ELECTROPHYSIOLOGICAL CORRELATES OF MULTIPLE OBJECT PROCESSING

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Abstract

Several daily activities like walking in a crowded street depend on our ability to process multiple objects simultaneously. According to some theories this ability relies on at least two stages or mechanisms related respectively to visual attention and visual working memory. The early stage of multiple object processing – individuation – is a function of attention that allows the visual system to represent multiple objects simultaneously by selecting a limited number of locations and binding them to basic visual features. A second later stage related to visual working memory encodes in greater detail the indexed objects leading to their full representation. In the present thesis I investigated the functioning of multiple object processing in a set of behavioral and electrophysiological studies focusing on the modulation of two component of the event-related potentials - N2pc and CDA – which have been associated respectively to individuation and visual working memory. In all the experiments of the present thesis I established that both N2pc and CDA were modulated by the number of relevant items during the execution of an enumeration task. I exploited this effect in each Chapter of the present thesis to investigate different aspects of multiple object processing.

In particular, in the first and second experiment (Chapter 2) I assessed the existence of a capacity limit in simultaneous processing as predicted by theories of individuation. In Chapter 3 I investigated the role of distracting information in simultaneous individuation. In Chapter 4 I focused on whether high-level features (such as semantic information) are incorporated in the representations produced at the stage of individuation. Finally in Chapter 5 I assessed the role of awareness in multiple object processing using a masking paradigm.

The results provided new information on the way early individuation and late WM stages interact for successful object perception, as well as on their functional dissociation during multiple object processing.

Chapter 1

General introduction

Several daily activities, like driving a car or walking in a crowded street, depend closely on our ability to analyze potentially relevant objects simultaneously. Although the visual input is a continuous stream of complex information, we are able to parse it and construct coherent representations of small portions of it, focusing on the relevant objects. Several theories of object recognition have proposed that multiple object processing can be divided in at least two stages: an early individuation stage of analysis and a late stage of processing mediated by visual working memory related mechanisms (Kahneman, Treisman, & Gibbs, 1992; Xu & Chun, 2009).

The early stage of multiple object processing – individuation– (Kahneman, Treisman, & Gibbs, 1992; Pylyshyn, 1989) is a function of attention that allows the visual system to represent multiple objects simultaneously by selecting a limited number of locations and binding them to basic visual features (Cavanagh & Alvarez, 2005; Cavanagh & He, 2011). Theories of individuation indicate that this early stage of processing cannot represent more than four or five items simultaneously (Kahneman et al., 1992; Pylyshyn, 1989; Trick & Pylyshyn, 1993). The representations produced during individuation underlie those tasks in which keeping separate multiple objects is crucial, like multiple object tracking (Chesney & Haladjian, 2011; Scholl & Pylyshyn, 1999) or visual enumeration (Trick & Pylyshyn, 1994a). When the task at hand requires a more detailed representation of the objects, like for instance during a memory task, the representations produced during individuation are not informative enough. For this reason, more features of the individuated objects need to be added and/or elaborated more deeply in order to have a complete representation, ultimately leading to the full object identification. This late stage of multiple object processing is likely mediated by mechanisms related to visual working memory (Xu, 2007).

The functioning of multiple object processing has been described by two main theories, which are based on empirical observations and behavioral evidence. Recent research has additionally tried to investigate the brain activations associated with multiple object processing. For instance, Xu and Chun (2009) have recently proposed that two specific portions of the intraparietal sulcus are respectively implicated in the individuation of multiple objects and in the detailed encoding procedures on the individuated objects. This and other evidence (Xu, 2007; 2009) concurred in the formulation of a neural model of multiple object processing based on functional Magnetic Resonance Imaging (fMRI) results. However, given the poor temporal resolution of fMRI, the time course of the processing stages underlying multiple object processing has received little investigation. Electroencephalographic (EEG) measures represent one of the best neuroimaging techniques to unravel this aspect, but so far only a few studies (Drew, Horowitz, Wolfe, & Vogel, 2011; Drew & Vogel, 2008; Mazza & Caramazza, 2011) have focused on the electrophysiological measurements of multiple object processing. For this reason, the present thesis will use EEG measures to investigate the temporal dynamics of the various stages implicated in the analysis of the multiple objects.

In the present chapter I will review some basic behavioral paradigms used so far to investigate multiple object processing. Next, I will describe the main theories that have tried to bring together the contributions of the behavioral and fMRI studies to explain the functioning of multiple object processing. Finally, I will discuss the existing EEG studies and findings on the involvement of two specific electrophysiological responses associated with multiple object processing.

1.1 Experimental paradigms for the study of multiple object processing

Multiple object processing and its underlying stages are crucial for the implementation of several activities. As a consequence, there is a variety of experimental paradigms that have been employed so far to study this topic. In this section I will describe three of them: the object reviewing paradigm, the multiple object tracking (MOT) paradigm and the visual enumeration task. These paradigms have given a substantial contribution to the formulation of the theories discussed in the next section.

1.1.1 Reviewing paradigm

Kahneman, Treisman and Gibbs (1992) used the so-called reviewing paradigm to investigate how the visual system recognizes that the multiple instances of an object pertain to the same object. This paradigm is at the basis of the object-file theory, one of the most relevant theories on multiple object processing. This theory is centered on the idea that, when looking at a scene, we need to construct representations of the displayed objects in order to recognize them as the same individuals when they change position or size on the retina. To test this idea, Kahneman, Treisman and Gibbs (1992) presented observers with a display with some predefined positions.

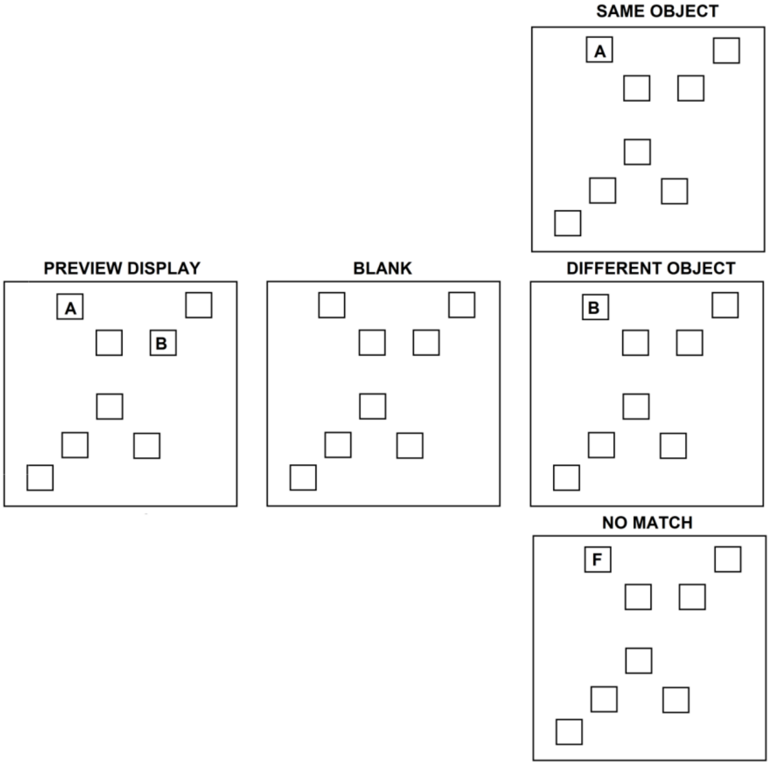

Figure 1.1 Schematic representation of the reviewing paradigm

Example of a preview display with letter A as target. The three possible test displays are depicted on the right (figure adapted from Kahneman, Treisman & Gibbs, 1992).

In the so-called preview display, two or more (up to eight) of these positions were filled with letters. After a blank, a target display was presented in which one letter appeared in one of the previewed positions. The letter could be the same one as in the preview display (*same object* condition), a different one chosen from the letter set of the preview display (*different object* condition), or a completely novel letter (*no match* condition). Participants' task was to name the target letter as fast as possible (see figure 1.1). The results showed that participants were fastest in naming the letter when the same object was displayed in the position corresponding to the previewed one. In addition, participants were faster in the different object condition with respect to the no-match condition. Interestingly, these effects disappeared when participants saw preview displays with more than four letters. This occurred both with static and moving stimuli.

Although this task required to focus on a single object, the results by Kahneman et al. (1992) are interesting for the study of multiple object processing as well. Indeed, they showed that the specific advantage for an object displayed in a previewed position disappears when more than four objects are originally presented. This result indicates that there is a limit in the number of objects that can be processed simultaneously, and that this limit is at approximately four objects. Interestingly, a similar limit has been found in other tasks requiring processing of multiple objects, such as visual enumeration (Kaufman, Lord, Reese, & Volkmann, 1949; Trick & Pylyshyn, 1994a) and visual working memory (Cowan, 2001; Luck & Vogel, 1997). This suggests the existence a common limit in the mechanism/s underlying the execution of these tasks.

1.1.2 Multiple object tracking

Multiple object tracking (MOT) is a task proposed by Pylyshyn & Storm (1998) that requires to actively track multiple moving targets. In a classical MOT experiment participants are presented with a display of targets and distractors. After an interval, all the objects displayed become identical and they start moving independently from one another. At the end of the trial participants are asked to recognize the target objects (e.g., by clicking on each of them or by indicating whether or not a highlighted item is a target; see figure 1.2).

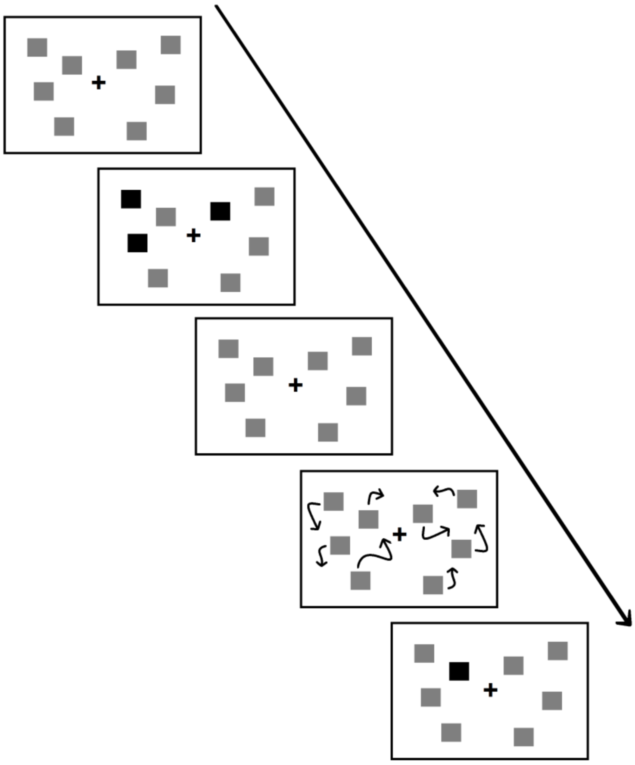

Figure 1.2 Schematic representation of a MOT task

Example of a MOT trial with three targets (black squares). Participants have to report whether the square highlighted in the last display is a target or not (figure modified from Cavanagh & Alvarez, 2005).

