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Attentional mechanisms and representation of number

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Summary

The work presented in this thesis has explored attentional mechanisms and numerosity representations in visual estimation through a variety of methods. After a brief literature review, in chapter 2 I present a study of visual attention that demonstrates a clear example of how perception is influenced by past experience (Priming of Pop-out). Besides the classical measures of Reaction Times, I investigated whether attentional mechanisms can be measured with pupillometry measures. The results suggest that pupillometry may be a valid, non-invasive and fast tool to evaluate some cognitive and perceptual processes, particularly in clinical populations (such as ASD) when behavioral measures may fail. The focus of the thesis then shifts to investigate another capacity of the visual system: estimating number of objects in a visual scene. In Chapter 3 I investigated whether reaction times, which have classically been used to assess differences between very low and intermediate number, can be used to prove the existence of a third regime of number perception, that comes in to play when the items on the scene are too packed to be perceived independently. The results show that not only do thresholds change from intermediate to high densities, but reaction times also follow this pattern. In Chapter 4 I present a study showing how linking elements influence number perception at various ranges of numerosity. Contribution of both number and texture-density are examined. This study strengthens the idea that the Approximate Number System operates only when items are sparse enough to permit spatial segregation. After that limit, ANS gives way to another separate perceptual system responding to texture-density: for sparse stimuli, numerosity – but not element density – can be directly perceived, without being calculated indirectly from other perceptual features. In the fifth and sixth Chapter, I move back to attentional mechanisms, with particular interest in number estimation processes.

In the fifth chapter, the role of visual and auditory attentional resources on discrimination thresholds over all the three ranges (subitizing, estimation and texture-density) was investigated. Attentional load greatly affected the subitizing range, to the extent that thresholds became similar to those of the estimation range. More important, numerosities higher than 60-80 dots were more affected by attentional load (both visual and auditory) than lower (non-subitizing) numerosities. Following this, the last empirical chapter assessed the contribution of increasing attentional engagement, instead of decreasing it, on enumeration of numerosity. Here, we examined whether presentation of a visual cue that increased attentional engagement in a given task can facilitate the estimation process, leading to less compressive representation of number in space compared to when attention is diverted elsewhere. Results revealed that enumeration of a collection of dots in the location previously cued led to more precise and accurate (and linear) judgements than enumeration in uncued locations.

Overall, this thesis assessed the distinction between intermediate and large numerosity using reaction times, precision, linking elements, and attentional techniques. All studies point to the existence of separate regimes of number perception. Moreover, data on location and object-based attention may suggest that researches focusing on a mechanism that can improve rather than impair enumeration processes could prove helpful when considering rehabilitation in conditions such as dyscalculia. Finally, data on priming effects support an increasing body of evidence that pupillometry can be very useful in tracking perceptual processes, providing information that cannot be gathered from standard psychophysics. Likewise, it would seem that these pupillometry measures may be more sensitive to variations in perceptual styles, and their dependency on personality traits.

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Publications

Parts of this thesis have been included in the following peer-reviewed journal publications.

Experiment in Chapter 2 was included in the following paper, that is currently under review. Analysis, data collection and writing were conducted by myself with editing for publication by supervisors:

Pomè, A., Binda, P., Cicchini, G.M., Burr. D.C. (2019) Perceptual expectancy is revealed by pupillometry and correlates with autistic traits. Journal of Vision. Under review

Experiment in Chapter 3 was included in the following publication. Analysis, data collection and writing were conducted by myself with editing for publication by supervisors:

Pomè, A., Anobile, G., Cicchini, G. M., & Burr, D.C. (2019). Different reaction-times for subitizing, estimation, and texture. Journal of Vision, 19(6), 14. https://doi.org/10.1167/19.6.14

Experiment in Chapter 4 was included in the following publication. Data collection and analyses were conducted by myself. Anobile and Cicchini wrote the research paper with comments and editing provided by myself:

Anobile, G., Cicchini, G. M., **Pomè, A.,** & Burr, D. C. (2017). Connecting visual objects reduces perceived numerosity and density for sparse but not dense patterns. Journal of Numerical Cognition, 3, 133–146.

Experiment in Chapter 5 was included in the following publication. Analysis, data collection and writing were conducted by myself with editing for publication by supervisors:

Pomè, A., Anobile, G., Cicchini, G. M., & Burr, D.C. (2019). Higher attentional costs for numerosity estimation at high densities. Attention, Perception & Psychophysics, 1-8.

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Declaration

I, the author, declare that the work presented in this thesis is my own and has not been submitted for a degree at any other institution.

Chapter 1

Introduction

1.1 Attentional mechanisms

Many tasks in daily life require visual search - that is, searching for a target amongst non-target items. There are many factors that can influence where one’s attention is drawn first in a scene when conducting such a search. Imagine you are going for an exam in a building you have never been before, your current goal is to find the room in which your exam will take place, so you won’t be late. While you are searching for the room, the fire alarm goes off and you are asked to evacuate the building. You momentarily forget about searching for your exam room and shift your search to move towards the nearest exit. In this example, the fire alarm captured your attention, even though you had different goals in mind; however, as soon as it is safe to go back into the building, and the salient irrelevant fire alarm cue is gone, you will resume your attentional focus on searching for your exam room.

How does visual attention guide us toward the fire alarm? Do we unconsciously orient to such salient stimuli in that particular moment? Or, is our attention shifted toward the salient cue, while still maintaining our initial goals?

Researchers have long debated whether attentional control is dominated by goal-driven processing, where we orient toward a known feature or quality (e.g., searching for the exam room), or if attentional control is dominated by stimulus-driven processing, where we orient to the most salient, or noticeable item in the display (e.g. the fire alarm). Visual salience can be thought of as distinct perceptual qualities that make some stimuli stand out from other stimuli in our environment, orienting our attention towards them. Another distinction in the attention literature is that attention can be either location-based, in which items are selected based on their spatial position, or object-based, in which items are selected based on shape properties. Moreover, unconscious biases that guide visual attention has been reported.

For the aim of this dissertation, the focus of the next two paragraphs will be on the processes that guide our visual attention to a particular object or location and to the unconscious effects that a recent stimulus has on altering the current perception (Árni & Campana, 2010).

1.1.1 Object based and location-based attention

Beyond these bottom-up and top-down control parameters, attentional control also involves different forms of attentional selection. A natural scene usually contains a vast amount of information. Dealing with different information at the same time can be very demanding, because of the limited processing capacity of the visual system. Attention serves as first step in order to allocate optimally resources for better use, depending on the most informative stimulus in that particular moment: for example, when looking for the bathroom in a restaurant, location information is more relevant; or looking for your friend in a crowded party benefits from object information. Location-based and object-based attentional control settings are likely to coexist and operate in different situations. A common way to measure the contributions of object and location-based attention is to use a cueing paradigm (Egly, Driver, & Rafal, 1994). (Figure 1.1)

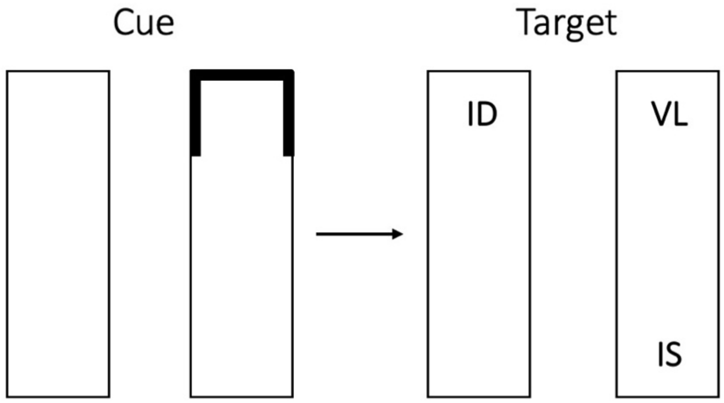

Figure 1.1 Sample displays from Egly et al. (1994). After a brief cue, a target is presented in one of three possible locations: the location of the target is represented here by VL for valid location trials, IS for invalid same-object trials, and ID for invalid different-object trials. Responses were faster on valid than on invalid trials and on invalid same-object than on invalid different-object trials.

In this paradigm a double rectangle display is shown, with one end of one rectangle brightened briefly, cuing the observer to direct attention to a specific location while maintaining fixation. After a delay, a target (solid square at one end of one rectangle) is presented in the location previously occupied by the cue (a validly cued location), or in the opposite end of the cued rectangle (an invalid same-object location), or in the other rectangle (an invalid different-object location) at the same distance from the cue as the invalid same-object location.

Reaction times (RT) for detecting the presence of the target are measured. This paradigm yields two main findings: a *spatial cueing effect*, shorter RT for items presented at the validly cued location than at the uncued locations; and a *same-object advantage*, shorter RT for target appearing at the uncued end of the cued rectangle rather than at the uncued reactangle, with an equal spatial distance between the cued location and the target. This latter finding reflect the fact that other dimensions of the object are facilitated just by being part of the cued object.

The mechanisms underlying the same-object advantage are still unknown. Shomstein and Yantis (2010; 2004) proposed two mechanisms that might give rise to an object-based advantage. The first mechanism states that this effect emerges because the attentional cue serves as a top down signal that guides attention and enhances the sensory representation at the attended object. So that attention spreads to other features or locations that are bound by the object, given the enhanced activation for a part of the object. A second proposed mechanism is that there is a predisposition to assign higher priority to locations of high importance (e.g., cued locations) and to within the attended object than to location elsewhere (see also Drummond & Shomstein, 2010). In this attentional prioritization view, unattended parts of an attended object will enjoy an attentional advantage over other objects and locations in a scene (Müller & Kleinschmidt, 2003). The results of the double display cueing paradigm are overall robust and have been extended to a series of studies using various stimuli, demonstrating both the spatial cueing effect and the same object advantage (Chou, Yeh, & Chen, 2014; Moore, Yantis, & Vaughan, 1998; Shomstein & Behrmann, 2008). However, as far as we know, all the studies assessing the contribution of object and location-based attention have used detection or discrimination task (i.e. Brawn & Snowden, 2000; Shomstein & Behrmann, 2008).

In Chapter 6, I will show the contribution of both object-based and location-based attention on higher level information, such as number estimation.

1.1.2 Unconscious biases: priming of pop-out

As discussed above, various types of guidance drive selective attention in a search. However, such guidance is not limited just to attributes of the stimuli or obligatory task demands stemming from the current trial or to the most informative location or object; indeed, it has been known for some time that repeated exposure to a stimulus feature can influence where attention is allocated in a visual scene, that is that past experience may also modulate the current selection. Sometimes, the guidance of past experience is not temporally confined to any one particular moment in the search. For example, in a series of trials of singleton search, performance on the current trial was significantly facilitated by recent responses (Maljkovic & Nakayama, 1994, 1996, 2000). In their seminal study, Maljkovic and Nakayama (1994) had participants identify the shape of a singleton target stimulus defined as the one different in color: repeating target color across trials led to a speeding of responses (Figure 1.2).

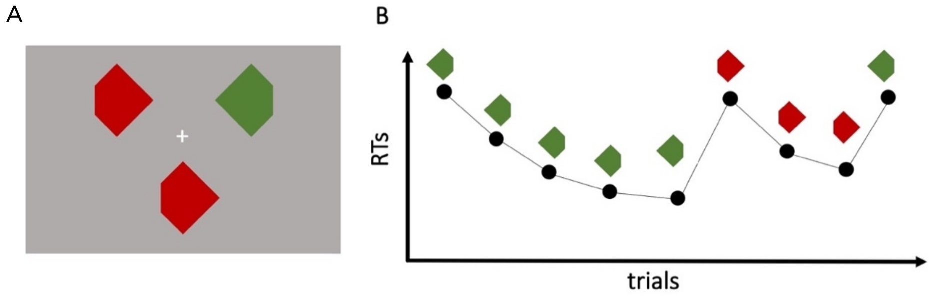

Figure 1.2 An example of Priming of pop-out. (A) Visual search task in which the odd colored diamond is to be found and the task is to indicate whether it has a notch on the left or on the right side (paradigm based on (Maljkovic & Nakayama, 1994). **(B)** Illustration of reaction time curve as the target color is repeated across consecutive trials or when the target color changes (simulated data).

A series of studies has delineated several characteristics of Priming of Pop-out. First, the duration of Priming of Pop-out is relatively short, five to eight trials (Maljkovic & Nakayama, 1994, 1996, 2000), unlike other memory effects induced by past experience (i.e. semantic priming, Squire, Shimamura, & Graft, 1987). According to Maljkovic and Nakayama (1994), the memory trace of a target feature lasts for only five to eight trials, or 15 to 30 seconds. And the advantages for RTs of presenting the same color for more than once led Maljkovic and Nakayama to propose that Priming of Pop-out may rely on a type of short-lived memory, and this short-lived memory must be different from the long-lasting memory responsible for traditional priming effects. The second characteristic of Priming of Pop-out is that it does not rely on explicit, voluntary control. In one experiment, Maljkovic and Nakayama (1994) tested whether explicitly knowing the identity of the upcoming target facilitated a search. In one block, the target color stayed the same without exception, enabling participants to anticipate the color of the target in the next trial. In another block, the target color alternated between two colors on every trial, so participants were still able to predict the color of an upcoming trial. Contrasting with those two conditions, there was a block where the target color was determined with complete randomness (i.e. 50% chance of switch). If Priming of Pop-out occurs based on explicit predictability, search would be facilitated when participants had perfect knowledge of the upcoming target color. That is, RTs should be faster when the target color either always stayed the same, or regularly alternated from one to another, than when the target's color switched at random. In contrast to predictions, however, results of the study showed that the RTs of trials with the predictable color switch (i.e. 100% alternation) were slower than the RTs of trials with a single color (i.e. 100% stay). Between these two extremes, RTs increased linearly as the number of alternations increased. In sum, Priming of Pop-out was not affected by the predictability of the target color in the next trial, indicating that Priming of Pop-out is immune to the observer's explicit knowledge or expectations, and rather is solely driven by the repetition or switch of the target color. Right now, the idea that Priming of Pop-out is a completely unconscious bias is not completely shared, leading to some theories that argues for multiple sources of priming: both bottom-up (Huang, Holcombe, & Pashler, 2004; Maljkovic & Nakayama, 1994, 1996, 2000; Meeter & Olivers, 2006), accounting for Priming of Pop-out as the result of stimulus-driven, automatic, and implicit attentional control; and top-down (Fecteau, 2007; Folk, Remington, & Johnston, 1992), emphasizing the role of goal-driven and voluntary attentional control.

1.1.3 Pupillometry correlates of attention modulation

Besides from behavioral measures of Reaction Times and accuracy, it has been demonstrated that attentional modulations can also be measured without relying of participants responses. Recent data suggests that spatial extent of attention is reflected in brain activity, both measuring event related potentials (Shioiri, Honjyo, Kashiwase, Matsumiya, & Kuriki, 2016), single-voxel fMRI (Puckett & Deyoe, 2015); as well as eye-movements measurements (Eckstein, Guerra-Carrillo, Miller Singley, & Bunge, 2017).

The saccadic and smooth-pursuit eye movements that control gaze direction have been extensively studied (e.g. Kowler, 2011). Since the limited capacity of our visual system (it is impossible to focus on every object in the field), we need to select which object to attend. Once our attention has been directed at an object of interest, our eyes continue to move to locations of interest to retrieve information and provide a stable image of the object: the curvature of the lens accommodates to control focus; and pupils dilate or constrict to control how much light enters the eye.

For the purpose of this dissertation, I will focus on pupil response. The pupil responds primarily to changes in light (the pupil light response, or PLR), to near fixation (the pupil near response, or

PNR); and to increases cognitive activity, such as increased levels of arousal or mental effort, cognitive and emotional load, and reaction to the unexpected (Binda, Pereverzeva, & Murray, 2014; Bradley, Miccoli, Escrig, & Lang, 2008; Chiew & Braver, 2014; Lavín, San Martín, & Rosales Jubal, 2014; Preuschoff, 't Hart, & Einhäuser, 2011; Renninger, Carney, Privitera, Klein, & Aguilar, 2010). Moreover, recent evidence suggests that pupil dilation may be particularly correlated to the demands on sustained attention (Hopstaken, van der Linden, Bakker, & Kompier, 2015; Sarter, Givens, & Bruno, 2001). Non-luminance mediated pupil response has been suggested to provide an index of the locus coeruleus–norepinephrine (LC-NE) neuromodulatory system, which is thought to be important for regulating attentional resources to maintain alertness and task engagement in a variety of situations (Aston-Jones & Cohen, 2005; Gilzenrat, Nieuwenhuis, Jepma, & Cohen, 2010; Murphy, Robertson, Balsters, & O'connell, 2011; Sara, 2009). A great deal of recent research suggests that there is an inverted-U relationship between LC tonic activity and performance on various cognitive tasks, consistent with the Yerkes & Dodson (1908) curve. Specifically, it is assumed that when tonic LC activity is low, individuals are inattentive and non-alert, leading to poor behavioral performance. As tonic LC activity increases to an intermediate range (phasic mode), attention becomes more focused and behavioral performance becomes optimal. However, as tonic LC activity increases further, the individual experiences a more distractible attentional state, leading to task disengagement (tonic mode) and a reduction in behavioral performance. In accord with these ideas, prior research has consistently shown that under conditions of low levels of alertness (or inattention), the baseline pupil diameter is smaller and more variable than when one is alert (Morad, Lemberg, Yofe, & Dagan, 2000). The LC is thought to be an essential area within the neural system which also controls the muscles in the iris (Laeng, Sirois, & Gredebäck, 2012). This relationship provides a way for researchers to observe changes within the LC through pupil dilation, an externally measurable response to internal LC activation. Thus, this LC-NE-pupil connection means researchers can measure pupil diameter in order to observe shifts in attention. This is supported by decades of studies which have shown that pupil diameter is directly correlated with changes in LC neurons (Laeng et al., 2012; J. Rajkowski, Kubiak, & Aston-Jones, 1993; Janusz Rajkowski, Majczynski, Clayton, & Aston-Jones, 2004). Even before the LC-pupil connection was established, Hay & Sokolov (1966) indicated that pupil dilation was a component of attention orienting to novel stimuli. During phasic LC activity there are large pupillary increases. Particularly salient stimuli also cause pupil dilation (Laeng et al., 2012). Rajkowski et al. (1993) also showed the link between the LC-NE system and pupillary responses in non-human primates. Additionally, Einhäuser, Stout, Koch, & Carter

(2008) used bistable images (two different percepts within one image) to observe pupillary changes alongside shifts in perception. Asking subjects to press a button at the time of perceptual switching revealed that pupil diameter increased significantly around 100 ms before the perceptual shift and the larger the pupil diameter at this time, the more stable the perception subsequently (Einhäuser et al., 2008). This demonstrates the role of pupillary responses in attentional shifting and recognition of relevant events.

In sum, pupillometry can be a useful tool in cognitive neuroscience research because it is a measure of preconscious processing and cognitive events. In addition, it is non-invasive and relatively inexpensive. It is especially useful in nonverbal populations such as infants or severely developmentally disabled patients, since it does not require conscious, verbal response. Finally, it is also especially useful when studying patients with autism given that it is minimally stimulating and thus is not likely to cause anxiety and the resulting potentially interfering brain signals (as opposed to loud, confined machines as in functional magnetic resonance imaging (fMRI), or novel physical sensations such as electroencephalography (EEG)).

In Chapter 2, I will elucidate more in detail how attention, in particular shifts in attention by repeating or switching the target features, can be measured by pupillometry and whether pupillometry can show differences in personality traits when behavioral measures may fail.

1.2 Number representation

When faced with a scene dense with information, the visual system tends to group all the kind of redundant information and to perceive them in the form of summary statistics. So that if we are at the market, we can rapidly make judgments on the face expression of the cashiers, or on the average color of strawberries, or on the size of the baguettes. Moreover, it seems adaptative for us to choose the line with less people waiting, hence we can rapidly estimate how many people are in the line or making a judgment on which of the two lines is less numerous.

That is a clear example of the "Approximate Number Estimation", our ability to produce raw estimates of the quantity of a collection of objects, without counting. Although humans are the only species with a linguistically mediated code for numbers, we share an approximate, nonverbal representation of number with many animal species and with young infants (Dehaene, 2011; Nieder, 2005, 2013;

Whalen, Gallistel, & Gelman, 1999; Xu, Spelke, & Goddard, 2005). The evolutionary advantage of this capacity is obvious, allowing animals to choose zones with more food, and quickly determine which group of competitors is more numerous. However, the mechanisms underlying number perception are still highly debated. Estimation of the number of items extends over a wide range, from a few units to hundreds of items. Much evidence shows that numerical estimation is subserved by two separate systems: one fast and errorless, handling very few items (usually up to four) termed subitizing (Jevons, 1871; Kaufman & Lord, 1949); the other slower and error-prone, estimating higher numerosities, often termed the Approximate Number System (Butterworth, 2011; Feigenson, Dehaene, & Spelke, 2004; Gallistel & Gelman, 1992). However, numerosity seems to be intrinsically correlated with many other physical features. For example, if we continuously keep increasing the amount of food in our bag at the market, we change not only the number of items we are going to buy but also decrease the distance between them, increase the total cover area and also the density (numbers of items/area). It seems thus plausible that numerosity is not sensed as such, but indirectly via other features of the object.

Does it mean that numerosity does not exist as a primary visual perceptual attribute and can just be inferred indirectly? In the next paragraph I will show evidence for separate (but sometimes overlapping) regimes of number perception, depending on the quantity of items presented on a scene (from very few and segregable quantities to very dense and packed one). I will review some milestone studies on the debate between intermediate and large numbers with particular interests on the mechanisms and the techniques used to distinguish between them.

1.2.1 Evidence for three systems of number perception

It is now well known that enumeration of very small numbers is fast and errorless (Kaufman & Lord, 1949), while representing ensemble of larger quantities come at a cost: ensemble representations of numerosity are slower and imprecise (Alvarez & Oliva, 2008; Feigenson et al., 2004). Although this dichotomy seems to be nowadays a sharable thought, the idea of a sense of number outside the subitizing regimes is not commonly shared. Considerable evidence has accumulated to reinforce the idea that number is encoded directly at moderate densities. For example, Stoianov & Zorzi (2012) have shown that number (rather than density) emerges spontaneously within an unsupervised learning algorithm. If numerosity was a sensory by-product of density and area, as suggested by several research groups (Dakin, Tibber, Greenwood, Kingdom, & Morgan, 2011; Durgin, 2008; Morgan, Raphael, Tibber, & Dakin, 2014; Tibber, Greenwood, & Dakin, 2012) sensitivity for numerosity should be predictable from the independent measures of area and density. A recent study directly tested this hypothesis and showed that when subjects discriminate items varying in the space spanned by number, density and area, discrimination thresholds are far lower for number than for density of area, suggesting that number rather than density is sensed spontaneously (Cicchini, Anobile, & Burr, 2016). When subjects were specifically asked to make numerosity, density and area judgments in a range of sparse stimuli varying in all three dimensions, all three dimensions interacted with each other. However, number had a much stronger effect on density and area than vice versa. Density judgements were biased towards numerosity by about 78% and area by 53%, whereas number judgements were biased towards area by only 15%. This is consistent with several studies that showed small biases of numerosity estimates towards area (DeWind, Adams, Platt, & Brannon, 2015; Gebuis & Reynvoet, 2012a, 2012b), but stronger effects of numerosity on area judgements (Hurewitz, Gelman, & Schnitzer, 2006; Nys & Content, 2012) and density judgments (Dakin et al., 2011). Importantly, the selective sensitivity for numerosity over density is far less pronounced with dense stimuli, where the results are consistent with independent analyses of density and area (Cicchini et al., 2016).This is supported by several other studies showing clear differences in the psychophysical laws governing visibility at high and low densities of dot patterns (Anobile, Turi, Cicchini, & Burr, 2015; Anobile, Cicchini, & Burr, 2014;Cicchini et al., 2016), leading to the suggestion of two different regimes of analysis (Anobile, Cicchini, & Burr, 2016).

A particularly clear demonstration that numerosity mechanisms need not to involve texture density is the cross- modal and cross-format adaptation study of Arrighi, Togoli, & Burr (2014). Adaptation is one of the clearest signatures of the existence of a dedicated system for the encoding of a particular feature (Clifford & Rhodes, 2005; Mollon, 1974; Thompson & Burr, 2009). This widely used method involves the quantitative measurement of the perceptual distortion caused by the previous exposure to a given stimulus. For example, inspecting for a few seconds the downward motion of a waterfall (adapter stimulus), the surrounding rocks will be perceived as moving upwards. This is the signature of a neural system dedicated to those motion directions. Numerosity is also susceptible to adaptation: viewing large numbers of dots for a few seconds (adapter stimulus) makes subsequent smaller groups of dots seem to contain fewer dots than they actually do (Burr, Anobile, & Turi, 2011; Burr & Ross, 2008; Schwiedrzik, Bernstein, & Melloni, 2016). Recently, Arrighi et al. (2014) extended the technique to demonstrate adaptation to temporal numerosity sequences: adapting to a sequence of tones for few seconds changed the apparent numerosity of subsequent streams of visual flashes, and vice-versa, even though no texture was involved (as stimuli were temporarily defined). Importantly, adapting to a series of flashes changes the apparent numerosity of dot arrays: again, there was no texture in the adaptor, yet a spatial pattern seemed to contain fewer dots. They have further extended the technique to show that action adaptation can change numerosity. After tapping for a period of time (either rapidly or slowly), the apparent numerosity of a sequence of flashes and of a dot array was strongly changed, in the opposite direction to the tapping speed (Anobile, Arrighi, Togoli, & Burr, 2016). All these adaptation effects are difficult to reconcile with the notion that numerosity is a surrogate of texture-density.

