentrate on two measures, reaction times and percent errors. As the dual task makes reaction times difficult in our paradigm, we concentrated on error rate. However, it is important to distinguish the two forms of error, accuracy and precision. The precision tells us how reliably subjects can make enumeration judgments. Systematic biases or inaccuracies are not related to precision but could reflect other processes. For example, after adapting to fields with large numbers of items, subjects underestimate numerosity, but do so reliably. Therefore looking only at error rate is very uninformative about underlying processes. Another problem with error rate is that the magnitude of the error is lost. For example, confusing 2 with 3 is a 50% error, whereas 10 with 11 is only 10%: yet when scoring error rate, both are scored equally, which leads to an overestimation of the imprecision in the larger range, which can be quite misleading. So while our results agree qualitatively with many previous studies looking at the effect of attention on enumeration, the important difference between the subitizing and estimation ranges is lost in many of those studies. Two main conclusions can be drawn from the present study: that subitizing and estimation are not identical processes, as they are differently affected by attentional load; and that subitizing, described by many as a pre-attentional process, relies heavily on attentional mechanisms (while estimation mechanisms do not). A parsimonious explanation of the current data would be that estimation processes work over all numerosity ranges, and this is broadly consistent with the animal neurophysiology (Nieder et al., 2002) and human imagining studies (Piazza et al., 2002). However, in the low number range, additional attention-based processes exist, and these have a very limited capacity, around four items. Our results are also in agreement with the recent evidence that the capacity of trans-saccadic perception, measured as the transfer of adaptation aftereffects across gaze shift, is around four items in single-task condition, instead with the addition of visual working memory or counting task this capacity decrease to only one item (Melcher, 2009). When attention is diverted on a demanding task, estimation mechanisms still operate, with lower precision.

Chapter 3 : Effect of cross-sensory attention on subitizing and mapping number

3.1 Abstract

Various aspects of numerosity judgments, especially *subitizing* and the mapping of number onto space, depend strongly on attentional resources. Here we use a dual-task paradigm to investigate the effects of cross-sensory attentional demands on visual subitizing and spatial mapping. The results show that subitizing is strongly dependent on attentional resources, far more so than is estimation of higher numerosities. But unlike many other sensory tasks, visual subitizing is equally affected by concurrent attentionally demanding auditory and tactile tasks as it is by visual tasks, suggesting that subitizing may be amodal. Mapping number onto space was also strongly affected by attention, but only when the dual-task was in the visual modality. The non-linearities in numberline mapping under attentional load are well explained by a Bayesian model of central tendency.

3.2 Introduction

In the previous experiment we demonstrated that subitizing strongly depend on visual attention. We suggested that subitizing and estimation are not identical processes and that a relatively attention-free estimation mechanism could operate over both high and low number ranges, but small numbers, within the subitizing range, can call on an additional attentive mechanism that operates when attentional resources permit over a range of up to four items. Interestingly, a body of research suggests that the capacity to rapidly enumerate low numbers of items many not be restricted to vision, but could reflect a general perceptual mechanism shared between different senses; subitizing has been shown to operate in audition (Camos & Tillmann, 2008; Repp, 2007), and also with haptic stimuli (Plaisier, Bergmann Tiest, & Kappers, 2009; Riggs et al., 2006). fMRI data also point to amodal representation of numbers. When subjects are asked to estimate numerosities of visual or auditory stimuli, both result in increased activity of a right lateralized fronto-parietal cortical network, independently of the modality of the stimuli (Piazza, Mechelli, Price, & Butterworth, 2006). Cross-modal interactions in subitizing have also been revealed in a study by Cordes, et al (2001a), who showed that precision in tactile number production is affected by a concurrent verbal task.

However, it is not clear whether the attentional effects are modality specific, or whether they transfer across modalities. This question is particularly relevant to recent work showing that subitizing is not strictly visual, but also seems to operate in audition (Camos & Tillmann, 2008; Repp, 2007) and touch (Plaisier et al., 2009; Riggs et al., 2006).

Cross-modal attentional effects

Concurrent perceptual tasks of the same sensory modality interfere with each other to degrade performance (Pashler, 1992, 1994). However, evidence for cross-modal interference is conflicting. Bonnel and Hafter (1998) found evidence for audio-visual cross-modal interference for detecting the sign of a magnitude change (luminance in vision and intensity in audition). Spence, Ranson and Driver (2000) found that selecting an auditory stream of words presented concurrently with a second (distractor) stream is more difficult if a video of moving lips mimicking the distracting sounds it is also displayed. These psychophysical findings are not only consistent with some of the cognitive literature of the 1970s and 1980s (Taylor, Lindsay, & Forbes, 1967; Tulving & Lindsay, 1967), but also with recent neurophysiological and imaging results. For example, Joassin, Maurage, Bruyer, Crommerlink and Campanella (2004) examined the electrophysiological correlates of auditory interference on vision in an identification task of non-ambiguous complex stimuli, such as faces and voices, and showed that cross-modal interactions occur at various different stages, involving brain areas such as the fusiform gyrus, associative auditory areas (BA 22), and the superior frontal gyri. Hein, Alink, Kleinschmidt and Muller (2007) showed with a functional magnetic resonance (fMRI) study, that even without competing motor responses, a simple auditory decision interferes with visual processing at neural levels including prefrontal cortex, middle temporal cortex, and other visual regions. Taken together these results imply that limitations on resources for vision and audition operate at a central level of processing, rather than in the auditory and visual peripheral senses.

However, much evidence also suggests independence of attentional resources for vision and audition. For example, Larsen, Mclhagga, Baert and Bundesen (2003) compared subject accuracy for identifying two concurrent stimuli (such as a visual and spoken letter) relative to performance in a single-task. They found that the proportion of correct responses was almost the same for all experimental conditions, either single-task or divided-attention. Similarly, Bonnel and Hafter (1998) used an audio-visual dual-task paradigm to show that when identification of the direction of a stimulus change is capacity-limited, simple detection of visual and auditory patterns is governed by “capacity-free” processes, as in the detection task there was no performance drop compared with single-task controls. Alais, Morrone and Burr (2006) measured discrimination thresholds for visual contrast and auditory pitch, and showed that visual thresholds were unaffected by concurrent pitch discrimination of chords and vice versa, while when two tasks were performed within the same modality, thresholds increased by a factor of around two for visual discrimination and four for auditory discrimination. Also for sustained attentional tasks (such as 4 seconds of the *Moving-Objects-Tracking* task of Pylyshyn and Storm (1988) separate attentional resources seem to be allocated to vision and audition (Arrighi et al., 2011). Many of these results are in line with imaging studies suggesting that attention can act at early levels, including primary cortices A1 and V1 (Jancke, Mirzazade, & Shah, 1999; Posner & Gilbert, 1999; Somers, Dale, Seiffert, & Tootell, 1999).

Mapping numbers onto space

An interesting aspect of numerosity perception is our ready capacity to map numbers into space, pointing to intrinsic interconnections between number and space (Burr, Ross, Binda, & Morrone, 2010; Butterworth, 1999; Dehaene, 1997). Experimentally, this is studied with the so-called “numberline”, where subjects are asked to position appropriately on the line numeric digits, or clouds of dots. Educated adults have no difficulty in doing this accurately, whereas the mapping of young children, children with dyscalculia and unschooled adults show distinct compressive, logarithmic-like non-linearities (Ashkenazi & Henik, 2010; Booth & Siegler, 2006; Dehaene et al., 2008; Geary, Hoard, Byrd-Craven, Nugent, & Numtee, 2007; Geary, Hoard, Nugent, & Byrd-Craven, 2008; Siegler & Booth, 2004; 2003). Recently, we showed that limiting attentional resources by a dual-task also results in logarithmic-like numberline mapping (Anobile, Cicchini, & Burr, 2012).

However, the fact that the function follows a logarithmic form does not necessarily imply an intrinsic logarithmic representation of numerosity (Gallistel & Gelman, 1992; Karolis, Iuculano, & Butterworth, 2011). Several alternate explanations have also been put forward, including proportional judgments relative to the ends and centres of the numberline (Barth & Paladino, 2011), related to the well known *central tendency of judgment* (Hollingworth, (1910). We (Anobile et al) have also explained the non-linearities in numberline-mapping caused by attention deprivation as a Bayesian model of central tendency, similar to that introduced by Jazayeri and Shadlen (2010) to model interval reproduction judgments. The results were well fit by a simple Bayesian model of central tendency, where *central tendency* is a *prior* of variable width, that effectively pulls the higher numbers towards the centre of the numberline (while the lower number remain anchored). We use this model again in this study (see methods section for details).

Goals of this study

The current study was designed to examine the role of cross-modal attentional competition in visual numerosity estimation, using dual-tasks with visual, auditory and haptic distractors on several number paradigms. We had three specific aims: (1) to test the effects of cross-modal attention on numerosity perception for both small (subitizing) and large item sets; (2) study the effects of cross-modal attention on mapping of numbers onto space; and (3) model the mapping effects within a Bayesian framework. We confirm our previous results, showing that high numbers are less affected by attentional demands, while the subitizing range is far more vulnerable. In the low subitizing range, the auditory and haptic distractors were as effective as visual distractors in decreasing precision. The results reinforce other studies in suggesting that subitizing may be an amodal capacity, not restricted to vision. We also replicate our previous results showing that dual-task attention to a concurrent visual task affects numberline mapping (well-modelled by a Bayesian model), but further show that there is little cross-modal attentional effects from a concurrent auditory task to the visual numberline mapping.

3.3 Methods

Stimuli were presented in a dimly lit room on a 23-inch liquid crystal monitor (ACER) with 1280 X 1024 resolution, mean luminance 60 cd/m^2, refresh rate 60 Hz. Subjects viewed the screen binocularly at a distance of 57 cm. Stimuli were generated and presented with Matlab 7.6, using PsychToolbox routines (Brainard, 1997) running on a Macintosh laptop. Sounds were played by two loudspeakers (Trust SP-2420) flanking the computer screen. Speaker separation was around 80 cm and intensity 75 dB at the sound source. Haptic stimuli were delivered by a modified speaker resting on the index finger of the non-dominant hand (the left, for all the participants).

Experiment I: enumeration

Participants

Ten naive subjects (mean age: 26±3) with normal or corrected-to-normal vision participated. Four subjects were tested in the visual attentional load and in one (of the two) auditory distractor paradigms (frequency discrimination). Four subjects (including three new) were tested on a different auditory attentional load task (time bisection). Finally, three new subjects performed the haptic load task (time bisection). All subjects performed the single task condition.

Stimuli and procedure

Each trial started with a fixation point (randomly displayed for a random interval from 200 to 2000 ms), followed by the simultaneous presentation of both distractors and numerosity task, both lasting 230 ms, followed immediately by a mask (600 X 600 pixels, randomly black or white) for 250 ms. The *numerosity stimulus* was a cloud of non-overlapping dots varying in number from one to ten, which subjects were required to enumerate. Dots were half-white and half-black so luminance was not a cue to number. Each dot was 0.4° in diameter, with position chosen at random within a matrix of 18° diameter. The visual distractor comprised four centrally positioned coloured squares, each subtending 3° of visual angle. The stimulus was classed as a target if a specific conjunction of colour and spatial arrangement was satisfied: two green squares along the right diagonal or two yellow squares along the left diagonal. Two separate auditory distractors were used: pitch discrimination and interval discrimination. For the pitch discrimination, three tones (each 30 ms) were played equi-spaced within 250 ms. Two reference stimuli had the same frequency, while the target to be detected (chosen at random) differed by ±40% Hz. Both the sign of the increase (increase or decrease) and the reference frequency (400 to 1000 Hz) were chosen randomly on each trial. For the auditory interval discrimination task, we performed *interval bisection* of three 1300 Hz, 10 ms tones. The first and the third were always played at 0 and 250 ms, the second at a variable interval (60, 80, 90, 110, 120 or 140 ms): subjects reported whether it was closer to the first or third tone. The haptic distractor task was like the auditory time bisection, with taps to the hand instead of tones. Taps were delivered by the coil of a small speaker resting on the hand, through which a 10 ms tone of 80 Hz was played. Like the auditory time bisection task, subjects determined whether the second tap was nearer in time to the first or third (same conditions as for audition). To prevent the use of auditory cues, subjects wore noise-reduction headphones that played white noise. In the Single Task condition, distractor stimuli were presented on all trials, but subjects were instructed to ignore them. These conditions were re-run separately for all distractor conditions (visual, auditory and tactile).