The MOT task offers a good tool to investigate multiple object processing in dynamic contexts in which there is a continuous update of the spatial information, like in real-life situations. Some of the classical results about MOT fit well with the idea that multiple object processing is a mechanism based on individuation. First, several studies indicated that there is a limit in the number of targets than can be successfully tracked and that such limit is at around four or five targets (Alvarez & Cavanagh, 2005; Storm & Pylyshyn, 1988), in line with the assumptions of individuation theories. Second, successful tracking can be dissociated from the detailed encoding of the targets features (Pylyshyn, 2004), thus suggesting that individuation, rather than working-memory related operations, is the perceptual stage mainly involved in tracking of moving objects. More recent studies have shown that MOT capacity can vary by splitting attention among the two visual hemifields (Alvarez & Cavanagh, 2005), modifying objects spacing (Franconeri, Jonathan, & Scimeca, 2010) objects velocity (Alvarez & Franconeri, 2007) or targets and distractors saliency (Bettencourt & Somers, 2009), leading to a debate on whether or not there is a fixed capacity limit in MOT task. Recent accounts explain these contrasting findings by proposing that there is a fixed number of attentional foci that can be used to track multiple objects and that these channels are flexible in the number of features they can encode or select (Cavanagh & Alvarez, 2005; Xu & Chun, 2009).

1.1.3 Enumeration tasks

The processing of multiple objects is intrinsically related to visual enumeration. During enumeration our visual system needs to tag and keep separate several objects in order to count them once and only once, and to finally retrieve the numerosity of a set. For this reason visual enumeration is one of the simplest, yet more effective, paradigms to study multiple object processing. This is a well-known paradigm in which a variety of features can be easily changed to assess different aspects of multiple object processing. Moreover, decades of studies on enumeration (e.g. Jensen, Reese, & Reese, 1950; Kaufman et al., 1949) have produced a large corpus of data to be used as a basis for the investigation of several issues. For these reasons, I chose to use this paradigm for exploring the questions addressed in the present thesis. Typically, in this paradigm a display with a variable number of objects is shown and participants are required to report the numerosity of the items displayed (e.g. Mandler & Shebo, 1982; Trick & Pylyshyn, 1993; 1994b; see figure 1.3).

Studies on visual enumeration usually report a dissociation between a fast and relatively error-free type of enumeration, called “subitizing”, and a slower and error-prone one, known as counting (Kaufman et al., 1949). Interestingly, subitizing involves the range between one and four-five items, whereas counting is the term that refers to the precise enumeration of larger quantities. In the literature the dissociation between subitizing and counting has been interpreted as evidence of the functioning of two different enumeration processes (Mandler & Shebo, 1982; Trick, 2008; Trick & Pylyshyn, 1993, 1994a, 1994b).

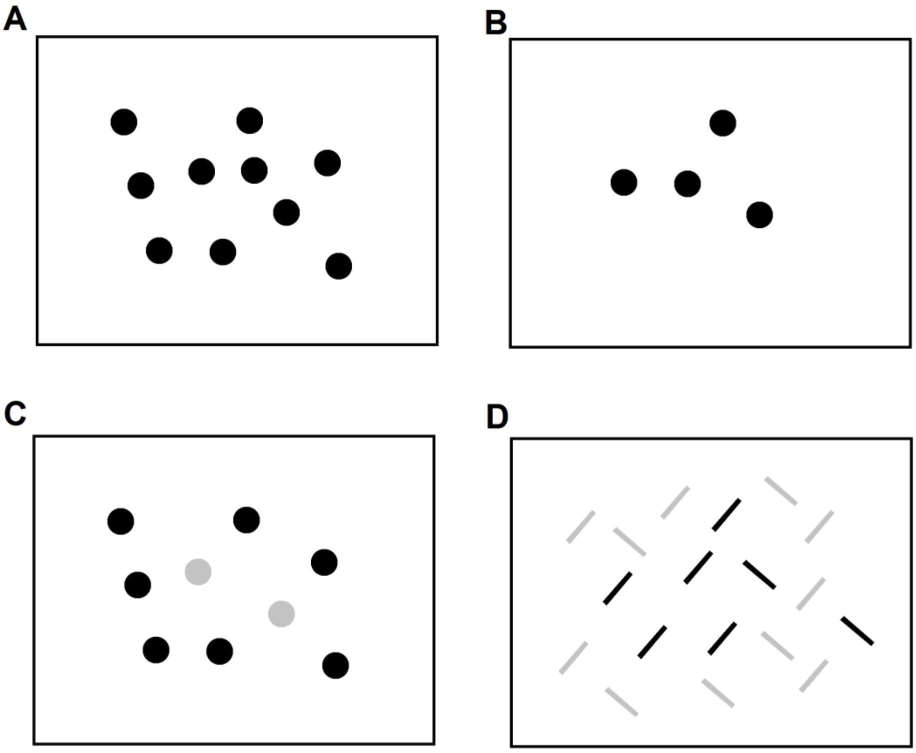

Figure 1.3 Example of different enumeration tasks

The top line shows enumeration displays without distractors representing a typical condition in which counting (A) or subitizing (B) are observed. The bottom line represent enumeration displays of targets among distractors in a "pop-out" (C) and in a feature conjunction (D) condition (modified figures from Trick & Pylyshyn, 1993).

If the number of displayed objects is within the subitizing range, a fast indexing system is supposed to be at work, tagging multiple objects and then retrieving their numerosity (Trick & Pylyshyn, 1993). If the number of displayed objects is in the counting range the indexing process must be reiterated over the whole set, keeping track of the objects already indexed, thus consuming more time and leading to more errors. Another account (e.g. Mandler & Shebo, 1982) explained the dichotomy between subitizing and counting by suggesting that small object numerosities are ascribable to simple shapes or pattern (like the ones in a dice) that are easily recognizable and thus enumerated fast and with no errors. In line with this account, some studies (Logan & Zbrodoff, 2003; Mandler & Shebo, 1982) showed that if several dots are arranged in a recognizable pattern they are enumerated as fast and as accurately as small quantities.

While the idea of the dichotomy between subitizing and counting has dominated in the literature for a long period, some studies have recently challenged this hypothesis, considering the existence of a double enumeration mechanism too redundant (Cordes, Gelman, Gallistel, & Whalen, 2001; Railo, Koivisto, Revonsuo, & Hannula, 2008; Vetter, Butterworth, & Bahrami, 2008; Whalen, Gallistel, & Gelman, 1999). These studies propose the existence of a single enumeration mechanism whose precision varies with the number of to-be-enumerated items. The precision of this mechanism is extremely high for small numerosities, leading to a fast and error-less performance. For large numerosities, the precision of this mechanism decreases as a function of object numerosity, thus causing more errors during enumeration (see Whalen et al., 1999). In general, precision refers to the fact that there is a limit in the amount of resources available to process multiple objects. Thus, if the number of objects is small, all resources available can be used to fully process those objects, leading to their precise representation. On the other hand, when the number of objects is large, resources are not enough to fully process the whole group of items, leading to a more coarse representation. This idea is supported by a growing number of studies showing that subitizing disappears when the amount of resources available is reduced (for example, by adding a secondary task, see Vetter et al., 2008; by manipulating attentional resources deployed to the targets, see Egeth, Leonard, & Palomares, 2008;

Olivers & Watson, 2008; Poiese, Spalek, & Di Lollo, 2008; or during inattentional blindness, see Railo et al., 2008).

Yet, there is a vast corpus of behavioral and imaging data showing a consistent discrepancy in the way small (1-4) versus large numerosities are enumerated (Dehaene & Cohen, 1994; Dehaene, Piazza, Pinel, & Cohen, 2003; Logan & Zbrodoff, 2003; Sathian et al., 1999). The apparent discrepancy between these two theoretical positions can be reconciled by hypothesizing that the phenomenon of subitizing is not due to a capacity limit specific for enumeration but rather to a limit in a more general perceptual mechanism, such as individuation. This hypothesis is based on the fact that a limit of four items in processing capacity have been found in a variety of tasks that rely on the ability to simultaneously elaborate multiple objects, such as multiple object tracking (Storm & Pylyshyn, 1988), memory tasks (Cowan, 2001) and reviewing paradigm (Kahneman et al., 1992). If enumeration depends on individuation, than the capacity limit of this latter mechanism can easily explain the phenomenon of subitizing. Recent behavioral findings (Chesney & Haladjian, 2011; Piazza, Fumarola, Chinello, & Melcher, 2011), as well as some imaging studies (Sathian et al., 1999; Vetter, Butterworth, & Bahrami, 2011) have indeed confirmed this idea by showing that the capacity limit of the individuation stage is the best predictor of subitizing performances. However electrophysiological studies about the specific role of individuation supporting this idea are still few (see Ester, Drew, Klee, Vogel, & Awh, 2012; Hyde & Spelke, 2009; Mazza & Caramazza, 2011).

A final remark about visual enumeration studies concerns the use of distracting information. In everyday life, relevant objects are always surrounded by other distracting items. This means that usually we need to select the relevant items from the irrelevant objects. In an experimental setting, this situation can be mimicked by presenting distractors together with the targets. Although visual enumeration has been thoroughly investigated, so far only a few studies have used distractors, thus leaving out the important aspect of target selection during enumeration. The majority of the studies have investigated subitizing and visual enumeration using target items displayed in isolation (Kaufman et al., 1949; Mandler & Shebo, 1982; Trick & Pylyshyn, 1994b). The few behavioral (e.g. Trick & Pylyshyn, 1993) and electrophysiological (Nan, Knösche, & Luo, 2006) studies with cluttered scenes seem to suggest that distractors can change the way targets are enumerated. However, it is still unclear whether and how the presence of distractors affects the functioning of the various stages of processing involved in multiple object enumeration.

Overall, the reviewing paradigm, MOT and visual enumeration show that there is a common limit in the processing of multiple objects. Whether this limit can be attributed to the capacity limit of early individuation mechanisms (versus late stages of processing) is still a matter of debate, although some behavioral studies indicate that this may indeed be the case (Chesney & Haladjian, 2011; Piazza et al., 2011). This issue will be addressed in Chapter 2. In addition, the role of distracting information during multiple target processing is still unclear. This issue will be examined in Chapter 3.

1.2 Theories of multiple object processing

Multiple object processing has been studied so far using two different perspectives that focused on spatial indexes (FINST theory) and on feature-to-location binding (object-file theory). In the next section I will describe both theories highlighting their differences as well as their similarities. Finally, I will report on a neural model of multiple object processing based on recent neuroimaging studies that tries to summarize both the FINST and object-file approaches.