The main idea here is that three different regimes in number perception may exist. Beside the well know phenomenon of subitizing (up to four items), there is a range where items are discernable as unique from each other (the ANS). But what happens if we keep increasing the amount of item on the scene? It is likely to think that when the ensembles become too crowded, another system seems to come into play, encoding texture-density. Most of the psychophysical evidence from the idea of a third regime of number perception comes from simple measurements of Weber fractions—the minimal detectable change in numerosity, normalized by point of subjective equality—over a large range of numerosities and densities (Anobile et al., 2014). Although it is commonly assumed that Weber fractions for numerosity are constant (Dehaene, 2011; Ross, 2003; Whalen et al., 1999), when carefully measured over a wide range, it is clear that this is not strictly true. Weber's law holds for a while, then after a critical point, Weber fractions decrease at a rate proportional to the square root of numerosity. The critical numerosity is lower for smaller than for larger patches, corresponding to a critical density of about 0.3 dots deg^2: for example, 30 dots within 10 x 10 deg^2. When the experiments are repeated with test and probe patches of different sizes (so numerosity is not directly proportional to density), these predictions hold over an even wider range, extending past the boundary. These experiments with stimuli of mismatched area suggest that the two regimes are not mutually exclusive but overlap considerably. When the areas are matched and density can be used as a proxy for number, or vice versa, the more sensitive prevails (Figure 1.3).

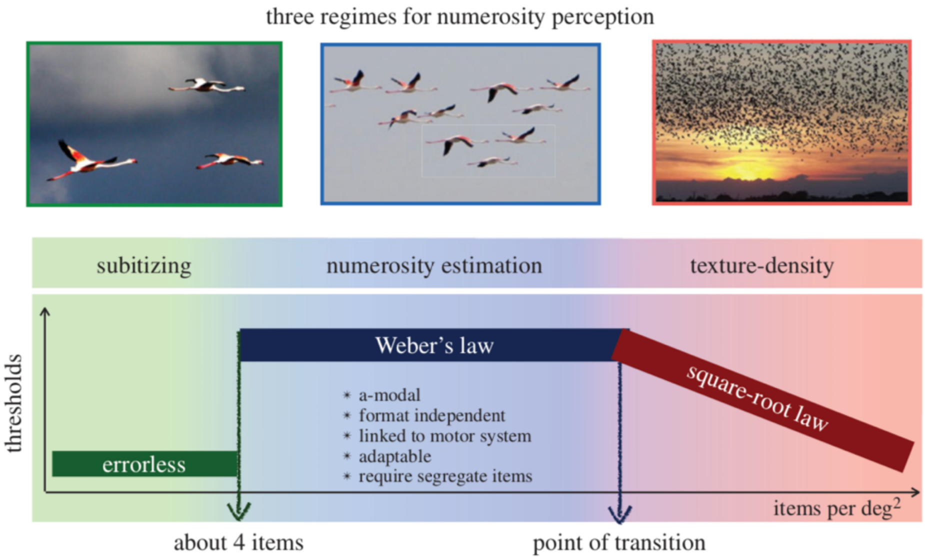

Figure 1.3 Illustration of the three regimes of numerosity perception: subitizing, estimation and texture. Reproduced with permission from Anobile et al. (2016).

The aim of some of the next chapters will be to show evidence of distinct mechanisms of perception of large quantities, using the classical psychophysical methods: reaction times and precision (Chapter 3); linking elements (Chapter 4); and attentional mechanisms (Chapter 5).

1.3 Aim and overview of the thesis

In this thesis, I aim to explore the attentional mechanisms underlying the selection of the targeted object to attend in a visual scene, while also assessing number perception over a wide range of numerosities through a variety of methods. After exploring the unconscious bias of attentional mechanisms, with particular interest in pupillometry measures and their correlates with autistic traits, a large part of the focus will be on the visual perception of quantities spanning from few to many items. The main questions here are: can the classic measures of numerosity perception for low and intermediate numbers explain the differences between segregable and very dense patterns? Moreover, can attentional mechanisms, apart from low level visual features, investigate the relationship between intermediate and large numbers? Finally, I ask whether there is a different type of number representation when people estimate numerosities when an enhancement (instead of deprivation) of attention is adopted.

In the first empirical chapter, I present a study of visual attention that demonstrates a clear example of how perception is influenced by past experience. I focused on the pioneering works of Maljkovich and Nakayama (1994), in which an automatic bias in visual selection is explored: repeating a target feature unconsciously speeds responses. Besides the classical measures of Reaction Times, I moved forward in order to investigate whether this attentional mechanism can be measured without relying on participants' responses, such as with pupillometry measures. Since pupillometry has been demonstrated to be a powerful tool in evaluating the role of past experience on perception, I measured pupil size of my sample while they were performing the behavioral task. Moreover, as visual attention is influenced also by individual differences and according to the fact that pupillometry can reveal personality traits of individuals, I analyzed the effect of repeating or switching a target feature with particular interest on low and high autistic personality traits (measured by the AQ questionnaire). I hypothesized that pupillometry could reveal individual differences and based on the suggestion that autism spectrum disorders are associated with weak or less adaptable priors (Pellicano & Burr, 2012), participants with high autistic traits would rely less on past experience and hence show a lower priming effect, compared to the low autistic traits subsample (this chapter is currently under review on Journal of Vision).

After presenting evidence of pupillometry being a powerful and relative recent tool to investigate the visual system's ability to allocate and shift attention during a Priming of Pop-out task, the focus of the thesis is shifted to investigate another capacity of the visual system: extracting measurements from a visual scene. In particular the focus of the next chapters will be on presenting evidence in favor of the hypothesis that number is a primary visual perceptual attribute, sensed directly and not inferred from other feature of the objects, with a particular look into the dichotomy between intermediate and large numerosities. In fact, in the second empirical chapter I investigated whether the classical measures of number perception, usually used to assess differences between very low and larger number, can be used to prove the existence of a third regime of number perception, that comes in to play when the items on the scene are too packed to be perceived independently. In this chapter, I measured participants' reaction times and precision over a wide range of numerosities at two different eccentricities. Are reaction times and precision different from estimation and texture-density? Is the shift between the two regimes depending on eccentricities? (this chapter is published in Journal of Vision). In the third empirical chapter, I present a study of how manipulation of the spatial arrangement of the element in the scene influences number perception at various ranges of numerosity. Here, I was further interested in a different question: is numerosity perceived different if subjects are asked to estimate the density of the array instead of its numerosity? Linking elements in the array, the contribution of both number and texture-density are examined. (this chapter is published in Journal of Numerical Cognition).

In the fourth and fifth empirical chapters, I move back to the different contributions of attention on number estimation. In the fourth chapter, I assess whether, when attention is deprived using a concomitant visual or auditory task, different pattern of results emerges for different quantities of numerosity, with particular interest on the dichotomy between estimation and texture-density (this chapter is published in Attention, Perception & Psychophysics). Following this, the last empirical chapter assessed the contribution of increasing attentional engagement, instead of decreasing it, on enumeration of numerosity. Overall, previous studies on the relationship between numerosity and attention, and also the previous chapter, have investigated only the cases in which attention is not fully available. Here, I was interested in examining whether enhancement of attention during an enumeration task can improve the estimation process. Using a visual cueing paradigm, I assessed the contribution of both object and location-based attention. I hypothesized that enumeration of quantities would benefit from the focusing of attention to a specific location, and that the advantages found here would spread to the whole object in which the cue was previously presented, leading to faster, more accurate (and linear) and precise estimations compared to the situation in which attention needed to be shifted to a different object.

Overall, the data presented in this thesis provide novel contributions to the longstanding debate on whether number is sensed directly, and whether the processes underlying perception of intermediate and large numerosities can rely on different mechanisms. The distinction between estimation and density was assessed using reaction times, precision, linking elements, and attentional techniques. All of them point to the existence of separate regimes of number perception. Moreover, data on priming effects support an increasing body of evidence that pupillometry can be very useful in tracking perceptual processes, providing information that cannot be gathered from standard psychophysics. Likewise, it would seem that these pupillometry measures may be more sensitive to variations in perceptual styles, and their dependency on personality traits.

Chapter 2

Priming of attention and dependency on autistic traits

2.1 Introduction

As mentioned in the general Introduction, both attention and perception can be strongly influenced by past perceptual history. Neurotypical adults track the statistics of the environment and combine past information with current sensory data to improve efficiency in processing of incoming stimuli (Cicchini, Anobile, & Burr, 2014; Cicchini, Mikellidou, & Burr, 2017; Fischer & Whitney, 2014) Imperfect predictions elicit a prediction error (Friston, 2005), which promotes learning through updating of an internal model (Nassar, Wilson, Heasly, & Gold, 2010). On this view, perceptual decisions are made by comparing the probability of the sensory evidence with prior experience. The Bayesian class of theories – including predictive coding and other generative models (Kersten, Mamassian, & Yuille, 2004; Knill & Pouget, 2004) – assumes that perception is an optimized combination of the likelihood (sensory data) and the prior (influences based on previous perceptual history). Importantly, the expectations are perceptual in nature, and seem to be obligatory, not under cognitive control. In a crucial experiment, Maljkovic and Nakayama (1994) alternated the target color between trials, so it was perfectly predictable but always changed: average reaction times under this condition were slower than totally unpredictable random alternation, showing that a cognitive knowledge of target color could not by itself prime the next trial to speed up responses.

Individuals vary considerably in perceptual style, especially in the extent that they use perceptual priors predictively. In particular, it has been suggested that autism spectrum disorders are associated with weak or less adaptable priors (Pellicano & Burr, 2012), so their perception is dominated more by sensory information than past experience. This concept has been reinforced by several other proposals along similar lines (Friston, Lawson, & Frith, 2013; Lawson, Rees, & Friston, 2014; Rosenberg, Patterson, & Angelaki, 2015; Sinha et al., 2014), and has received empirical support from studies showing diminished adaptation in autistic individuals in the processing of faces (Pellicano, Jeffery, Burr, & Rhodes, 2007; Pellicano, Rhodes, & Calder, 2013) and non-face stimuli (Turi et al., 2015; Turi, Karaminis, Pellicano, & Burr, 2016). This is in line with recent studies on how people on the autism spectrum use sensory statistics to update their internal model (for a review see Robertson & Baron-Cohen, 2017). Some evidence suggests that autistics are slower to update prediction, so it is more dominated by earlier past (Lieder et al., 2019), and that autistic adults tend to rely less on learned priors when asked to discriminate sensory representation in a volatile environment, showing less response to surprising events (Lawson, Mathys, & Rees, 2017). On the other hand orientation of attention in visual search was found to be intact in ASD (e.g. Grubb et al., 2013).

Pupillometry is proving to be a powerful tool for this line of research. Using pupillometry, Turi et al. (2018) showed that pupil diameter oscillated in phase with the ambiguous perception of a bistable rotating cylinder, more dilated when the black surface was in front. Importantly, the magnitude of oscillation varied between participants and was strongly correlated with autistic traits, defined by the Autism-Spectrum Quotient AQ (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). The effect was far stronger in participants with high AQ, consistent with high AQ (and autistic) individuals having a local, detail-oriented perceptual style. These and other results (eg Tortelli, Turi, Burr, & Binda, 2018) show that pupillometry can be more sensitive than standard behavioral measures (including RTs) in revealing subtle inter-individual differences in the deployment of attention and perception.

This chapter aims to investigate whether pupillometry can reveal the effects of perceptual priming, and whether the pupillometry and reaction-time effects co-vary with personality traits. Twenty-seven randomly selected neuro-typical adults with variable degrees of AQ-defined autistic traits were tested. It was hypothesized that change of the target color should cause a measurable increase in pupil size compared with repetition of target color, reflecting a “surprise” reaction to the violation of expectancy. I further speculated that there could be a reduced pupillary response to violation expectancy in the group with high autistic traits, reflecting their lesser dependency on prior information.

2.2 Methods

This experiment replicates the classical phenomenon of priming of pop-out of Maljkovic & Nakayama (1994), moreover it investigates the effects of perceptual priming on pupil size, with a specific look into the differences in participants personality traits.

Twenty-seven participants (22 female, age (mean ± SD): 24.4 ± 2.45) with corrected-to-normal vision took part in the experiment. All participants reported no diagnosed neurological condition. Experimental procedures were approved by the regional ethics committee (Comitato Etico Pediatrico Regionale—Azienda Ospedaliero-Universitaria Meyer—Florence) and are in line with the declaration of Helsinki; participants gave their written informed consent.

2.2.1 Procedure

Participants were seated in front of the computer monitor in a dark room with chin resting on a chin-rest at a distance of 57 cm. Stimuli were generated with the PsychoPhysics Toolbox routines (Brainard, 1997) for MATLAB (r2016b, The MathWorks) and presented on a 39 cm monitor (120 Hz, 800x600 pixels; Barco Calibrator). All trials started with a white fixation cross at screen center on a dark background following a search display containing three diamond shapes, 0.84° X 0.84°, with 0.15° cut off either the left or right side (Figure 2.1). Observers searched for the odd-colored diamond (either a red target among two green distractors or vice versa) and reported its shape (cutoff on left or right side) by rapidly pressing the appropriate button on the keyboard. As in the study of Maljkovic & Nakayama (1994) the test stimulus was always above the fixation cross, either left or right. A trial lasted 500 ms, with an inter-trial pause of 750 ms. The target color either switched or repeated on each trial with equal probability. After a 10-trial training session, participants performed four 80-trial sessions. While performing the behavioral task, pupil size of participants was recorded (see Apparatus). To prevent luminance driving pupil size, the background, the red and green diamonds all were equi-luminant at 14.8 cd/m^2.

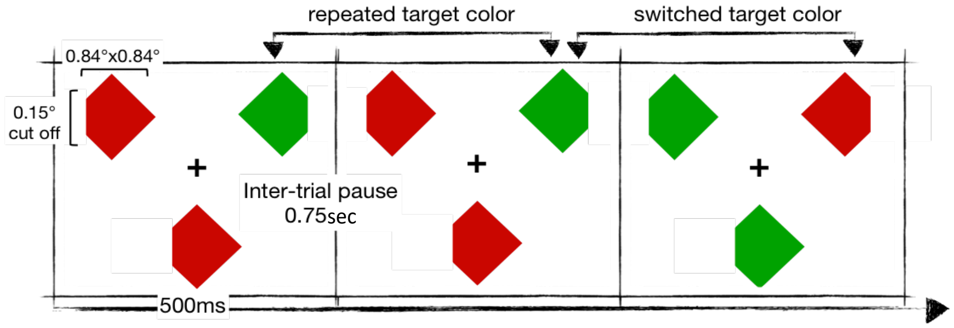

Figure 2.1 Schematic representation of the stimuli. The participant's task was to report which side of the odd-colored diamond was missing; after the response a blank display with fixation cross remained for 750 ms. The target was positioned randomly left or right, always above of fixation.

2.2.2 AQ score

All participants completed the self-administered Autistic Quotient questionnaire, in the validated Italian version (Ruta, Mazzone, Mazzone, Wheelwright, & Baron-Cohen, 2012). This contains 50 items, grouped in five subscales: Attention Switching, Attention to Detail, Imagination, Communication and Social Skills. For each question, participants read a statement and selected the degree to which the statement best described them: ''strongly agree'', ''slightly agree'', ''slightly disagree'', and ''strongly disagree'' (in Italian). The standard scoring described in the original paper was used: 1 when the participant's response was characteristic of ASD (slightly or strongly), 0 otherwise. Total scores ranged between 0 and 50, with higher scores indicating higher degrees of autistic traits. All except one participant (with AQ 37) scored below 32, the threshold above which a clinical assessment is recommended (Baron-Cohen et al., 2001). The median of the scores was 15, with lower and upper quartiles of 12.2 and 21.2. Scores were normally distributed, as measured by the Jarque-Bera goodness-of-fit test of composite normality (JB=4.1175, p = 0.13).

2.2.3 Apparatus and data analysis

Eye position and pupil diameter were monitored at 1000 Hz with an infrared camera mounted below the screen (Eyelink1000 Plus, SR Research). Pupil diameter measures were transformed from pixels to millimeters after calibrating the tracker with an artificial 4 mm pupil, positioned at the location of participant's left eye. Time points with unrealistic pupil size (less than 2 mm) were considered to be signal losses and were removed from the analysis. The first trial of each session was also excluded as there was no possibility of priming. To measure the change in pupil diameter evoked by the stimuli, individual data were baseline-corrected against a 100-ms window preceding the stimulus presentation. The time course of the pupillary response was determined by averaging baseline-corrected data in 150-ms bins. We restricted our analysis of pupil size to a specific time window from the stimulus onset to 600 ms (just after the stimulus disappearance, and before the button-press dominated the pupillary response). We verified that shifting this window or shrinking it by 100 ms did not change the pattern of results. Only data from correct trials were analyzed. Standard t-tests and correlation analyses were complemented with Bayes Factors estimation. The JZS Bayes Factor (Rouder, Speckman, Sun, Morey, & Iverson, 2009) quantifies the evidence for or against the null hypothesis as the ratio of the likelihoods for the experimental and the null hypothesis. It can be expressed as the logarithm of the ratio (Jeffreys, 1961; Kass & Raftery, 1995), where negative numbers indicate that the null hypothesis is likely to be true, positive that it is false. By convention, absolute log Bayes factors greater than 0.5 are considered substantial evidence for or against, and absolute log-factors greater than 1 strong evidence.

To estimate the effect of internal reliability on correlations, we also calculated the "disattenuated correlation" index, which takes into to account internal reliability by normalizing the geometric mean of estimates of the internal reliability of each measure. We assessed internal reliability with either Cronbach's alpha, for AQ, and with split-half reliability adjusted with the Spearman-Brown proficiency formula (Spearman, 1904, 1910), for pupil-change and reaction-times.

2.3 Results

Figure 2.2 shows for one example subject reaction time distributions for both repeated and switched trials. Responses for repeated trials were faster than to switched trials, in this case by nearly 100 ms (mean ± sem: repeated 591.9 ms ± 6.5; switched 672.1 ms ± 8.9), confirming previous results of reaction times advantages for repeated than switched target color (i.e. Maljkovic & Nakayama, 1994).

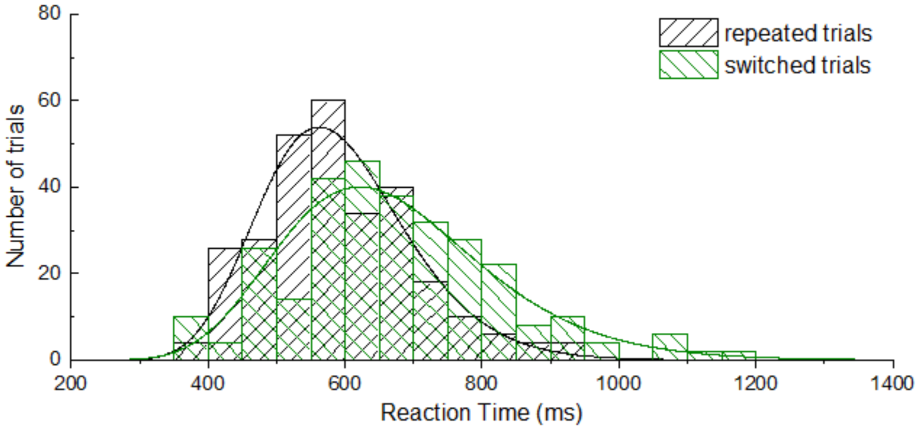

Figure 2.2 Example of subject reaction time distributions. *Distributions of reaction times for one example subject for both repeated trials (black) and switched trials (green), with best-fit Gaussian functions.*

Since we were interested in the effect of personality traits on the results, we divided participants into low AQ (blue) and high AQ (red), based on a median split of their AQ scores (above or below 15). Figure 2.3A plots individual reaction times to repeated trials against those to switched trials. The data of all except one participant fell below the equality line, showing that RTs were faster for the repeated condition. The blue and red data points are intermixed, with no clear difference in the performance of participants with low and high AQ scores. This is clear from the average data points in Figure 2.3B. There is a clear priming effect (shorter RTs in repeated trials), similar not depending on AQ. A mixed model two-way ANOVA shows a significant main effect of the within-subject factor "priming" (repeated vs. switch trials, $F_{(25,1)} = 51.73$, $p<0.001$), but no effect of the between-subject factor AQ (low or high, $F_{(25,1)} = 1.37$, $p = 0.25$), and no interaction between factors ($F_{(25,1)} = 0.082$, $p = 0.77$).

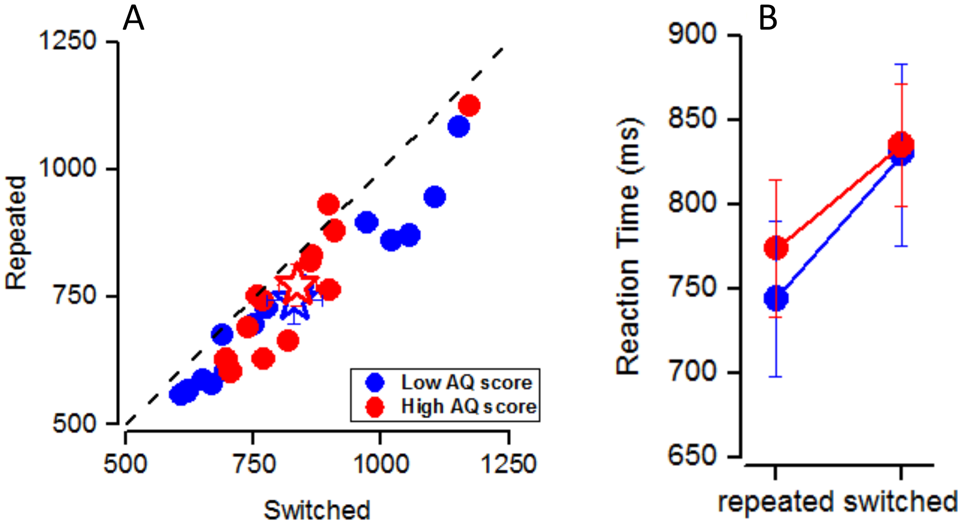

Figure 2.3 The effect of switching target color on reaction times. (A) Reaction times for repeated trials plotted against switched trials for the 27 participants. Blue refers to participants with low AQ, red to high AQ. Empty stars show the color-coded

means for the subsample of participants. **(B)** Mean reaction times for the two subsamples of participants for both repeated and switched trials.

We then examined in more detail the relationship between AQ and priming effects. Figure 2.4 plots the effect of priming on reaction times against AQ scores, showing substantive evidence of there being no correlation (r = −0.15 [−0.50 0.24] p = 0.458, log-BF = −0.7). The disattenuated correlation was 0.22, log-BF = −0.56.

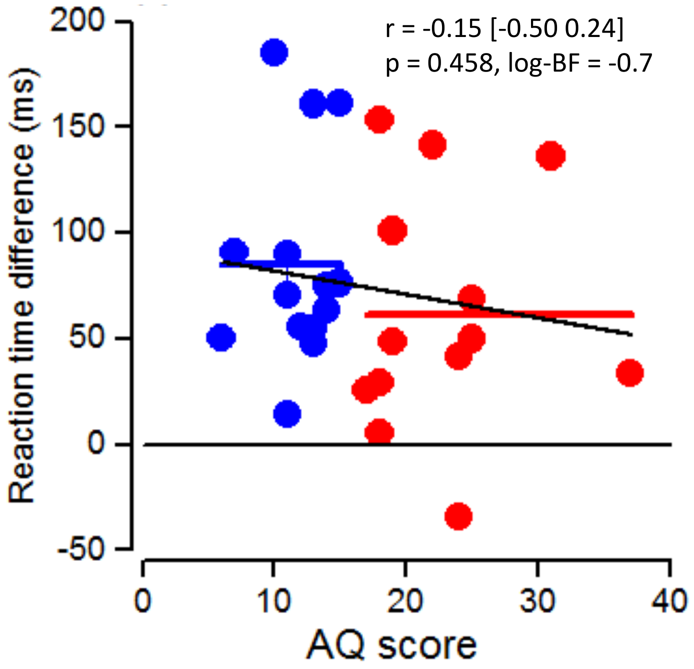

Figure 2.4 Correlations between Autistic Quotient and reaction times. Reaction time difference plotted against AQ scores for all participants (low AQ in blue and high AQ in red). Thick color-coded horizontal lines represent the means of the two groups. Text insets report Pearson's Rho values and associated p-values and Bayes Factors.