Numerosity responses were recorded only if the distractor task was correct. We measured 10 levels of numerosity (from one to ten) and 5 attentional conditions (visual, haptic, two different auditory dual-task and single-task), yielding a total of 5500 trials (equally divided between subjects and conditions). In separate sessions we measured enumerations where subjects were not required to do the distractor task (although the stimuli were always displayed).

In this experiment we also asked subjects to perform the auditory frequency-discrimination and visual conjunction task together, to verify that they did not interfere with each other (as others have previously reported).

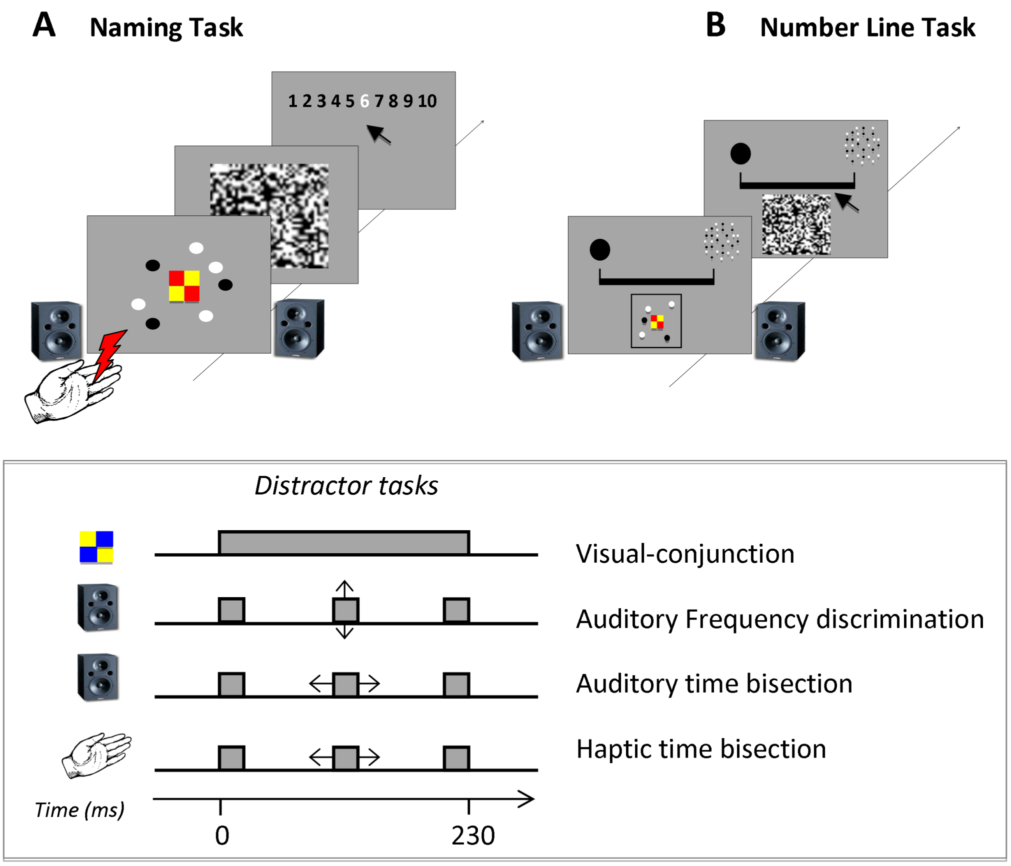

Figure 1. Illustration of stimulus sequences. Each trial starts with a fixation point (randomly displayed for 200–2000), followed by the numerosity stimulus (dot cloud), together with the distractor. Both last for 230 ms, immediately followed by a binary pixel mask (200 ms). Subjects responded first to the distractor task then enumerated the numerosity.

Experiment II: numberline mapping

Three new naive subjects were recruited (mean age: 26±2), with normal or corrected-to-normal vision, and who had not participated in the previous study participated in this one.

The general conditions (apparatus etc) were like the previous experiment, unless otherwise stated. Throughout each trial a “numberline” was displayed, a 25 cm line without markings, with sample dot-clouds representing the extremes: one dot on the left and 100 dots on the right (see Fig. 1). On subject initiation, both distractor and dot-cloud stimuli were presented for 230 ms, followed by a random-noise mask (described above) that remained on until the subject responded. In separate sessions we measured three different attentional conditions: single-task, visual distractor (described above) and auditory distractor (the frequency-discrimination task). As before, subjects responded first to the distractor task (when appropriate).

The numerosity stimulus was like the previous, a cloud of non-overlapping dots, half-white, half-black at 90% contrast, falling inside a circle of 8° diameter (sparing the central 1°). The numerosities were randomly selected from the set: 2, 3, 4, 5, 6, 18, 25, 42, 67, 71, 86 following Siegler and Opfer (2003) . To discourage observers using strategies other than numerosity (such as texture density), on each trial we kept constant either the total covered area at 8° by varying individual dot size, or constant individual dot size of 0.4°, varying total area covered), Thus on average, neither dot size nor total covered area correlated with numerosity. Subjects clicked a mouse pointer on the position of the numberline corresponding to the estimated numerosity. As before, numberline data were recorded only if the distractor task was correct.

Each block measured one of the 3 conditions (single and two dual-task), presenting ten test stimuli of different numerosity presented in random order once. About five blocks were run for each condition, order randomized between observers.

Bayesian modelling

We modelled numberline mapping with the Bayesian model developed by Anobile et al (2012), which assumes that subjects base their performance on a distribution that combines both their sensory estimates and an *apriori* hypothesis about the stimulus. Bayes' rule states that:

$$p(r \mid n) \propto p(n \mid r) p(r)$$

Eqn. 1

Where *r* is the response and *n* is the numerosity of the stimulus. *P(n|r)* is typically termed the likelihood, *p(r)* the *prior* and *p(r|n)* the *posterior*. We model likelihood with a gaussian distribution centred on the stimulus, with width given by Weber's law (Weber fraction times number). The *prior* is also modelled as a gaussian distribution centred on the mean of the stimulus range, with variable width (standard deviation).

Bayes' Law states that the optimal combination of information is obtained point-wise multiplication of the two gaussian distributions:

$$\phi(r\,|\,n) \propto N(\mu_r,\sigma_r^2)N(\mu_P,\sigma_P^2)$$

Eqn. 2

where N indicates the gaussian function [*printer's note: should be in* calligraphic *font*]. The resulting distribution is itself gaussian whose centre is given by a weighted average of the centres of the likelihood and that of the prior:

$$\hat{r} = \mu_P \frac{\sigma_r^2}{\sigma_r^2+\sigma_P^2} + \mu_r \frac{\sigma_P^2}{\sigma_r^2+\sigma_P^2}$$

Eqn. 3

$$\mu_r = n$$
$$\sigma_r = wn$$

Eqn. 4

where w is the *Weber fraction,* assumed constant. σ_r increases linearly with n, so the prior will have a weight proportional to n^2. For low numbers, the posterior distribution should be centred on the physical sensory number, while for higher numbers, the posterior estimates are attracted towards the prior (see Figure 3 A of Anobile et al (2012)).

The final equation for the curves of figure 3 is obtained by substituting eqn. 4 into eqn. 3 and simplifying:

$$\hat{r} = \frac{\mu_P w^2 n^2 + \sigma_P^2 n}{w^2 n^2 + \sigma_P^2}$$

Eqn. 5

The shape of the function depends only on the position and width of the prior. By inspection it is obvious that as $\sigma_P^2 \to 0$, $\hat{r} \to \mu_P$ (total regression to the mean), and as $\sigma_P^2 \to \infty$, $\hat{r} \to n$ (veridical response). For intermediate values, the equation follows a Naka-Rushton-like rule, compressing towards the mean of the prior (μ_P).

3.4 Results

Experiment I: enumeration of low numerosities

As detailed above, we asked subjects to estimate the numerosity of dot-clouds, both when presented alone and with the various distractor tasks: visual conjunction detection, auditory frequency discrimination, auditory interval bisection task and tactile interval bisection task. Figure 2 shows response distributions averaged over all subjects for two sample stimuli (3-dot and 6-dot), which we approximate by Gaussian distributions (on logarithmic abscissa). In the single task conditions the response distributions are narrow, particularly for the 3-dot stimulus (within the subitizing range). In the dual task conditions, the response distributions are broader. The effect of attention is clearly greater on the 3-dot than the 6-dot distribution, as they are so narrow without attentional load. With attentional load subjects begin to make errors in estimating the number of presented dots, deviating from veridicality by one or even more units. . However, the mean remains virtually unchanged, around three.

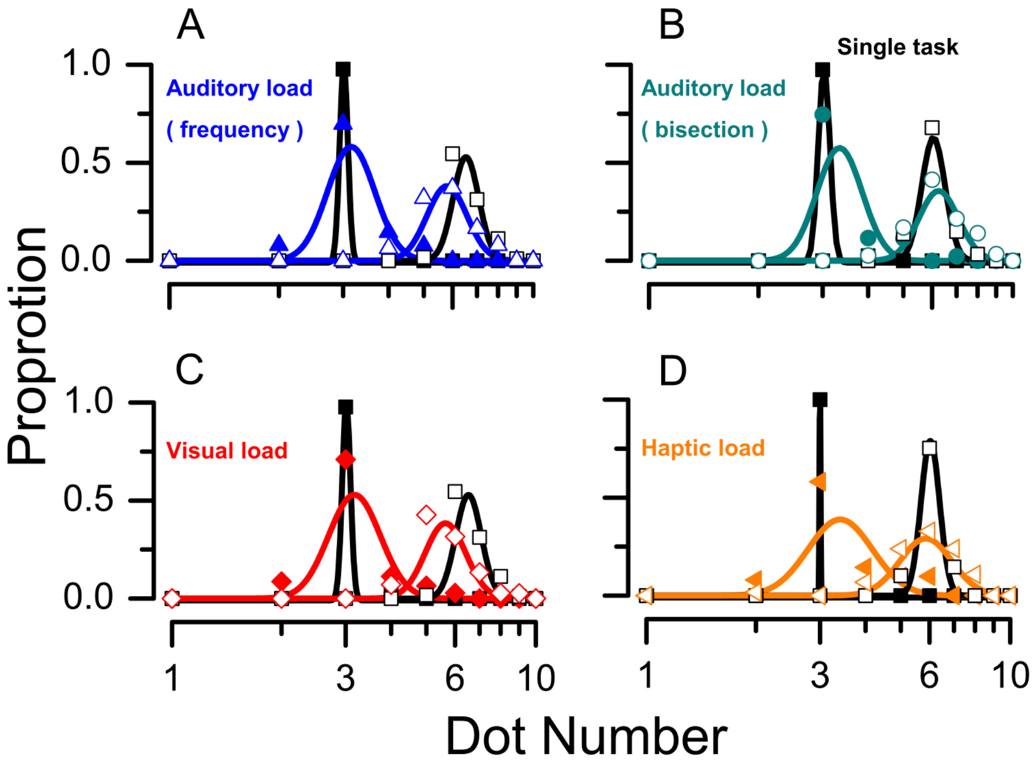

Figure 2. Sample response distribution for enumerating 3 or 6 dot stimuli numbers in single task (black) and dual task conditions. Filled symbols show responses to 3-dot stimuli, hollow symbols to 6-dot stimuli. Several dual task conditions are shown: (A) Auditory frequency discrimination (blue). (B) Auditory time bisection (cyan). (C) Visual conjunction (red). (D) Haptic time bisection (orange). Best fitting log-gaussian curves are shown as continuous lines

We calculated separately for each subject the mean and standard deviation, to yield respectively estimates of accuracy and precision, which were then averaged and shown in Figure 3. Fig. 3 A plots precision as average Weber fraction (standard deviation divided by dot number) of the subjects for each attentional condition, as a function of dot number (excluding the extremes 1 and 10), for the various conditions. For the single-task condition, Weber fractions are near zero in the subitizing range, but rise to about 0.1 for numbers 5 and higher. This pattern changes completely under attentional load. When subjects were required to perform a concomitant dual-task – visual, auditory or tactile – precision was severely impaired in the subitizing range, with Weber fractions rising to 0.2 or higher. Precision was also impaired for the higher numbers, but by a lesser extent. This confirms the results of Burr et al (2010), and further shows that a distractor task in any modality, not just vision, impacts heavily on subitizing. In fact the worst performance was obtained with the tactile distractors. It is not clear why this is so, but perhaps the tactile task was, for some reason, more demanding.