1.2.1 The FINSTs theory

Pylyshyn's theory of Fingers of Instantiation (FINST) was introduced to frame findings coming from different research fields, like attentional selection and enumeration, into a general theory of vision. In order to achieve this, FINST theory introduces the concept of "indexing" as a core process that is able to apprehend simultaneously a limited number of objects. According to Pylyshyn's idea, visual processing of multiple objects includes three stages. The first stage is preattentive and allows the visual system to index in parallel all the features and discontinuities in a scene, in order to create a feature map. The second stage requires attention and is spatially serial. Here the objects displayed can be processed only one at the time, without the possibility of being elaborated simultaneously. During this stage multiple features are integrated into a complete object representation. Although this second stage can produce detailed object representations, it cannot process multiple objects simultaneously. How can a set of targets, defined by a set of features, be successfully processed?

Pylyshyn hypothesized the existence of a third mechanism dedicated to this purpose. This intermediate process, represented by the so-called FINSTs, allows for the binding of features and locations, resulting in the simultaneous tagging of a set of objects (Pylyshyn, 1989; Trick & Pylyshyn, 1993, 1994a). FINSTs are pointers that individuate multiple objects and track them in space and time; as it is assumed that

FINSTs are limited in number (1-4), the overall indexing mechanism is therefore limited in capacity. Moreover, FINSTs stick to the indexed objects tracking them as they move even when the objects are occluded (Scholl & Pylyshyn, 1999). One of the distinctive features of FINSTs is that they operate preattentively. This means that they can only index objects on the basis of preattentive features (i.e. those feature that have been registered in the first stage of visual processing) and not on the basis of conjunctions of features (see figure 1.4). The ultimate goal of FINSTs is to isolate multiple objects simultaneously in order to “distinguish between different tokens of the same type, for example a given black dot from all other black dots” (Trick & Pylyshyn, 1993).

By hypothesizing that there is a fixed limit in the number of available FINSTs, this proposal explains why the limit of visual enumeration and of successful tracking is set at four items. In addition, as FINSTs stick to the objects when they move, it is also explains why objects can be isolated even during multiple object tracking tasks. However Pylyshyn’s theory has three major shortcomings.

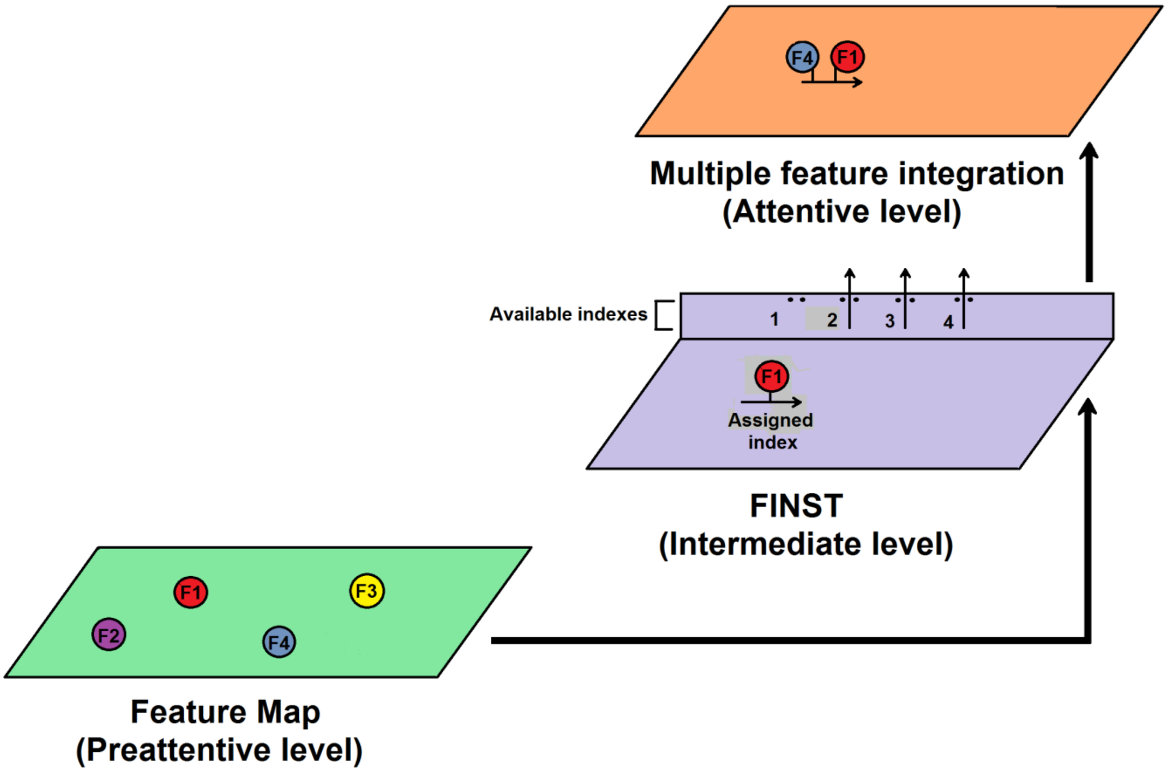

Figure 1.4 Schematic representation of the FINST model

The figure depicts the three main stages described by the FINST theory: in the Feature Map level all features are detected preattentively, the FINST level indexes up to four objects by feature-to-location binding, in the upper level multiple features are integrated in a full representation of a single object (figure modified from Leslie, Xu, Tremoulet & Scholl, 1998).

First, FINSTs are thought to operate in a preattentive manner. Trick and Pylyshyn (1993; 1994) based this idea on the fact that visual enumeration is highly influenced by the kind of features defining the to-be-enumerated targets. For instance, when targets are defined solely on the basis of one feature there is evidence of subitizing; conversely, when the targets are defined by a conjunction of features, enumeration of small quantities becomes slow and error-prone (Trick & Pylyshyn 1993). On the assumption that unique features can be detected preattentively (e.g. Treisman & Gelade, 1980), they reasoned that when a “pop-out” feature (such as color) defines the target(s), FINSTs can easily select up to four objects simultaneously. In contrast, when a feature conjunction defines the target(s), the slow attentional mechanism must intervene, searching for each of the targets and adding them one by one.

However, the preattentive view of subitizing has been recently challenged by several studies, indicating that attention is needed even when we have to enumerate or track small quantities (Burr, Turi, & Anobile, 2010; Egeth et al., 2008; Olivers & Watson, 2008; Railo et al., 2008; Vetter et al., 2008). Using different attentional load conditions during enumeration, some of these studies hypothesize that if FINSTs operate in parallel and without attention, they should index multiple targets even under conditions of high attentional load (Burr et al., 2010; Vetter et al., 2008). Interestingly, these studies found that when attention is deployed to a demanding secondary task, enumeration of small numerosities becomes slower and error prone. Taken together, these studies challenge the idea that individuation is preattentive and support the view that individuation is instead a key function of attention (Alvarez & Cavanagh, 2005; Cavanagh & He, 2011).

Second, it is not entirely clear which type of feature FINSTs can tag and the nature of the representations that are subsequently generated. In fact, features, feature clusters or objects can be indexed but it is not clearly defined whether or under what circumstances one should be privileged over the others. Related to this, the nature of the content of a FINST during visual enumeration still remains unclear.

Finally, FINST theory does not describe whether awareness is required during simultaneous individuation. So far, only few studies investigated this topic using behavioral paradigms (Bahrami et al., 2010; Koechlin, Naccache, Block, & Dehaene, 1999). Both studies showed that a group of masked dots can prime the response to another group of dots, provided that they share the same numerosity. Although these studies imply that multiple object processing can operate in the absence of awareness, there are currently no studies that have directly manipulated target awareness during visual enumeration. This topic will be addressed in Chapter 5.

To summarize, the FINST theory offers a relatively good model of multiple object processing. However the assumption of pre-attentive processing needs to be revised and the exact nature of the representations produced during the individuation stage remains to be clarified. This has partially been accomplished by the object-file theory that will be described in the next section.

1.2.2 The object-file theory

The object-file theory (Kahneman et al., 1992) proposes that individuation occurs through entities called “object-files”. According to the object-file theory, when we look at a scene we are able to select objects on the basis of their location. Whenever an object is encountered, the corresponding object-file is set up at that location, and then filled in with the featural information regarding that particular object as long as it is present in the visual field. The opening of an object file and the initial feature binding corresponds to the individuation stage. It is important to note that when all the object's features are bound to the object-file, a complete representation of the object is available for comparison with the representations stored in memory. Differently from the FINST proposal, the object-file theory assigns an important role to attention. Attention controls the object-file resolution and the level at which the object-file are set up (i.e., whether they concern the whole object or only its parts). As in Pylyhsyn's theory, object-files are also limited in number and only about four objects can be represented simultaneously. This idea derives from the fact that the previewing effects in the reviewing paradigm are reduced or disappear when the objects initially displayed are more than four or five (see section 1.1.1).

However, this theory remains unclear about the kind of features that are needed to initially set up an object-file. Kahneman, Treisman and Gibbs suggest that the simplest visual features are initially used, and that only later more complex features are added. However they do not describe when the switch from simple to complex should occur in time. Finally, as the FINST theory, the object-file theory does not specify the role of awareness in the setting up and filling in of object-files. Although some studies suggest that awareness is not crucial during these operations (Bahrami et al., 2010; Koechlin et al., 1999), further research is needed to address the question more extensively.

1.2.3 The neural object-file theory

The FINST (Pylyshyn, 1989) and object-file (Kahneman et al., 1992) theories have been the first systematic models of multiple object processing. Recent advances in cognitive neuroscience have made it possible to to test the classic cognitive models with neuroimaging techniques, in order to assess the brain dynamics associated with multiple object processing. This has brought to several new studies on multiple object processing using fMRI. These recent studies have discovered a network in parietal and occipital extrastriate areas of the brain that is active when multiple objects are selected and encoded (Xu, 2007, 2009). This new corpus of results has promoted the development of a new theoretical framework that tries to merge the contribution of behavioral studies on multiple object processing on one hand, and the findings of neuroimaging studies on individuation and visual working memory on the other hand.

In their “neural object-file” theory, Xu and Chun (2009) propose that our cognitive system selects and encodes multiple objects by means of two stages whose activity is mainly based in the parietal lobe. The first stage - individuation- is a capacity-limited mechanism through which we select object locations and set up the corresponding object files. At this stage, object-files contain only simple visual features of the objects, such as color or shape. During the second stage –identification- more complex features are added to the object-files by means of procedures that rely on working memory. This in turn leads to a complete representation of the individuated objects. Identification has a variable capacity depending on the complexity of the objects encoded and, according to the theory, this can vary from one to four items. On the basis of fMRI findings (Xu & Chun, 2006; Xu, 2009), individuation takes place in the inferior intraparietal sulcus (IPS), while identification is located in the superior IPS

(Xu, 2009). For instance, in an fMRI study by Xu (2009) participants were asked to observe either one object, four identical or four different objects. After a delay, they judged whether a probe object was present in the previous display. Interestingly, the inferior IPS was more active when both four identical and four different objects were displayed, while the superior IPS was maximally active only when four different objects were shown. This study suggests that different portions of IPS are selectively involved in individuation and identification of multiple targets, respectively.