We then conducted an analysis on the build-up of priming, looking at effect of past history up to 5 trials back. Figure 2.5A shows that the RT advantage caused by the presentation in a previous trial of the same target color is strongest when the prime immediately preceded the current stimulus ($t_{(13)} = 6.45$, $p<0.001$, log-BF=3.04), then decreases as a function of distance in the sequence. The difference remains significant for 2 trials back ($t_{(13)} = 4.54$, $p<0.001$,log-BF=1.81), then fails to reach statistical significance (all other $p > 0.1$, log-BF < 0.15).

Figure 2.5B plots the priming effect for sequences of the same color, as a function of the length of the preceding sequence of the same color. The priming effect is clearly cumulative, following closely the prediction obtained by integrating the individual effects of Figure 2.5A (shown by the dashed line). The linear regression of this function has a slope of 15.95 ms (±2.46) statistically different from zero ($t=6.48$, $p=0.007$).

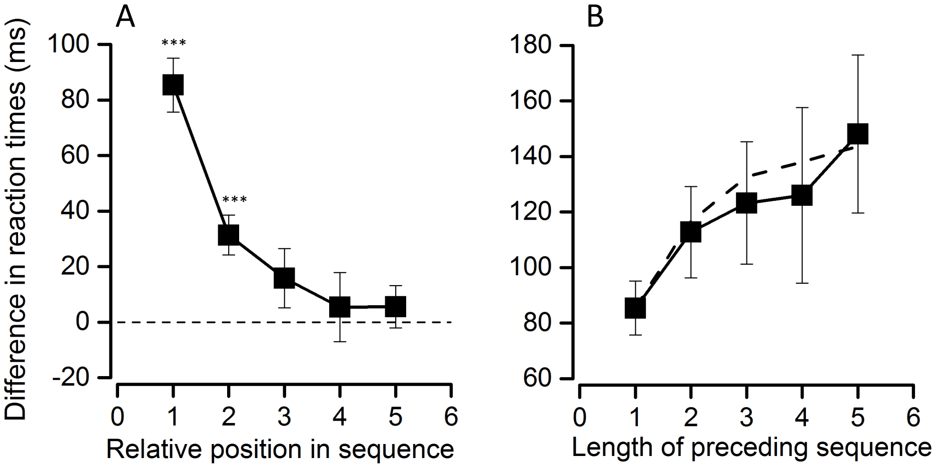

Figure 2.5 Serial dependence of repeating target color for reaction times. (A) Reaction time differences in ms (switched trials – repeated trials), as a function of the relative serial position of the repeated color in the trial sequence. **(B)** Reaction time differences in ms as a function of the length of the same-color sequence. Dashed line is the integral of data in panel A. Significance values refer to one sample T-test (**p<0.01, ***p<0.001).

2.3.2 Pupil size

Figure 2.6 illustrates the average time course of the pupillary response for the same example participant. There is a clear tendency for switch trials to elicit larger pupil dilation, averaged over the range of 0-600 ms (mean ± sem: repeated 0.0390 mm ± 0.0035; switched 0.0503 mm ± 0.0037).

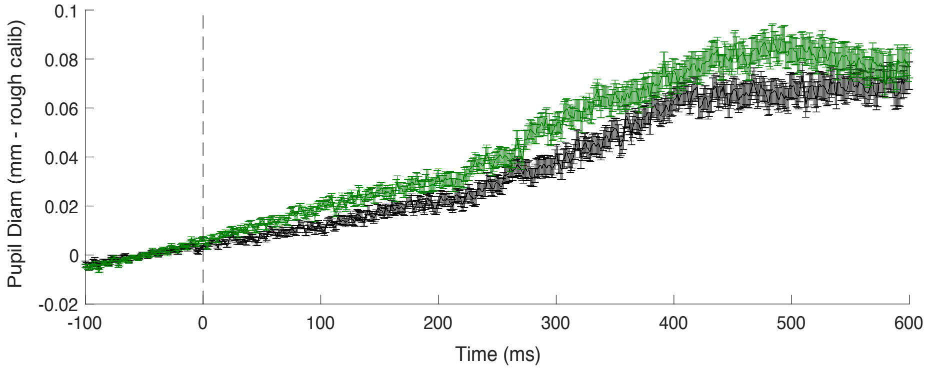

Figure 2.6 Example of one subject pupil modulations. Pupil size recordings plotted as a function on time from 100 ms before the trial onset (considered as baseline and subtracted from each trace and then averaged across subject) to the stimulus offset. Vertical dashed line marks the onset of the stimulus. Error bars show SEM.

As for reaction times results, we did a median split our sample of participants into low AQ and high AQ. Figure 2.7A plots pupil change for repeated against switched trials. Here, low and high AQ participants form distinct clusters, with low AQ points tending to fall below the equality line. Again, this is best seen in the plot of average results, shown by Figure 2.7B. There is stronger pupillary dilation in the switched-color trials, but only for the group of low AQ. This is confirmed by the two-way ANOVA, which reveals a significant interaction between the within-subject factor "priming" and the between-subject factor AQ ($F_{(25,1)}$ = 16.16, $p<0.001$), but no effect of the between-subject factor AQ ($F_{(25,1)}$=2.57; p=0.12) and no main effect of the within-subject factor "priming" ($F_{(25,1)}$= 1.42, p=0.24).

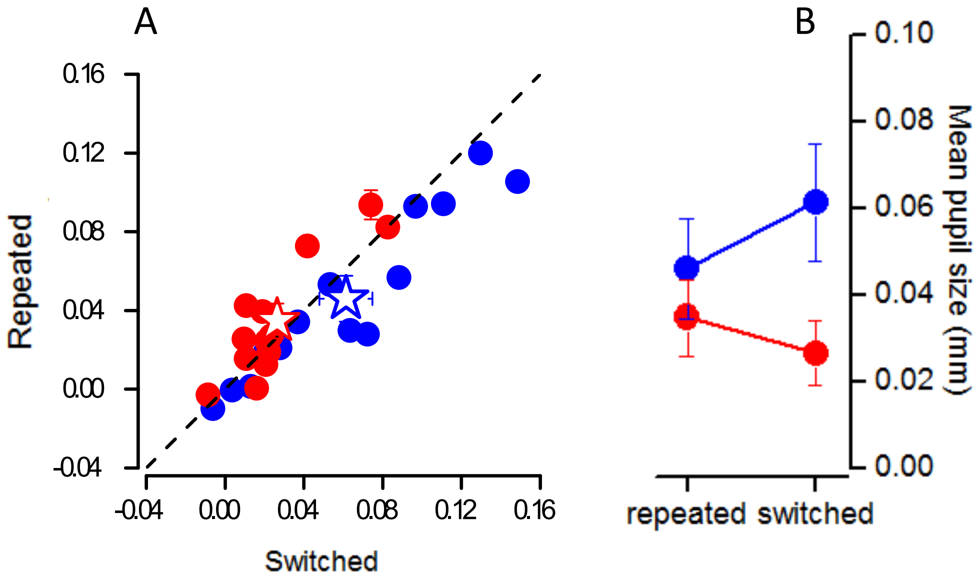

Figure 2.7 The effect of switching target color on pupil-size changes. (A) Changes in pupil size for repeated trials plotted against switched trials for the same participants (Blue refers to participants with low AQ, red to high AQ). **(B)** Mean pupil size for the two subsamples of participants for both repeated and switched trials.

Examination on the relationship between AQ and priming on pupil dilation shows that the priming effect on pupil dilation is substantially correlated with AQ scores ($r = -0.51$ $[-0.74\ -0.15]$ $p < 0.01$, log-BF = 0.72; disattenuated correlation > 1) (Figure 2.8). Reinforcing the results of the median split in Figure 2.7 A-B.

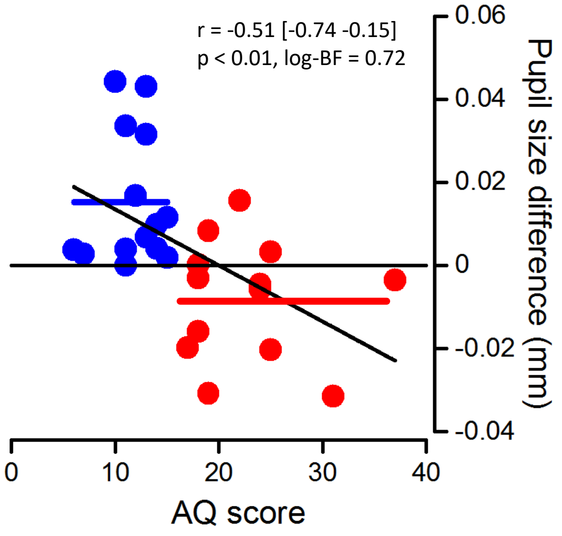

Figure 2.8 Correlations between Autistic Quotient and pupil-dilation. *Pupil size difference plotted against AQ scores for all participants (low AQ in blue and high AQ in red). Thick color-coded horizontal lines represent the means of the two groups. Text insets report Pearson's Rho values and associated p-values and Bayes Factors.*

We further explored the correlation separately for pupil changes during repeated (Figure 2.9A) and swapped trials (Figure 2.9B). While changes on repeated trials did not correlate with AQ scores ($r = -0.18$ [−0.52 0.22], $p = 0.376$, log-BF = −0.7), those during switched trials do show a negative correlation ($r = -0.38$ [−0.67 −0.00], $p<0.05$, log-BF = 0.0065). The attenuated correlations were $r = -0.23$ (log-BF = −0.52) and $r = -0.48$ (log-BF = 0.59) for repeated and switched trials. This is consistent with Figure 2.8B, showing a greater difference between the high and low AQ groups for switched than for repeated trials.

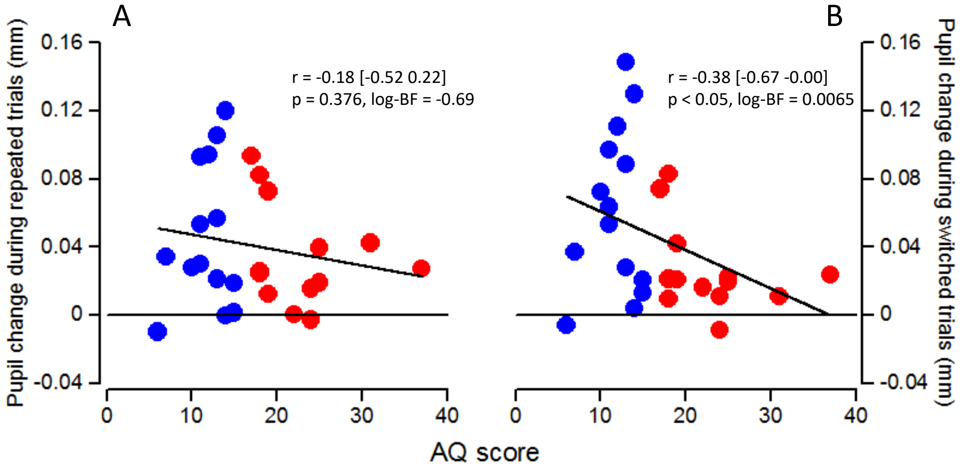

Figure 2.9 Correlations between repeated and switched trials and AQ. (A) Pupil changes during repeated trials and switched trials **(B)** plotted against AQ scores. Text insets report Pearson's Rho values and associated p-values and Bayes Factors. Thick black lines show the linear fit through the data.

Analysis on the effects of past history on pupil size (Figure 2.10 A-B), revealed that, unlike RTs, the effects on pupil-size do not last more than the immediate change. While the effects 1-back are significant ($t_{(13)} = 3.60$, $p<0.01$, log-BF=1.16), none of the other comparisons for trials further back in the sequence reach significance (all $p > 0.1$, log-BF < −0.5). Similarly, there was no accumulation of the effect for long repetitions (Figure 2.10B): the effects for all run-lengths of repeated sequences were statistically indistinguishable

($F_{(52,4)}$ = 0.069; p = 0.991) and the slope of this function was −0.001 mm (±0.001), not statistically different from 0 (t = −1, p>0.3).

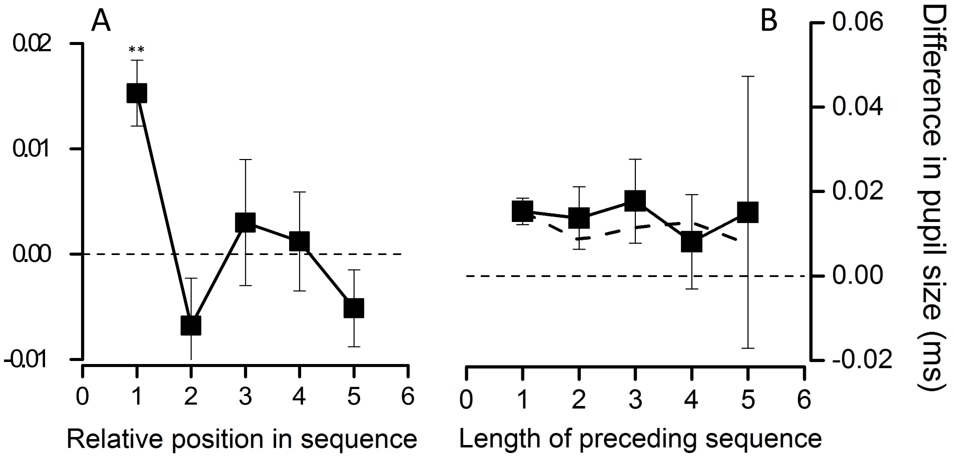

Figure 2.10 Serial dependence of repeating target color for pupil size. (A) Pupil size differences in mm (switched trials – repeated trials), as a function of the relative serial position of the repeated color in the trial sequence. **(B)** Pupil size differences in mm as a function of the length of the same-color sequence. Dashed line is the integral of data in panel A. Significance values refer to one sample T-test (**p<0.01, ***p<0.001).

2.3.3 Comparing reaction times and pupil size

Taken together our analysis suggests that both RTs and pupil dilation are related to priming effects, but in qualitatively different ways. To bring this out more clearly, Figure 2.11 plots the effect of priming on pupil dilation (the difference between the average change in pupil size for the switched and the repeated targets) as a function of the priming effect on reaction times (the difference of RT during switched trials and repeated trials). There is substantive evidence that the two measures do not correlate with each other (r = 0.15 [−0.24 0.50], p=0.440, log-BF = −0.7), suggesting that these two indices – pupillary and behavioral – capture different aspects of the priming phenomenon. To check that this lack of correlation did not result solely from poor internal reliability of our measures, we also calculated the "disattenuated correlation", which takes into to account internal reliability, by normalizing the geometric mean of Cronbach's alpha of each measure. The internal reliability (calculated by split-half reliability adjusted with Spearman-Brown proficiency formula) was 0.71 (logBF=2.86) for RTs and 0.35 (logBF = −0.14) for pupil size. Although these are not particularly high (especially pupil-size), normalizing by these leads to a disattenuated correlation of 0.30, Log-BF = −0.33. The Bayes factor is not substantial, but there is no evidence for a significant correlation between the two measures.

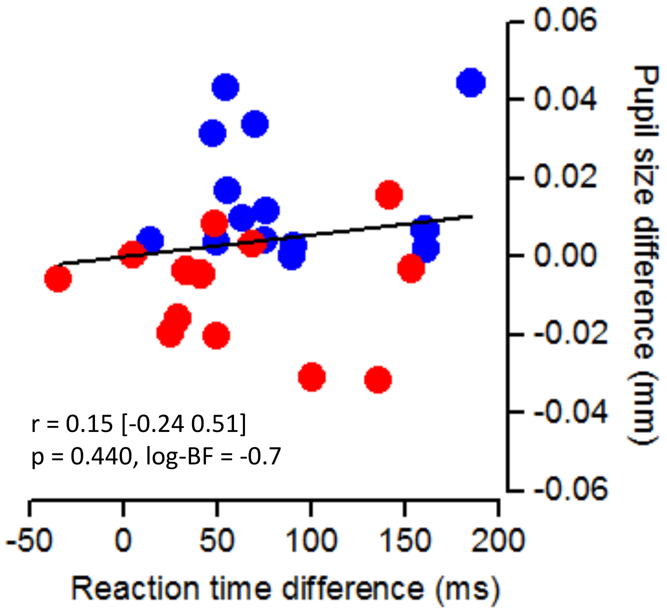

Figure 2.11 Correlation between the pupil dilation difference (measured as the difference between pupil size during switched and repeated trials) **and reaction time difference** (measured as the difference between reaction times during switched and repeated trials). Text inset reports Pearson's Rho value and associated p-value and Bayes Factor. Thick black line shows the linear fit through the data.

2.3.4 Potential artifacts

As a major conclusion of this paper is that the greater pupillary response to switched than to repeated trials depended on AQ, it is important to exclude the possibility that the pupillary dependency on AQ did not result from a generalized AQ-dependent difference in pupil responsivity. This is not implausible, as it has been reported that pupil metrics such as baseline pupil size and stimulus-evoked changes are abnormal among autistic individuals (Anderson, Colombo, & Unruh, 2013; Martineau et al., 2011). However, we believe this is unlikely in this study. Firstly, AQ correlated only with responses to switched trials, not to repeated trials, as would be expected if there were a generalized change in responsivity. We also ran two further analyses, correlating both baseline pupil size (averaged over the 100 ms preceding the response) and the late pupillary response (averaged over the time window 1000-1500 ms after stimulus presentation), mainly generated by button-press. Neither correlation approached significance: baseline $r = 0.23$; $p = 0.25$; $\log BF = -0.5$ (disattenuated $r = 0.28$; $\log BF = -0.37$); response to button-press $r = 0.08$; $p = 0.69$; $\log BF = -0.8$ (disattenuated $r = 0.10$; $\log BF = -0.77$). These non-correlations preclude the possibility that the results are driven by a generalized dependency of either baseline or stimulus-evoked pupil response on AQ.

Subjects were asked to fixate throughout the trials, and eye-movements were monitored. The average root-mean squared deviation from fixation was 0.77°. As eye-movements can change the estimate of pupil size (Hayes & Petrov, 2016), which could in turn artificially drive our results, we checked whether eye-movement amplitude correlated with any relevant variables. It did not. The correlation with AQ was $r = -0.05$; $p=0.80$; $\log BF = -0.8$; disattenuated $r= 0.06$; log-BF= -0.80), and the correlation with average pupil-size was ($r = -0.25$, $p = 0.20$, log-BF = -0.5; disattenuated $r= -0.26$; log-BF = -0.44). Nor was there a correlation with difference in pupil-size ($r = -0.30$, $p = 0.12$, log-BF = -0.3; disattenuated $r = 0.60$; log-BF = 1.56). We can therefore safely rule out the possibility that eye-movement related artifacts in pupil-size influenced our results.

Moreover, since in the original work of Maljkovic and Nakayama (1996) showed that there was a reaction-time advantage not only when the target color was repeated, but also a smaller advantage when the position of the target was repeated, we also analyzed positional priming and the dependency of priming on repetition of motor responses. We found a significant main effect of position and a significant interaction with the target color for reaction times measures, but we found no effect of positional priming when analyzing pupil changes. For both the two measures there was no interaction with AQ. Further analyses and details are shown in Appendix (A1).

2.4 Discussion

This study used pupillometry to investigate perceptual priming of pop-out. Our results show that priming does affect pupillometry indices, but these effects are different from those on reaction times. We replicated Maljkovic and Nakayama study (1994), showing robust speeding of reaction times on repetition of the priming color. This priming effect did not depend on autistic-like personality traits, as measured by AQ scores. As shown by the results on pupil size, pupillary dilation on stimulus presentation was greater for trials when the test-color switched than when it remained the same as the previous trial. Importantly, this effect clearly depended on the AQ of participants, to the extent that it was observed only in participants with lower than median AQ. The dependence on AQ was strongest for the switched trials, suggesting that it was the switch that drove the effect, consistent with a response to violation of expectancy.

The two effects of priming – reaction times and pupil dilation – seem to be independent. The two measures did not correlate with each other across participants, as would be expected if they shared common mechanisms. One effect depended on AQ, the other did not. And whereas the effect on reaction times occurred for stimuli two or three trials back in the sequence, and accumulated over trials (agreeing with Maljkovic and Nakayama (1994)), the effect on pupil dilation depended only on the previous trial being different, with no accumulation over trials.

Chapter 3

Using reaction times to dissociate estimation and texture-density

3.1 Introduction

Classical studies describing the dichotomy between subitizing and estimation are based mainly on Reaction Times. The time taken by people to count visual stimuli varies in a highly systematic fashion as a function of the number of stimuli present: reaction times (RTs) show only a small rise as the number of stimuli increases from 1 to 4 (typically at a rate of around 50-80 ms per item), while for larger numbers there is a slower and more clearly linear increase in RT for every item that is enumerated (typically increasing at a rate of about 200 ms/item) (Mandler & Shebo, 1982; Trick & Pylyshyn, 1994). This generates a characteristic 'dog leg' function, from a shallow to a steep enumeration slope. Many studies have reinforced these findings by showing that both reaction times and precision differ from small to large sets of items. For example, with a number-naming task over the range of 1 to 8 (grain of 1) or 10 to 80 (grain of 10), Revkin, Piazza, Izard, Cohen, & Dehaene (2008) found that precision was higher and reaction times faster in the range 1 to 4 than 10 to 40. Also Choo & Franconeri (2014) showed that comparing 2 versus 3 elements was much faster and more accurate then comparing 20 versus 30. Furthermore, individual subitizing capacity and numerosity comparison thresholds were not correlated (Piazza, Fumarola, Chinello, & Melcher, 2011; Revkin et al., 2008). These distinct patterns indicate the involvement of different processes. Not all studies confirm the idea that subitizing and estimation are driven by completely separate processes. For example, Sengupta, Bapiraju, & Melcher (2017) recently showed that a single flexible network can allow different number ranges to emerge through a self-organization of the same network. Similarly, Balakrishnanl & Ashby (1992) have questioned the existence of a single mechanism for subitizing, showing a lack in discontinuity in RT data inside the subitizing range. Interestingly for larger quantities outside the subitizing range, most of the studies proposing separate mechanisms between estimation and texture-density employed sensory thresholds: numerosity discrimination thresholds tend to obey Weber's law, increasing with perceived numerosity, up to a point at which Weber fractions cease to be constant but decrease with the square-root of numerosity (Anobile, Cicchini, & Burr, 2014; Anobile et al., 2015). The fact that intermediate and large numerosities follow two psychophysical regimes suggest two separate mechanisms: one for estimating numerosity at moderate densities, the other for estimating the density of textures at higher densities. The transition from estimation mechanisms (following Weber's law) to texture-like mechanisms (following a square-root law) occurs when the individual items are no longer discernable as separate items. In other words, when the items become 'crowded'. Crowding is a well-studied visual phenomenon, referring to the fact that stimuli, typically letters, that are easily discerned when displayed individually, can become indiscriminable when embedded in other letters (Levi, 2008). Previous studies questioned whether similar process governs the transition from numerosity to density. According to crowding-like mechanisms, the transition between numerosity should depend on eccentricity, occurring at lower densities in the periphery; and it should depend on center-to-center spacing rather than edge-to-edge separation, or total coverage of dots. Both these predictions were verified by recent data (Anobile et al., 2015): texture mechanisms came into play far earlier in the periphery than with central vision, and the effects did not depend on stimulus size. For numerosity mechanisms to operate, the items to be enumerated need to be perceptually segregated.

Here I investigate the transaction between the two different regimes using the classical method of reaction times and, taking advantage on previous studies on the effect of eccentricity on the transaction, I tested a wide range of numbers at two different eccentricities (fovea vs periphery). I hypothesized that if reaction times vary in the same way that thresholds do, they should follow the same trend, and begin to decrease for high numerosities and that the point of transaction between the two ranges should occur at lower densities in the periphery of the visual field.

3.2 Methods

This experiment reports reaction times and precision measures during an enumeration task for a wide range of numerosities displayed at two eccentricities, separately. Sixteen subjects (9 male, mean age: 28; SD=2.50) with normal or corrected-to-normal vision participated. Eight (5 males, mean age: 28; SD=1.70) completed the central viewing condition, other nine (one shared, 4 males, mean age: 28; SD=2.4) were tested in the peripheral condition. All participants gave written informed consent. Experimental procedures were approved by the local ethics committee (Comitato Etico Pediatrico Regionale—Azienda Ospedaliero-Universitaria Meyer—Firenze) and are in line with the declaration of Helsinki.

3.2.1 Apparatus and stimuli

All trials started with a central fixation-cross presented on a grey screen, on which subjects maintained fixation throughout the trial. On initiation by the experimenter, a cloud of dots was presented for 400 ms, and subjects called out how many dots they had seen.

Subjects were instructed to respond as fast and accurately as possible. All participants started with a training phase of 10 trials in which they were shown a subset of the stimuli used in the actual experiment (numerosities of roughly ½, ¼, 1/5 and 1/8 of the maximal stimulus in the range) and were given feedback of the actual numerosity of the stimulus.