Figure 3 B plots the average perceived numerosity, the mean responses for each numerosity, averaged over subjects. In general, these estimates were quite accurate (bias-free) in all conditions, following reasonably closely the actual target number (dashed diagonal). The only small deviation from veridicality was for the higher numbers (7-8-9), which tended to be slightly underestimated. This shows that the errors in the subitizing range were not simply due to some elements not being seen, as this would have lead to a systematic under-estimation of numerosity.

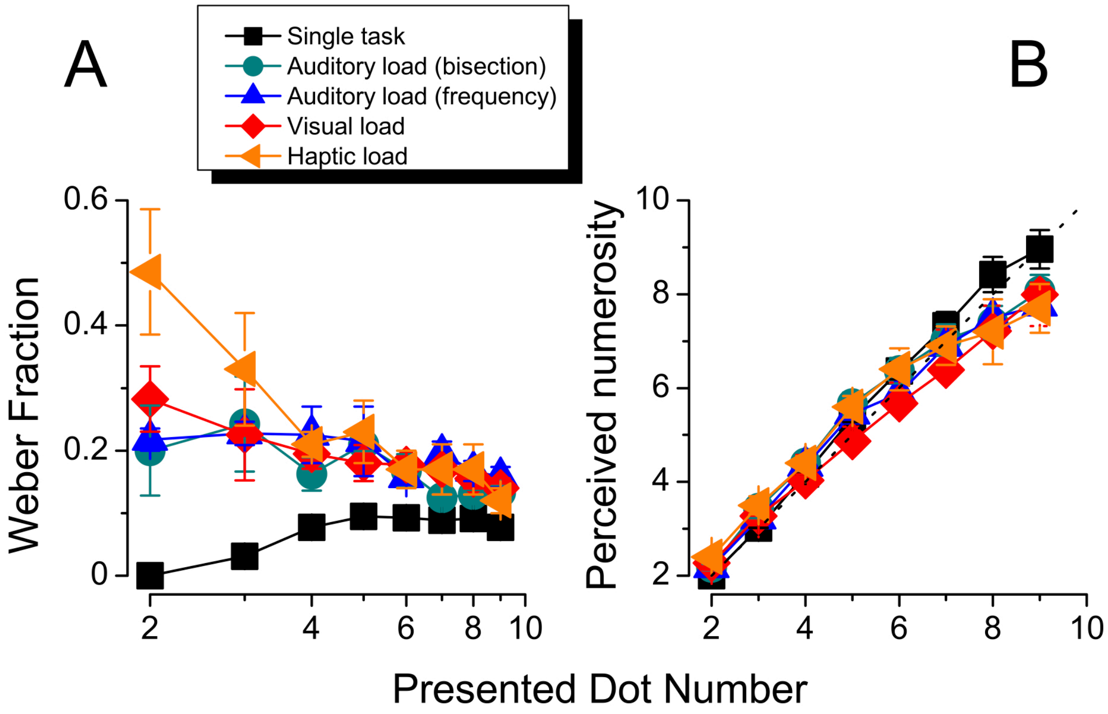

Figure 3. Number enumeration. (A) Mean Weber fraction (standard deviation divided by physical number) as a function of target number, for the various distractor conditions. Attentional load strongly impairs precision in the subitizing range (4 and below), irrespective of the modality or type of distractor task. The effect at high numerosities was much less. (B) Attention had a little effect on average accuracy, with mean perceived numerosity nearly veridical over the range.

To be certain that the distractors tasks were performed appropriately during the dual-task conditions, we also measured in separate sessions the baseline performance of on the different distractor tasks. Performance on average does not change when these tasks were performed alone or within dual-task paradigm. Mean performances were 98, 77, 83 and 83% respectively for the visual colour-orientation conjunction, auditory frequency discrimination, auditory time bisection and haptic time bisection task when performed alone, compared with 97, 75, 80 and 81% when performed in the dual-task paradigm. The similar performance suggests that they made similar attentional demands on the subjects. As a final test of the independence of auditory and visual attention, we measured performance on the two distractor-stimuli – visual conjunction and auditory frequency discrimination – in the presence of the other. The methodology was exactly as before, except that subjects had to report on the conjunction task and the auditory-frequency task (and ignore the numerosity. Figure 4 shows the results, for the auditory (A) and visual (B) tasks, measured alone and together with the task in the other modality. Clearly, doing two tasks in different modalities incurs little cost: performance, shown as percent correct responses, is little affected by the concomitant task.

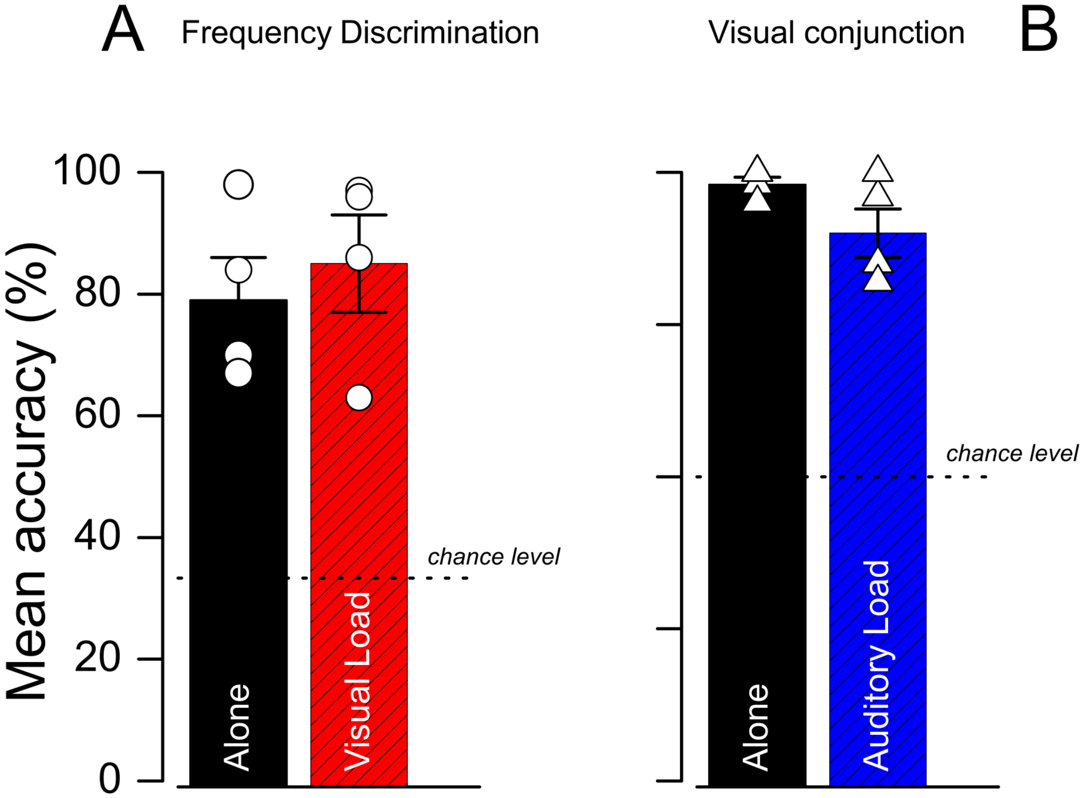

Figure 4. (A) Average performance (shown as percent correct) for four subjects on the

auditory distractor task (frequency discrimination), measured either alone (black) or in dual-task with the visual conjunction task (right-slanting red). The cross-modal distractor clearly did not affect performance. (B) The converse of (A): percent correct on the visual conjunction task measured either alone (black) and or in dual-task condition (right-slanting blue). Again, auditory attention had little effect on visual performance

Experiment II: mapping numbers onto space

Mapping onto the numberline is a standard task in number research. Subjects view a cloud of dots, estimate its numerosity and map that onto a line. Here we asked subjects to perform the task under dual-task conditions, with a visual or an auditory distractor. Figures 5A-C show numberline judgements for all three conditions (single-task, and visual and auditory frequency-discrimination distractors), averaged over all subjects. Without attentional load (A), the numberline is quite linear. With a concomitant visual conjunction task (B), the mapping shows a clear compressive non-linearity, as previous observed (Anobile et al., 2012). However, the auditory distractor (C) had very little effect, leaving the mapping almost linear.

The curves are fits of the Bayesian model described in Anobile et al. (2012) and methods section (eqn. 5). Best fits of the data were obtained with priors centred at 52 for single and auditory, and 40 for visual distractors: both near the mid-point of the stimulus range (2-86). If we assume a Weber fraction of 0.25 (agreeing with Ross (2003), and many other estimates), *prior* widths giving best fits are of 130, 34 and 10 for the single, auditory distractor and visual distractor respectively (the more narrow the prior, the greater the deviation from linearity). Assuming a higher or lower Weber would require the priors to be scaled commensurably.

Figures 5D-F plot the precision of the mapping, expressed as Weber Fraction (standard deviation normalized by dot number), with dot-number on a logarithmic abscissa (to bring out better the effects at low numbers). These results confirm those of experiment I. Without attentional load (D), Weber fraction is low everywhere, including the subitizing range (slightly higher here than in experiment I, presumably reflecting noise in positioning the pointer). However, with both visual and auditory distractors

(E&F respectively), the Weber fraction increased considerably in the low number range, as in the previous experiment.

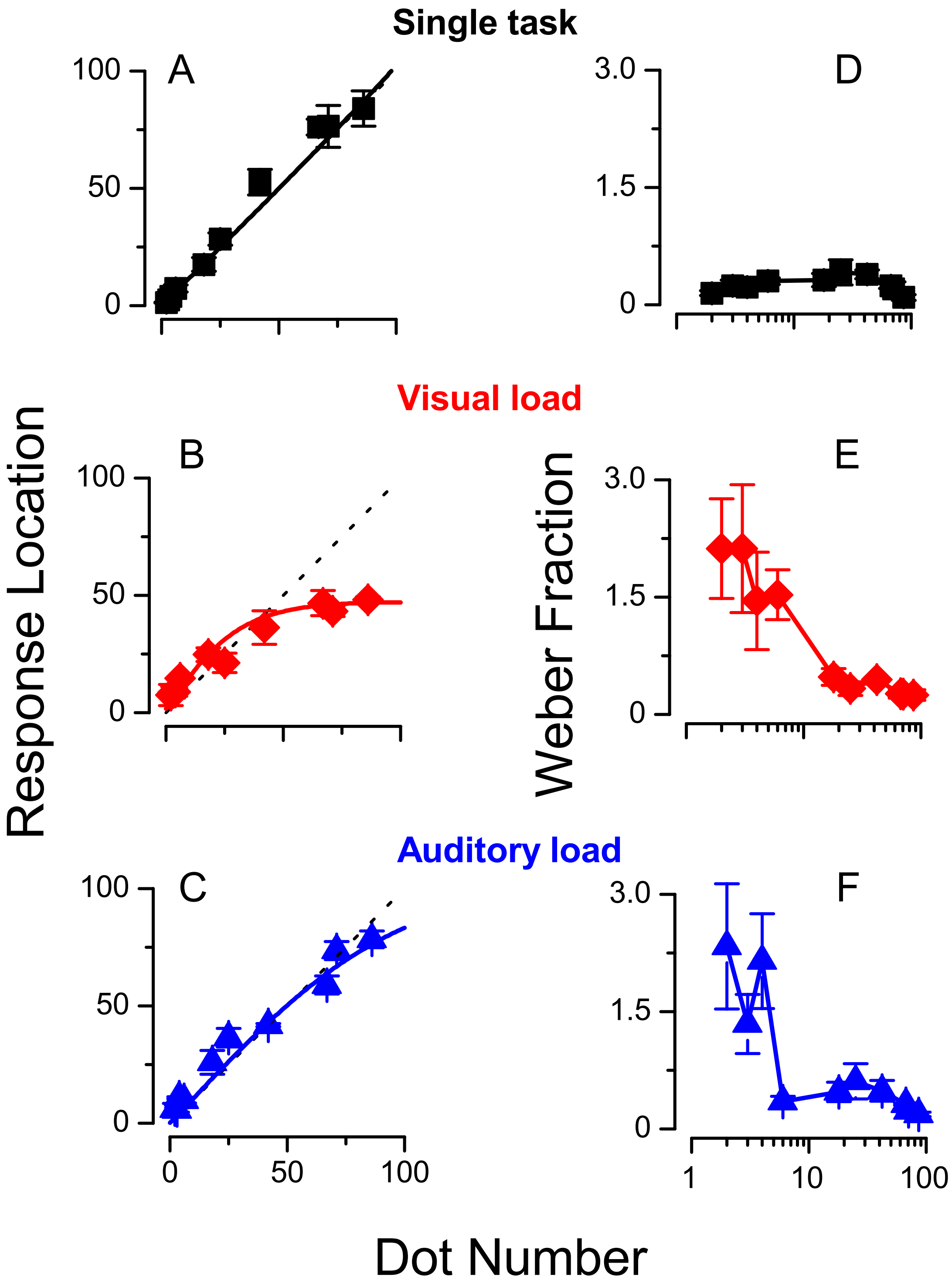

Figure 5. Numberline. (A–C) Mapped response (averaged across subjects), as a function of physical dot-number for different attentional load conditions: single task (A), visual

conjunction (B) and auditory dual-task (C). The continuous curves are the fits of the Bayesian central tendency model, described in Section 2. (D–F) Mean Weber fraction as a function of numerosity (on logarithmic scale to display more clearly low numbers), again for single-task (D), visual (E) and auditory (F) distractors. Attentional load affects Weber fraction more for low (2–4) than high (6–98) numbers. Error bars represent ±1 s.e.m.