The neural object-file theory is different from FINST in several aspects. First, according to this theory, the results of the individuation stage represent a sort of "proto-objects", namely not simply indexes but actual object representations. In addition, this proposal highlights the central role of attention for individuation for two reasons. First, because the neural object-file theory acknowledges the results of several recent studies (for a review see Cavanagh & Alvarez, 2005) showing that attention can be deployed simultaneously to multiple focal parts of a scene, thus suggesting that attention can have a role in the processing of multiple objects. Second, the spatial proximity and partially overlapping of the brain structures traditionally associated with "selective attention" (for a review see Behrmann, Geng, & Shomstein, 2004) with the areas activated during individuation, suggest that these two mechanism are tightly linked.

Finally, the neural-object file theory argues that only during identification we become aware of the object identities. Differently from the other theories of multiple object processing, this is the first theory that makes specific assumptions on the role of awareness, stating that awareness is necessary only after individuation.

1.3 Electrophysiological correlates of multiple object processing

Although the neural object-file theory complements previous behavioral theories by providing important hints on the neural structures associated with multiple object processing, it is entirely based on fMRI studies. Thus, it cannot provide the fine-grained information on the temporal brain dynamics associated with the various processing stages involved in the analysis of multiple objects. The electrophysiological measures would be perfectly suitable to this extent given their high temporal resolution.

Previous Event-Related Potential (ERP) studies on visual search with single target presentations (Mazza, Turatto, & Caramazza, 2009a; Mazza, Turatto, Umiltà, & Eimer, 2007) have indicated that two temporally distinct neural activations- the N2pc and the CDA- are tightly correlated, respectively, with the object individuation mechanism and with the maintenance of the individuated object for subsequent cognitive operations required for computing more detailed representations of the objects. In the subsequent paragraphs I will review the main findings on these two components, highlighting the links to multiple object processing.

1.3.1 N2pc

N2pc (N200 posterior contralateral) is a lateralized negative component of the ERPs that arises at approximately 200 ms post-stimulus onset (Eimer, 1996; Luck & Hillyard, 1994) when the relevant information (i.e., a target element) is displayed in one visual hemifield. More precisely, the N2pc is defined as a difference in the activity of the two hemispheres, with the posterior electrodes contralateral to the target side more negative than the ipsilateral ones (see figure 1.5).

Typically, the N2pc has been measured during visual search tasks and it has been associated with attentional selection/individuation processes. The first studies on N2pc showed that this component is visible when a target presented with distractors must be either detected or localized (Luck, Girelli, McDermott, & Ford, 1997; Luck & Hillyard, 1994). Given that N2pc occurred only in the presence of distractors, the first accounts proposed that N2pc reflected a mechanism of distractor suppression during attentional selection (Luck et al., 1997). This account was based on the fact that N2pc disappeared when distractors are eliminated, or when they carry information relevant for the task (Luck & Hillyard, 1994). Moreover, N2pc typically increases when the number of distractor increases (Luck et al., 1997), leading to the idea that this component represents a mechanism suppressing irrelevant information.

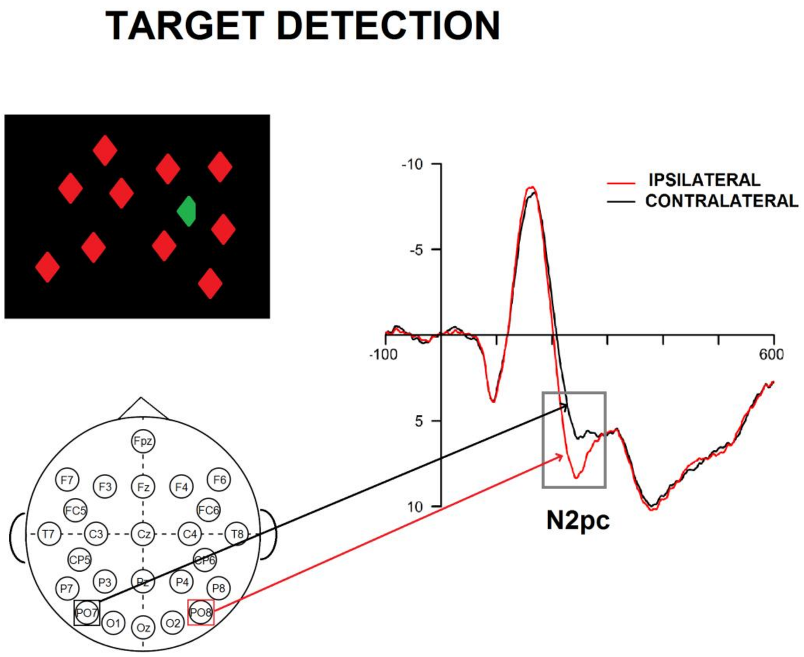

Figure 1.5 N2pc as elicited by a target detection task

Typical task and scenario eliciting a N2pc waveform using a target detection task. Notice how the activity corresponding to the electrode ipsilateral to target position (PO8) is less negative than the activity in the relative contralateral electrode (PO7) in the highlighted window.

However, subsequent studies (Eimer, 1996) showed that N2pc appeared also when one target was displayed together with a single distractor in the opposite hemifield. In this context there is a reduced need for suppression of irrelevant information; yet, the N2pc was still visible. Together with other evidence (e.g., Hickey, McDonald, & Theeuwes, 2006; Mazza, Turatto, Caramazza, 2009a; 2009b) this suggests that N2pc may reflect target enhancement rather than distractor suppression (for an “intermediate” proposal that the N2pc may reflect a summation of distractor-related and target-related activities, see Hickey, Di Lollo, & McDonald, 2009).

Given that the N2pc has been associated with attentional functions, and on the assumption that attention is intrinsically related to individuation, this component is an ideal candidate for testing the role of individuation in multiple object processing. However, the majority of studies on the N2pc (Eimer, 1996; Hickey et al., 2006; Luck & Hillyard, 1994; Mazza et al., 2009; Mazza, Turatto, Umiltà, & Eimer, 2007) have used single target presentations. Thus, the temporal dynamics of multiple object individuation have remained largely unexplored.

Two recent studies have shown that N2pc amplitudes are modulated by the number of targets to be processed (Drew & Vogel, 2008; Mazza & Caramazza, 2011). In the study by Drew and Vogel (2008) participants performed an MOT task with a variable number of targets (up to five). Results showed that the amplitude of this component was modulated by the number of tracked targets, increasing as the number of targets increased. N2pc amplitudes also reached an asymptote between 3 and 5 tracked elements, indicating a capacity limit similar to the one proposed by models of individuation. The findings of Drew and Vogel (2008) on N2pc were extended by a study of Mazza and Caramazza (2011) using an enumeration task. In their study, Mazza and Caramazza asked participants to count the number of uniquely colored targets displayed among distractors. Similar to Drew and Vogel (2008), they found that N2pc amplitude was modulated by target numerosity, increasing as the number of targets increased.

Taken together, these two studies provided evidence that individuation, as reflected by N2pc, has an active role in multiple object processing. However, Mazza and Caramazza (2011) used a relatively small range of target numerosities (i.e., 1-3), thus leaving unexplored whether individuation during visual enumeration is limited in its ability to process objects simultaneously. A study addressing this issue is presented in Chapter 2 of the present thesis.

1.3.2 CDA

CDA (Contralateral Delay Activity, also known as SPCN, Sustained Posterior Contralateral Negativity) is a lateralized and sustained component arising at around 400 ms post stimulus onset (Jolicoeur, Brisson, & Robitaille, 2008; Vogel & Machizawa, 2004). Like N2pc, CDA represents a difference in the activity of the two posterior sites of the hemispheres with respect to target side, with the contralateral sites being more negative than the ipsilateral ones.

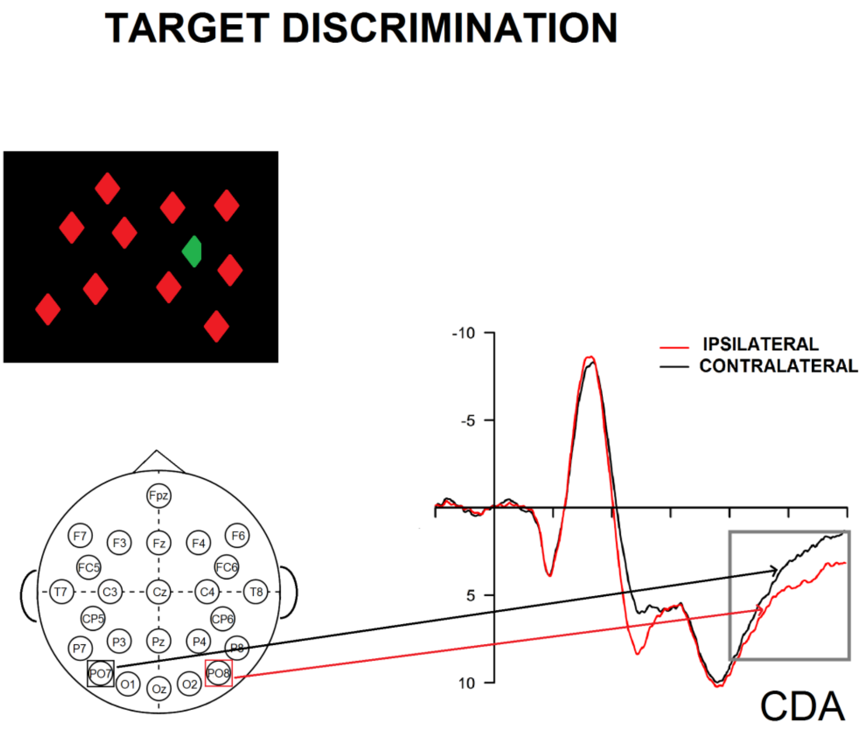

Figure 1.6 CDA as elicited by a target discrimination task

Schematic representation of an EEG setting eliciting CDA using a single target. Participants have to discriminate which side of the uniquely colored target is cut. Activity in the posterior electrode contralateral to target side (PO7) is more negative than correspondent activity the ipsilateral site (PO8) in the N2pc and CDA (400-600 ms) time windows.