In the main experiment, thirty-one numerosities were used, roughly equi-spaced on a logarithmic scale (N= 1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 13, 15, 17, 19, 22, 26, 29, 34, 39, 45, 52, 60, 69, 79, 91, 105, 121, 139, 160, 184, 212). Three 62-trials sessions were run (each numerosity was presented 6 times). Importantly, subjects were never instructed about the actual range used to avoid edge effects (Jazayeri & Shadlen, 2010; Poulton, 1973; Teghtsoonian & Teghtsoonian, 1978), which might contaminate precision measures. To test the prediction that the switching from estimation to density range depends on eccentricity, we tested additional subjects on a different range of numerosities from the previous experiment, asking them to report the estimated number of dots confined within circular regions alternated randomly on either side of a central fixation cross at 15° of eccentricity. We tested twelve different numerosities (N= 3, 6, 12, 24, 32, 50, 64, 75, 100, 125, 150, 200). Three 72-trials sessions were run for each condition. Stimuli were generated with the Psychophysics Toolbox (Brainard, 1997) and presented at a viewing distance of 57 cm on a 23 inch LCD Acer monitor (resolution = 1.920x1.080 pixels; refresh rate = 60 Hz), run by a Macintosh laptop (MacBookAir, Apple, Cupertino, CA). Half of the dots were white, the other half black, to avoid luminance being a cue for numerosity. Each dot had a diameter of 10 pixels (0.25 degrees) and were always separated from each other by at least 0.25°. Dots were randomly displayed within a virtual circular patch with a diameter of 6°. (Figure 3.1)

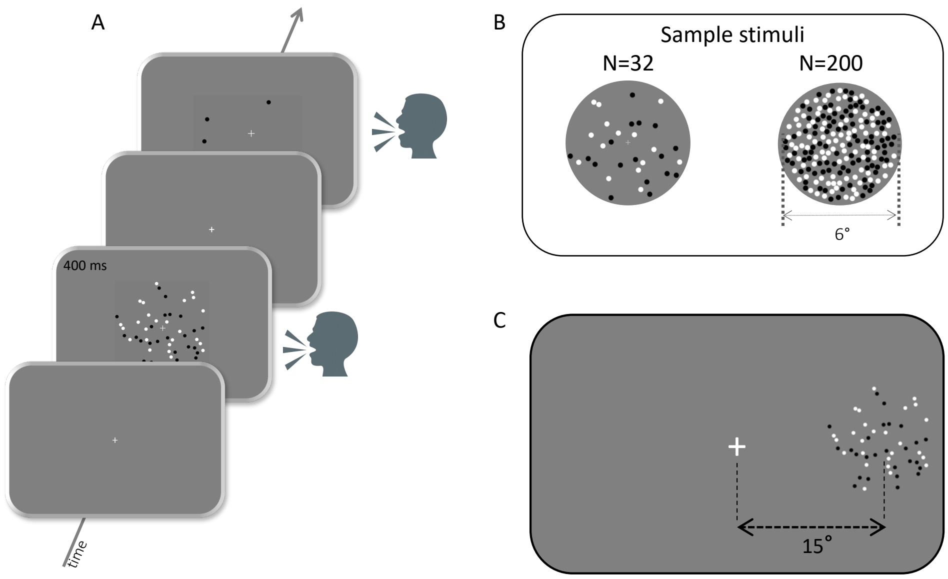

Figure 3.1 Illustration of the stimulus sequence. Each trial started with a cloud of dots presented for 400ms either in central viewing **(A)** or at 15° of eccentricity **(C)**. The subjects were asked to voice the numerosity of the patch. **(B)** Sample stimuli (N=32 and N=200).

3.2.2 Data analysis

The computer detected the onset of the vocal response, from which reaction times were computed, and the experimenter recorded the responses on a keyboard. Reaction times were measured by voice onset and averaged for each condition. Vocal responses were recorded using a Psychotoolbox function on MATLAB, which records audio data from the internal microphone of the computer. Subjects were instructed to call out swiftly and cleanly the number, which nearly always yielded neat soundtracks to estimate reaction times from (checked manually by experimenter). Sound thresholds for detection of responses were set to about 1/10th of the typical vocal intensity, which excluded the rare environmental sounds in the experimental room. In the event of coughing, unclear utterances or particularly loud noises, the experimenter tagged the response, which was excluded from analyses. Trials with response times outside ±2 standard deviation from the mean of each subject were considered outliers and also excluded from the analysis (a total of 354 trials, 9.7 % in total). Data were analyzed separately for each subject and numerosity, and then averaged over subjects. Responses were pooled for each condition and numerosity, from which the mean and standard deviation were estimated. The mean reflects systematic biases in judgments, while the standard deviation provides an estimate of response precision which, normalized by the numerosity for each condition, yields the Coefficient of Variation.

3.3 Results

3.3.1 Reaction time measures

We measured numerosity estimation thresholds and reaction times by asking subjects to call out as quickly and accurately as possible the numerosity of a briefly presented cloud of dots. We tested a large range of numerosities at two stimulus eccentricities (0 and 15°), in two separate conditions. Figure 3.2 shows the average perceived numerosity for each physical numerosity, averaged over subjects. In general, these estimates were quite accurate (bias-free) for both conditions, following the physical numerosity tested (dashed diagonal), and showing no sign of edge effects (Jazayeri & Shadlen, 2010; Poulton, 1973; Teghtsoonian & Teghtsoonian, 1978) indicating that training the subjects with a smaller range of stimuli was sufficient to obtain unbiased estimates.

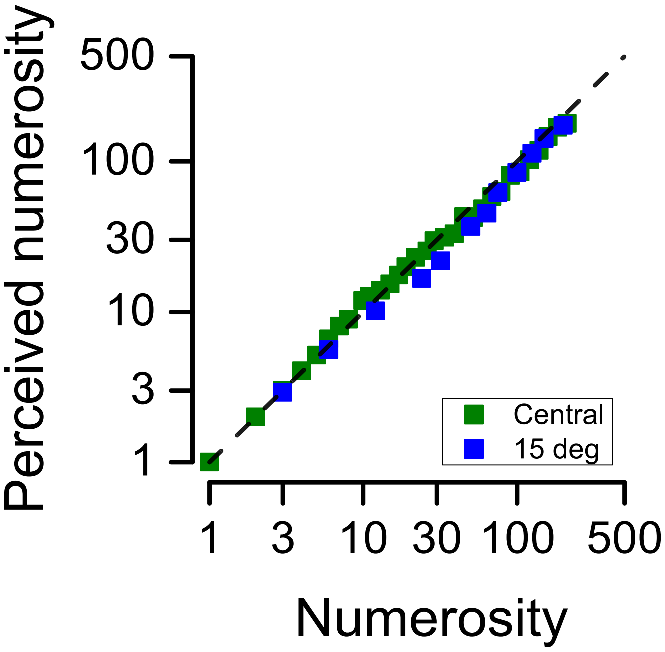

Figure 3.2 Accuracy for verbal numerosity estimation. Average perceived numerosity for central (green squares) and 15° peripheral viewing (blue squares). Eccentricity had no effect on average accuracy.

Figure 3.3 shows reaction times data averaged over all subject as a function of numerosity for both central and eccentric viewing. Mean reaction times increase with dot number, from about 700 ms in the subitizing range (1-4 dots), to around 1300 ms over the range 10 - 100 dots (for central viewing), first sharply then more gradually. They then decline sharply for higher numerosities. To verify that there is a significant modulation of reaction times outside of the subitizing range, we fitted a two-limbed linear function and pitted it against a simple linear regression. For eccentric presentation, we found that a two-limbed function predicted the data much better (R^2=0.90 vs 0.45). To verify that this is statistically significant we bootstrapped the data 10000 times and compared the residuals of the two fits. Since the two-limbed function has two more degrees of freedom, we fixed two parameters (the peak of the curve and the rising part) to make a fair comparison with the linear model. The analysis revealed that even when the two-limbed function was run with only two free parameters, it still yielded a better R^2 in virtually all cases ($p < 0.0001$). Also, in the case of central viewing, the R^2 of the two-limbed function predicted much better the data (R^2=0.45 vs 0.25). Bootstrap resampling demonstrated that also this difference in fitting performance is statistically significant (p=0.044).

The fits were similar for the two eccentricities, except that the change in slope at 15° eccentricity occurred at a lower numerosity. The reaction time results parallel those of the coefficient of variation, in showing a steep decrease as the numerosity become dense. When fitting average data, the points where the curve sharply changes slope are similar for CV and RTs: 101 and 105 respectively for coefficient of variation and reaction time in the central viewing condition; 75 and 82 elements for CV and RTs in the peripheral viewing.

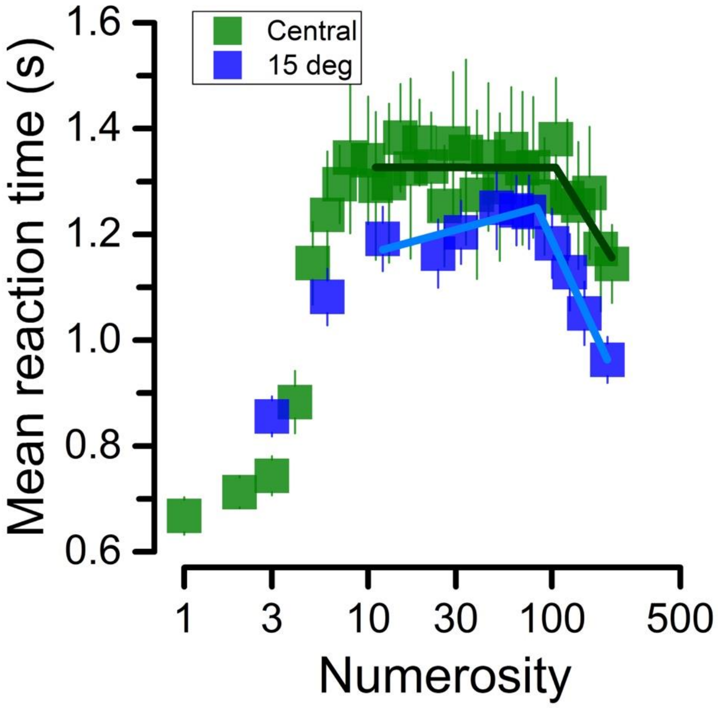

Figure 3.3 Reaction times for verbal numerosity estimation. Means of reaction times (in secs) as a function of numerosity, for the two conditions (central-green and 15° eccentricity-blue). Continuous lines are two-limb linear functions (both slopes free to vary on semi-log coordinates) that best fit the data.

Bootstrap t-tests confirmed that the difference of the knee points on RTs data was significantly different between the two presentation conditions (114±15 central vs 84±11 peripheral, sign test p = 0.049). On the other hand, the slopes of the curve fits, both before and after the knee point were statistically indistinguishable (before: –0.01±0.04 central vs 0.09±0.07 peripheral, sign test p-value= 0.10 ; after: –0.63±0.25 central vs –0.76±0.14 peripheral, bootstrap p-value>0.4).

Inspection of the reaction time curves of Figure 3.4 suggests that they were generally faster in peripheral than central viewing. This difference was significant with a bootstrap sign test (p<0.05). We have no clear explanation for this difference. However, the two conditions were measured in different sessions, with partly different groups of participants. It is possible that different strategies were employed, resulting in a faster reaction time for the peripheral stimuli.

3.3.2 Precision measures

Figure 3.4 shows average numerosity estimation precision, expressed as the Coefficient of Variation (CV: standard deviation normalized by numerosity), as a function of numerosity, separately for the two eccentricity conditions. As we previously demonstrated (Anobile et al., 2014), CV remains stable (following Weber's Law) over the low numerosity range, then starts to decrease. To estimate where thresholds switched from one regime to another, we fitted the data with a two-limb piecewise linear function, with the slope of the first limb fixed at zero and that of the second fixed at −0.5 (on logarithmic coordinates), as our previous studies showing that the decrease followed an approximate square-root law (Anobile et al., 2014, 2015). The goodness of fit had a coefficient of determination (R^2) of 0.41 and 0.63 for the data of central and peripheral viewing respectively.

Previous work (Anobile et al., 2015) has shown that the break in the two-limb function determining the point where Weber's law gives way to the square-root law depends on eccentricity, occurring at lower numerosities in the periphery than in central vision. In the current study, the change in psychophysical regime occurs at 101 elements in the central condition (green square) and at 75 elements in the 15° eccentricity condition. This extends the previous study by showing the effect of eccentricity on numerosity judgments also occurs when subjects are required to estimate numerosities, rather than discriminate them with a two-alternative forced-choice task. Also replicating previous work, the effect of eccentricity is different for numerosities either side of the knee-point. For lower numerosities (i.e $9<N<68$), the CVs are not only flat but also dependent on eccentricity, with better performance for central viewing conditions (0.24 vs 0.3, KS-test= 0.29, p= 0.007). For numerosities above the turning points (i.e $N>105$) the slope in the two viewing conditions are statistically indistinguishable (0.206 vs 0.200 KS-test= 0.14, p= 0.85).

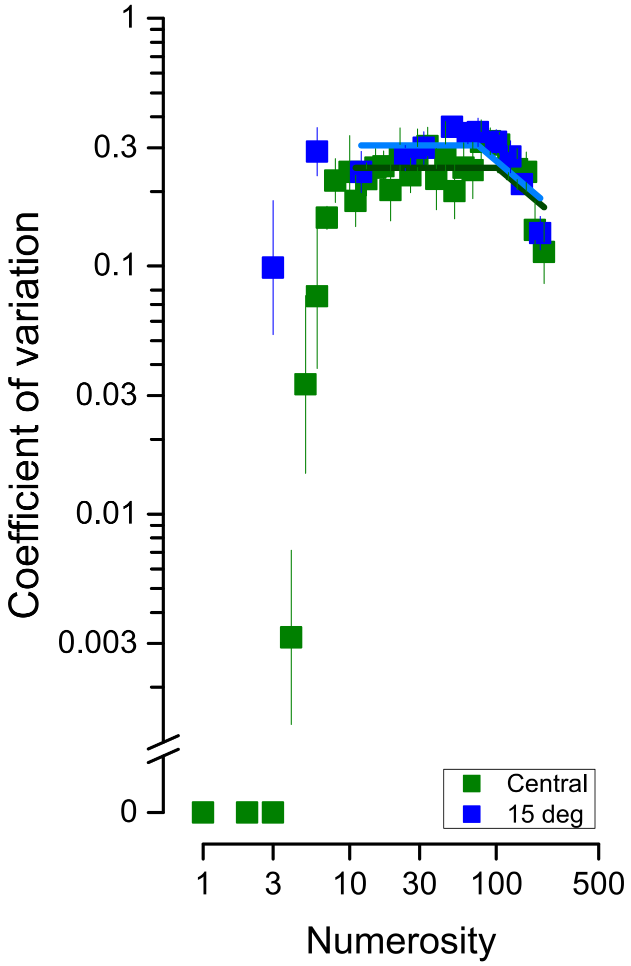

Figure 3.4 Precision for verbal numerosity estimation. Means of CV (standard deviation divided by numerosity) as a function of numerosity, for the two conditions (central-green and 15° eccentricity-blue). Numerosity ranged from 1 to 212 for the central presentation condition and from 3 to 200 for the 15° condition. Continuous lines are two-limb linear functions (slope 0 and −0.5 on log coordinates) that best fit the data.

Given the similarity in the pattern of results for precision and reaction times, we examined the correlation between the two measures across the whole dataset (Figure 3.5 A-B). In order to obtain a more robust fit, we excluded the first four numerosities of the central condition, where estimation was nearly perfect, and quantification depends crucially on the occurrence of rare errors. The correlation between the two was positive for both the conditions (r = 0.67 and r = 0.94 respectively for central and 15° of eccentricity; p < 0.001). This correlation shows that there is no speed-accuracy tradeoff, and that the improvements of performance in the density-perception regime go together with a speeding of responses.

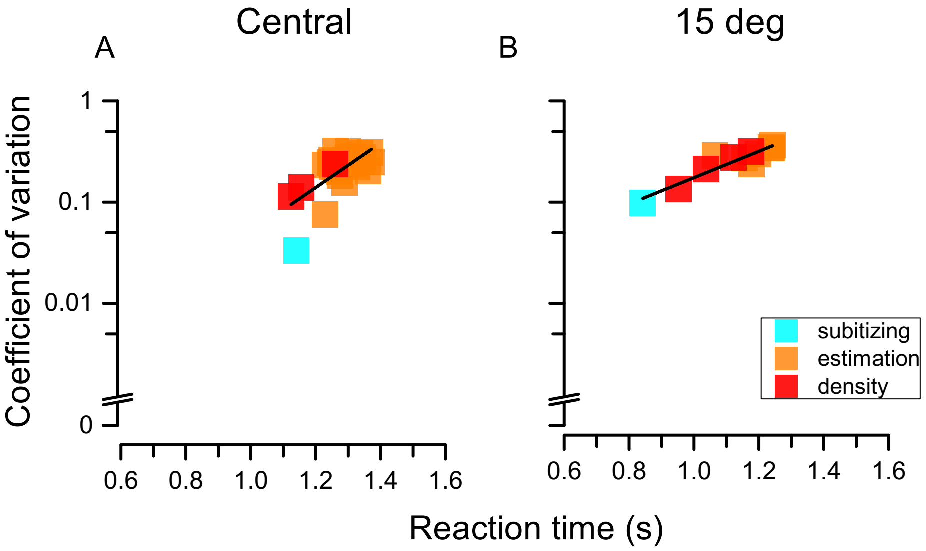

Figure 3.5 Correlations between reaction times and coefficient of variation. (A-B) Correlations of mean reaction times with coefficients of variation separately for the two different conditions (central and 15° of eccentricity). Different colors refer to different numerosity ranges, calculated from the point in which the slopes fall. Black continuous lines are linear functions that best fit the data.

3.4 Discussion

In this experiment, we asked subject to estimate numerosity, as quickly and accurately as possible, and measured both reaction times and precision. The precision estimates confirmed previous study showing that while Weber's law describes well the results for relatively sparse numerosities, it gives way to a square-root law for higher numerosities (Anobile et al., 2014). Importantly, however, reaction times, which have traditionally defined subitizing, also followed the same trend. They increased from the subitizing range as numerosities increased, but only up to a point, then decreased, in a similar manner to the Coefficients of Variation. The point where reaction times started to decrease was similar to where Weber's law gives way to a square-root law (a possible signature of the texture-density system). Indeed, the two measures – reaction times and Coefficient of Variation – correlate positively with each other, with no "speed-accuracy trade-off". These data extend and reinforce some previous findings (Anobile et al., 2014, 2015) indicating that the lowering of precision at high numerosities is genuine and does not come at the expenses of higher reaction times. Moreover, since it was hypothesized that numerosity perception at high densities may follow the same crowding-like rules (Anobile et al., 2015), we were interested in test this prediction also on a enumeration task, instead of a usually used forced choice task. We demonstrate that also enumeration of quantities is subject to eccentricity and, as predicted, the both reaction times and precision trends depend on eccentric: both measures, indeed, began to decrease at lower numerosity for the more eccentric stimuli.

Chapter 4

Linking elements influences sparse but dense patterns

4.1 Introduction

One important feature of number estimation is the effect of visual grouping on number judgments. Approximate number estimation is modulated by how elements are grouped and bound together into higher-order objects. The same number of items will look more numerous when regularly arranged than when randomly distributed (Ginsburg, 1976; Taves, 1941), and random patterns look more numerous than clustered patterns (Ginsburg & Goldstein, 1987). It has also been shown that when higher-order objects are presented, simply by joining the items with lines, the apparent numerosity of the connected items is greatly reduced (Franconeri, Bemis, & Alvarez, 2009; He, Zhang, Zhou, & Chen, 2009; He, Zhou, Zhou, He, & Chen, 2015). In fact, the lines do not need to be physically present: the effect works well with illusory contours as well (Kirjakovski & Matsumoto, 2016). Connecting dots not only changes the perceived numerosity of a pattern, but also the selectivity of the fMRI BOLD response. Connecting three dot-pairs in a pattern of ten dots causes the maximum repetition adaptation to occur at eight rather than ten dots (He et al., 2015). Similarly, while adapting to a 20-dot field does not change the apparent numerosity of a 20 isolated dots (as adaptation to the same number has no net effect), it does reduce the apparent numerosity of 10 dot-pairs, which appear less numerous than 10 isolated dots, and even less numerous after adaptation (Fornaciai, Cicchini, & Burr, 2016). These studies are particularly interesting in the context of the numerosity texture-density debate: adding connectors increases the amount of texture on the screen, particularly at high spatial frequencies. Dakin et al. (2011) have proposed that numerosity can be derived from the power spectrum of the stimulus, essentially the magnitude of high spatial frequencies normalized by the low frequency content. This theory makes very clear and testable predictions: adding visual items to the scene, especially those having greater energy in the higher spatial frequencies, should make the stimulus as more dense – and hence more numerous.

In this chapter, I specifically test this prediction, varying the spatial configuration of the element on the scene adding connectors. In particular, I ask whether the connectedness effect (underestimation of numerosity due by connecting the items with thin lines) also occurs with dense pattern, where texture mechanisms may come into play. The prediction is that the effect of connectivity on numerosity should be strongly reduced at high numerosities, where the Approximate Number System gives way to texture-density mechanisms. Moreover, for dense patterns, where texture-density mechanisms predominate, subjects should see the connected patterns as denser than the isolated patterns: the reverse would hold true for sparse patterns. Therefore, both apparent numerosity and apparent density in dot clouds with items connected was measured, over a wide range of numerosities.

4.2 Methods

Here I tested whether the spatial configuration of the elements in a scene affects dense pattern, monitoring the effect of connecting dots with thin lines. Five subjects (1 male, 4 females, all naïve to the goals of the experiment, mean age 25 years) took part in the study. All had normal or corrected-to-normal visual acuity and no major visual impairment. All participants gave written informed consent. Experimental procedures were approved by the local ethics committee (Comitato Etico Pediatrico Regionale—Azienda Ospedaliero-Universitaria Meyer, Florence), and are in line with the declaration of Helsinki.

4.2.1 Apparatus, stimuli and procedure

Numerosity and density thresholds were measured with a classical two alternative forced choice method (2AFC): participants were asked to report (by appropriate keypress) which of two stimuli (clouds of dots, diameter 6.2 degrees) seemed to be more numerous or more dense, guessing whether uncertain. Stimuli were presented simultaneously on both sides of a central fixation point (8 degrees eccentricity), too fast to make single elements serially countable (500 ms). Subjects sat at 57 cm from a calibrated LCD screen (35 x 19 degrees) running at 60 Hz and 1366 X 768 resolution (1 pixel = 0.025 degrees). Stimuli were generated under Matlab 7.6 using PsychToolbox routines (Brainard, 1997). One of the two dot clouds, the reference, remained of fixed numerosity throughout the session, while the probe varied in numerosity throughout the session, guided by the adaptive Quest routine (Watson & Pelli, 1983) which homed in on the Point of Subjective Equality (PSE). The probe comprised only isolated dots, whereas the reference comprised either isolated dots, or patterns with 40% dots connected by joined by lines (Figure 4.1).

In separate runs the experiment was performed with reference stimuli of 15, 25, 50 and 100 items, corresponding to densities of 0.5, 0.83, 1.67 and 3.3 items/deg^2. For density judgements, to maximize information while keeping the number of conditions reasonably low, only the two extreme values were tested (0.5 and 3.3 items/deg^2). Each participant performed 100 trials for each numerosity/density condition, for both connected and isolated dots resulting in a total of 1200 trials for each participant (6000 trials across participants and conditions, half trials connected and half isolated). Dots were small disks of 0.25 degrees diameter, half white, half black (so that luminance did not vary with number, providing a potential cue). Dot position was calculated online for each trial. For patches containing isolated dots, dot positions were generated sequentially, respecting the sole condition that two items could not be closers than 0.25 degrees (10 pixels) thus forbidding overlap of dots. For patches with connectors, dot position was calculated in two stages: first couples of dots (40% of the total dots of the reference stimulus) were cast and connected via a line, with the constraints that line length was comprised between 1 and 1.5 degrees, with no lines crossing; in the second stage, the remaining 60% of the dots were cast with the constraint of not overlapping either the other dots or the connecting lines. The connector line width was fixed at 0.05 degrees (2 pixels). Figure 4.1 shows examples of the patterns used in the experiments.

4.2.2 Data analysis

Data were analyzed separately for each subject. For each condition (numerosity or density judgments, with connected or isolated items) and reference numerosity, the responses were plotted as function of the probe numerosity on a logarithmic scale and fitted with a cumulative Gaussian distribution, whose median estimates the Point of Subjective Equality (PSE).

An example of psychometric functions is shown in Appendix (A2). In our paradigm the connected dots were always the reference: underestimation of the reference results in a PSE below the true numerosity of the patch. The effect of connectivity was defined as:

$$connectivity = \frac{PSE_{connected}}{PSE_{isolated}} \times 100 \qquad \text{[Eq 4.1]}$$

The effect of item connection and numerosity were analyzed by two-way repeated measures ANOVA, conducted with Sigmaplot 12 for Windows (Systat Software, Inc, California, USA).