Following Shadlen and Jazayeri (2010), we partitioned error into two components: bias (inaccuracy) – the distance of the average mapping from the true value – and root-variance (imprecision) – the standard deviation of the individual trials. Figure 6 shows the results of the numberline, partitioned in this way, separately for low (2-6) and for high numbers (18-86). This representation is revealing. For low numbers, the attentional demand increases both the bias and root-variance slightly more for vision modality compared with the single task condition. However, for high numbers only the visual attentional load increases the bias, the auditory distractors affecting only the root-variance (slightly). This is reflected in the non-linear mapping so clear in Figure 5C, but not Figure 5E.

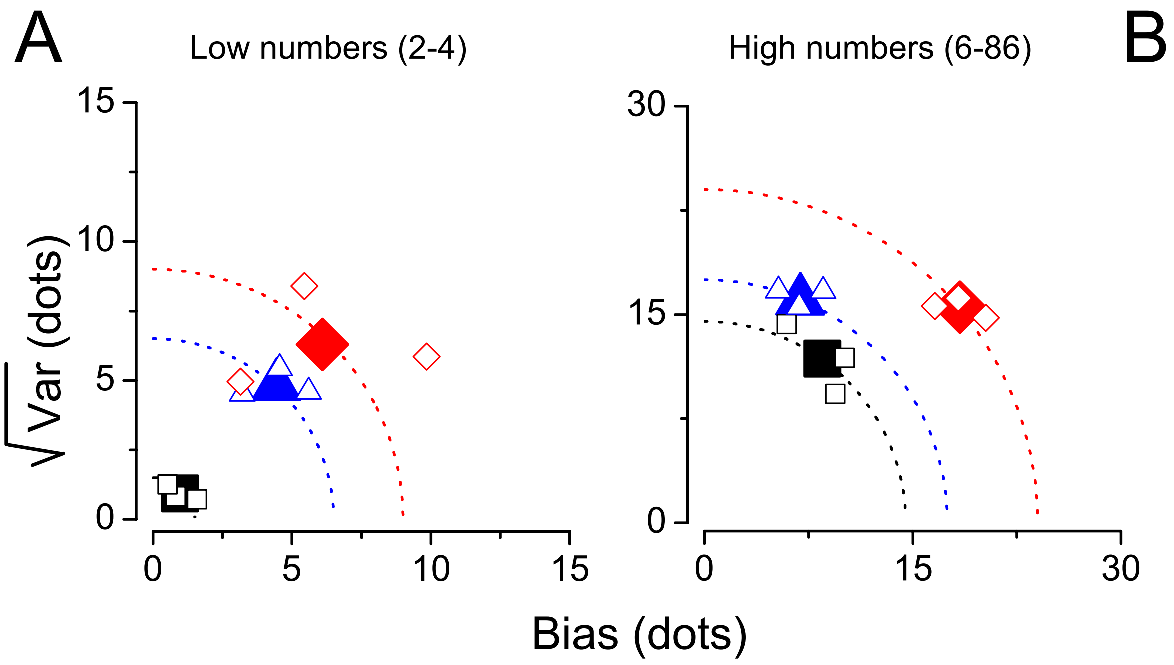

Figure 6. Partitioning of the error of the numberline task into root-variance (average standard deviation of trials at a particular numerosity) and bias (average distance of the mean response from the physical numerosity), plotted separately for low numbers (2–4: panel A) and high numbers (6–86: panel B). Open symbols represent data of individual subjects, filled the average over subjects for each condition. Colour-coding as before: single – task black squares; visual – red diamonds; auditory – blue triangles. Total error is given by the distance of each symbol from the origin.

3.5 Discussion

One of the main results of this study is to show that subitizing is affected by cross-attentional demands. While we confirmed previous work showing independent attentional resources for visual and auditory tasks for estimation of moderately high numerosities, *subitizing* of small quantities of visual items was strongly affected by concurrent attentionally demanding tasks in vision, audition (frequency discrimination or interval discrimination) or touch. For the distractor stimuli we used, all had similar effects, raising Weber fractions from virtually 0 to more than 30%.

This suggests that subitizing may be an *amodal* phenomenon, rather than strictly visual, an idea that finds support in some recent research showing that subitizing processes also operate in audition (Camos & Tillmann, 2008; Repp, 2007) and touch (Plaisier et al., 2009; Riggs et al., 2006). Estimating the numerosity of either visual or auditory stimuli causes increased activity of a right-lateralized fronto-parietal cortical network, independently of the modality of the stimuli (Piazza et al., 2006). All this suggests that subitizing may rely on supra-modal attentional resources. Estimation, however, was little affected by cross-modal attention, further evidence that it is an independent process.

It is not clear why subitizing is more affected by attention than estimation. One possibility is that it is a qualitatively different process, requiring more attentional resources than estimation. Indeed, it has been suggested that subitizing is directly linked to the capacity to individuate objects (Piazza, Fumarola, Chinello, & Melcher, 2011). The cross-modal interference reported here tends to support this view, as all modalities may be contributing to object individuation. However, we cannot exclude other possibilities, such as there being some form of pre-normalization noise, highly dependent on attention, that would affect the low range of numbers more than the higher range. Further experimentation may be able to tease out these two possibilities.

A second goal of the study was to examine the effects of intra- and cross-modal attentional demand on mapping number onto space. Here we found that visual, but not auditory attentional load caused the mapping process to become strongly non-linear, with a logarithmic-like compression. Both auditory and visual distractors impaired the precision (Weber fraction) in the low numerosity range, agreeing with the previous result showing that cross-modal attentional load affects subitizing.

The compressive non-linearity we observed with visual attentional load is similar to the non-linearities observed with young children (Booth & Siegler, 2006; Siegler & Booth, 2004; Siegler & Opfer, 2003) children with dyscalculia (Ashkenazi & Henik, 2010; Geary et al., 2007; Geary et al., 2008) and adults without mathematical schooling (Dehaene et al., 2008). In all these cases, the mapping process has been described as "logarithmic". However, the fact that a logarithm describes the function does not necessarily imply that it reflects underlying logarithmic transformation. Anobile et al. (2012) have suggested that the compression may reflect a "central tendency of judgements", which has been studied for at least 100 years (Hollingworth, 1910) and recently revived in Bayesian terms (Jazayeri & Shadlen, 2010). In their version, the central tendency is a *Bayesian prior*, which combines with the sensory likelihood to produce a *posterior* biased towards the mean. Given that the likelihood is essentially the product of the Weber constant and dot number, and Weber fraction is fairly constant, the likelihood is much broader at the higher number range, and therefore more influenced by the prior. We modelled our numberline data with a simple Bayesian model that predicted both the compressive shape, and fitted the data well, accounting for about 95% of the variance.

What function does the *prior* serve? Shadlen and Jazayeri suggest that it serves to optimize performance, defined as the total error. Error can be partitioned into accuracy and precision, or bias and root-variance, as shown in Figure 6. Total error is the Pythagorean sum of the two, the distance of the points from the origin. At low numerosities, both visual and auditory attentional loads affect performance, and they affect root-variance and bias in very similar amounts. As has been shown elsewhere (Cicchini, Arrighi, Cecchetti, Giusti, & Burr, 2012; Jazayeri & Shadlen, 2010), increasing bias towards the mean optimizes performance, measured by total error. For high numerosities, however, the results were quite different. Visual attentional load caused a small increase in variance, but a large increase in bias, reflected in the compressive, non-linear mapping. Auditory attention had little effect on either bias or variance, agreeing with previous studies showing visual tasks to have separate attentional resources from audition.

In summary, this study examined how attentional tasks, either in the same and different sensory modalities, can affect numerosity perception. We show that enumerating numbers in the subitizing range is highly dependent on attentional resources, and these resources seem to be shared by the auditory and haptic systems. Attention also affects the higher range of numerosities, particularly when subjects are required to map number onto space. However, in this case, the attention-dependence seems to be specific for vision.

4. Adaptation Affects Both High and Low (Subitized) Numbers Under Conditions of High Attentional Load

4.1 Abstract

It has recently been reported that, like most sensory systems, numerosity is subject to adaptation. However, the effect seemed to be limited to numerosity estimation outside the subitizing range. In this study we show that low numbers, clearly in the subitizing range, are adaptable under conditions of high attentional load. These results support the idea that numerosity is detected by a perceptual mechanism that operates over the entire range of numbers, supplemented by an attention-based system for small numbers, (subitizing).

4.2 Introduction

Numerosity perception like all primary sensory properties, is susceptible to adaptation: the prolonged exposure to a more numerous visual stimulus makes the current stimulus appear less numerous, and *vice versa* (Burr & Ross, 2008b). Interestigly, low numbers (<4) were not susceptible to adaptation. In the previous experiments we shown that dual-task paradigms affect precision performance (Weber Fraction) in the subitizing range far more than in a higher range. Under attentional load, precision in the subitizing range deteriorated considerably to approach that of the higher estimation range. The results imply that two systems are involved with numerosity. However, we do not believe that the two number ranges are processed by completely independent mechanisms. We suggested that there may exist a preattentive estimation mechanism operating over the entire range of numbers, both large and small, and that this system is supplemented by an additional attentive mechanism with very limited capacity, capable of attending to up to about four items: the attentive mechanism makes performance virtually perfect over this low range. In this study we test directly this hypothesis by measuring adaptation to numerosity under demanding attentional load conditions.