Different from N2pc, CDA has been first shown in tasks requiring multiple object processing (Vogel & Machizawa, 2004). In their study, Vogel and Machizawa (2004) asked participants to memorize half display (left or right with respect to a fixation point) with a variable number (1 to 10) of colored squares. After a delay in time, a new display was shown and it was asked to indicate whether it was identical or not to the one previously displayed. Vogel and Machizawa found a difference in the activity of the two hemispheres at posterior electrodes – CDA - in the time interval corresponding to the delay. Crucially, this activity was modulated by the number of squares to be memorized and reached a plateau at approximately four elements. This study interprets the CDA as reflecting nueral activity linked to the encoding and maintenance of multiple objects in visual working memory. However the task proposed by Vogel and Machizawa required an explicit memory encoding of the items.

The two studies described above (Drew & Vogel, 2008; Mazza & Caramazza, 2011) showed that CDA modulations are visible also during MOT and visual enumeration. The study by Drew and Vogel (2008) found that CDA was elicited by the MOT task during the tracking period, suggesting that CDA represents a mechanism that encodes and maintain multiple objects simultaneously. Interestingly, in this study CDA was also modulated by the number of objects to be tracked, increasing in amplitude as the number of targets increased. A similar finding was shown by Mazza and Caramazza (2011). In their study CDA was elicited during visual enumeration and increased as the number of to-be-enumerated targets increased. However, when participants were simply asked to detect the presence of at least one target, no CDA was visible at all. These findings provide further support to the idea that CDA represents the second stage of multiple object processing, in which the individuated targets are encoded in greater detail and maintained for further operations. These issues will be further discussed in Chapter 2.

1.4 Rationale of the present thesis

In a series of five electrophysiological experiments and two behavioral studies, the present thesis will focus on N2pc and CDA to investigate the involvement of early individuation mechanisms and late working-memory related procedures during multiple target enumeration.

In Chapter 2 I will describe two ERP experiments aimed at establishing the involvement of both early and late mechanisms in response to changes in the numerosity of the target elements. As highlighted before, only two electrophysiological studies have specifically focused on this issue (Drew & Vogel, 2008; Mazza & Caramazza, 2011), showing that N2pc and, to some extent, CDA can track the number of individuated items either in an enumeration task or in a MOT task. However, as far as enumeration is concerned, previous experiments used only a small number of items without exploring one of the defining features of multiple object processing, namely its limit in capacity. In Chapter 2 I will present a first experiment (Experiment 1) in which the number of to-be-processed items was increased up to seven items in order to observe whether N2pc and CDA amplitudes showed modulations compatible with the predictions of theories of multiple object analysis. In Experiment 2 I will use a more continuous and extended range of numerosities to further test whether N2pc and CDA are directly involved in enumeration.

In Chapter 3 I will focus on the role of distracting information during individuation. As discussed previously (see section 1.1.3) the presence of distracting information characterizes most of the real life situations in which the relevant objects must be selected from the irrelevant ones. Some research has shown that indeed the presence of distractors can influence the way targets are enumerated (Nan et al., 2006; Trick & Pylyshyn, 1993). By manipulating the presence of distractors in the target hemifield I specifically focused on the issue of whether the selection of multiple relevant elements can be distinguished from the computation of the general (target and distractor) numerosity of objects.

In Chapter 4 I will present an experiment that investigated the role of semantic information during simultaneous target individuation. As previously discussed, little is known about the exact contents of the representations produced during individuation. While some studies on MOT showed that we can successfully track multiple objects without encoding all their features (Annan & Pylyshyn, 2006), so far there are no exhaustive investigations on whether high-level features (such as semantic information) are incorporated in the representations produced at the stage of individuation. Thus, by means of a number-Stroop paradigm in Experiment 4 I asked whether semantic information is encoded during individuation, as reflected by N2pc.

Finally, as I have already discussed (see section 1.2), theories of individuation did not make specific assumptions on the role of awareness during multiple object processing. This is an interesting question that so far has received little investigation. Some behavioral studies indirectly suggested that individuation can operated in the absence of awareness (see Bahrami et al., 2010). Consistently, some studies using single target presentations indicated that N2pc is elicited even when awareness is reduced (Prime, Pluchino, Eimer, Dell’Acqua, & Jolicœur, 2011; Woodman & Luck, 2003), but so far no investigation has been made using multiple targets. In Chapter 5 I will present an EEG experiment (together with two behavioral studies) that investigated this topic using a paradigm that combined masking with an enumeration task.

Chapter 2

The role of individuation during multiple object processing

2.1 Experiment 1

Computation of quantities is essential in daily life and, as some studies suggest, it is necessary to develop symbolic representations of numbers (e.g., Carey & Xu, 2001; Feigenson & Carey, 2005; Leslie, Xu, Tremoulet, & Scholl, 1998; Piazza & Izard, 2009). A topic that is still debated in the literature is whether visual enumeration relies on a single mechanism that covers both small and large quantities (Cordes, Gelman, Gallistel, & Whalen, 2001; Whalen, Gallistel, & Gelman, 1999) or whether small quantities are (at least initially) processed through a more general individuation mechanism that is common to other activities, such as object tracking, visual search and short-term memory tasks (Hyde & Wood, 2011; Piazza et al., 2011; Trick & Pylyshyn, 1993, 1994a).

The individuation mechanism relies on the ability to distinguish an object from the others and is assumed to operate relatively early and simultaneously on a small set of objects (approximately four), leading to a fairly accurate representation of their properties (Hyde & Wood, 2011; Piazza et al., 2011; Trick & Pylyshyn, 1993, 1994a). While the earlier proposals argued that individuation operates separately from attention (Pylyshyn, 1989; Trick & Pylyshyn, 1993; see also Doran & Hoffman, 2010), recent research has suggested that simultaneous indexing of relevant items is tightly related to attention, being indeed one of its key functions (Alvarez & Cavanagh, 2005; Burr, Turi, & Anobile, 2010; Cavanagh & He, 2011; Olivers & Watson, 2008; Vetter, Butterworth, & Bahrami, 2008; Xu & Chun, 2009). Thus, according to this view enumeration of small quantities depends on a capacity-limited ability of the visual attention system to individuate simultaneously approximately four items.

How does the individuation mechanism operate and how is its operation related to visual enumeration of small quantities? Some models of object analysis assume that individuation is a multifaceted process that is decomposable into various subcomponents each dedicated to a different aspect of object processing. For instance, the object file theory (Kahneman et al., 1992), as well as other models (Pylyshyn, 1989; Pylyshyn, 2001), argues that the earliest encoding of objects is based on spatio-temporal aspects alone. Subsequently, these object files are filled with feature information resulting in an approximate representation of the objects. The latter subcomponent may take place through binding of specific features to their respective locations (Mazza & Caramazza, 2011).

As far as enumeration of small quantities is concerned, previous studies (Trick, 2008; Trick & Pylyshyn, 1994) have suggested that it relies on the first component of individuation, the one that initially opens a small set of indexes on the basis of the spatio-temporal information of the objects. However, it is unclear whether additional subcomponents of individuation, such as feature-to-location binding, also have a role in visual enumeration. For instance, feature-to-location indexing may be particularly important when quantities need to be extracted from a complex scene, namely when distractors are presented together with the targets. In such situations, binding may be crucial in order to select and distinguish the relevant from the non-relevant objects. In line with this observation, recent studies on multiple object tracking suggest that the presence of distractors may change the way multiple targets are individuated (e.g., see Doran & Hoffman, 2010).

However, in the majority of the studies on visual enumeration (e.g., Mandler & Shebo, 1982; Piazza et al., 2011; Trick, 2008; Trick & Pylyshyn, 1994b) the elements to be enumerated were presented in isolation, thus leaving unexplored how enumeration occurs when the number of elements to be counted does not coincide with the overall number of elements presented. In addition, most of the previous evidence is based on behavioral measures, which represent the final product of effects potentially taking place at several stages of processing. Therefore, it is unclear whether the advantage in processing small quantities can be really attributed to a relatively early stage, such as the one represented by individuation and its subcomponents, or whether later stages are mainly involved in enumeration of small quantities. To address these aspects, in Experiment 1 I investigated how multiple object individuation is accomplished during visual enumeration of targets presented in cluttered scenes. I adopted an Event-Related Potential (ERP) approach that, given its excellent temporal resolution in recording brain activity, is well-suited to isolate the effects taking place at different stages of stimulus processing.

Previous ERP research on number-related tasks (Dehaene, 1996; Hyde & Spelke, 2009; Hyde & Wood, 2011; Libertus, Woldorff, & Brannon, 2007; Nan et al., 2006; Szucs & Csépe, 2004; Temple & Posner, 1998) has used numerical distance paradigms to infer the cognitive operations related to symbolic number processing. The most consistent result from these studies is a modulation of the brain activity at posterior sites at approximately 200 ms (P2p component) as a function of the distance between a specific symbolic or non-symbolic numerosity and a predefined number or numerical distance in adaptation paradigms (Hyde & Spelke, 2009). Interestingly, some studies (e.g., Hyde & Spelke, 2009; Libertus et al., 2007) additionally found an earlier modulation (N1 range, 140-200 ms) related to the absolute cardinality of the object sets. However, the tasks used by previous studies (e.g., parity judgment, passive viewing) required only an implicit quantification and not an explicit enumeration of the object sets. In addition, the sets of elements were always presented in isolation, thus leaving unexplored how relevant quantities are extracted in a complex scene (i.e., when the relevant object sets are presented among distractors). The only exception is the study of Nan et al. (2006), which showed that the N1 increase is related to the overall number of elements presented in the visual display, regardless of whether these are targets or distractors.

Given my interest in individuation of targets when these are presented with irrelevant objects, in the present study I used an explicit enumeration task of target elements presented among distractors. My main focus in terms of ERPs was on the N2pc component (N2 posterior contralateral- arising at approximately 200 ms), a lateralized ERP response that occurs whenever a relevant object is presented in one hemifield together with distractors (Eimer, 1996; Luck & Hillyard, 1994). The fact that the N2pc is elicited in the presence of distractors and in a wide range of tasks used to study attention makes this ERP response an ideal tool to investigate how targets are individuated in complex scenes.

The N2pc has typically been interpreted as the neural correlate of attention selection in the visual field, either through distractor suppression (see Luck, Girelli, McDermott, & Ford, 1997) or through target enhancement (see Eimer, 1996; Mazza, Turatto, & Caramazza, 2009). The lateralized nature of the N2pc indicates that the visual hemifield where the relevant stimulus occurs is processed differently from the other hemifield, thus implying that (at least coarsely) the location of this object plays an important role in the functioning of the mechanism reflected by this ERP response. Interestingly, recent studies (e.g., Woodman, Arita, & Luck, 2009) have shown that the N2pc is elicited only when a potentially relevant location is specifically marked by an object (i.e., a set of features in a specific location), thus indicating that the mechanism reflected by the N2pc is not exclusively based on location coding. This in turn suggests that this ERP component reflects the working of a mechanism that integrates spatial and non-spatial features and through which potential targets are indexed and distinguished from distractors.