4.3 Results

Figure 4.1 shows examples of the patterns used in the experiments, both high and low densities with connected and unconnected dots, along with the amplitude spectra of the patterns: isolated dots in black, connected in red (on the right side). It is clear from inspection that connecting three dot-pairs (20%) of the low-density pattern (Figure 4.B) visibly reduces apparent numerosity, while the effect of connecting 20 dot-pairs at high densities (again 20%:

Figure 4.1E) is far less obvious. The Figures at right show the amplitude spectra of the patterns: isolated dots in black, connected in red. The amplitude spectra were calculated by Fourier analysis, which essentially decomposes the images into a series of sinusoidal waveforms, of different spatial frequencies, orientations and amplitudes. This analysis yielded two-dimensional amplitude spectra, which were averaged over all orientations to yield the one-dimensional amplitude plots of Figure 4.1C&F. At both densities the spectra are similar: amplitudes decrease with spatial frequency, similarly to most natural images (Field, 1989; Tolhurst, Tadmor, & Chao, 1992). There is also a clear dip in amplitude around 4 c/deg, largely driven by the size of the dots (0.3 deg diameter). Importantly, the spectra for the connected dots have higher amplitude over this high frequency range (4-6 c/deg). According to some previous studies (Dakin et al., 2011; Morgan et al., 2014), these patterns should appear more numerous than those with isolated dots.

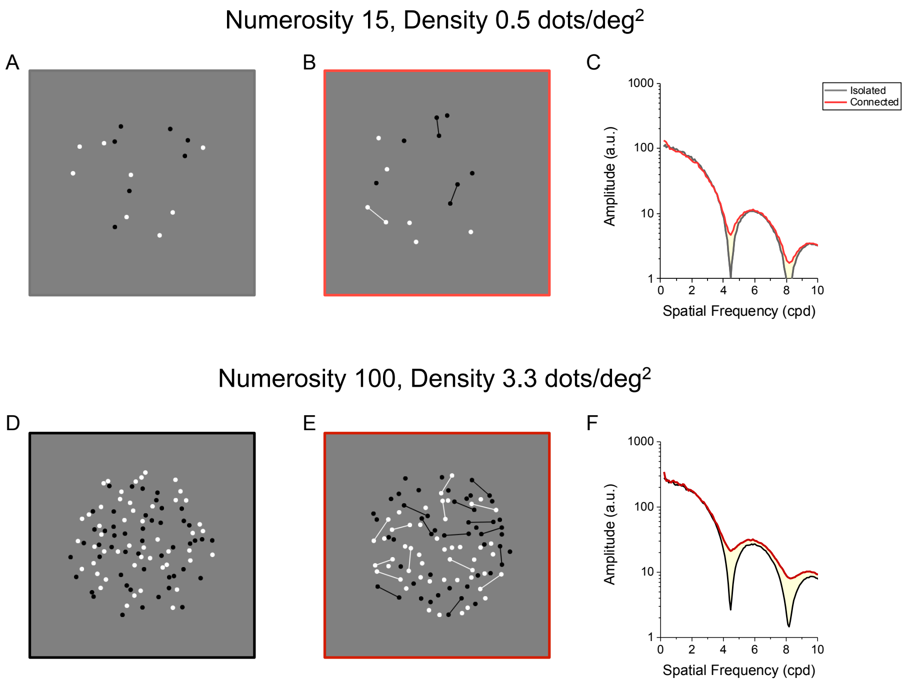

Figure 4.1 Illustration of stimuli and their Fourier transforms. Top row: Stimuli at low numerosity/density. **(A)** Sample patch containing only isolated dots (Numerosity=15, Density=0.5 dots/deg^2). **(B)** Stimulus of same numerosity but with 6 dots (40%) connected by thin lines. **(C)** Radial Fourier Spectra of the two patches: isolated dots (black), connectors (red). Note that the connected patterns have more energy at relatively high spatial frequencies, 4-6 c/deg. Bottom row **(D-F)**: Stimuli at high numerosity/density (Numerosity=100, Density=3.3 dots/deg^2).

The main analysis was performed on the data of individual participants. For each participant and condition, we fitted psychometric functions (for an example of a psychometric function see (Appendix, A2), from which we extracted estimates of PSE for the various conditions. The effect of connectivity from the PSEs for the connected and isolated dots (Eq 4.1) was then calculated. Figure 4.2

shows the results averaged over subjects as a function of numerosity and density. Figure 4.2A-B report the biases for the connected and isolated conditions, and Figure 4.2C the connectivity effect (Eq 4.1). In all cases, the data were obtained from averaging the PSEs of individual subjects, rather than from the aggregate subject. For both numerosity and density judgements, the isolated condition had almost no bias. And for both judgements, the bias of the connected stimuli decreased with numerosity. For numerosity judgments the bias remained negative for 100-dot stimuli, while for density the effect crosses over, so the connected patterns appear denser. These clear effects result in statistically significant interactions between numerosity and biases (two-way repeated measures ANOVA: $F_{(3,12)=}4.049$, p=0.033 and $F_{(1,4)=}44.548$, p=0.003 for numerosity and density tasks respectively). Figure 4.2C shows connectivity effect (difference between isolated and connected conditions) for the two tasks. Two way repeated measures ANOVA with factors Dot Number and Task revealed a significant main effect of dot number ($F_{(1,4)}=52.1$ p=0.002) consistent with the idea that the connectivity effect is modulated by stimulus density (number of dots).

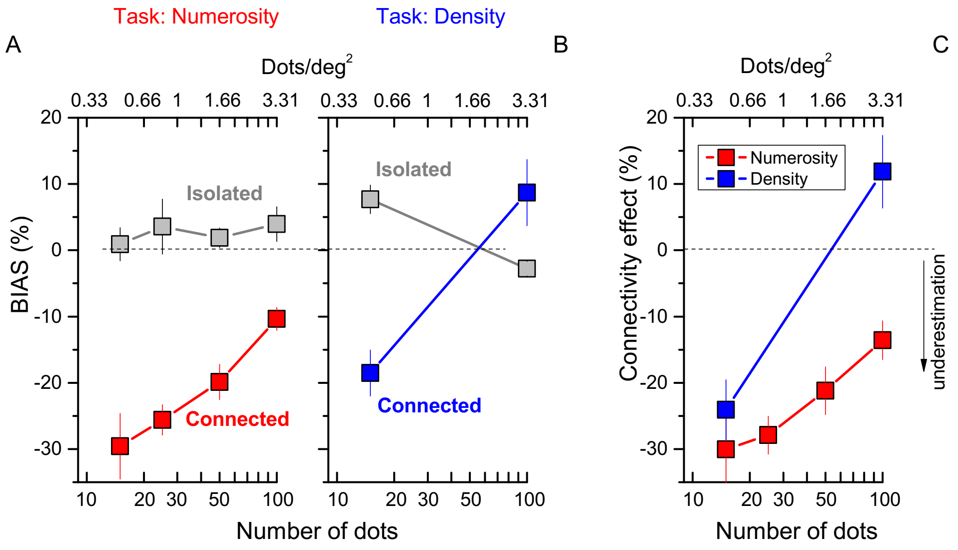

Figure 4.2 Bias and connectivity effect for both numerosity and density task. (A-B) Average PSEs expressed as percentage difference from the reference number/density levels (on the abscissae). The isolated dots condition (baseline) is reported in grey. Numerosity judgements for connected stimuli are shown in red, density judgments in blue. I Effect of connecting dots expressed as % difference from PSEs in the isolated and connected conditions.

4.4 Discussion

Here, we studied the effect of stimulus connectivity on numerosity and density judgments in adult subjects, for various dot densities. Previous studies showing that connecting items in the visual scene results in a strong and reliable underestimation of numerosity were confirmed (Fornaciai et al., 2016; Franconeri et al., 2009; He et al., 2009, 2015). We expanded these results to show that: 1) this effect is strongly reduced at higher numerosities; 2) when asked to judge density rather than numerosity, participants underestimated the density as well as the numerosity of stimuli with connectors for sparse patterns; 3) as for numerosity, the effect of connectivity on apparent density depends on item spacing: for sparse items, density was underestimated, switching to overestimation for denser stimuli. This study strengthens the idea that the Approximate Number System operates only when items are sparse enough to permit spatial segregation. After that limit, ANS gives way to another separate perceptual system responding to texture-density. We also suggest that for sparse stimuli, numerosity – but not element density – can be directly perceived, without being calculated indirectly from other perceptual features.

Chapter 5

Using attention to dissociate between numerosity and texture-density

5.1 Introduction

As shown in Chapter 3, the classical measures (RT and precision) that have been used for differentiating the subitizing from the estimation range also differentiate very dense from sparse arrays: reaction times are faster and thresholds are lower for vary large items in the texture density regime compared to segregable numerosities in the estimation range. Moreover, as demonstrated in Chapter 4, linking elements leads to overestimation of numerosities for very dense arrays but not for sparse ones in the estimation range (as it would have been if intermediate and large numerosities relied on the same mechanisms as suggested by Dakin et al. (2011)).

A further potential method for identifying different mechanisms is to examine the dependency on attention. It has been shown that depriving visual attentional resources leads to massive detrimental effects of performance thresholds in the subitizing range, but far less for larger numbers (Burr, Turi, & Anobile, 2010; Egeth, Leonard, & Palomares, 2008; Olivers & Watson, 2008; Railo, Koivisto, Revonsuo, & Hannula, 2008; Vetter, Butterworth, & Bahrami, 2008). The same differential effects of attentional load have been detected cross-modally: visual subitizing suffers greatly with both auditory and haptic distractors, while the estimation range is affected very little (Anobile, Turi, Cicchini, & Burr, 2012). Similarly, visual subitizing, but not estimation of larger numerosities, has been shown to be strongly impaired by concurrent visual working memory load (Piazza et al., 2011). These results have been interpreted as a signature of partially independent systems for subitizing and estimation regimes. Here we tested whether manipulation of attentional load can support the idea of different mechanisms for intermediate and very large numerosities, as well as it does for very small and larger numbers. This experiment investigates the effects of visual and auditory attentional load on a wide range of numerosities. I hypothesized different effects of deprivation of attention on intermediate and large numbers, supporting the idea of different regimes of number perception.

5.2 Methods

This experiment investigates the effects of visual and acoustic attentional load over a wide range of numerosities. Seven participants (2 males, mean age: 26; SD=2.08) with normal or corrected-to-normal vision were tested on the visual spatial attention task; 5 of these were tested on the auditory time bisection task (2 subjects did not give consent for the whole protocol). All subjects performed the single task control. All participants gave written informed consent, and experimental procedures were approved by the local ethics committee (Comitato Etico Pediatrico Regionale—Azienda Ospedaliero-Universitaria Meyer—Firenze).

5.2.1 Apparatus and stimuli

The experiment was run in a dimly lit room with stimuli presented on a 13-inch Macintosh monitor with 1440 x 900 resolution at 60 Hz refresh rate, mean luminance 60 cd/m^2. Subjects viewed the stimuli binocularly at distance of 57 cm from the screen. Stimuli were generated and presented under Matlab 9.1 using PsychToolbox routines.

The stimuli for the numerosity task were two dot clouds of 6° diameter centered 10° right and lefts of a central fixation point (Figure 5.1A). Each dot was positioned pseudo-randomly within the dot-cloud, respecting only the condition that two dots (center-to-center) could not be separated by less than 0.25°. In a particular session, one cloud of dots (the reference, randomly right or left) maintained the particular numerosity across trials, while the other (the probe) varied around this numerosity. The number of dots in the probe patch varied by the QUEST adaptive algorithm (Watson & Pelli, 1983), perturbed with a Gaussian noise with a standard deviation 0.15 log-units. In separate blocks 14 different reference numerosities were tested: 3, 6, 8, 12, 18, 24, 32, 50, 64, 75, 100, 125, 150 or 200. Probe numerosities were curtailed to be within one and 600.

The dot stimuli were presented for 500 ms, simultaneously with a visual or auditory distractor. The visual distractors (Figure 5.1B) comprised 4 centrally positioned colored squares (3° × 3°), which could take up eight color combinations. 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. The auditory interval discrimination task was an interval bisection of three 1300 Hz, 10 ms tones (Figure 5.1C). 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). Participants were asked to report (by appropriate key press) whether the second tone was temporally closer to the first or third tone.

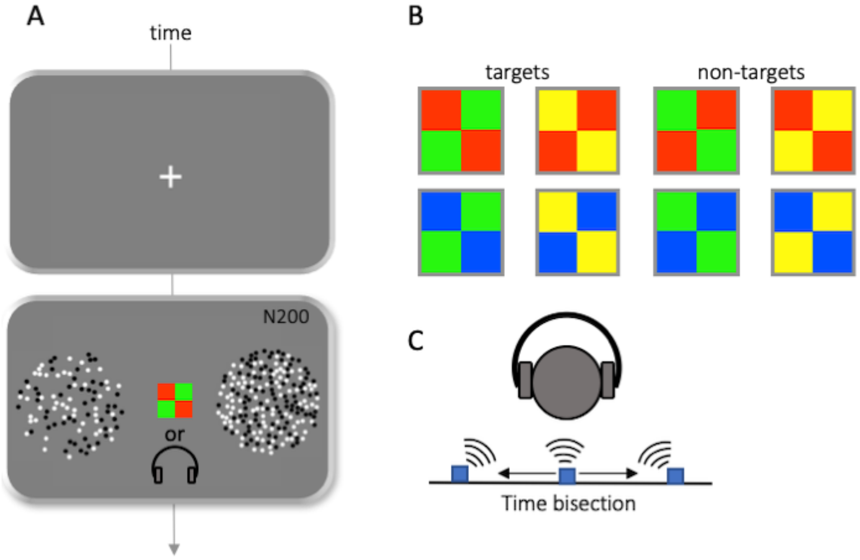

Figure 5.1 Example of the stimuli and distractor used. (A) Each trial started with a fixation point followed by two dot clouds, presented together with the distractor. Both lasted for 500 ms. In the dual-task condition, participants responded first to the distractor task then indicated which of the two clouds of dots seemed more numerous. In the single task they performed only the numerosity task (see Procedure for more details). **(B)** Conjunction stimuli displayed in the center of the screen for the Visual Distractor task. The stimulus was a target if it satisfied a specific conjunction of colors and orientations. **(C)** Time bisection judgment in the Auditory Distractor condition. Participants were asked to perform an interval discrimination task, judging whether the middle tone was closer in time to the first or the third tone.

5.2.2 Procedure

In the single task condition, participants were told to ignore the central distractor task and indicated which of the two peripheral dot-clouds contained more dots. In the dual-task conditions, participants first responded to the distractor task, then indicated which of the two arrays was more numerous. The order of tasks was pseudorandom across participants.

Before starting the experimental condition, all subjects performed 30 training trials, in which they were asked to judge if the central colored square was a target or not for the visual spatial attention task, or to report whether the second tone was temporally closer to the first or third tone for the auditory time bisection task (if 75% accuracy was not attained the session was repeated). In the main experiment, all trials started with a fixation point presented until the subject pressed a key to start the experiment, then the primary and secondary stimuli were presented for 500 ms. Participants were tested with 14 different reference numerosities levels. The order with which each numerosity was tested was pseudorandom across participants and attentional conditions.

Three sessions of 30 trials each were run for each numerosity level and each attentional condition, yielding a psychometric function for that condition. The function was plotted and inspected visually, to ensure that it was monotonically ascending and well behaved. We also checked the estimate of the standard error of the mean: if this was greater than 30% of the estimate of JND, we added another session of 30 trials. In practice this happened on only 4% of psychometric functions. On average, each participant ran 1260 trials.

5.2.3 Data analyses

For each participant, the proportion of trials where the probe appeared more numerous than the reference was plotted against the number of reference dots on logarithmic scale and fit with a cumulative Gaussian error function. The median (the numerosity corresponding to 50% responses left) gives the point of subjective equality (PSE), and the difference in numerosity required to pass from 50% to 75% correct responses defines the just-noticeable difference (JND), a measure of precision. JND divided by the reference numerosity yields the coefficient of variation (CV), a dimensionless index of precision that allows comparison of performance across numerosities. Where performance was errorless (often in the subitizing range in single task) JND was arbitrarily assigned as 0.001 dots.

Biases in PSE were tested by a series of Wilcoxon signed-rank tests (two tailed) comparing, separately for each numerosity (14 levels) and attentional conditions, PSEs shifts from the physical reference numerosity. The alpha level was Bonferroni-corrected according to 0.05/14 (0.0035).

To model numerosity-dependent changes in thresholds, CV versus numerosity curves above the subitizing range ($N \geq 6$) were fitted with two-segment piecewise linear fits, with slope of the first segment set to zero and the second free to vary. Standard Error estimates for all fit parameters were obtained by bootstrap resampling of subjects (10,000 reiterations) and fitting the data to the average group performance. The same iterations were used to calculate bootstrap sign-test p-values. Residuals of the two-segment function (3 parameters, baseline, knee point and high-numerosity slope) were compared to those of a simple linear fit (2 parameters) by means of Akaike Information Criterion (AIC). By definition Akaike Information Criterion of each model is:

$$AIC = 2k - 2\ln(\mathcal{L}) \qquad \text{[Eq 5.1]}$$

Where $\mathcal{L}$ is the maximal of the log-likelihood function and k is the number parameters in the model. The maximal of log-likelihood can be derived from the residual sum of squares according to the following formula:

$$\mathcal{L} = -\frac{n}{2}\ln(RSS/n) + C \qquad \text{[Eq 5.2]}$$

Where RSS is the residual sum of squares, n is the number of datapoints and C is a constant which depends solely on the data and does not vary from model to model. Overall, save for a common constant term $C + \ln(n)$, the Akaike information criterion of a model is:

$$AIC = 2k + n\ln(RSS) \qquad \text{[Eq 5. 3]}$$

The attentional cost was measured for each individual as the ratio between CVs in the single and dual task conditions. Statistical significance of the attentional cost within numerosity-range was measured by bootstrap sign test (BST) by resampling (10,000 times, with replacement) subjects and numerosities in the range (except for the subitizing where only one numerosity was tested). The proportion of times in which the cost was less than or equal to unity (null hypothesis) are taken as BST p-value.

The differential attentional cost between numerosity regimes was also measured by a similar procedure to yield average CVs for each numerosity range, which were then pitted against each other. By convention, reported p-values represent the proportion of times the attentional cost of the estimation regime exceeded that in the other regime (10,000 iterations).

5.2.4 Sample size

To determine the appropriate sample size, we ran two bootstrap power analysis for the two analyses on attentional costs. The first is a comparison of CVs of single and dual tasks within one numerosity-regime. To mirror our paradigm, we assumed each subject would be tested over a broad range of numerosities with a psychometric curve based on 90 2AFC trials at each numerosity. Given previous literature and the current choice of reference numerosities it is reasonable to assume that, at least three would fall in one regime and three into the other. Thus conservatively, we assumed that the measure of attentional costs within one regime would be based on the average CVs in three psychometric curves in single and dual task. Population variance was derived by previous literature (Burr et al., 2010; Tibber, Greenwood, & Dakin, 2012), and was assumed to be 20%. Lastly, we assumed that attentional costs to be detected would be a factor of 1.2 (less than half of the effect documented by Burr et al). Simulations demonstrated that a sample size of 4 subjects would be sufficient to return a true positive on 91% of the cases.

In the second power analysis we applied similar reasoning to comparison between the attentional costs across regimes. We assumed the attentional costs in the two regimes may differ by 25%, as a smaller difference would be of little importance. Simulations showed that 4 subjects were sufficient to detect such a difference with a power of 94%. Hence a sample size of 5 was deemed appropriate to address the experimental questions posed in the Chapter. Nevertheless, as replicability is important, we ran an addition study to replicate our main results, with an additional 9 naïve participants.

5.3 Results

We tested the effect of attentional load on numerosity perception over a wide range of numerosities. We first examined whether the attentional manipulations affected points of subjective equality (PSEs). We found no significant deviation from the physical reference numerosity (all $p>0.01$, two tailed Z-tests, corrected $\alpha=0.05/13= \sim 0.004$). However, this is to be expected as the probe and reference stimuli were randomized in position.

We then looked at sensory thresholds. Figure 5.2A-B plot average normalized discrimination thresholds (Coefficient of Variation, CV), separately for the two attentional conditions (visual and auditory), as a function of dot numerosity. The curves passing through the data are two-segment piecewise linear fits that exclude the subitizing range (≥6), the first of slope zero and the second free to vary. For the single-task condition, CVs are near zero in the subitizing range then rise to about 0.18 for numbers above 6, remaining constant over the estimation range. For numerosities higher than 60, CVs decreased steadily with numerosity, with log-log slopes of –0.65±0.07. The two-limbed function fitted the data better than a single linear function (taking into account the degrees of freedom), both in log-log (AIC –42 vs –15, fit residuals 0.02 L.U. vs 0.223 L.U.) and lin-lin coordinates (AIC –69 vs –56, residuals 0.0036 vs 0.0099). This reinforces the idea of two separate psychophysical regimes. Precision for the two attentional conditions also followed two-limbed functions, with log-log slopes of –0.47±0.07 and –0.65±0.17. Interestingly, the knee points for the two conditions (64±15 and 81±16 for visual and auditory) fell close to those of the single task condition (statistically indistinguishable, all p-value>0.1), indicating that the boundaries of the three regimes are similar in the two different conditions.

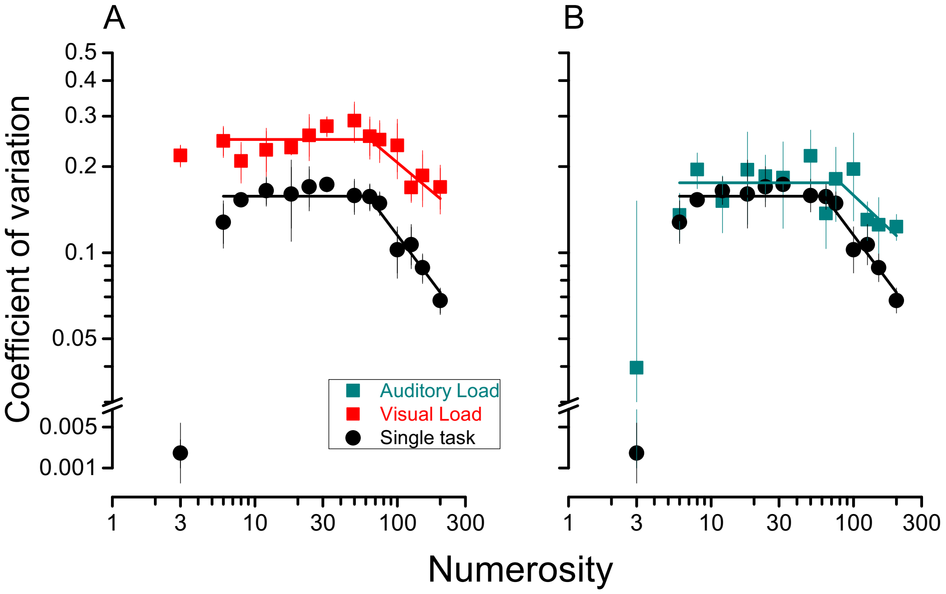

Figure 5.2 Precision for both visual and auditory load. (A-B) Mean CV (JND normalized by numerosity) as a function of target number, for the single task and the distractor conditions (A visual, B auditory). Visual attentional load strongly impairs precision in the subitizing range (4 and below) and also in the density-perception range (from 100 dots); a smaller but similar effect occurs for the auditory load condition.

5.3 The effect of visual and auditory attentional load

To examine more closely the effects of visual and auditory attention we calculated the visual and auditory attentional costs as the ratio of the dual to single CVs (Figure 5.3). At low numerosities (N<6), the visual dual-task raises CV from ~0 to 0.22, a factor of 121 (BST $p < 0.001$), and the auditory task by a factor of 11.2 (from ~0 to 0.039, BST $p = 0.018$). In the estimation range (6<N<60) the visual dual-task had less effect than in the subitizing range, raising CVs from 0.16 to 0.25 (a factor of 1.6, BST $p < 0.001$). The auditory dual task had negligible impact on CVs in this range (factor of 1.02, BST $p = 0.5$). In the texture density regime (N>75), attentional costs rose again (visual dual task a factor of 2, BST $p < 0.001$, auditory dual task a factor of 1.58, BST $p = 0.036$).

Bootstrap t-test on attentional costs revealed that the effect of the dual tasks in the three regimes were different from each other. In particular, the cost in the estimation and density-regime differed both for the visual distractor ($p = 0.037$) and the auditory distractor ($p = 0.005$). The attentional cost in the subitizing range was markedly higher than in the estimation range ($p = 0.0006$, visual distractor; $p = 0.047$, auditory distractor).