4.3 Methods

The stimuli were presented in a dimly lit room on a 15-inch Macintosh monitor with 1440 × 900 resolution at refresh rate of 60 Hz and mean luminance of 60 cd/m^2, and viewed binocularly by subjects from 57 cm. Stimuli were generated and presented under Matlab 7.6 using PsychToolbox routines (Brainard, 1997). Three subjects with normal or corrected-to-normal vision participated in this study, two authors and one naïve to the goals of the study (all male, mean age 26). The experiment used a dual-task paradigm: subjects first performed a difficult conjunction task, then a numerosity judgment (see Figure. 1). The stimuli for the primary task comprised 4 centrally positioned colored squares, each subtending 1° of visual angle, presented concurrently with the numerosity matching task (lasting the entire duration of both test and probe). The squares could be arranged in eight different color combinations. If two green squares fell along the right-sloping diagonal *or* two yellow squares fell along the left diagonal, the stimulus was a target. In the single-task condition, the conjunction stimulus was presented as before, but subjects were instructed to ignore them. The *test* stimulus for the secondary task (numerosity comparison) was a cloud of non-overlapping dots (diameter 10 arcmin), half white and half black at 90% contrast. The dots were constrained to fall within a virtual circle of 4° visual angle, and were always separated from each other by at least 12 arcmin. The *adaptation* and probe stimuli were similar to the test, with the probe comprising 3, 6, 12 or 24 dots (depending on adaptation condition), and the *adaptor* 200 dots. Each session started with 40 s of the adaptor presented 6◦ left of fixation; in subsequent trials it appeared for only 6 s (top-up adaptation). 150 ms after the adaptor disappeared, the test appeared for 200 ms in the same position as the adaptor, and the primary task (colored-squares) in the centre of the screen for 550 ms. 150 ms after the test was extinguished, a probe stimulus was presented for 200 ms, 6◦ right of fixation. The probe was also a dot pattern, similar to the test, with numerosity 3, 6, 12, 24 dots depending on condition. In the dual-task condition, subjects were required first to report whether the central stimulus was a target (by appropriate mouse-click), then respond whether the test or probe appeared to be more numerous. All subjects were about 90% correct on the conjunction task, with no differences between conditions: responses were recorded to the number task only if the response to the conjunction task was correct. In the no-load condition, subjects performed only the numerosity task. The number of dots in the test was initially equal to the probe, then varied from trial to trial depending on subject response, with numerosity determined by the QUEST algorithm (Watson and Pelli, 1983), and with parameters initial numerosity = probe numerosity, standard deviation = 0.5 log-units; beta = 3.5; epsilon = 0.01; gamma = 0. To determine the numerosity of the next trial, the algorithm estimated the point of subjective equality (PSE) after each trial, then perturbed that with a random number drawn from a Gaussian distribution of standard deviation 0.15 log-units. At the end of each session, data were analyzed separately for each subject and condition. The proportions of trials where the test appeared more numerous than the probe was plotted against test numerosity and fitted with cumulative Gaussian functions like those of Figure. 2, yielding estimates of PSEs (median of psychometric function) and precision (standard deviation). Statistical testing was performed by bootstrapped sign test of the whole procedure that led to the particular measure. For example, to test whether adaptation had a significant effect in the single task condition at N = 6, we calculated for each subject the PSE in that condition with a sample of data (with replacement, equal to the number of trials), and computed the average across subjects. The same was done for the no-adaptation single-task condition. The process was reiterated 10 000 times, counting which was the higher average on each reiteration. The proportion of times when the non-adapted condition had a higher mean than the adapted condition is the significance value. For each subject there were two adaptation conditions, two attention conditions and 4 numerosities, yielding 16 conditions for each subject (with about sixty trials for each condition). The conditions were blocked into separate sessions, two sessions per condition, with order of conditions randomized between subjects. There was always a considerable pause (hours) between the adapted and non-adapted conditions to ensure that the effects did not carry over.

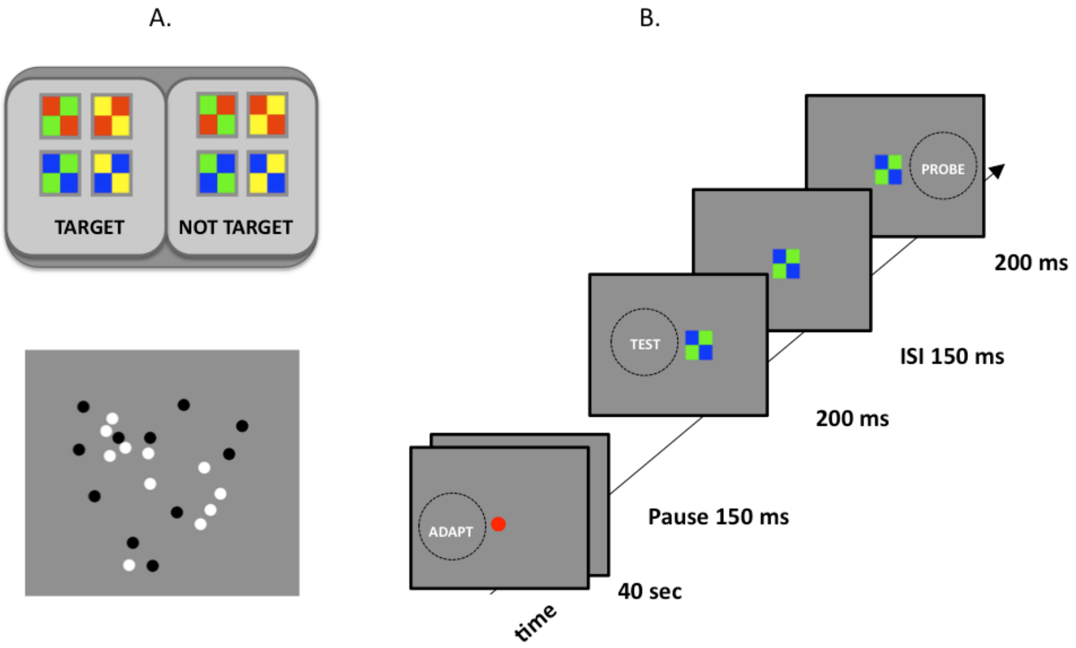

Figure 1. (A) Illustrations of primary (upper) and secondary (lower) stimuli. Primary stimuli were classed as targets if there were two green squares along the right-to-left diagonal *or* two yellow squares along the left-to-right diagonal. (B) Trial sequence: after adaptation (40 s on first trial, 6 s thereafter) to 200 dots, the *test*-stimulus was presented in the adapt region (200 ms); after 150 ms inter stimulus interval, the *probe* was displayed in the opposite field (200 ms). The colored squares remained on for 550 ms.

4.4 Results

Figure 2 shows sample psychometric functions for 1 subject, for three relevant conditions at two numerosities. At the highest numerosity measured (24 dots), the PSE in the no-adapt, single-task condition was 32, close to the veridical value of 24. After adaptation to 200 dots, 50 dots were required to match to 24, implying that the apparent numerosity of stimuli in the adapted region was greatly reduced. The result in the dual-task condition was also similar (54 dots). However, the pattern of results in for probe numerosity of three (subitizing range) was quite different. In the single-task condition, adaptation had only a weak effect (PSE = 3.8, compared with no-adapted PSE = 3.4), while in the dual-task condition the adaptation was as strong as for larger numerosities (PSE = 6.3). The results of all subjects are summarized in Fig. 3, both for the three individual subjects (symbols) and averages across subjects (bars). The ordinate reports the ratio of the PSE of the particular condition to that of the baseline for that numerosity (single-task, no adaptation). A value of one means that the adaptation and/or dual-task had no effect, greater than one means that the apparent numerosity of the test was *reduced* by that factor (so the test numerosity was increased to obtain the match). As the example psychometric functions of Fig. 2 show, attentional load affected adaptation in the subitizing range. In the single-task condition, adaptation affected perceived numerosity for large numerosities (Bootstrap t -test with: N (6) $p = 0.03$; N (12 and 24) $p < 0.01$), but very little effect where $N = 3$ ($p = 0.38$). However, under attentional load the effect of the adaptation increased considerably for low numbers to 40%, nearly as much as for the large numbers (50%). The effects of attentional-load by itself are shown by the black right-slanting bars. For low number ($n = 3$), the double-task by itself had very little effect, but at higher numerosities it caused a slight underestimation, by about 25% at $N = 24$. Figure 4 reports the geometric means of Weber Fraction against numerosity for all four conditions. Note that there are four rather than three conditions here, as the Weber fraction for the baseline is also shown. As previously reported, the strongest effects of attentional-load were in the subitizing range: there the Weber Fraction increases from 7% in the no-load condition to 16% in the double-task, while for the larger ranges it remains about in the order of 22–24% irrespective of attentional demand. The only significant effect of attentional load was in the subitizing range (see t -tests in figure caption), agreeing with our previous study (Burr, Turi, et al., 2010).

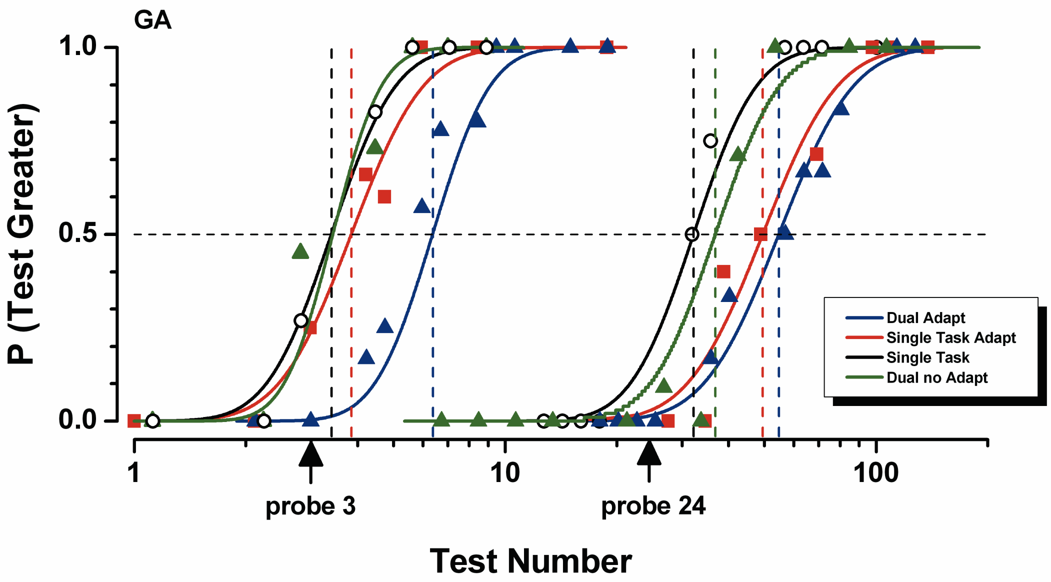

Figure 2. Example psychometric functions for subject GA for two numerosities (3 and 24) and four conditions. In all cases the proportion of times the subject reported the *test* to be more numerous than the probe (fixed at 3 or 24 dots) is plotted as a function of *test* number. The various conditions are indicated by the colors described in the legend. The effect of adaptation was far greater in the dual-task than in the single-task condition at low, but not high numerosities.

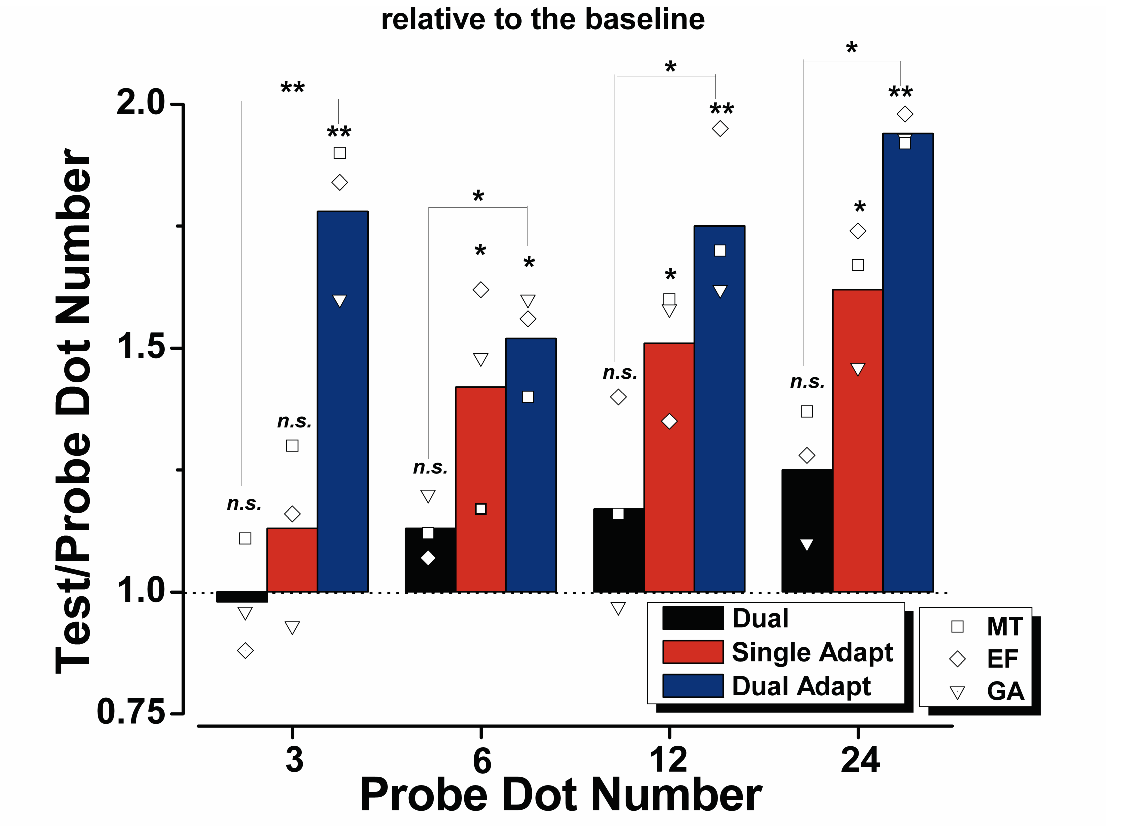

Figure 3. Effect of attention and adaptation on number estimation. Symbols report individual results (EF is the naïve subject); bars indicate averages of the three subjects. All data show the PSE for that particular condition divided by the PSE for the single-task, no adaptation condition at that numerosity. Values greater than unity mean that the perceived numerosity of the *test* is proportionally less than of the probe. (Color coding: right-slanting black — dual task, no adaptation; red left-slanting — adaptation, single-task; blue cross-hatched — adaptation, dual-task.) The values of all conditions were tested for statistical difference from 1 by bootstrap sign-test (see methods), and the result reported by the symbols above each bar: *n.s.* $p > 0.05$; $*$ $p < 0.05$; $**$ $p < 0.01$).