Although most of the studies on the N2pc have used single-target presentations, recent research (Drew & Vogel, 2008; Mazza & Caramazza, 2011) has shown that the N2pc is sensitive to target numerosity, making it a good candidate for investigating the mechanisms involved in multiple target individuation. Drew and Vogel (2008) showed that in a multiple object tracking task the N2pc amplitude is modulated by the number of objects that are tracked, reaching a plateau at approximately four elements. While these results support the idea that the N2pc component might reflect the functioning of a stage of multiple object individuation, the study did not address the role of this process during explicit object enumeration. The study by Mazza and Camarazza (2011) found that the N2pc amplitude is modulated by target numerosity during an enumeration task, suggesting an important role of feature-to-location binding in quantity computation. However that study manipulated a small range of target numerosities (i.e., 0-3), leaving unexplored one of the defining features of the individuation mechanism, namely its limit in simultaneous processing. The present study filled this gap by using an enumeration task with an extended range of target numerosities (i.e., 1, 3, 5 and 7). To further explore the involvement of the feature-to-location binding stage of individuation (as reflected by the N2pc) in target enumeration I assessed the relationship between the N2pc pattern and participants' enumeration efficiency as revealed by behavioral performance. On the basis of the foregoing, I expected that the pattern of the N2pc activity would change not only as a function of target numerosity but also according to individuals' enumeration performance.

Finally, some studies have underlined a close relationship among enumeration, visual working memory (VWM) and individuation (e.g., Piazza et al., 2011; Whalen, Gallistel & Gelman, 1999). More specifically a VWM buffer may be crucial in maintaining active the individuated items during the process of mapping the set of elements onto a specific numerical value. For this reason I additionally assessed another lateralized component, the CDA (Contralateral Delayed Activity- also called SPCN, Sustained Posterior Contralateral Negativity- arising at approximately 350-400 ms post-stimulus). This is a sustained lateralized response elicited in memory tasks, as well as in other "attention" paradigms in which further elaboration of the relevant object(s) is carried out (Drew & Vogel, 2008; Jolicoeur et al., 2008; Vogel & Machizawa, 2004). It has been proposed that CDA is related to cognitive operations involved in a more detailed elaboration of the individuated objects (Jolicoeur, Sessa, Dell'Acqua, & Robitaille, 2006; Kiss, Van Velzen, & Eimer, 2008; Mazza et al., 2007). Recent studies have shown that the CDA is modulated by the numerosity of the items to be memorized or tracked (Drew & Vogel, 2008; Ikkai, McCollough, & Vogel, 2010) making it a good candidate for assessing the role of VWM in quantity computation.

2.1.1 Methods

2.1.1.1 Participants

Twenty-four healthy volunteers (15 female; aged 19–35) with normal or corrected-to-normal vision participated in the study after providing informed consent. The study was approved by the local ethics committee.

2.1.1.2 Stimuli and procedure

A total of 32 equiluminant green and red dots (8 cd/m²) were presented on a dark grey background (6 cd/m²), equally distributed to the left and right side of the fixation cross (Figure 2.1 A). The dots appeared within an invisible 10 (rows) x 8 (columns) grid (10.7° × 5.4°). On each trial, one, three, five or seven dots (the targets) had a unique color (either red or green) relative to the homogenously colored distractors, and appeared with equal probability and in random order to the left or right of fixation, but never in the two extreme columns and rows of the grid, nor in the two columns closest to fixation. The color of the target(s) and of the distractors was counterbalanced across participants. The display duration was 300 ms. Participants’ task was to report the number of targets by pressing one of four vertically arranged keys on a keyboard with their index or middle fingers of both hands. Response assignment was counterbalanced across participants. Speed and accuracy were emphasized equally, and maximum time for responding was 1500 ms. The inter-trial interval was 1500 ms. Participants performed eight blocks of trials with 104 trials per block (26 one-target trials, 26 three-target trials, 26 five-target trials and 26 seven-target trials). One practice block was delivered before the first block of the experimental session.

A problematic aspect when measuring lateralized ERP activity concerns the lateralized electrical artifacts created by the participant’s eye movements, especially in tasks (such as the present one) that might increase the likelihood of systematic eye movements towards the target(s) location. Thus, in addition to the standard off-line procedures for removing eye movement artifacts (see below) we recorded eye movements with a remote eye-tracking device and used these measurements as an on-line feedback to the participants in order to minimize their tendency to make eye movements. In each block, the device delivered a visual feedback to the participants every five consecutive saccades.

2.1.1.3 EEG recording and data analysis

EEG was recorded from the scalp with 25 electrodes (including PO7 and PO8) and a left earlobe electrode, with a right earlobe reference (bandpass filter: 0.01- 200 Hz; A/D rate: 1000 Hz). EEG data were re-referenced offline to the average of right and left earlobe electrodes and filtered with a 40 Hz low-pass filter. Horizontal electro-oculogram (HEOG) was recorded from two electrodes placed on the external canthi of both eyes. Impedance was kept below 5 KΩ for all electrodes. Trials with horizontal eye movements (HEOG exceeding ± 30 µV), head movements, eye blinks or other movement artifacts (any channel exceeding ± 80 µV) were discarded. The average number of retained trials for each participant was 80%.

ERP averages for correct responses were computed relative to a time window starting 100 ms before stimulus onset, separately for each target numerosity (one, three, five, seven) and target side (left, right). Statistical analyses for the lateralized activations (N2pc and CDA) were carried out on mean difference amplitude values at posterior electrode sites (PO7 and PO8) obtained by subtracting the activity at the ipsilateral electrodes relative to the target side (e.g., PO8 for right targets) from that recorded at the contralateral sites (e.g., PO7 for right targets), collapsed across target side and for the following time windows: 206-286 ms (N2pc), and 400-800 ms (CDA). The N2pc time range was defined as the 80 ms interval centered on the N2pc peak amplitude calculated from the grand-average waveforms. To compare the present results with previous research (e.g., Hyde & Spelke, 2009; Libertus et al., 2007), I also analyzed the (non-lateralized) mean amplitude values for the following time windows: 139-199 ms (N1), and 175-250 ms (P2p). The N1 and P2p time range were defined as in Hyde and Spelke (2009). These mean amplitude values (as well as behavioral data) were submitted to a repeated measures ANOVA with numerosity (one, three, five, seven) and ERP response (N1, P2p, N2pc, CDA, for ERP data only) as factors. When appropriate, the Greenhouse–Geisser method for the violation of the sphericity assumption was applied, and only corrected p values are reported. Further analyses were conducted by means of pairwise comparisons (t-tests). To correct for multiple comparisons I followed the False Discovery Rate method (Benjamini & Hochberg, 1995). Only corrected *p* values are reported.

A second set of analyses evaluated the relationship between the N2pc, CDA, N1 and P2p patterns and the individual efficiency in enumeration performance (Section 2.1.2.2). Here, I divided participants into two groups (high versus low performance, each with an equal number of individuals) on the basis of their rank value on efficiency based on their behavioral performance. The procedure to obtain such indexes was twofold. First, following (Franconeri, Alvarez, & Enns, 2007), each participant's efficiency value was computed as the first numerosity that elicited less than 90% of correct responses. For example, in case of a participant with 98%, 97%, 89%, 80% correct responses for one-, three-, five-, and seven-element targets respectively, the efficiency value of that participant was defined as five elements[1]. Second, to take into account possible fluctuations in performance (e.g., participants that responded with less than 90% accuracy for a numerosity but whose accuracy increased for greater numerosities) and to obtain a more continuous index, for each participant I multiplied this "discrete" efficiency value by the value of the total accuracy across all target set sizes. An ANOVA with group (high, low) as between-subject factor and numerosity

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[1] Previous studies (e.g., Drew and Vogel, 2008; Vogel & Machizawa, 2004) have estimated the individual capacity limit by means of the K index (Cowan, 2001). However, unlike the procedure used in those studies (a yes/no response task) the four-choice response alternatives used in the present task did not allow for the computation of this more traditional measure of performance. Two participants scored more than 90% of correct responses for all numerosities (the lowest value being 91% for seven targets for both participants). However, I decided to adopt a conservative criterion considering their efficiency value as 7, and to leave these participants in the sample. This was motivated by the fact that the same statistical patterns were found when excluding these two participants from the data sets, both in the ANOVA and in the correlational analyses.

(three, five, seven) as within-subject factor was performed on mean amplitudes separately for each ERP response (N1, P2p, N2pc and CDA; Section 3.3). Trials with one target were excluded from the analysis given that none of the participants showed a decrease below 90% of correct responses for this numerosity. In addition, previous research has shown that there is no difference between high and low efficiency groups in the individuation of only one target (Drew & Vogel, 2008). Follow-up analyses were conducted as in the main analysis. To further assess the relationship between the neural and behavioral responses, for each ERP response I additionally performed correlational analyses between the individual efficiency index and the difference in the ERP response between the smallest (i.e., 3) and largest (i.e., 7) numerosities in the set.

2.1.2 Results

2.1.2.1 Behavioral results

2.1.2.1.1 RTs

The ANOVA on mean RTs for correct responses between 200 and 1500 ms showed a significant effect of numerosity, *F*(3,69)=143.12, *p*<.001: participants were progressively slower as target numerosity increased, all *ps*<.001 (paired t-tests), except for the largest numerosity in the set, which yielded RTs similar to the condition with three targets, *p*=.43 (Figure 2.1 B). This pattern is consistent with the so-called “end effect” (Trick, 2008).

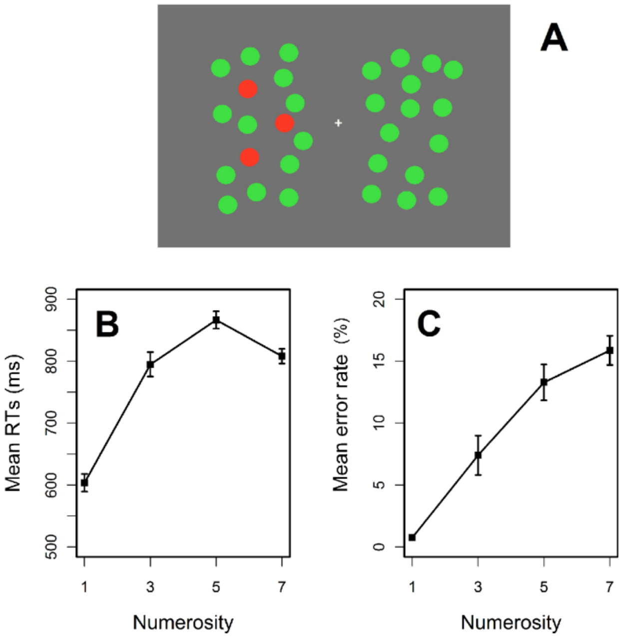

Figure 2.1 Stimulus display and behavioral results Experiment 1

Example of a stimulus display with three targets on the left side (A). Mean RTs as a function of target numerosity (B). Error rate percentage as a function of target numerosity. Error bars represent standard error of the mean (C).