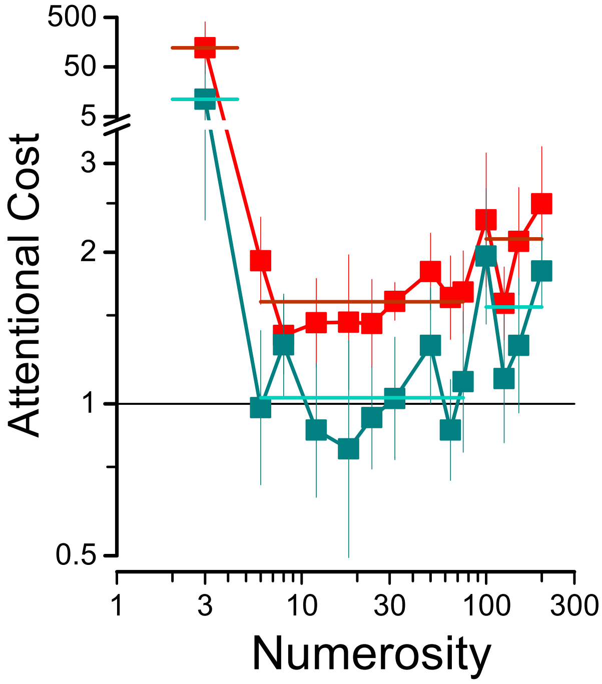

Figure 5.3 Attentional cost for both visual and auditory load. *Attentional cost (precision in the dual-task condition divided by the precision in the single-task condition). Numerosity precision was more affected by visual (red) that auditory load (cyan). The continuous lines show the mean per range for both the conditions, showing the mean over that range: subitizing (up to 3); estimation (up to ~80); and texture density (up to 200).*

To verify that the differences of attentional costs between ranges did not result from a change in the resources allocated to the primary task we calculated the average accuracy in the three regimes for both types of distractor: performance on the distractor visual task was 92%, 96% and 96.2% respectively for subitizing, estimation and density-perception; and 98%, 97% and 97% for the three regimes for the auditory distractors. Bootstrap t-tests revealed that none of these was statistically significant (all $p > 0.15$).

5.4 Replication

Replicability is important. We therefore ran a replication study on nine new naïve participants to verify the main results of this study: that attentional costs were different for the three regimes of numerosity perception. We tested three sample numerosities, representative of the subitizing, estimation and texture ranges: 3, 24 and 150. Figure 5.4 shows that this supplementary study replicated completely the main result. For the visual distractor (Figure 5.4A), the greatest cost was in the subitizing range, a factor of 6.75, supporting this and previous research (Anobile et al., 2012; Burr, Turi, & Anobile, 2010; Burr, Anobile, & Turi, 2011). Similarly, the attentional cost in the texture range was more than twice that of the numerosity range, a factor of 3.04 compared with 1.25. This difference was highly significant (one-tailed t-test: $t(8) = 6.278$, $p = 0.0013$). The trend of results with the auditory distractor (Figure 5.4B) was similar, although the effects were weaker. The attentional cost was highest for subitizing (7.8), and higher for texture than for estimation (1.6 and 1.19 respectively). The difference between texture and estimation, while smaller than that for vision, remained significant (t(8) = 2.89, p = 0.015).

Figure 5.4C shows the individual results. For all nine subjects, the attentional cost of the visual task was higher in the texture than the estimation range; the cost of the auditory task was in general much less, but for seven out of nine subjects greater in the texture condition. Thus, the trend of the main results was amply confirmed on replication.

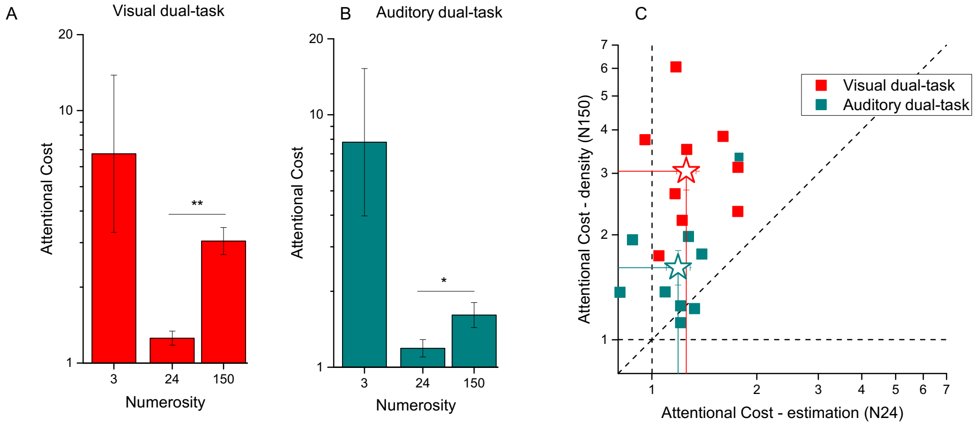

Figure 5.4 Replication study. (A-B) Geometric average of attentional costs (ratio of dual-task to single-task thresholds) measured on nine new participants for three representative target numbers (N3 for subitizing, N24 for the estimation range and N150 for the density range). Stars show significance (one-tailed paired t-tests): * $p < 0.05$; ** $p < 0.01$. **(C)** Attentional costs in the density range plotted against that for the estimation range, for all nine participants (square symbols). Stars show geometric means.

5.5 Discussion

This study tested the effects of visual and auditory attention on a wide range of numerosities spanning from the subitizing range to very large numbers. The effect of attentional deprivation has been usually used as a tool to study the dichotomy between subitizing and estimation. Here, we provide further evidence for separate mechanisms for intermediate and very large numerosities by investigating the role of visual and auditory attentional resources on discrimination thresholds over all the three suggested ranges (subitizing, estimation and texture-density). We first replicated earlier study showing different psychophysical laws for thresholds in the three regimes. In the baseline condition, as expected, discrimination thresholds were near zero in the subitizing range, obeyed Weber's law for intermediate numerosities, then decreased with a square-root law for denser stimuli. Attentional load changed completely this pattern of results. As previously shown for magnitude estimation tasks, attentional load greatly affected the subitizing range, to the extent that thresholds became similar to those of the estimation range (Burr et al., 2010), implying the existence of two separate but partially overlapping systems: estimation mechanisms, which probably extend into the subitizing range (Burr, Anobile, & Turi, 2011), supplemented by the attention-dependent subitizing system. When subitizing is compromised by depriving attention, estimation remains possible and yields similar coefficients of variation to the estimation range.

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Attentional load (visual and auditory) had a greater effect on subitizing than estimation and increased again at higher densities. Numerosities higher than 60-80 dots were more affected by attentional load (both visual and auditory) than lower (non-subitizing) numerosities. This major result was confirmed on replication of key numerosities with an addition nine naïve participants. These results reinforce suggestions for a third regime of numerosity perception.

Chapter 6

Effect of location and object-based attention on number estimation

6.1 Introduction

There is increasing evidence highlighting the role of visual attention in enumeration, in particular for small numerosities. Depriving visual attentional resources with a concomitant visual or auditory dual task leads to large detrimental effects in the subitizing range, but far less for larger numbers (Burr et al., 2010; Egeth et al., 2008; Olivers & Watson, 2008; Railo et al., 2008; Vetter et al., 2008). The results in Chapter 5 demonstrate how depriving attention leads to different outcomes for intermediate and very large numbers, further evidence in favor of the distinction between estimation and texture density mechanisms.

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, 2011; Butterworth & Walsh, 2011; Dehaene, 2001). Experimentally, this is usually 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, Izard, Spelke, & Pica, 2008; Geary, Hoard, Nugent, & Byrd-Craven, 2008). 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 centers of the numberline (Barth & Paladino, 2011).

In addition, the capacity to map number onto space requires attention: merely looking at numbers causes a shift in covert attention to the left or right side, depending on number magnitude (Fischer, Castel, Dodd, & Pratt, 2003). Anobile et al. (2012) showed that deprivation of attention causes strong non-linearities in numberline-mapping. While this is consistent with a logarithmic compression, they pointed out that it is also consistent with "regression to the mean". Hollingworth (1910) noted that judgements of almost all properties – size, duration, speed etc – tend to regress towards the mean. This tendency has been modelled within the Bayesian framework, where the mean is considered to be a prior (Anobile, Cicchini, & Burr, 2012). The authors modeled the effects attention deprivation on reproduction judgments as a Bayesian model of central tendency. 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 center of the numberline (while the lower number remain anchored). They also used the same model to investigate the role of cross-modal attention in mapping number into space. They showed 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 (Anobile et al., 2012). They also pointed out that the nonlinear representation of number onto space (under conditions of deprivation of attention) does not necessarily reflect the action of a static logarithmic transformation. In a subsequent study, they showed that the response to the current trial was well correlated with the magnitude of the previous stimuli, suggesting that subjects compute a weighted average of current and recent stimuli. In this view, mapping number into space seems to be more a dynamic process that incorporates past history into numerosity judgments (Cicchini et al., 2014). This evidence reveals a strong connection between the representations of numbers, space, and the deprivation of attentional resources.

Nevertheless, only one study has so far investigated the role of increasing attentional engagement in a number task. The authors demonstrate that enhancement of attention through an alertness paradigm can improve subitizing processes. To a lesser extent the improvement also occurred in the estimation (from 5 to 9 elements) range, particularly when elements were presented in a canonical arrangement (Gliksman, Weinbach, & Henik, 2016).

Here I used a cueing paradigm to increase the attentional engagement during enumeration of intermediate numerosities. Taking advantage of the contribution of both object- and location-based attention, I hypothesized that enumeration of quantities would benefit from focusing attention on a specific location, and that the advantages found there would spread to the whole object to which the cue had been presented. This should lead to faster, more accurate and precise estimations compared to when attention needs to be shifted to a different object. Moreover, I also explored the possibility that, especially in the condition of switching attention to a different object, the spatial representation of number would show a non-linear compression resulting from a central tendency like that described by previous works (Hollingworth ,1910) for many sensory judgments, which we model within the Bayesian context.

6.2 Methods

Using a visual cue paradigm, this experiment examines whether enumeration performance can be modulated by allocating attention to a specific location previously cued and by the shift in attention from the previous cued location to the whole cued object. Fifteen subjects (mean age: 22.26; SD: 3.61) took part in the study. All the informed consent forms were obtained from participants in accordance with the Declaration of Helsinki. Since twelve participants were recruited at Johns Hopkins University (Baltimore, MD) and three from the University of Florence (Florence, IT), the experimental protocol was approved by both the Institutional Review Board of Johns Hopkins University and the Italian regional ethics committee (Comitato Etico Pediatrico Regionale—Azienda Ospedaliero-Universitaria Meyer—Florence).

6.2.1 Apparatus, stimuli and procedure

Stimuli were generated using MATLAB software together with the Psychophysics Toolbox extensions (Brainard, 1997) and displayed on an LCD monitor driven by a Macintosh iMac computer (with a resolution of 1920x1080 pixels, refresh rate = 60 Hz). The subjects were seated approximately 50 cm from the screen and viewed the display binocularly. The displays comprised a pair of adjacent black rectangles oriented either vertically or horizontally with equal probability. Each rectangle (4.8° x 18.2°) was centered 4.81° from fixation. The fixation was a white cross (0.48° x 0.48°). The cue (three 4.8° x 0.28° white lines, overlapping one end of a rectangle) and the target, consisted of a collection of dots displayed in a circular region of 4°, were located at the end of the two rectangles. The background of all displays was grey. Default diameter of the dots was 0.25° end the maximum variability in size between dots was ±31%.

As previous research has found that non-numerical aspects of an array can affect numerical performance (Clayton, Gilmore, & Inglis, 2015; Gebuis & Reynvoet, 2012b; Smets, Sasanguie, Szücs, & Reynvoet, 2015), on half of the trials the two arrays were equated for individual dot size (i.e., the average size of the dots in each collection was equal), and on the other half the cumulative surface area of dots was equated. The minimum distance between dots was 0.15°. Dot position was randomly determined with the constraint that dots never overlapped.

Each trial began with a fixation display comprising the central cross and two rectangles from 500 to 1000 ms, to avoid subjects predicting the onset of the cue. Following the fixation display, the cue was presented for 100 ms and then replaced by the fixation display for another 200 ms. The target comprised a cloud of yellow dots and was presented for 200 ms followed by a number line with extremes of 1 and 35, which extended 56° (Figure 6.1)

At the beginning of the session participants pressed the space bar when ready. They were asked to fixate on the central cross throughout each trial, and to position and click a mouse pointer on the position of the number line corresponding to the estimated numerosity. Participants ran 4 blocks of 150 trials each, with numerosities ranging from 5 to 30, presented in random order.

Each block consisted of 75% of valid trials, in which the cue and the target (cloud of dots) appeared in the same location (Valid same location, VSL); 25% of trials in which the cue and the target did not appear in the same location: 12.5% of trials the target appeared in the cued object but at a different location (Invalid same object, IS), the other 12.5% the target appeared in the un-cued object but equally distant from the cue (Invalid different object, ID).

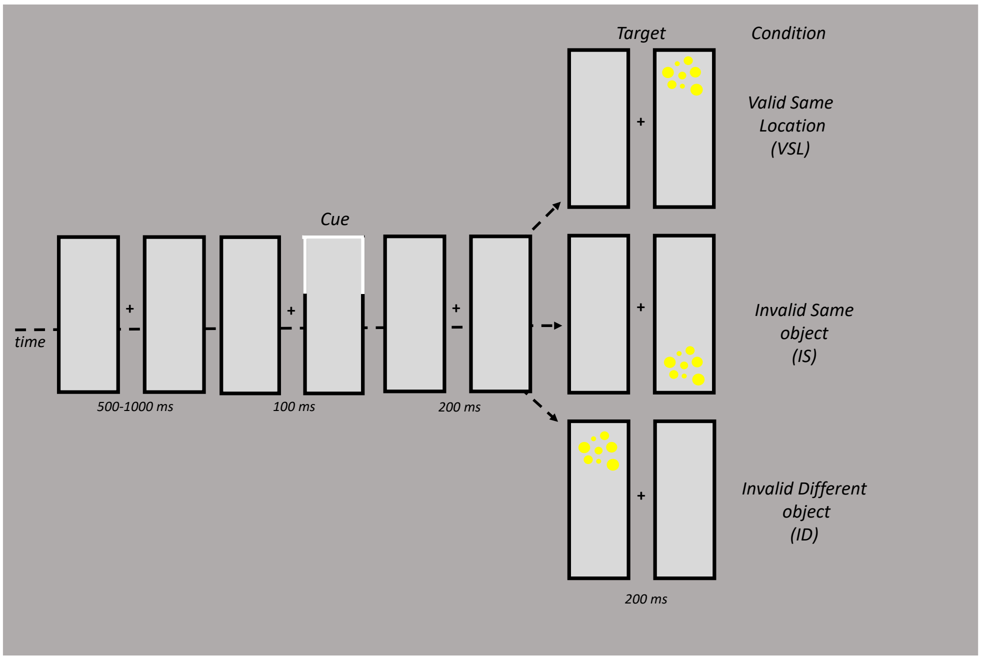


Figure 6.1 Schematic illustration of the stimulus sequence. At the beginning of the session participants pressed the space bar when ready. A fixation display stayed on for 500 – 100ms, a cue appeared for 100 ms followed by a fixation display and then a collection of dots could appear in the previously cued location (VSL) or in the cued object but at a different location (IS) or in the uncued object but at the same distance from the cue (ID).

6.2.2 Data analysis

For each participant, data that exceeded ±2 std from the mean of number estimates and the first 20 trials of each session (treated as training) were excluded.

In order to estimate the slope, intercept and sigma of each subject estimates we used a maximum-likelihood estimation approach, using an R-based package (PsiMLE, Odic et al., 2015). This method maximizes the parameters that fit the normal distribution CDF (cumulative distribution function), with intercept (**α**), slope (**β**) and an extra parameter **σ** that describes the variability of the estimates of each dot quantity given the actual dot quantities (N) and participants responses (R) with a likelihood function:

$$L(\alpha, \beta, \sigma | N, R) = \prod_{k=1}^{n} \frac{1}{\sqrt{2\pi(\alpha+\beta*N_k*\sigma)^2}} \exp\left(-\frac{(R_k-\alpha+\beta*N_k)^2}{2*(\alpha+\beta*N_k*\sigma)^2}\right). \qquad \text{[Eq 6.1]}$$

Here, *N* corresponds to the number of dots presented (ranged from 5 to 30), **α** corresponds to the intercept of the linear regression, **β** corresponds to the slope, **σ** corresponds to the linearly increasing scalar variability (equivalent to CV, coefficient of variation), and *R* corresponds to participants' number response on the number line. PsiMLE simultaneously estimates all three parameters of interest. We fitted each participant's estimates with the best fitting power function and obtained the corresponding three parameters of interest (exponent, scaling factor and variability). We first removed outliers from the estimates of each dot quantity for each participant. For all the trials with the same dot quantity, the estimates that were more than two standard deviations above or below the mean were removed.

In order to calculate the person's perceived dot quantity of each actual numerosity tested, we used each participant's best fitting power function:

$$Y = \alpha x^{\beta} \qquad \text{[Eq 6.2]}$$

where α is the scaling factor, x the actual numerosity tested and β the exponent. Then, we used these estimates to calculate the average perceived dot quantities across our entire sample that are listed in Table A3 (Appendix, A3).

We separately analyzed mean reaction times. Following the standard practice in the literature on cueing paradigm, data that exceeded 2 std from the mean and reaction times less than 150 ms were removed from the analysis.

We conducted all the analyses separately for the three different positions of cue and target: Valid same location (VSL), in which the target (cloud of dots) appeared at the same location of the cue; Invalid same object (IS), in which the target appeared in the same cued object but at a different location; and Invalid different object (ID), in which the target appeared in a different object than the cue.

6.3 Results

6.3.1 Accuracy

Figure 6.2 shows average accuracy in estimating dot number. Here the mean numerosity estimates are plotted as a function of the actual numerosity, for the three different conditions (VSL in dark green; IS in blue; and ID in red). The average data from each condition are fitted with a power function (Eq 6.2), pooling together responses from all participants, separately for each condition. The continuous curves show these fits (values of exponents in caption).

We also fitted the data of individual participants with the same equation. The average exponents of the individual fit of the power function (**β** of Eq 6.2) were respectively 0.68 (sem=0.03), for the VSL condition; 0.63, (sem=0.03)for the IS condition; and 0.51, (sem=0.02) for the ID condition (showed in the bar graph right side of the Figure 6.2). The exponents reveal the non-linearity of the relationship, with 1 corresponding to a linear relationship and lower values to progressively increasing compressive non-linearities.

We then tested for significant differences in the exponents with a one-way ANOVA. Within-subject factor cue validity revealed a significant effect of cue on non-linearity ($F_{(1,43)} = 6.92$; p=0.01), with the response to validly cued targets more linear than that for invalidly cued targets. Post-hoc comparisons showed a significant difference in non-linearity between the condition in which the target appeared in the cued object but in a different location compared to the condition in which the target appeared in a different object (t=2.57; p_{tukey}=0.03), and a further significant spatial cuing effect with VSL trials being more linear than ID (t=3.7; p_{tukey}=0.002), but not significantly more linear than IS trials (t=1.13; p_{tukey}=0.49).

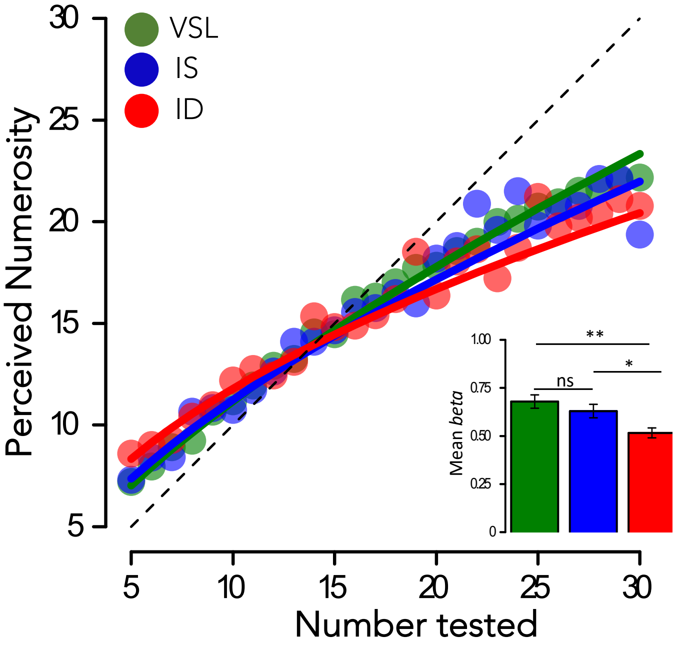


Figure 6.2 Relation between number presented and participants' estimates separately for the three conditions (valid same location in green, invalid same object in blue and invalid different object in red) . Continuous lines represent the power fitting function, with exponents of 0.68, 0.63, and 0.50 respectively for the VSL, IS and ID condition. The small insert on the bottom right side shows the mean exponents of the power function (**β**). Significance values refer to post-hoc comparisons (*p<0.05, **p<0.01, ns p>0.05).

6.3.2 Precision

We used the PsiMLE package to calculate the variability (***σ***) estimations. We found a strong effect of cue validity ($F_{(1,43)}$=7.09 p=0.01), with performance on valid trials being more precise than invalid trials overall. Mean estimation variabilities for the three conditions are presented in Figure 6.3: sigma increases as the attention is diverted from the cued location to the un-cued object, yielding to less precise estimation. In particular we found (post-hoc comparisons) a less precise estimation for ID trials, compared to both VSL (t=3.65; p_{tukey}=0.002) and IS (t=2.44; p_{tukey}=0.04) trials. Again, presenting the target in the previous cued location or in the cued object did not affect subject' precision (t=1.21; p_{tukey}=0.45). A very similar pattern of results was observed when we calculated another index of precision, the coefficient of variation (CV). The coefficient of variation was obtained dividing the raw responses for the actual number tested and then computing the standard deviation (SD) for the three condition separately. Again, we found a strong effect of cue validity ($F_{(1,43)}$=6.57; p=0.003). In particular, CV measure show a significant difference between VSL and ID trials (post hoc comparisons, t=3.56; p=0.003) and between IS and ID trials (post-hoc comparisons, t=2.36; p=0.05). Moreover, we found no difference between VSL and IS trials (post-hoc comparisons, t=-1.2; p=0.45).

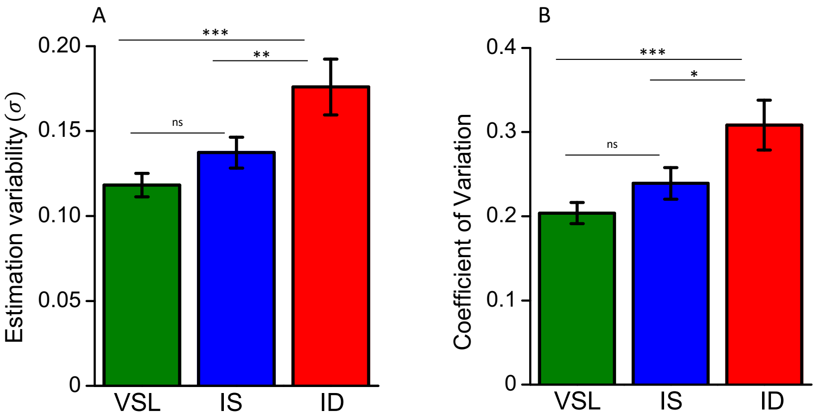


Figure 6.3 Precision measures. **(A)** Estimation variability (σ)obtained from the PsiMLE package. **(B)** Coefficient of variation (CV). Both the measures of precision show an increase as the attention is diverted from the cued location to the un-cued object. A. Significance values refer to post-hoc comparisons (*p<0.05, **p<0.01, ns p>0.05).

Overall, both measures of precision confirm the hypotheses that estimation of numerosity is improved by the spread of attention within the all cued object, to the expenses of the object outside the focus of attention.

6.3.3 Reaction Times

Since the previous literature on location- and object-based attention have focused on the differences in reaction times between the condition tested (suggesting a reaction time advantage for target presented in the same previously cued location or the same previously cued object compared to the uncued object), we also analyzed subjects' reaction times in computing the responses on the number line.

Data in Figure 6.4 shows averaged reaction times calculated for each participant and each condition. We submitted the data to one-way analysis of variance (ANOVA) with a within-subjects factor of cue validity. The analysis revealed a main effect of cue validity ($F_{(43,1)}$= 5.44; p=0.02): RTs for validly cued targets (mean±SD= 1.07 sec; 0.14) were faster than those for invalidly cued targets (mean±SD= 1.2 sec; 0.18), resulting in an overall validity effect of 12ms. Data from the invalidly cue conditions were then subjected to a one-way ANOVA in order to reveal the effects of the single conditions. Post-hoc comparisons showed a significant 0.19 ms cueing effect (t=3.44; p_{tukey}=0.004), with valid same location RTs (mean±SD= 1.07; 0.14) being faster than invalid different object (mean±SD= 1.27; 0.20). The cue, also, led to faster responses when the target appeared at the cued object (IS) than un-cued object (ID) (t=2.58; p_{tukey}=0.03), with a 0.14 ms advantage. These results suggest that estimation of numerosities suffers from the shift of attention to one cued object to another un-cued object, leading to slower reaction times in computing the estimation (same-object advantage). Moreover, a comparison between the VSL and IS revealed that participants reaction times were not significantly faster when the target appeared at the cued location compared to the cued object (t=-0.85; p_{tukey}=0.67). It may be that both location-based and object-based cues are informative, and that attention spread from the cued location to the whole object.