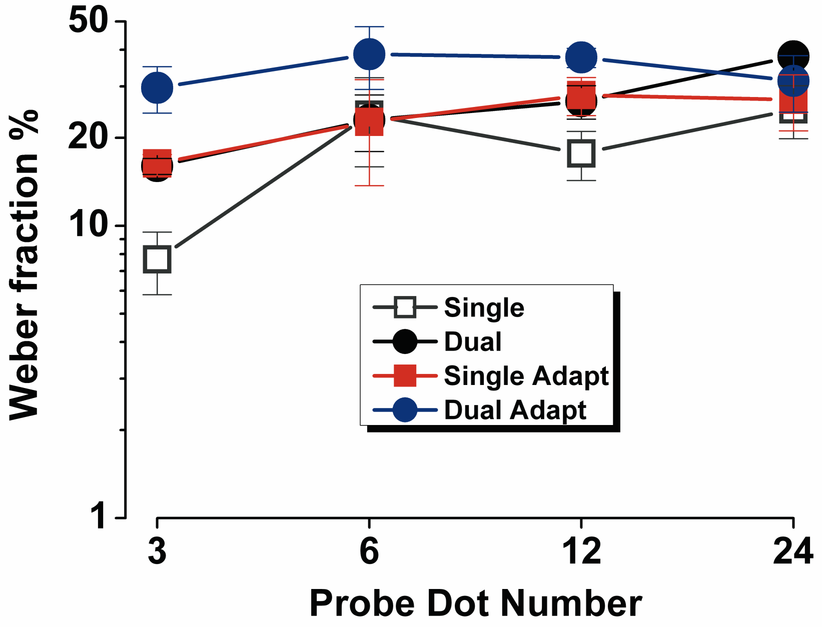

Figure 4. Mean Weber Fraction (*std/tested number*): color-coding as Fig. 3, with the single-task no adaptation condition shown by open symbols. The strongest effects of attentional load were for the low numbers. T-tests between single and dual (non-adapted conditions) revealed significant effects only for the smallest numerosity: N (3): t= 3.93, p= 0.017; N (6): t= 0.10, p= 0.92; N (12): t = 1.84, p = 0.14; N (24): t = 2.33, p = 0.09.

4.5 Discussion

In our previous study we presented evidence that subitizing depends strongly on attentional resources, whereas estimation of larger numbers was much less affected. We suggested that an estimation mechanism senses number directly over all ranges of numbers, but the low subitizing range benefit from an additional attention based mechanism. A direct prediction of this idea was that under conditions of high attentional load, the low subitizing range should also be strongly susceptible to visual adaptation. Our results verify this prediction, showing very strong effects of adaptation in the subitizing range in high-load, dual-task conditions, but very little in the single-task condition. Attention also affected adaptation of larger numbers, but the effects were much weaker. We also showed that precision was affected by attention more in the subitizing than estimation range, supporting our previous study (Burr, Turi, et al., 2010) and those of others (Egeth et al., 2008; Juan et al., 2000; Olivers & Watson, 2008; Railo et al., 2008; Vetter et al., 2008; Xu & Liu, 2008a). There is a long-standing debate regarding the possible existence of two neural systems for number processing — one precise and dedicated to numbers of items less than three/four and another one approximate system, dedicated to large sets (Feigenson et al., 2004). On the other hand, that the estimation mechanism operates over both large and small number ranges is consistent with fMRI studies suggesting that the two ranges share common mechanisms (Piazza et al., 2002). It is also con- sistent with more recent studies of neural correlates of visual enumeration under different attentional load (Vetter et al., 2010), showing that the temporal-parietal junction (rTPJ), an area implicated in stimulus-driven attention (Corbetta & Shulman, 2002), responds to small numbers only in conditions of low attentional load, suggesting that this area could be the neural substrate for the attention-assisted boost in number-naming performance in the subitizing range. Evoked potential studies in humans have also provided evidence for separate neural mechanisms for the subitizing and estimation ranges. For example, Hyde and Spelke (2009) all have demonstrated that an early (N1) component is modulated by absolute number with small, but not large, number arrays, while a later component (P2p) is modulated by the ratio between arrays for small but not large numbers. Most interestingly, under dual-task conditions, the late component P2p is also modulated by small, as well as large numbers (Hyde & Wood, 2011), suggesting that under these conditions, where the subitizing system is rendered ineffective, the estimation system continues to function, and dominates the evoked response. Single-unit physiology (Nieder et al., 2002) and behavioral data (Nieder & Miller, 2004a) of macaque monkeys also suggest that estimation mechanisms work over both large and small number ranges. Two classes of number neurons have been described in monkeys: neurons in areas IPS with overlapping log-normal tuning curves each tuned to a specific number (Nieder, 2005); and a different type of neuron in area LIP, which responds in a graded manner to number, some maximally to large numbers some to small (Roitman, Brannon, & Platt, 2007). These neurons have clearly defined receptive fields, and have been suggested as being the site of adaptation to numerosity. We (Burr, Turi, et al., 2010) have previously shown that attentional load affects the capacity to estimate number most in the subitizing range, causing resolution thresholds to increase to the levels of estimation of larger numbers. We suggested that this implicated the existence of two separate mechanisms: one working over the entire range of numerosity (including subitizing), assisted by an attentional-based sys-tem of subitizing that operated for small numbers, no more than about four. One system, subitizing, is an exact and robust system, highly resistant to change by processes such as adaptation. However, during very demanding dual-task conditions, the attentional-based subitizing system cannot operate, and even this range is subject to adaptation.

5. Number adaptation in Typical Children and Children with Autism Spectrum disorder

5.1 Abstract

As mentionated before, like most sensory systems, numerosity is susceptible to adaptation: apparent numerosity is decreased after adaptating to large numbers of dots, and increased after adaptating to small numbers. Here we investigated number adaptation in children with a diagnosis of autistic spectrum disorder (ASD) and typically developing children of similar age and ability. We asked children to discriminate between two numerosities with and without prior adaptation to numerosity, using a child-friendly technique. Children adapted to two patches of dots, containing 80 and 20 dots, presented to the two visual hemifields for 3 seconds. ASD children discriminated numerosity with the same precision as the typical children, but showed much less (about half) the levels of adaptation to number than the control group. This result is in line with recent findings showing weak adaptation to facial identity in ASD (Pellicano, Jeffery, Burr, & Rhodes, 2007). These new results show that adaptation, processes, fundamental for efficient processing of variable sensory inputs, is diminished in autism. Importantly, we show for the first time that this phenomenon is not unique to faces (which have a special significance in autism), but seems to occur more generally.

5.2 Introduction

As mentionated before in the introduction and showed in the previous experiment, numerosity is susceptible to adaptation like all primary sensory properties. In the current study, we examined whether children with autism show adaptation to numerosity. Autism is a neurodevelopmental condition characterised by a range of social difficulties, as well as non-social symptoms, including repetitive behaviours and restricted activities and unusual reactions to sensory input. These latter sensory sensitivities, which include hypersensitivities to sensory input, as well as hyposensitivities and sensory seeking behaviours, which have only recently been included in the diagnostic criteria for autism (American Psychiatric Association Arlington, 2013), represent some of the most puzzling features of the condition (Pellicano, 2013). There is renewed interest in these symptoms from researchers, prompted largely by the possibility that the sensory and other non-social symptoms of autism might be caused by fundamental differences in sensation and perception. We have suggested that atypicalities in adaptation, which is held to pose numerous functional advantages (Kohn, 2007), might be one such difference (Pellicano & Burr, 2012; Pellicano et al., 2007). Adaptation helps to improve neuronal efficiency by dynamically tuning its responses to match the distribution of stimuli to make maximal use out of the limited working range of the system (Barlow, 1990; Clifford et al., 2007; Webster MA, 2005). Any failure to continuously adapt to the current environment should also increase the transmission of redundant information, rendering one less able to distinguish irrelevant from relevant stimuli: which would have profound effects for how an individual might perceive and interpret incoming sensory information. Research has shown much empirical support for this hypothesis – at least for high-level social stimuli. Children with autism have been found to show diminished adaptation in the coding of facial identity (Pellicano et al., 2007) though see (Cook, Brewer, Shah, & Bird, 2014), in adults with autism), facial configuration (Ewing, Pellicano, & Rhodes, 2013) and eye-gaze direction (Pellicano, Rhodes, & Calder, 2013), while adults with autism have been found to present atypical adaptation to emotional categories (e.g., happy, sad; (Rutherford, Troubridge, & Walsh, 2012) but see also (Cook et al., 2014), for an account suggesting more general difficulties in the use of emotional labels). Adaptation to facial identity was also attenuated in relatives of children with autism compared with relatives of typical children, pointing towards the possibility of reduced adaptation as a potential endophenotype for autism (Fiorentini, Gray, Rhodes, Jeffery, & Pellicano, 2012). These findings suggest that individuals with autism show diminished adaptation for high-level stimuli, at least those with social relevance. Since adaptation is ubiquitous in perceptual systems, these findings further raise the possibility that a reduced ability to adapt flexibly to incoming sensory input might be pervasive in autism. In this study we test directly this hypothesis by measuring adaptation to numerosity in typical develop childred and children with ASD.

5.3 Methods

Stimuli were generated with the Psychophysics Toolbox (Brainard, 1997) and presented at a viewing distance of 57 cm on a 23” LCD Acer monitor (resolution = 1,920 × 1,080 pixels; refresh rate = 60 Hz; mean luminance = 60 cd/m^2), run by a Macintosh laptop.

Participants

We tested 15 high functioning children with autistic spectrum disorder (ASD), aged 7-14 (M age 10.30 years; SD = 2.18) and 14 age-and ability-matched (M age 11.2 years; SD = 2.32) typical developing children (TD) with no current or past medical or psychiatric diagnoses. None of the children had a diagnosis of any learning or attention disorder and all had both nonverbal intelligence in the normal range and normal visual acuity. All participants met Diagnostic and Statistical Manual of Mental Disorders, Fourth Edition (DSM-IV) criteria (American Psychiatric Association Arlington, 2013) for autism according to an independent clinician, and the Autism Diagnostic Interview - Revised, and were considered high-functioning. We formed a comparison group of 14 typically developing children, who were individually matched with children with autism in terms of chronological age, t(44)=0.23, p=0.82 and full-scale IQ, t(44)=0.49, p=0.63 (independent samples t-test, two tailed), as measured by the Wechsler Abbreviated Scales of Intelligence (Wisc-IV; Wechsler, 2003), see Table 1. All children were therefore considered to be cognitively able. Moreover all children obtained a total IQ score above 80. No child had a medical or developmental disorder other than ASD, not was on medication. Participants were tested individually in a quiet room either at home or at the university.