2.1.2.1.2 Accuracy

The ANOVA on percentage of correct responses revealed a significant effect of numerosity, *F*(3, 69)=38.83, *p*<.00. Pairwise comparisons showed that participants were less accurate as the number of targets increased, all *ps*<.01, but they were equally accurate for the two largest numerosities (i.e., five and seven targets), *p*=.13 (Figure 2.1 C).

2.1.2.2 ERP results

In the non-lateralized activations, an increasing trend in the N1 amplitude emerged between the single and multiple target conditions, while the P2p amplitudes showed a decreasing trend as a function of numerosity (Figure 2.2 A). In the lateralized activities, the N2pc increased as a function of numerosity, reaching an asymptote at five targets. In contrast, the CDA showed an inverted U-shape trend, with an increase in amplitudes for numerosities from one to five, and a drop for the largest numerosity (Figure 2.2 B and Figure 2.3). Statistical analyses confirmed these observations.

The overall ANOVA with numerosity and ERP response as factors revealed a significant effect of numerosity $F(3,69)=38.2$, $p<.001$ and a significant ERP response x numerosity interaction, $F(9,207)=3.4$, $p<.001$. Therefore, I explored the effect of numerosity separately for each ERP response.

2.1.2.2.1 N1

The ANOVA on N1 mean amplitudes showed a significant effect of numerosity, $F(3,69)=7.9$, $p<.001$, with pairwise comparisons indicating only a difference between one target and all the other numerosities, all *ps*<.05. No differences emerged among three, five and seven targets, all *ps*>.10 (Figure 2.2 A). To compare the present results with those of Hyde and Spelke (2009) I additionally conducted a contrast analysis, which showed a significant linear trend, $F(1,23)=23.48$, $p<.01$.

2.1.2.2.2 P2p

The ANOVA on P2p mean amplitudes showed a significant effect of numerosity, *F*(3,69)=14.4, *p*<.001, with follow-up comparisons indicating more pronounced amplitudes for one target than for all the other numerosities, all *ps*<.001. Three targets marginally elicited more positive amplitudes than five targets, *p*=.09. The same pattern was marginally significant for five and seven targets, *p*=.08 (Figure 2.2 A). The contrast analysis showed a significant linear trend, *F*(1,23)=30.34, *p*<.01.

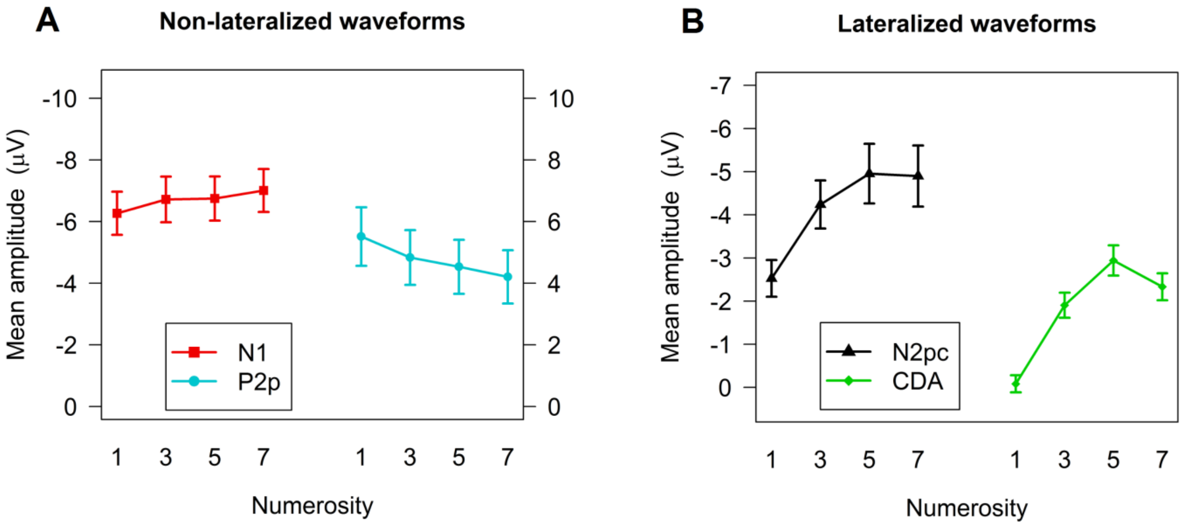

Figure 2.2 ERP main results Experiment 1

(A) ERP mean amplitudes for the non-lateralized (N1 and P2p) and (B) lateralized (N2pc and CDA) brain activities as a function of target numerosity.

2.1.2.2.3 N2pc

The ANOVA on the N2pc showed that it was modulated by numerosity, $F(3,69)=21.6$, $p<.001$, with paired t-tests confirming that the N2pc was greater for three, five or seven targets than for one-target trials, all *ps*<.001, and for five or seven targets relative to three-target trials, both *ps*<.01. In contrast, no difference emerged between five and seven targets, $p=.84$ (Figure 2b and Figure 3). In line with these results, the contrast analysis showed a significant quadratic trend, $F(1,23)=14.5$, $p<.01$.

2.1.2.2.4 CDA

The ANOVA on CDA mean amplitudes showed a significant main effect of numerosity, $F(3,69)= 44.91$, $p<.001$. Further comparisons confirmed the inverted U-shape trend, with significant differences between one-target and all the other numerosities, all *ps*<.001, as well as greater amplitudes for five relative to three targets, $p=.001$. Five-target trials elicited a more pronounced CDA than seven-target trials, $p=.01$, which in turn were marginally significantly different from trials with three targets, $p=.09$ (Figure 2.2 B). A significant quadratic trend emerged from the contrast analysis, $F(1,23)=50.63$, $p<.01$.

2.1.2.3 Group analysis

Here I evaluated the relationship between the ERP patterns and the individual enumeration efficiency by means of an ANOVA with group and numerosity as factors.

For completeness, behavioral data were also analyzed (Figure 2.4 D and E). The ANOVA on RTs revealed only a significant effect of numerosity, *F*(2,44)=15.21, *p*<.001, indicating the same pattern as in the main analysis. The ANOVA on accuracy data showed significant effects of group, *F*(1,22)=29.11, *p*<.001, numerosity, *F*(2,44)=14.56, *p*<.001, and a marginally significant numerosity x group interaction, *F*(2,44)=2.4, *p*=.09, due to the fact that participants in the high group were more accurate for five than for seven targets, p<.05, whereas participants in the low group did not show such a difference, p=.6.

The ANOVAs on the N1, P2p and CDA revealed no significant effects of group or numerosity x group interaction, all *p*s>.20, but only a main effect of numerosity for the P2p and CDA (*F*(2,44)=5.8, *p*<.01 and *F*(2,44)=10.3, *p*<.001, respectively), in line with the main analyses.

In contrast, the ANOVA on the N2pc revealed a significant group x numerosity interaction, *F*(2,44)=3.5, *p*<.05, indicating that numerosity had differential effects as a function of participants' efficiency in enumerating targets (Figure 2.4 C). This was confirmed by follow-up analyses (t-tests). In the high-performance group (mean enumeration capacity: 6.1 items) the N2pc reached an asymptote at approximately five elements: the N2pc was greater for five and seven targets than three targets, all *ps*<.01, but five and seven targets were not different from each other, *p*>.5 (Figure 2.4 A and Figure 2.4 C left side). In contrast, in the low-performance group (mean enumeration capacity: 3.4 items; Figure 2.4 B and Figure 2.4 C right side) the N2pc reached a plateau at approximately three elements: three, five and seven targets were not different from one another, all *ps*>.2.

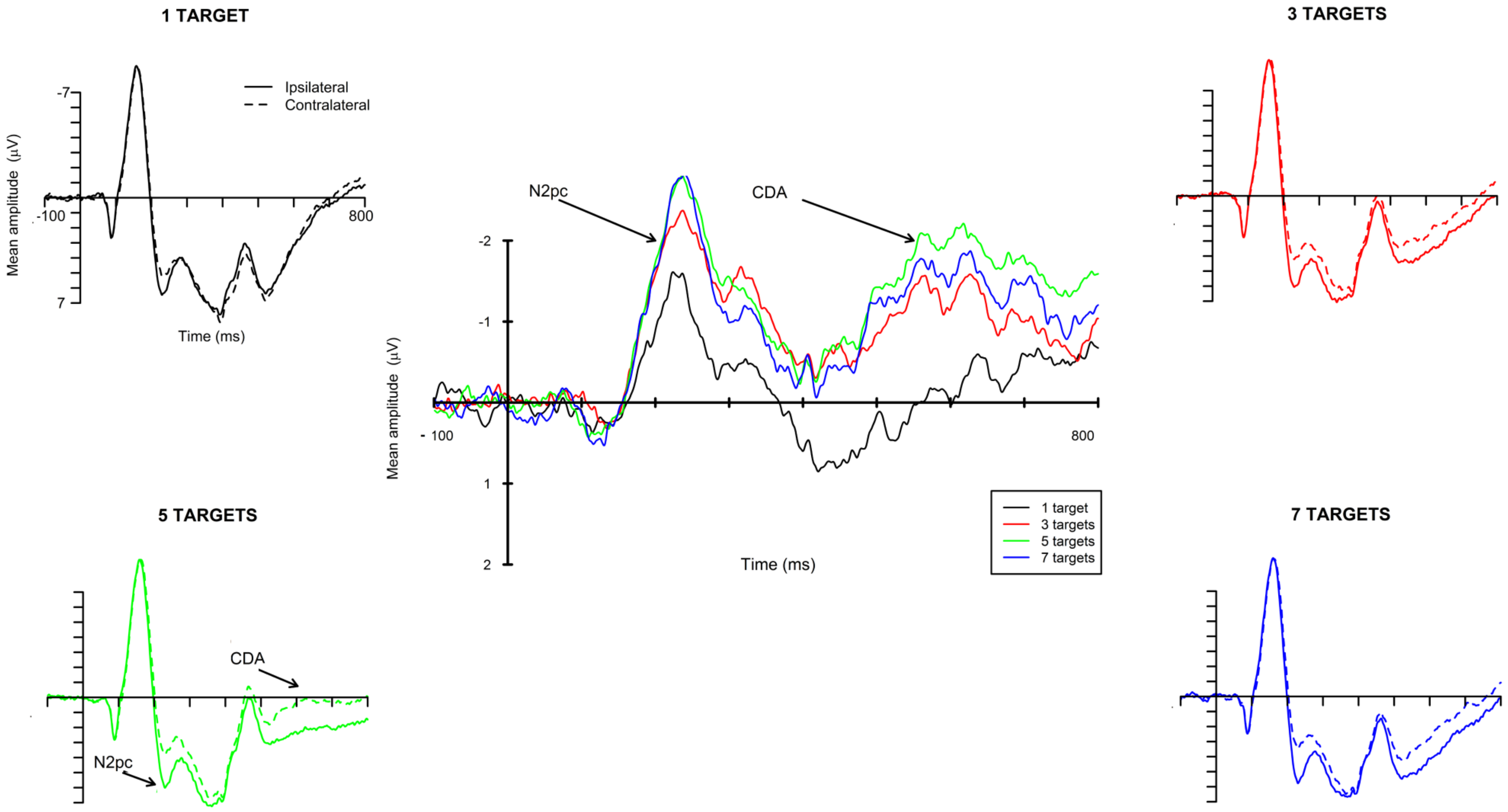

Figure 2.3 Grand Average waveforms Experiment 1

Both the grand-average ERP waveforms (graphs at the four corners), -representing ipsilateral (continous line) and contrateral (dashed line) activity for PO7 and PO8 electrodes (separately for each target numerosity), -and the grand-average differential waveforms (middle graph), -obtained by subtracting the activity of the contralateral sites from the ipsilateral ones for PO7 and PO8 electrodes in the 800 ms post-stimulus interval, -show that the N2pc amplitudes reach an asymptote at five elements. An inverted U-shape pattern is visible for the CDA.