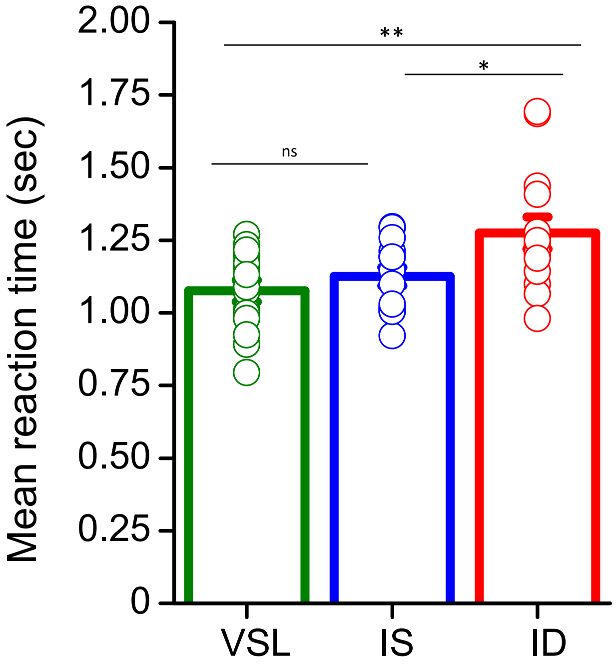


Figure 6.4 Mean reaction times for the three conditions. The bars show the averaged reaction times, and the symbols the individual data of each participants each condition (Valid same location, in green; invalid same object in blue; invalid different object in red). Significance values refer to post-hoc comparisons (*p<0.05, **p<0.01, ns p>0.05).

6.3.4 Bayesian model

To explore the possibility that the non-linear compression of the spatial representation of number could result from dynamic temporal context, producing regression to the mean, we modelled our numberline mapping with a Bayesian model similar to that used by Anobile, Cicchini, and Burr (2012), which assumes that subjects base their performance on an estimate that combines both their sensory estimates and an *apriori* hypothesis about the stimulus.

Bayes' rule states that:

$$p(R|N) \propto p(R)p(N|R) \qquad \text{[Eq 6.3]}$$

where R is the response and N is the numerosity of the stimulus. $p(N|R)$ is termed the *likelihood*, $p(R)$ the *prior* and $p(R|N)$ the *posterior*. We model likelihood with a gaussian distribution centered on the stimulus, whose width is estimated from the variance of the estimates, averaged over participants. The *prior* is also modelled as a gaussian distribution centered on the mean of the stimulus range, with standard deviation free to vary to best fit the data. (Figure 6.5)

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

$$\emptyset p(R|N) \propto \varphi\ (x)(\mu_{R,}\ \sigma_{\mathbf{R}}^{2}\ )\ \varphi\ (x)(\mu_{p,}\ \sigma_{\mathbf{p}}^{2}) \qquad \text{[Eq 6.4]}$$

where $\varphi(x)$ indicates the gaussian function, whose center is given by a weighted average of the centers of the likelihood and that of the prior. The resulting distribution is itself a Gaussian probability density function, whose mean will be between the sensory estimate and the central prior with standard deviation ωN.

The extent to which the prior draws the results towards the mean depends on the relative widths of the prior and sensory likelihood functions. As the width of the sensory pdf increases with N, the effect will be stronger for large than for small numerosities, resulting in a compressive function.

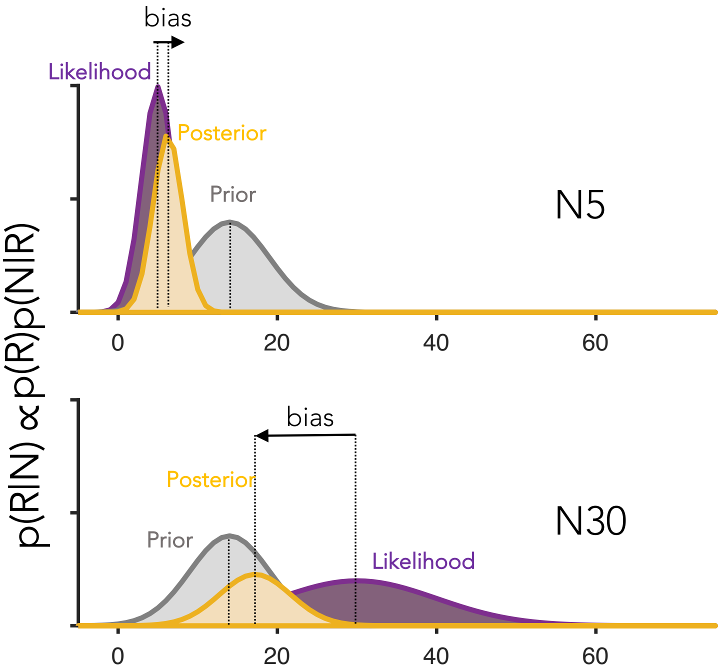


Figure 6.5 Illustration of the central-tendency model of non-linear mapping. Probability density functions for *likelihood*, *prior* and *posterior* (Eq 6.3), for two physical displays of 5 or 30 dots to be mapped onto a 1–75 numberline. For all three numberlines, the prior is a Gaussian pdf centered at 14 dots on the number line with standard deviation of 5 (determined by best fit to data). The likelihood was also Gaussian, centered at the physical number *L*, with standard deviation increasing with N (3 at N=5 and 6 at N=30). The posterior is the product of the sensory likelihood and the prior. If the prior is closer to the center of the test range, the posterior will be biased towards the center of the distribution. The strength of the bias depends on the relative uncertainty of likelihood and prior. As the standard deviation of the likelihood for larger magnitudes increases, the bias towards the prior also increases.

The data were fitted by a simple model based on the principle illustrated in Figure 6.5. Specifically, the predicted estimation of numerosity $\hat{R}$ was given by:

$$\hat{R} = \frac{N\sigma_{prior}^2}{\mu\sigma_{lik}^2 + N\sigma_{prior}^2} \qquad \text{[Eq 6.5]}$$

Where N is the numerosity; σ_{prior} the width of the prior, which was the only free variable; σ_{lik} is the root variance of the likelihood, calculated from the data. The measured standard deviations were fit (separately for the three conditions) with a power function of exponent 0.5, corresponding to a square-root fit. This fit, derived from the actual data, was used as the best-predictor of the root variance of the likelihood. The only parameter free to vary was the root variance of the prior. Best fits of the data were obtained with prior width of 17 dots.

The fits, shown in Figure 6.6, capture the data well. In the condition of VSL and IS both the data and the fits of the numberline are quite linear (dark green and blue continuous lines), while for ID trials (red line) data and the fit show a clear compressive non-linearity, as previous observed (Anobile et al., 2012).

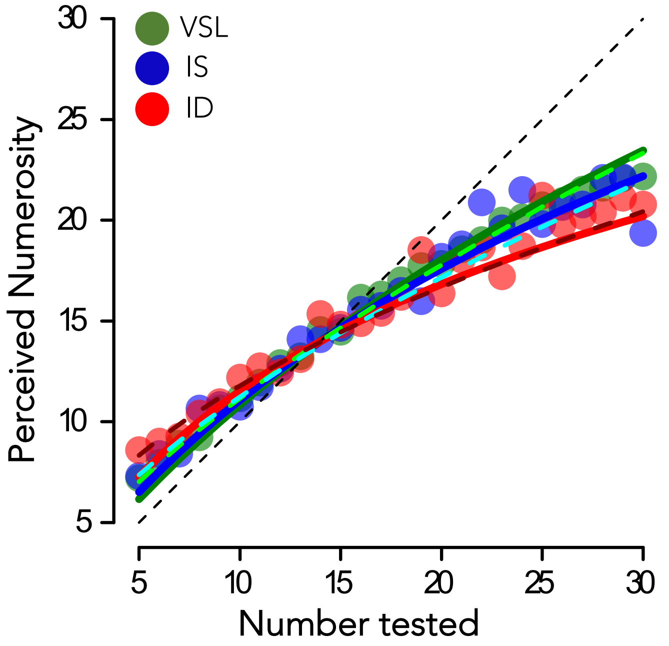
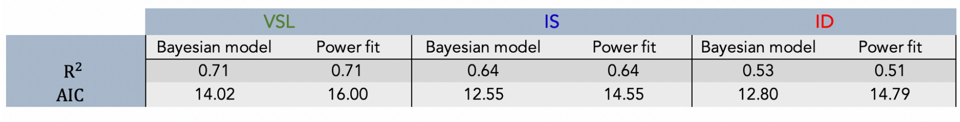


Figure 6.6 Mean perceived numerosity as a function of number tested (valid same location in green, invalid same object in blue and invalid different object in red). Continuous lines represent the Bayesian model of central tendency while dashed lines represent the power fitting function.

Fits were assessed calculating the coefficient of determination, R^2: 1 minus the ratio between the Explained and the total variance. The fit for the Bayesian predictions (continuous lines), with only 1 degree of freedom, were as good as the power function (with two degrees of freedom). Table 6.1 reports the R^2 for the two fits and also the means of Akaike Information Criterion (AIC). The formula used here is the same of Chapter 5 [Eq 5.1]). Overall, for all the three conditions tested the Bayesian predictions resulted to be ~3 times more probable to minimize the information loss than the power function.



	VSL		IS		ID	
	Bayesian model	Power fit	Bayesian model	Power fit	Bayesian model	Power fit
R^2	0.71	0.71	0.64	0.64	0.53	0.51
AIC	14.02	16.00	12.55	14.55	12.80	14.79

Table 6.1 R^2 of Bayesian and MLE fits and AIC. Coefficient of determinations for the three different conditions separately. Both the fits capture the data well. Residuals of the Bayesian model of central tendency were compared to those of the MLE by the means of Akaike Information Criterion (AIC). The formula used was the same of Chapter 5 [Eq 5.1].

The Bayesian model predicts explicitly that the magnitude of mapping distortions should depend on sensory noise level. We therefore looked at the correlation between model outcome and individual sensory thresholds. Figure 6.7 shows the relationship between non-linearity strength and discrimination thresholds. As predicted, subjects with higher discrimination thresholds also had higher non-linearity ($r = 0.45$, $p = 0.002$). Furthermore, it is possible to predict the amount of non-linearity of an ideal observer model.

To compute the fit, we used the model outlined in Cicchini, Anobile, & Burr (2018) which simulates the behavior of an ideal observer who blends current noisy sensory information with a central prior. Given that the current sensory likelihood is characterized by a certain precision level σ_L and that the central prior is also associated with a given uncertainty level σ_P and given that σ_L depends on numerosity and follows Weber's Law:

$$W_L = \frac{\sigma_P^2}{x^2 * WF^2 + \sigma_P^2} \qquad \text{[Eq 6.5]}$$

The Bayesian model, with just one degree of freedom (width of the prior), fitted the data well, both qualitatively (capturing the undulation of the data) and quantitatively, with coefficient of determination $R^2 = 0.15$. This suggests that the notion that the non-linearity in the mapping of number to space is well explained by the Bayesian model simulating regression to the mean.

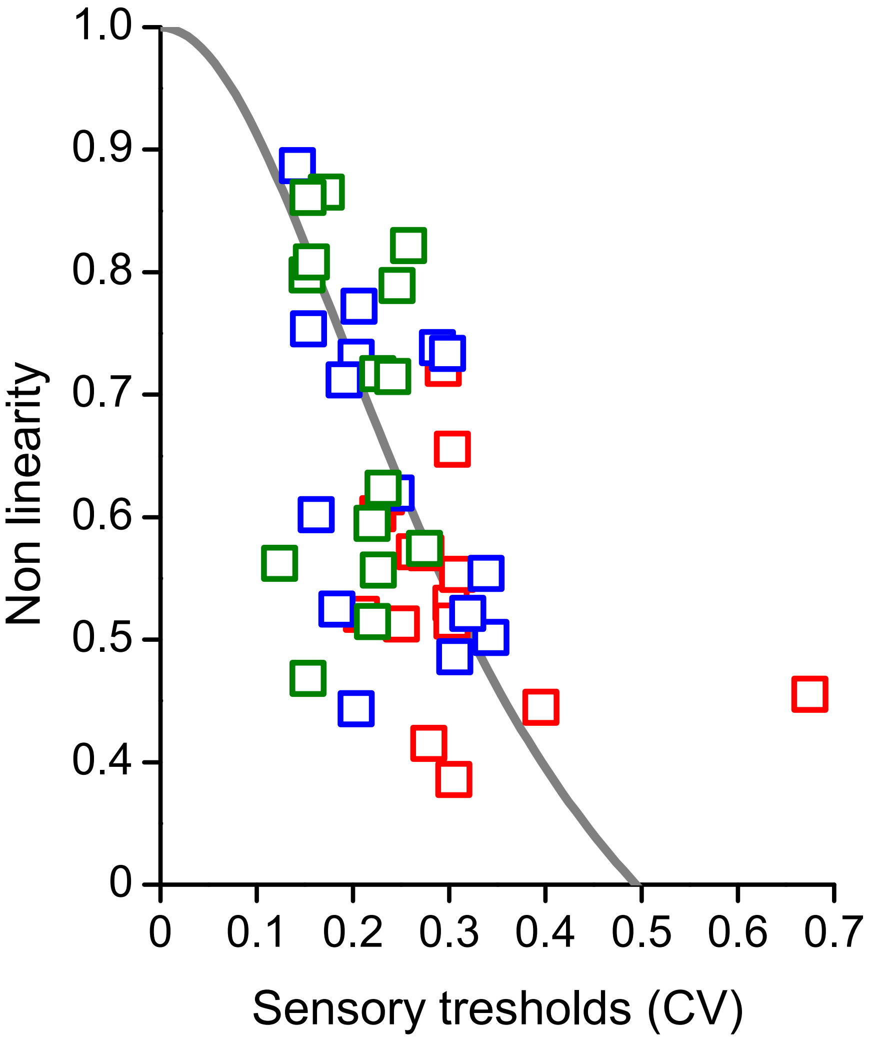


Figure 6.7 Non-linearity index plotted against sensory thresholds (CV). The grey curve shows Bayesian model predictions (see Eq 6.5); color coded squares refer to the different condition tested (valid same location green; invalid same object blue and invalid different object red).

6.4 Discussion

The present study aimed to examine the role of attention in enumeration process. Previous studies (including the experiment of Chapter 5) showed that when attention is disengaged from a numerosity task, the subitizing process is impaired. Much less impairment was found in the estimation process (see Figure 5.3). Here, we examined whether presentation of a visual cue that increases attentional engagement in a given task can facilitate the estimation process, leading to less compressive representation of number into space compared to when attention is diverted elsewhere. The results revealed that enumeration of a collection of dots in the location previously cued led to more precise and accurate judgements than enumeration in uncued locations. In particular, the visual cue facilitated the estimation process when both the cue and the target was presented in the same previously cued object.

Since the classical literature on object and location-based attention has tended to examine the effects of attention by measuring participants' reaction times, we also calculated the time participants took to report their responses on the number line. Consistent with previous findings, reaction times were faster when the target appeared in the previously cued location compared with uncued locations, with an advantage also when the target was presented in the cued object compared to uncued object.

Findings of previous literature on the contribution of object and location based attention have pointed out two main effects: a spatial cueing effect and a same-object advantage (the first referring to advantages in detecting the target when it appears in the cued location; and the latter referring to advantages in detecting the target when it appears in the cued object rather than the uncued object). Here, we first demonstrated that these results expanded to the extraction of higher level information, such as number estimation, and we also demonstrated that numerosity benefits from the availability of both location and object-based attentional resources. In particular, the same-object advantage found here suggests that attention to number seems to spread from the cued location to the whole cued object.

As previously mentioned, studies on the contribution of attention on numerosity perception have mainly focused on the effect of depriving attentional resources on a number task. An effect of enhancing rather than depriving attention can be seen in the effect of alertness on enumeration within the subitizing range. Gliksman et al., (2016) examined the effect of pre-target warning cues on the subitizing process. They found that cued arrays within the subitizing range were enumerated faster than uncued arrays, indicating that subitizing is an attention-dependent process and can be manipulated through enhanced alertness. This alerting effect, when enumerating arrays within the subitizing range, has also been found in individuals diagnosed with developmental dyscalculia, although such cuing did not expand their smaller-than-normal subitizing range (Gliksman & Henik, 2018). Here we extended these results to show that also within the estimation range previously cued arrays are enumerated faster, more precisely and more accurately than uncued array, indicating that estimation processes are facilitated by inducing a manipulation that increases attentional engagement during an enumeration task.

When asked to position a cloud of dots on a number line, humans normally do so accurately: that is, linearly. However, when attentional resources are diverted by a concurrent demanding conjunction task, the judgments become distinctly non-linear, well described by a logarithmic relationship. This suggests that both linear and compressed maps can coexist, and the use of one or the other may be due to a variety of task-driven strategic factors. It has been suggested that the neural substrate underlying the logarithmic mapping of number may reflect the bandwidth of neurons selective to number. In both non-human and human primates, neural responses in the intraparietal sulcus show a logarithmic-like tuning, with bandwidth proportional to preferred number (Nieder, 2005; Nieder & Merten, 2007; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004), consistent with a pre-attentive logarithmic mapping onto the numberline. A native logarithmic representation is also consistent with the fact that numerosity discrimination in both monkeys and humans shows Weber-Law behavior, with the root-variance of the discrimination increasing directly with numerosity.

Here we tested the possibility 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). That numerosity may be subject to the central tendency is further support for the notion of number being a visual sensory attribute (Burr & Ross, 2008; Dehaene, 2001). 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 60% of the variance.

What purpose does the prior – and central tendency in general – serve? As others have argued, a prior based on the statistics of the sensory events can improve performance – measured as the sum of total error – at the expense of reducing veridicality (see Jazayeri &

Shadlen, 2010). Effectively, under conditions of great uncertainty, performance can be improved by considering the past history of events. This could explain why under the condition of invalid different object, given that the precision is higher, the prior becomes more effective (as it is the relative widths of prior and sensory likelihood that determines the extent of central tendency). Another possibility is that engagement of attention induces a more qualitative change in the processing, acting on the *prior* itself by reducing its width, and hence the mode of mapping numbers.

To conclude, the present study revealed that the estimation process could be facilitated by inducing a manipulation that increases attentional engagement during an enumeration task. Research focusing on a mechanism that can improve rather than impair enumeration processes could prove helpful when considering rehabilitation in conditions such as dyscalculia. Future research can examine whether procedures that act to increase attention can also improve enumeration in healthy individuals and the ability to map number into space in special populations such as those with dyscalculia.

Chapter 7

General Discussion

7.1 Overview of the findings

The work presented in this thesis has explored attentional mechanisms and number representations in visual estimation through a variety of methods. I first investigated the attentional mechanisms underlying the selection of the targeted object in a visual scene, using both behavioral measures and pupillometry and correlating the effects with personality traits of participants. The results suggest that pupillometry may be a valid, non- invasive and fast tool to evaluate some cognitive and perceptual processes, particularly in clinical populations (such as ASD) when behavioral measures may fail. I then focused on the visual system's ability to estimate numerosities in a visual scene, with particular interest on how relatively small and large quantities are processed. I demonstrated that, outside the subitizing range, estimation of moderate and large quantities are dissociable processes that rely on different mechanisms, which sometimes overlap. This was done using the classical methods of reaction times and precision, as well as linking objects and depriving attentional resources. Using these methods, the findings suggest that number can be directly extracted from the visual scene without relying on other features of the objects, such as density or area. Mechanisms based on density and area seem to come into play when the items are too crowded to be perceived separately, leading to more precise, faster and more attentional dependent judgments than moderate densities. Finally, a study on enhancement of attentional resources during visual enumeration of dots highlighted the contribution of focused attention on estimation processes. This provided converging evidence for enhancement of attention-improving enumeration processes that could prove helpful when considering rehabilitation in conditions such as DD (developmental dyscalculia).

7.2 Exploring attentional mechanisms using pupillometry and their correlation with autistic traits

Priming of pop-out is a specific example of the effect of history on performance. Unlike other examples where history affects perception directly, such as serial dependence (Cicchini et al., 2014; Fischer & Whitney, 2014), priming of pop-out is considered to result from the effect of history on attention, which in turn affects reaction times. The past years have seen an increasing body of evidence exploring behavioral measures of priming of pop-out. In the first empirical chapter (Chapter 2) I aimed to investigate whether effects of perceptual priming could be revealed without relying on participant responses, such as pupil size measures, and whether pupillometry and the classical measures of reaction-time effects co-vary with personality traits. It was hypothesized that pupillometry could reveal individual differences and, based on the suggestion that autism spectrum disorders are associated with weak or less adaptable priors (Pellicano & Burr, 2012), participants with high autistic traits would rely less on past experience and hence show a lower priming effect, compared to the low autistic traits subsample. Results of Chapter 2 confirmed this prediction but only for priming effect on pupil change. That the magnitude of the reaction time priming did not depend on AQ is interesting, especially in the light of Pellicano and Burr's (2012) theory of autism being associated with reduced priors. Although all the participants of this study were neurotypical, those with high AQ may have been expected to show less reaction time priming than those with low, if they relied less on historical prior information. It is hard to speculate why this did not occur; perhaps the proposed underuse of priors in autism does not extend to priming of attention. Or perhaps the effects do not extend to the neurotypical population with high AQ. Most interestingly, the difference in pupillary response was strongly related to AQ, occurring only in individuals with low AQ. It is not clear exactly what drives this response, but as the difference was strongest for the switched trials, it seems reasonable to assume that it is the change in target color that drives increased pupillary dilation. This could be considered a "violation of expectation", much like the "odd-ball" p300 response that can be recorded by EEG (Verleger &

Śmigasiewicz, 2016). However, there are clear differences. Whereas P300 is strongest after a long series of similar trials followed by an "odd-ball", there was no measurable accumulation of the pupillary effect over sequences of trials. If the response relates to expectation (like mismatched negativity), then the expectation should increase with increased presentations of the same target color, as indeed does the reaction-time advantage. The "surprise" on color change should be greater after a long run of the same color, like mismatched negativity and also other odd-ball effects, such as increased apparent duration for odd-balls (Tse, Intriligator, Rivest, & Cavanagh, 2004). Rather than reflecting expectation violation, it is possible that the increased pupillary dilation on switching of test color is driven by the operation of resetting the target color. This operation must occur on every switch, irrespective of the length of the previous run, and would seem to be independent of the priming effects on attention. We can only speculate on the connection between the increased pupillary response and AQ. It is highly unlikely that the pupillary response of high AQ individuals is damped or sluggish, as there was no dependency on AQ of pupil dilation to repeated trials. In addition, Turi et al. (2018) found no dependency of pupil dilation on AQ to switches in percept of a bistable illusion, showing that the pupillary response per se is intact. It would appear more likely that the difference in this experiment reflects the action of different mechanisms involved in reassigning the color driving the attentional search. It would be interesting to repeat the experiment with a group of clinically diagnosed autistic patients, to see if they behave like the neurotypicals with high AQ or show different properties. The current study encourages the use of pupillometry in autism research. This study supports an increasing body of evidence that pupillometry can be very useful in tracking perceptual processes, providing information that cannot be gathered from standard psychophysics. It would seem that these pupillometry measures may be more sensitive to variations in perceptual styles, and their dependency on personality traits.

7.3 Estimation and texture density: dissociable processes

Even under conditions where individual items are uncountable, humans can make rapid and reasonably accurate estimates of the number of items in a scene, as can young infants and many animal species (Gallistel & Gelman, 1992; Nieder, 2005, 2013; Tall & Dehaene, 1998; Whalen et al., 1999; Xu et al., 2005). Estimation of the number of items extends over a wide range, from a few units to hundreds of items. Much evidence shows that numerical estimation is subserved by two separate systems: one fast and errorless, handling very few items (usually up to four) termed *subitizing* (Jevons, 1871; Kaufman &

Lord, 1949); the other slower and error-prone, estimating higher numerosities, often termed the Approximate Number System (Butterworth, 2011; Feigenson et al., 2004; Gallistel & Gelman, 1992). However, numerosity is intrinsically correlated with many other physical features. A vast body of literature suggests that numerosity is not sensed as such, but indirectly via other features of the object. Does it mean that numerosity does not exist as a primary visual perceptual attribute and can just be inferred indirectly? In three empirical Chapters I provide evidence for separate (but sometimes overlapping) regimes of number perception, depending on the quantity of items presented on a scene (from very few and segregable quantities to very dense and packed). In the second empirical chapter (Chapter 3), subjects were asked to estimate numerosity as quickly and accurately as possible while both reaction times and precision were recorded. The precision of estimates confirmed previous studies showing that while Weber's law describes well the results for relatively sparse numerosities, it gives way to a square-root law for higher numerosities (Anobile et al., 2014). Importantly, however, reaction times, which have traditionally defined subitizing, also followed the same trend. They increased from the subitizing range as numerosities increased, but only up to a point, then decreased, in a similar manner to the Coefficients of Variation. The point where reaction times started to decrease was similar to where Weber's law gives way to a square-root law (a possible signature of the texture-density system). Indeed, the two measures – reaction times and Coefficient of Variation – correlate positively with each other, with no "speed-accuracy trade-off". These data extend and reinforce previous findings (Anobile et al., 2014, 2015) indicating that the lowering of precision at high numerosities is genuine and does not come at the expenses of higher reaction times. As the point where CV gives way to a square-root law depends on eccentricity (Anobile et al., 2015), we measured reaction times at two different eccentricities. As predicted, reaction times began to decrease at a lower numerosity for the more eccentric stimuli.