Table 1. Descriptive statistics for developmental variables for children with autism and typically developing children.

Measures	**Children with autism**	**Typically developing children**
Number	15	14
Gender (male : female)	12 : 3	9 : 5
Age (years)		
Mean (SD)	10.30 (2.18)	11.2 (2.32)
Range	7 - 14	7 - 14
Full-Scale IQ		
Mean (SD)	98.95(14.82)	101.45 (10.19)
ADOS score		
Mean (SD)	11.75 (3.6)	-
Range	7 - 18	-

Stimuli and Procedure

We measured children's judgements in numerosity discrimination with a child-friendly computer game in which to earn point the children were required to help an animated fish (Freddy) shown on the screen to find the most food. The game consisted of an initial Baseline phase, to measure participants initial Weber fraction and numerosity thresholds, followed by an adaptation phase where the changes in the perception that number adaptation elicited was examined. The two tasks were administered sequentially within a single session that lasted 15-20 min. The stimuli used throughout the experiment were two clouds of non-overlapping dots (diameter 10 arcmin), half white and half black at 90% contrast, covering 10° of visual angle, with all dots separated from one another by at least 0.10°. To encourage participants to maintain fixation in the center of the screen the fixation point was an animation of a fish which, during pauses in a trial, could jump, bounce, slide, or roll to attract attention..

On each trial two sets of stimulus pairs were shown: the first an adapting set and the second a test. At the begining of each trial, participants were asked to fixate upon the animation of the fish in the center of the screen. After 1000 ms, the adaptation set began (for 0.5 or 3s for Baseline phase or Adaptation Phase respectively) after which subjects were asked to indicate by which cloud of dots was more numerous ("Which side has the most food") using the arrow keys. In the Baseline phase the adaptation set consisted of a single 0.5s display of neutral numerosity stimuli consisting of 40 dots on each side (identical to the standard). Instead in the Adaptation set there were 6 consecutive 0.5s displays (lasting 3s in total) of 20 dots at one location and 80 dots in the other. After a fixed 1000 ms delay the second test set was shown for 500 ms and participants were asked to respond which side was the most numerous. In the test set the number of dots in the probe patch was varied according to the QUEST adaptive algorithm (Watson & Pelli, 1983), perturbed by a Gaussian jitter ($\sigma = 0.15$ log units) such that both patches were initially 40 dots (the test numerosity) and an inversly symetrical log change could be made for each of the two clouds in the set. This method of adapting one location to a high number, the other to a low number and then testing the percentage change in numerosity required in order for both locations to appear identical was found to be the most effective based on previous work (Aagten-Murphy D, 2011). The paradigm uses symetrical adaptation to a high (right) and low (left) numerosity adapter – however to make the psychometric curves more intuitive it is expressed as a function of the right patch (adaptation to high number with the adaptation to low number effect inverted and combined). The proportion of responses that the right hand side was greater or less than the left hand side was plotted against the number of the right hand patch relative to a 40 dot standard and fitted with a Gaussian error function. The median of this function estimates the point of subjective equality, and the standard deviation estimates the precision threshold (i.e., a just-noticeable difference), which was divided by point of subjective equality (a measure of perceived numerosity) to estimate the Weber fraction. A total of 50 trials were presented to children, in one session. Examiners monitored the children during this phase and ensured that children fixated on the centre of the screen.

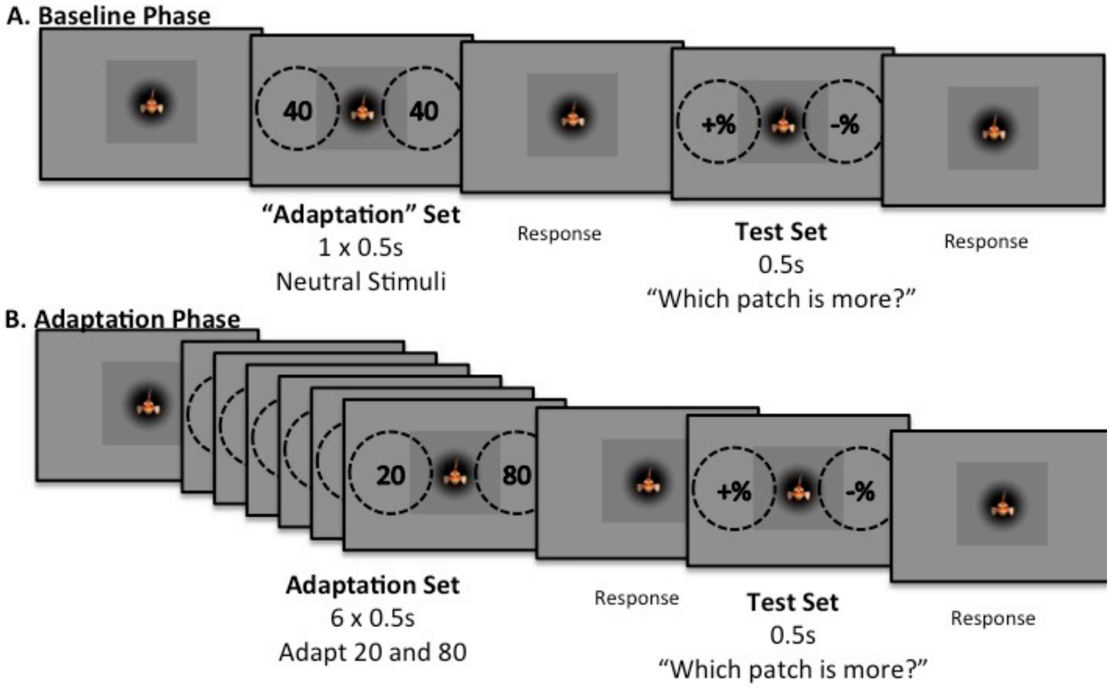

Figure 1. The paradigm used to measure the numerosity effect in children. Panel A shows the baseline phase, where subjects saw a single presentation of a neutral stimulus (with both sides equal to 40) followed by a 1000 ms pause, followed by test set, where the percentage difference from the 40 (the standard) between the left and right patch was varied in opposite directions on each trial and participants were required to respond

which patch was more numerous. Panel B shows the adaptation phase, which was identical to the Baseline Phase, however the adaptation set consisted of 6 brief presentations of a 20 and 80 dot adapter.

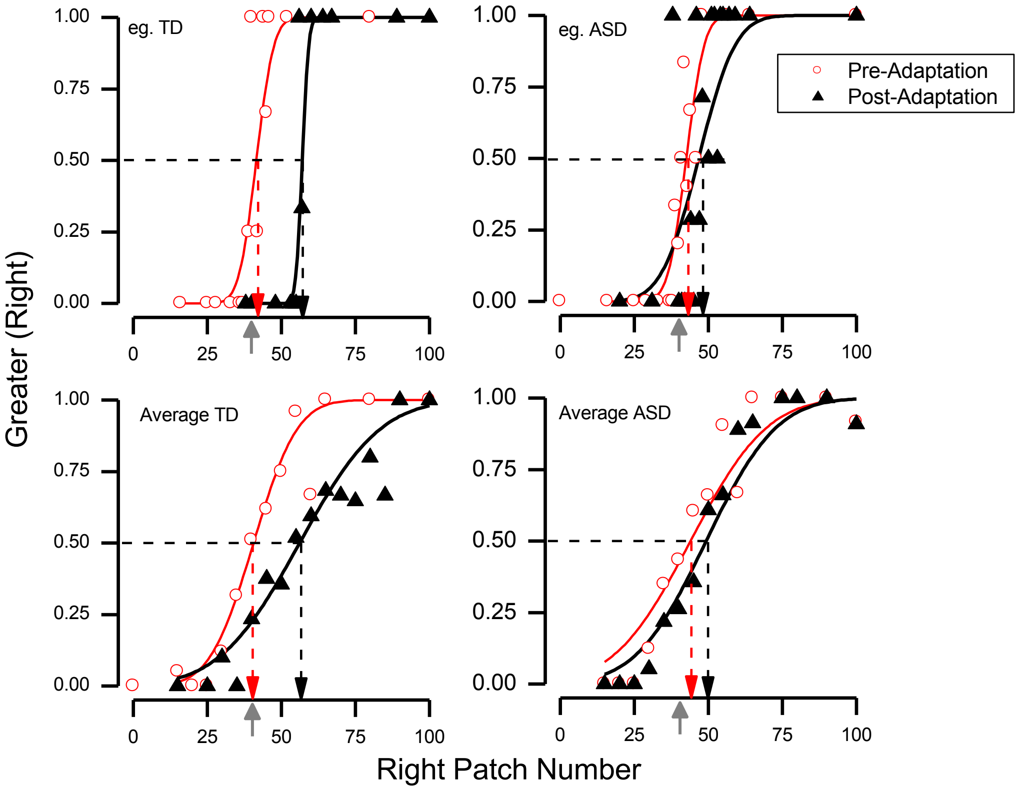

Figure 2. Sample Individual and Average Psychometrics Function. The top part of the panels shows example psychometric functions from one typically developing child (top left) and one child with ASD (top right) for the pre-adaptation baseline condition (close triangles) and for the adapting condition (open circles). The paradigm uses symetrical adaptation to a high (right) and low (left) numerosity adapter – however to make the psychometric curves more intuitive it is expressed as a function of the right patch (adaptation to high number with the adaptation to low number effect inverted and combined). Thus the x-axis represents the number of the right hand patch relative to a 40 dot standard (in grey) while the y-axis is the proportion of responses that the right hand side was greater or less than the left hand side. The bottom panels show data pooled over all TD children (left) and all children with ASD (right). If expressed as a function of the left patch (adaptation to low number) the black line would be displaced a proportionate distance from the red line in the other direction. The data are fitted with

two-parameter (mean and standard deviation) cumulative Gaussian functions, whose means estimate PSE and standard deviations estimate precision.

5.4 Results.

The proportion of responses where the right side was greater than the left side was plotted against the number of the right hand patch relative to a 40 dot standard and fitted with cumulative Gaussian functions whose mean estimates the point of subjective equality (PSE) and standard deviation the threshold for discriminating between the two (the just-noticeable difference [jnd]).

Figure 2 shows results for two representative children (top panels), and for the two groups, pooled across all children in each group (lower panels). The individual data were well fit by cumulative Gaussian functions (mean R^2 over all conditions= 0.94 ± 0.05 typical, 0.94 ± 0.04 autism group), and the fits for the pooled group data were excellent (all $R^2 > 0.95$). As previously reported in adults (Burr & Ross, 2008a), adaptation to numerosity caused probe appear less numerous. For example, for the typically developing child to perceive the two probe trials as being equal in numerosity they would need to be 48 and 32 for the adapted to high number and adapted to low number locations respectively. This is because, after adapting to high number, the patch of 48 dots at that location would be perceived with its numerosity such that is appears as 40 dots, while after adapting to low number, the patch of 32 dots at that location would be perceived to have an increase in numerosity such that it also appear 40.

It is clear from inspection of both the individual examples and group data (Figure 2) that the difference in the position of the psychometric functions after adaptation to numerosity is larger for typically developing children than it is for children with ASD. The position of the curves can be quantified by the point of subjective equality (PSE), defined as the mean of the cumulative Gaussian. We defined the adaptation aftereffect based on the PSEs in the pre-adaptation (PSEpre) and the post-adaptation (PSEpost) conditions as follows: 1- (PSEpre/PSEpost).