One important feature of number estimation is the effect of visual grouping on number judgments. It was previously demonstrated (Franconeri et al., 2009; He et al., 2009) that linking objects with thin lines (or with illusory contours (Kirjakovski & Matsumoto, 2016)) lead to an underestimation of the number of objects presented. Why should the connected or partially connected pattern appear less numerous? These studies are particularly interesting in the context of the numerosity texture-density debate: if numerosity is based—even partially—on texture density, adding lines to the pattern should increase numerosity (as it clearly increases the amount of ''stuff'' in the pattern). Presumably linking the dots with a line perceptually converts two dots into a single unit. The estimate of numerosity seems to be based on the number of separable items, rather than how much stuff is in the field.

In Chapter 4 I directly tested this prediction on a wide range of numerosities spanning moderate to very large. The displays contained either isolated dots and dots connected by thin lines. At modest numerosities, connecting 40% of dots led to a 30% reduction in apparent number, agreeing with previous work (Franconeri et al., 2009; He et al., 2009). This is interesting, as the Fourier transforms show that the connected patterns contain more energy at high spatial frequencies which, according to the influential model of Dakin et al. (2011), should lead to an increase, rather than a decrease in perceived numerosity. However, when we measured the apparent numerosities of higher densities, the effect was reduced, being only 15% with of 100 dots (3.3 dots deg^2). We also asked subjects to judge the density of the patterns. At low densities, the connected patterns seemed about 25% less dense, despite the fact that they were in fact denser, as they have more patterning within the same area. However, at higher densities, the results inverted, with the connected patterns appearing to be denser, corresponding to the physical reality. Thus, at modest densities, it would seem that perceived density was driven by perceived numerosity, rather than the other way round. At high densities, on the other hand, perception corresponds much more closely to physical reality. Overall, these results confirm the predictions that number is directly sensed only if the density is low enough to permit segregation: for highly packed stimuli, the Approximate Number System – which operates on segregated items – seems to be less active, so estimates were less influenced by the manipulation affecting segregation. However, for sparse stimuli, numerosity mechanisms dominate, and estimates followed what would be expected if numerosity were based on segregable units, with connected items perceptually merged. It is particularly interesting that texture-density estimates for sparse stimuli did not follow the overall energy in the stimulus, which is higher for connected patches, particularly at high spatial frequencies (Figure 4.1), but was also affected by item-connectivity. As mentioned, the influential theory (Dakin et al., 2011) suggesting that numerosity could be calculated from the power spectrum of the stimulus, makes the prediction that connected items, which have greater energy in the higher spatial frequencies, should appear more dense – and hence more numerous. Indeed, this prediction is upheld for dense patterns, at least for density judgments: but for low and modest densities it fails completely. This result not only shows that numerosity is not derived indirectly from density, texture or other low-level features, but also casts doubts on the idea that density is a primary visual feature: rather, density seems to be derived indirectly from numerosity, reinforcing previous evidence showing that at low numerosities, density judgments are particularly unreliable and are often surrogated by number judgments (Cicchini et al., 2016).

A further potential method for identifying different mechanisms of number perception is to examine the dependency on attention. It has been shown that depriving visual attentional resources leads to massive detrimental effects of performance thresholds in the subitizing range, but far less for larger numbers (Burr, Turi, & Anobile, 2010; Egeth, Leonard, & Palomares, 2008; Olivers & Watson, 2008; Railo, Koivisto, Revonsuo, & Hannula, 2008; Vetter, Butterworth, & Bahrami, 2008). In Chapter 5, I provide further evidence for separate mechanism underpinning three regimes of numerosity perception (subitizing, estimation, and texture-density) by investigating the role of visual and auditory attentional resources on discrimination thresholds over these ranges. First, earlier studies showing different psychophysical laws for thresholds in the three regimes were replicated. In the baseline condition, as expected, discrimination thresholds were near zero in the subitizing range, obeyed Weber's law for intermediate numerosities, then decreased with a square-root law for denser stimuli. Attentional load changed completely this pattern of results. It is interesting that the mechanism that suffered least from depriving attentional resources was the "estimation range", which suffers only a slight cost with the Visual Task, and no cost at all with the Auditory task. Given that the two distractor tasks were different in nature (visuo-spatial vs auditory-temporal), we cannot directly compare modality-specific costs with each other. However, it is interesting that these diverse distractors led to qualitatively similar relative effects on thresholds over the three ranges. There is now a better understanding of the involvement of attentional and visual-working-memory in the judgment of numerosities within the subitizing range (Anobile et al., 2012; Burr et al., 2010; Burr, Anobile, & Turi, 2011; Eger, Knops, Sengupta, Melcher, & Piazza, 2014; Piazza et al., 2011; Vetter et al., 2008; Vetter, Butterworth, & Bahrami, 2011). But why do judgments of very high numerosities (density regime) require more attentional resources than intermediate (estimation regime) numerosities? It has been previously demonstrated that for tightly packed stimuli the number of items is not perceived directly, but stimulus density (e.g. inter-dot distance) dominates judgments (Anobile et al., 2014; Anobile, Castaldi, Turi, Tinelli, & Burr, 2016; Burr, Anobile, & Arrighi, 2017; Cicchini et al., 2016). Other studies have shown that texture segregation and discrimination tasks require attentional resources (Landy & Graham, 1991; Yeshurun & Carrasco, 2000). Indeed, Tibber et al. (2012) found profound attentional costs in a dot-array density comparison task. Together, these results suggest that numerosity judgments for dense patterns require more attentional resources than for sparse stimuli, because they tap an attention-dependent system encoding texture-density rather than numerosity. It has been shown that primary sensory attributes are robust to cross-modal attentional interference (Alais, Morrone, & Burr, 2006). The results of Chapter 5 are consistent with this, and further support the notion that number estimation is a primary visual attribute, which is extracted spontaneously from the visual scene, at least for intermediate numerosities (Cicchini et al., 2016), without heavy recourse to attentional resources. The discontinuity in psychophysical performance between estimation and texture-density does not necessarily imply the existence of three totally independent systems. It is possible, indeed most probable, that estimation mechanisms operate over the entire range, but that this system are supplemented by attentional mechanisms at low and very high numerosities. There is good evidence for attention-dependent subitizing mechanism in the low range, allowing for perfect enumeration; but when attention is drawn from this mechanism by dual-tasks, the estimation system continues to operate (Burr et al., 2011). The same may occur at the high range: texture mechanisms may normally operate on local texture, but when these are impaired, estimation mechanisms could take over. The numerosity system may be always active, but not always called into play.

It should be noted that I am not proposing the existence of three completely independent and non-overlapping mechanisms for subitizing, estimation and texture. On the contrary, I believe, with good evidence, that there is considerable overlap of the mechanisms, but the most sensitive will dominate a particular task. For very small numbers, the attentional-based subitizing system is the most sensitive and will dominate. However, under conditions of attentional deprivation, this system cannot operate, and numerosity estimates will be based on the estimation system. Evidence for this comes from studies showing that during dual-task (which inhibits subitizing), adaptation (a signature of the estimation system) also occurs for numerosities in the subitizing range (Burr, Anobile, & Turi, 2011). Similarly, the estimation system (which obeys Weber's law) is typically more sensitive at lower numerosities, giving way to a density-based system (following a square-root law) at higher densities. But under conditions of area mismatch, where one system cannot act as a proxy for the other, it can be shown that both systems cover a very wide range (Anobile et al., 2014). For example, data of Chapter 3 expand on this suggestion by showing that advantages in precision are accompanied by faster response times: again, it is the faster response that will dominate the reaction-time measures, even though both systems may be activated.

Having demonstrated the existence of three regimes for numerosity discrimination, it is reasonable to ask what the mechanisms behind each are. Subitizing clearly relies on attentional mechanisms (Burr et al., 2010; Vetter et al., 2008), which can operate on up to 4 to 5 elements. The high-density range is probably subserved by a mechanism sensitive to texture, which could be based on several properties, such as the Fourier energy or the statistical properties of inter-dot distance, both leading to a square-root dependence on numerosity (Anobile et al., 2014). The mechanism for numerosity discrimination is harder to define. There exist several models, such as the classic model of Dehaene & Changeux (1993), which is constrained to have Weber-law behavior (quite different from models of texture discrimination). Similarly, it has been shown that numerosity discrimination, with Weber-law properties, can emerge spontaneously from neural networks designed for other, non-numerical functions (Hannagan, Nieder, Viswanathan, & Dehaene, 2018; Stoianov & Zorzi, 2012). A common principle of all of these models is a segregation stage, in which inhibitory surround regions play an important role (Sengupta, Surampudi, & Melcher, 2014; Stoianov & Zorzi, 2012). When segregation is impossible (for example at high densities), these purported mechanisms will clearly break down. However, while these models all are quite successful up to a point, it is clear that much more work is needed in uncovering the precise mechanisms responsible for estimation of numerosities, higher than those that can be subitized, but too low to define texture.

7.4 Attentional enhancement and mapping number into space

In the last part of this thesis we demonstrated that directing attention to a specific location leads to more accurate, precise and fast estimation judgements, and that attention spreads over the entire cued object. This reinforces previous evidence (Anobile et al., 2012a; Anobile et al., 2012b) showing that the ability to accurately map numbers onto space depends on attentional resources. Attentional engagement serves as a tool to map number onto space more linearly, compared with when attention is diverted elsewhere. We show that the non-linearity is consistent with the general perceptual principle of central tendency, observed in almost all sensory systems. This effect can be seen as merger of the current signals with a running average over the immediate past, which leads to an overestimation of lower magnitudes, and an underestimation of the higher, result in a compressed logarithmic-like response function.

It is clear now that number, space and attention are interconnected. Number acuity, which improves during development

(Halberda & Feigenson, 2008), correlates with formal mathematics achievement (Mazzocco, Feigenson, & Halberda, 2011) and predicts math skills years later (Halberda, Mazzocco, & Feigenson, 2008). (Halberda et al., 2008). It is clear that numerosity representation plays a key role in the acquisition of formal mathematical ability (Mazzocco et al., 2011; Piazza et al., 2010). Conceptions of how numbers map onto space develop during school years (Booth & Siegler, 2006; Siegler & Booth, 2004; Siegler & Opfer, 2003); kindergarten children represent numbers in space in a compressed, seemingly logarithmic scale (e.g., placing the number 10 near the midpoint of a 1–100 scale). The scale becomes progressively more linear over the first 3 or 4 years of schooling. Interestingly, dyscalculic children (those who suffer from a specific mathematical learning disability) show poor number acuity (Piazza et al., 2010) and a more logarithmic representation of the number line than controls (Ashkenazi & Henik, 2010; Geary, Hoard, Byrd-Craven, Nugent, & Numtee, 2007; Geary et al., 2008). Recent studies have shown that, along with deficits in numerical processing, people suffering from dyscalculia also have deficits in attention (Ashkenazi & Henik, 2010). As Anobile et al. (2013) have pointed to the interplay between attention and math skills, it would be interesting to study the relationship between attention enhancement and dysregulation in math abilities.

7.5 Conclusion

In brief, in this thesis we demonstrate that the estimation of very small (subitizing), intermediate and large quantities are subserved by three different but overlapped systems: *subitizing* (for numbers up to four) – very fast, precise and dependent on attention; *estimation* – slower, less precise and less attentionally dependent, also operating on segregated items; and *texture-density*, which comes into play when the single items form an amorphic mosaic, which is faster, more precise and more attentional dependent than intermediate numerosity in the estimation range and operates on unsegregable items. We also demonstrated that the ability to transform numbers onto spatial coordinates is highly dynamic and dependent on the focus of attention. Enhancement of attention results in faster, more precise and more linear estimates than diverted attention. Future research can examine whether procedures that acts to increase attention can also improve enumeration in healthy individuals, and the ability to map number into space in special populations such as those with dyscalculia. Moreover, we demonstrated that attentional mechanisms guiding the selection of a visual stimulus can be revealed by pupillometry indices, suggesting that pupillometry may emerge as a peripheral indicator of psychological and neurobiological processes related to perception and visual selection. We also suggest that measuring pupil changes may be helpful in examining where attention is deployed and in responding to variation in perceptual style, in a more reliable, flexible and non-invasive way than other behavioral and neurotomical measures, in particular in clinical populations.

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Appendix

A1 Position priming and dependency on response

In their original studies, Maljkovic and Nakayama (1996) showed that there was a reaction-time advantage not only when the target color was repeated, but also a smaller advantage when the position of the target was repeated. Figure 2.3A shows that our RT results also show positional priming. However, in our experiment, the positional priming seems to be confined to trials that did not switch color. Reaction times were about 46 ms faster when the target was presented to the same position for conditions when the target color did not change, but very similar when the target color did change (with a difference of about 10 ms). Three-way ANOVA revealed a significant within-group main effect of position ($F_{(25,1)} = 10.24$, $p = 0.004$), as well as a significant interaction with color ($F_{(25,1)} = 5.93$, $p=0.02$). However, there was no interaction with AQ ($F_{(25,1)}=3.55$, $p=0.07$), nor was there a significant correlation between AQ and the reaction-time advantage for position ($r= -0.08$, $p= 0.05$, log-BF = 0.006 – not shown).

Figures A1 show the dependence of pupil diameter on repetition of position. A three-way ANOVA shows no main effect of AQ ($F_{(25,1)} = 3.02$, $p = 0.09$). Nor was there a main effect of target position ($F_{(25,1)} = 0.67$, $p = 0.41$), or an interaction between AQ and position ($F_{(25,1)} = 0.001$, $p = 0.97$).

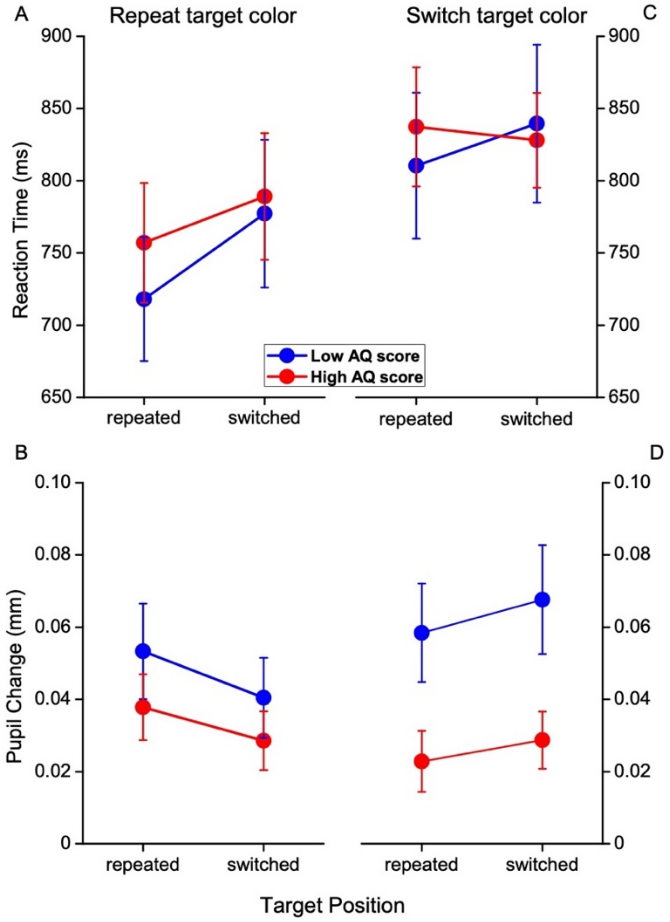


Figure A1 Priming of position for reaction time and pupil size. Mean reaction time **(A)** and mean pupil size **(B)** for repeated color trials as a function of the position of the target in the sequence. Mean reaction time **(C)** and mean pupil size **(D)** for switched color trials as a function of the position of the target in the sequence. Different colors represent different Autistic Traits (low AQ score in blue; high AQ score in red).

As some recent evidence (Yashar & Lamy, 2011) suggests that repetitions of motor responses interacts with the repetitions of the target defining features, we performed a 2-way repeated measures ANOVA, with between subject factor AQ, for both reaction times and pupil size separately. We found no interaction between repeating the target feature and repeating the motor response, neither for RTs ($F_{(25,1)} = 0.345$; $p = 0.56$) nor pupil size ($F_{(25,1)} = 0.287$; $p = 0.6$). Nor did we find any main effects of motor response ($F_{(25,1)} = 3.94$; $p = 0.06$ for RT; $F_{(25,1)} = 0.05$; $p = 0.8$ for pupil size), nor an interaction between the two measures and AQ (RTs: $F_{(25,1)} = 0.44$; $p = 0.5$; Pupil size: $F_{(25,1)} = 0.62$; $p = 0.4$). We also analyzed the effect of long runs of motor repetitions on both RTs and pupil size, as studies (Lamy, Bar-Anan, & Egeth, 2008) have reported stronger effects after consecutive repetition. We found that motor repetition facilitation of reaction times became apparent only after four response repetitions ($F_{(78,3)} = 4.26$; $p = 0.008$). However, even for four repetitions, there was no effect on pupil size ($F_{(78,3)}=1.052$; $p=0.37$).

A2 Example for psychometric curves of Chapter 4

Figure A2 shows psychometric functions for the tasks. These example functions plot aggregate data, pooling over all subjects to illustrate the technique: but all subsequent analysis was done with similar functions for individual subjects. The upper panels (A-B) show data for 15-dot stimuli (0.5 dots/deg^2), bottom panels (C-D) for 100-dot stimuli (3.33 dots/deg^2). For the sparse patterns, the PSEs for numerosity judgements are clearly shifted to the left for the connected stimuli, implying that they seem to contain fewer elements, agreeing with all the previous literature (Fornaciai et al., 2016; Franconeri et al., 2009; He et al., 2009, 2015; Kirjakovski & Matsumoto, 2016). For the dense pattern there is still a difference in PSEs, but the difference is much reduced, from about 40% for 15 dots to about 17% for 100 dots.

In separate sessions we also asked subjects to judge the apparent density of the patches. The results for the aggregate observer are shown on the right panels of Figure A2 (B and D). Despite the fact that the connected patterns contain more “stuff”, particularly at high spatial frequencies, shown clearly by their Fourier transforms (Figure 4.1), participants under-estimated rather than overestimated the density of the 15-dot pattern when dots were connected, by about 30%. However, they overestimated the density of the 100-dot pattern, as predicted by the power spectrum.

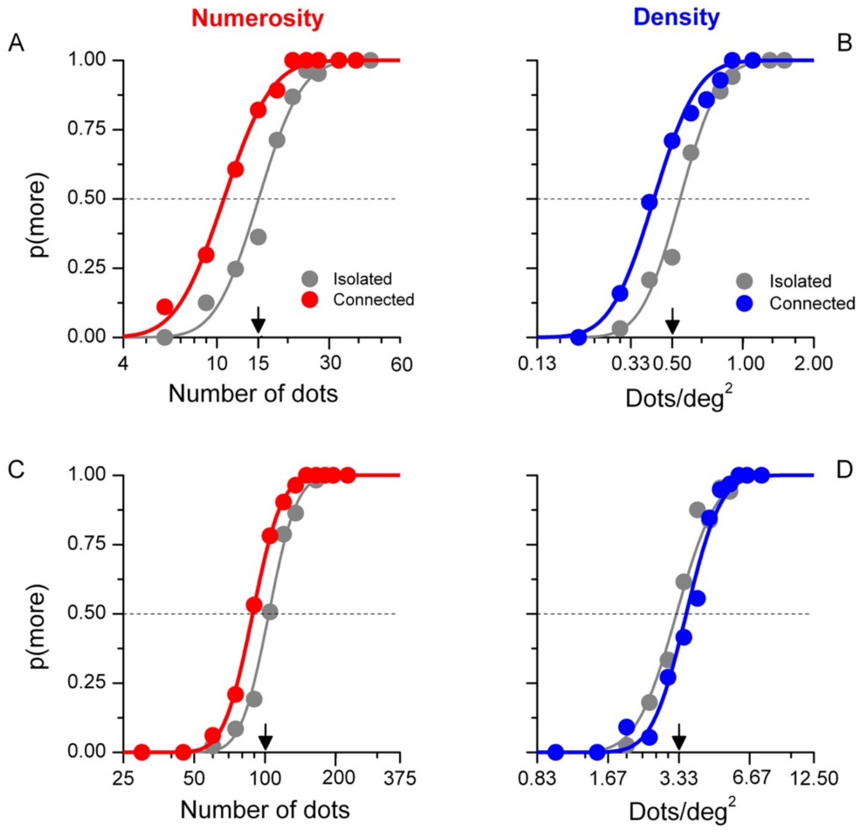
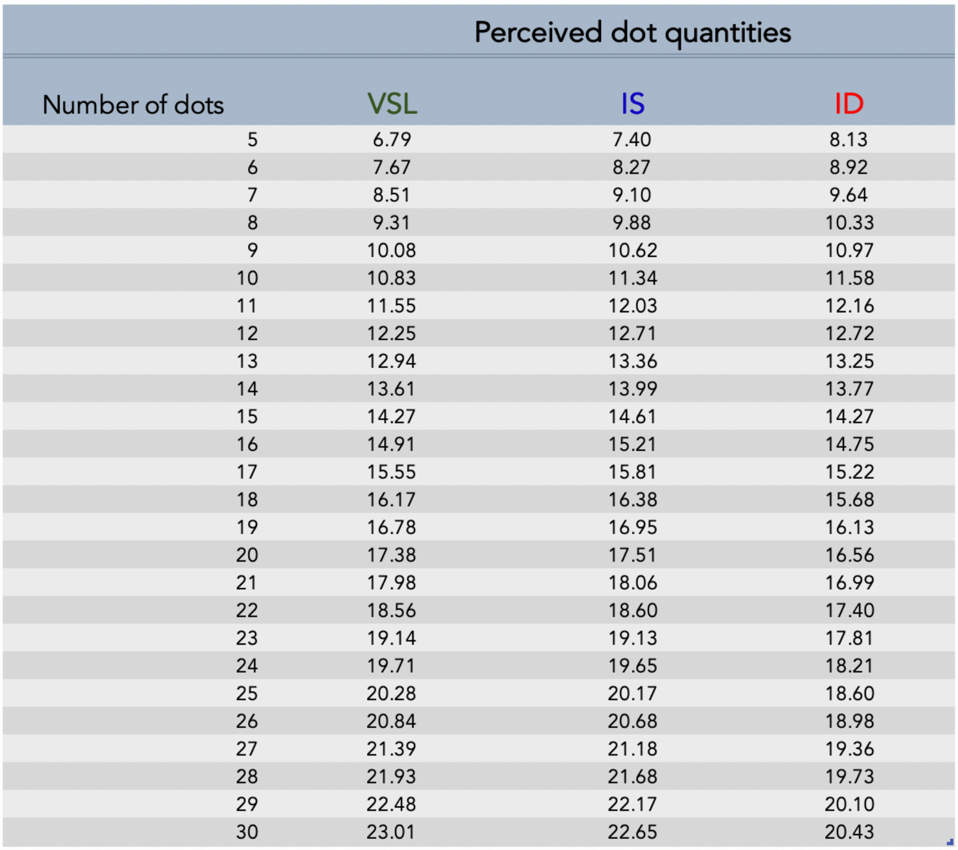


Figure A2 Aggregate psychometric functions for low and high numerosities: (A-B) 15 dots (density 0.5 dots/deg^2). **(C-D)** 100 dots (density 3.3 dots/deg^2). A & C show judgements of numerosity, B & D density (in separate sessions). All graphs plot the proportion of times the subject reported the probe to be more numerous (or more dense) than the reference, as a function of probe number. Colored lines refer to the connected condition (reference containing 40% of connected dots), greys lines to the isolated dots condition (baseline). Leftward shifts of colored curves imply underestimation of the connected-dot stimulus.

A3 Mean perceived numerosity and coefficient of determination of the fits



	Perceived dot quantities		
Number of dots	VSL	IS	ID
5	6.79	7.40	8.13
6	7.67	8.27	8.92
7	8.51	9.10	9.64
8	9.31	9.88	10.33
9	10.08	10.62	10.97
10	10.83	11.34	11.58
11	11.55	12.03	12.16
12	12.25	12.71	12.72
13	12.94	13.36	13.25
14	13.61	13.99	13.77
15	14.27	14.61	14.27
16	14.91	15.21	14.75
17	15.55	15.81	15.22
18	16.17	16.38	15.68
19	16.78	16.95	16.13
20	17.38	17.51	16.56
21	17.98	18.06	16.99
22	18.56	18.60	17.40
23	19.14	19.13	17.81
24	19.71	19.65	18.21
25	20.28	20.17	18.60
26	20.84	20.68	18.98
27	21.39	21.18	19.36
28	21.93	21.68	19.73
29	22.48	22.17	20.10
30	23.01	22.65	20.43

Table A3 Mean perceived numerosity separately for the three conditions tested. The first column represents the number of dots in the array. From the second to the third means perceived numerosity are showed. The perceived dot quantity of each actual dot quantity was calculated using each participant's best fitting power function to calculate the perceived dot quantity and average the perceived dot quantity for each actual dot quantity across all participants. There is a clear overestimation of smaller dots quantities and an underestimation of larger dot quantities (more pronounced when attention shifts from the cued to the uncued object).