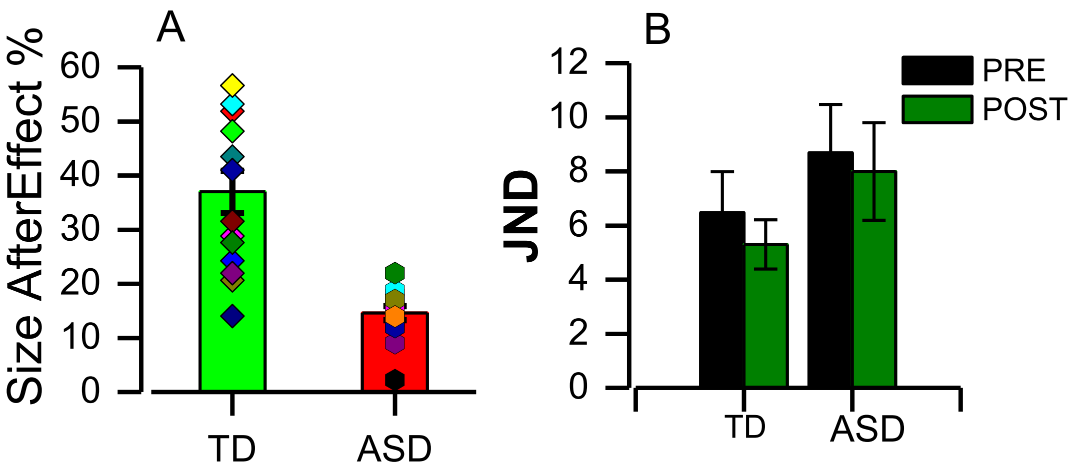

Figure 3. A) Size of the aftereffect for the groups of typically developing comparison children and children with ASD. The size of the aftereffect was defined as 1-(*PSEpre/PSEpost)*, where *PSEpre* and *PSEpost* were the PSEs in the baseline and adapted conditions, correspondingly. Error bars correspond to ± 1 SEM. B) Mean precision for discriminating numerosities (mean of standard deviations of the fitted psychometric curves) in the pre- and post-adaptation conditions for the group children with autism (left) and the group of typically developing comparison children (right). Error bars correspond to ± 1 SEM.

Figure 3A shows the magnitude of the aftereffect for children with autism (M = 37, SD = 3.9) and typically developing children (M = 14.6, SD = 1.3). Aftereffects were significant for both groups (*autism: t(11.14) p<0.001, typical: t(9.3) p<0.001*), in line with our prediction.

Importantly, however, there were significant group differences in the size of the aftereffect, t(5.51) p<0.001. Indeed, the aftereffect was significantly reduced for the ASD group t(5.30) p<0.00001, effect size, Cohen's d = 7.82]. The psychometric functions provide not only an estimate of PSE, but also of precision thresholds, given by the standard deviation of the cumulative Gaussian functions.

We therefore examined group differences in precision in discriminating number. Precision thresholds in the pre- (autism: M =8.68, SD =1.8; typical: M = 6.48, SD = 1.51) and post- (autism: M =8.00, SD =1.8; typical: M = 5.3, SD =0.91) adaptation conditions for the two groups of children are shown in Figure 3B. Precision thresholds did not differ for the ASD and control groups (F(1, 27) = 0.83, p = 0.37), indicating that the ASD group was as precise as was the typically developing group in discriminating number on this 2AFC task, in baseline and adaptation conditions.

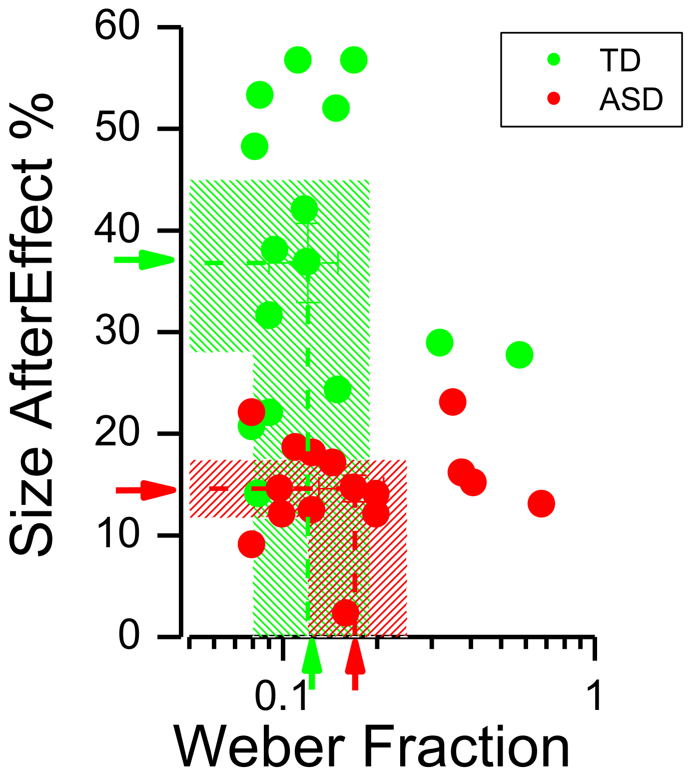

Figure 4. Scatter plot of Weber Fraction in post-adaptation (*std/tested number*) against size of the aftereffect (1-PsePre/PsePost). Arrow indicate the mean between the two groups and symblos indicated individual subjects. Weber Fraction is similar between typically developing comparison children and children with ASD, whereas the size of

the adaptation is different between the two groups.

Normalizing the standard deviation of the cumulative Guassian function, (that provide an estimate of response precision) by the PSE in that condition, we obtained an estimate of the Weber fraction, the standard parameter of precision performance that is often independent of magnitude. Figure 4 show individual results for both groups, plotting magnitude of the adaptation effect against Weber Fraction in Post-Adaptation condition. The graphs show clearly that children with autism and typical children have same precision in discriminating numerosities t(-0.94 p=0.329), but at the same time they have completely different magnitudes of adaptation. Similar precision thresholds for the two groups show that the reduced aftereffects in the ASD children cannot be attributed to poorer abilty in discrimination or task motivation. The magnitude of the aftereffect did not correlate significantly with chronological age, verbal ability, or nonverbal ability in either group of children ($p> 0.18$ in all cases).

5.5 Discussion

Previous studies on adaptation in autism have provided evidence for diminished adaptive coding of high-level (social) stimuli, including facial identity (Pellicano et al., 2007); see also (Fiorentini et al., 2012), for similar findings in relatives of children with autism), facial configuration (Ewing et al., 2013), and eye-gaze direction (Pellicano et al., 2013). Since adaptation is ubiquitous in perceptual systems, we reasoned that diminished adaptive coding might be pervasive in autism and extend beyond faces. To test this possibility, we developed a child-friendly task to examine adaptation to numerosity in children with autism and typically developing children of similar age and ability.

Numerosity is supported by a composite of different processes, including basic perceptual and high-level brain networks (e.g., temporal and parietal regions (Harvey, Klein, Petridou, & Dumoulin, 2013; Meaux, Taylor, Pang, Vara, & Batty, 2014);. Findings that numerosity is subject to adaptation (Burr & Ross, 2008a) are suggestive of a primary visual process, which is independent of mechanisms related to visual features, such as texture perception (Anobile, Cicchini, & Burr, 2014).

Our results indicate, that children with autism adapted to numerosity less than typical children. The fact that precision of discrimination was similar across groups suggests that the results do not reflect inattention in our participants. We also found that the two groups were indistinguishable in precision in discriminating numerosities. This is consistent with what foud by Pellicano et al. for faces (Pellicano et al., 2007). They show that children with autism were less adaptable to face-identity, but as precise as typically developing children of similar age and ability in identifying faces.

The fact that precision in estimating number is similar between autism and controls children is consistent with what found by Meux et al. (2014), who found that adults with autism made error in estimation number similarly to their matched control subjects for numerosities less than 100 dots.

However, among visuo-spatial investigations in ASD, numerosity estimation has been rarely assessed. There are a some reports of superior and highly specialized capacities. For example, Sacks (1985) described 26-year-old twins brothers with ASD (IQs 5 60) who spontaneously guessed the number of matches (111) dropped on the floor. Sacks (1985), and Smith (1983) reported the case of Zacharias Dase, who demonstrated the same ability, but for large quantities of peas (i.e., 79 and 183). How could they count so quickly? Questioned by the authors, these number prodigies indicated, as best they could, that they did not "work it out," but just "saw" their number, in a flash (Sacks, 1985), suggesting a possible link between numerosity estimation and perceptual processes. In the same vein, Soulieres et al. (2010) reported remarkable abilities in estimation for several quantifiable dimensions (rank, numerosity, time, weight, length, surface, distance) in two children with ASD at 9 years of age.

Our findings are also inconsistent with many prominent theories of autistic perception, such as the weak central coherence theory, which suggests reduced global processing in autism (Happe & Frith, 2006), and the enhanced perceptual functioning account (Mottron, Dawson, Soulieres, Hubert, & Burack, 2006), which posits that a local-processing bias leads to strengths in the processing of simple stimuli and to weaknesses in the processing of more complex stimuli. These two theories are similar in assuming difficulties in the integration of local sensory signals, which compromise the formation of global percepts in autism. Our paradigm therefore involved complex stimuli and relied upon global processing. The finding that children with autism were indistinguishable from typically developing children in terms of their precision in discriminating number challenges accounts assuming difficulties in the integration of local sensory input in autism – at least at low perceptual levels.

Our study clearly shows that adaptation to numerosity is attenuated in autism. This finding is consistent with a recent account proposed by Pellicano and Burr (2012). They proposed that Baysian models can be applied to autism, suggesting that attenuated Bayesian priors may be responsible for the unique perceptual experience of autistic people, leading to a tendency to perceive the world more accurately rather than modulated by prior experience.

General Discussion

In this thesis, the role of attention in visual enumeration was studied, with particular emphasis on the subitizing process, i.e. the judgement of small numerosities. Specifically, the hypothesis of a parallel and pre-attentive subitizing mechanism was tested as traditionally proposed in many enumeration studies (Dehaene & Cohen, 1994; Piazza, Giacomini, Le Bihan, & Dehaene, 2003; Sagi & Julesz, 1985; Sathian et al., 1999; Simon & Vaishnavi, 1996). Using psychophysical paradigms we have shown that attention is strictly related to many aspects of numerical cognition and that attentional manipulations can be used as a strong tool to reveal unexpected features of this ability. We started this work studying the nature and the possible dicotomy between the systems dedicated to the numerical estimation of low (<4, subitizing) and relatively high numbers (>4, estimation). We found that subitizing strongly depends on attentional resources, while estimation of larger quantities depend to a few lesser extent. Exactly the same results were found when the attentional resources dedicated to the visual numerical estimation task were limited to other sensory modalities: visual, auditory and also haptic attentional load strongly and similarly impaired visual subitizing but much less high numbers. Crucially, we found that under attentional load (visual, auditory or haptic), the sensory precision (Weber Fraction) with which we estimate quantities inside the subitizing range declines rapidly to approach that measured for number that exceed this range. We suggest that this implicates the existence of two separate mechanisms: one working over the entire range of numerosity (including subitizing), assisted by an attentional-based system of subitizing that operated for small numbers, no more than about four. In line with this we also demonstrated that visual adaptation to numerosity, absent in the subitizing range under normal condition, emerges under attentional load with a magnitude of the effect highly comparable to that measured for high numbers (>4). On the basis of these results, we advanced two ideas: Adaptable numerosity-estimation mechanisms operate over the entire range, with similar sensory precision, but at low numerosities these mechanisms are supplemented by attentional mechanisms, mechanisms that identify and enumerate very precisely, but have a very low capacity, around four items; Subitizing may reflect an amodal phenomenon, rather than a strictly visual one.

In the second part of this thesis we first demonstrate that the ability to accurately map numbers onto space also depends on attentional resources, showing that the assumption that performance on the ‘numberline task’ is the direct reflection of the internal numeric representation form could be misleading. We demonstrate that the non-linearity arises from a general perceptual principle: *central tendency*, observed in almost all sensory systems. This effect could be seen as a sort of running average between the stimuli, which leads to an overestimation of lower magnitude stimuli, and an underestimation of the higer, mirroring a compressed logarithmic response function. In brief, in this thesis we demonstrate that the estimation of small (subitizing) and large quantities are subserved by two different but overlapped systems and that subitizing reflect an amodal process. We showed that the ability to transform numbers onto spatial coordinates is a highly dynamic and attention-dependent system. Moreover, performance on the numberline task obeys the general perceptual principle of *central tendency* (observed in almost all sensory systems), and this effect explains completely the pattern of results previously differently interpreded. Finally, we found that ASD children discriminated numerosity with the same precision as the typical children, but showed much less (about half) adaptation to number than the control group. This result is in line with recent findings showing weak adaptation to facial identity in ASD (Pellicano et al., 2007). These new results show that adaptation, processes, fundamental for efficient processing of variable sensory inputs, is diminished in autism. Importantly, we show for the first time that this phenomenon is not unique to faces (which have a special significance in autism), but seems to occur more generally.

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