2.1.2.4 Correlational analyses

In line with the results of the group analysis, I found a significant correlation between the behavioral capacity index and the N2pc difference between 7 and 3 targets, r=.49, *p*<.05, such that the amplitude difference increased with the increase in the enumeration efficiency. The smaller difference in amplitude for participants with low efficiency in enumerating invites the inference that three targets consumed more resources than for the high-capacity participants. Together with the results of the group analysis, these results suggest that the N2pc for low performance individuals reached a plateau at smaller set sizes with respect to high performance individuals.

No significant results emerged for the other ERP responses, all ps>.2.

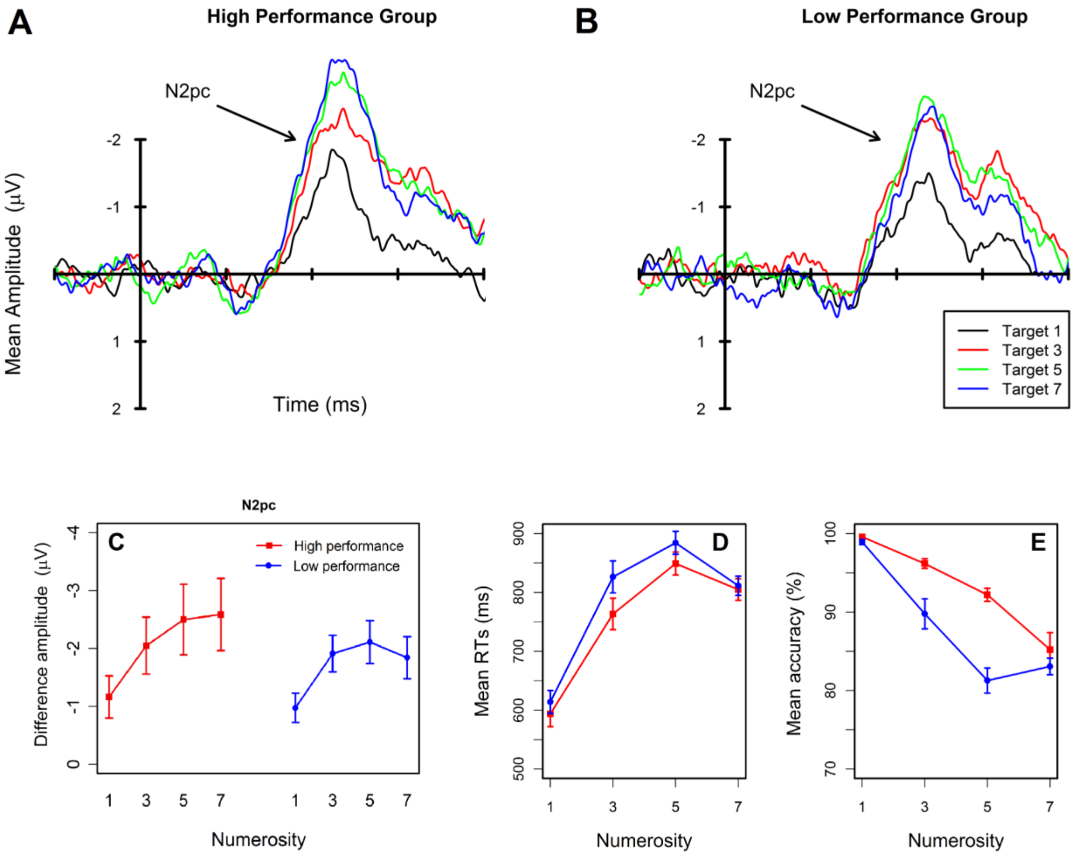

Figure 2.4 Group analyses results Experiment 1

(A) and (B) Grand-average differential waveforms as a function of target numerosity for the high (A) and low (B) group. (C) N2pc mean amplitudes in the 206–86 ms post stimulus interval as a function of target numerosity and group. Consistently with their enumeration capacity, the N2pc of the participants in the low performance group reached an asymptote before those in the high performance group. (D) and (E) Reaction times (D) and accuracy (E) for high and low group.

2.1.3 Discussion

The results of the present study shed new light on the mechanisms involved in enumeration of small quantities[2] in cluttered scenes.

First, the behavioral results showed a decrease in performance as a function of target numerosity and, in line with previous research, an end effect for the largest numerosity (Mandler & Shebo, 1982; Trick, 2008).

Second, the electrophysiological data on N2pc and CDA[3] provided information on how multiple target processing occurs in complex scenes during enumeration. The N2pc amplitude was modulated by the number of targets, supporting the idea that feature-to-location binding (as reflected by the N2pc) is a critical process during enumeration of small quantities in cluttered scenes (see also Mazza & Caramazza, 2011; Piazza et al., 2011). In addition, the N2pc reached a plateau at about five elements, in line with the limit of simultaneous processing proposed by some models of individuation (Pylyshyn, 1989; Kahneman et al., 1992). These results are strengthened by the results of the group analysis that revealed different N2pc asymptotes as a function of the participants' behavioral efficiency in enumeration. Specifically, N2pc for the low-performance group reached an asymptote at smaller quantities (i.e., three targets) with respect to the high-performance group, in line with the idea that participants with lower enumeration efficiency also possess a relatively low limit in the ability to individuate.

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[2] Given the difference between the present behavioral pattern and the typical subitizing pattern I have chosen to use the term "enumeration of small quantities" throughout the chapter rather than referring to "subitizing".

[3] Results on N1 and P2p will be fully discussed in the General discussion (section 2.3)

Finally, CDA amplitudes were modulated by target numerosity, suggesting that the maintenance of the target elements in VWM during the matching of the set to a specific numerical value contributes to quantity enumeration. However, the modulation showed an atypical pattern, with a marked decrease in amplitudes for the largest numerosity in the set (Figure 2.2). This inverted U-shaped trend invites the inference that participants used different quantity enumeration procedures in assigning numerical values to the smaller versus largest set sizes. However this specific hypotheses should be tested in an experimental contest. To this extent, and to further support the general findings about the role of individuation in visual enumeration I performed Experiment 2.

2.2 Experiment 2

Experiment 2 had three main purposes specifically related to the N2pc and CDA results found in Experiment 1.

First, I wanted to replicate the N2pc results using a more extended range of numerosities. This was motivated by the fact that the N2pc results of Experiment 1 showed that only one target numerosity (i.e., 7) was clearly above the “neural” capacity limit of individuation. Therefore, having a more extended number of targets would allow for a more direct and precise testing of the N2pc plateau. Second, in Experiment 1 target numerosities were not presented along a continuum, thus preventing very fine-grained comparisons in the neural activity between a given numerosity and the next one. Additionally, the use of only four numerosities presented in a “discrete” rather than continuous fashion may have potentially induced the functioning of a different cognitive process for the analysis of multiple target objects relative to typical enumeration contexts. For these reasons, in Experiment 2 I manipulated the numerosities of the targets by having 1 to 9 elements.

Finally, the use of a wide range of numerosities may additionally help clarifying the nature of the inverted U-shaped pattern of the CDA found in Experiment 1. The results showed the presence of a pronounced decrease in amplitudes for the largest numerosity (i.e. 7). This trend was tentatively interpreted as the consequence of a guessing strategy related to the largest numerosity in the set (the so-called “end effect”). Having an extended range of numerosities may either eliminate the guessing strategy (and the corresponding “end-effect”) or alternatively may shift it for the largest numerosity presented. In both cases, this leaves a consistent number (e.g., 5,6,7) of small and large target quantities for a clearer assessment of the involvement of working memory procedures, as reflected by the CDA, in the enumeration of visual quantities.

2.2.1 Participants

Eleven participants (all females, mean age= 22.6) were tested in two sessions with an interval of 7 days. All participants provided written informed consent. The study was approved by the local ethics committee.

2.2.2 Stimuli and procedure

Stimuli and procedure were identical to Experiment 1 except for the following aspects. First, the number of targets varied within a continuous range from 1 to 9 elements. Second, on the basis of the results of a pilot experiment (not reported here) the display duration was set at 400 ms, in order to give participants more time to enumerate, thus increasing their accuracy performance. This in turn gave the possibility to have a adequate number of correct trials for the EEG analysis. Third, response assignments were based on accuracy only. This was done in order to avoid the presence of an excessive number of eye movement artifacts. In fact, as participants provided their response using the keys of a computer keyboard, and given that in this experiments they had several relevant buttons (i.e., 9), they might tend to move their eyes in order to search for the correct response button. Therefore, the response requirements were modified in a way that the presence of an eye movement would not interfere with the

EEG measurements in the critical time windows for N2pc and CDA. After stimulus presentation, a blank screen appeared for 500 ms, during which participants were required to refrain from responding and from moving their eyes. A display with the question “How many targets?” prompted participants to give their response by pressing one of the nine buttons. After a practice session, participants completed a total of 1728 trials divided in two sessions (each of 12 blocks) for a total of 24 blocks. Each numerosity was repeated 192 times.

2.2.3 EEG recordings and analysis

EEG recordings and analysis were the same as in the previous experiment. The only difference with Experiment 1 was in the definition of the time windows representing N2pc and CDA activity. On the basis of visual inspection of the grand-average waveforms, N2pc was defined as the difference between contralateral and ipsilateral activity (PO7/8) in a time interval ranging from 180 to 300 ms post stimulus, whereas CDA was measured between 400 and 600 ms post stimulus, time-locked to the stimulus onset.

N2pc and CDA mean amplitudes, as well as accuracy data, were submitted to two separate repeated measures ANOVA, one for the subiziting range (1,2,3,4 targets) and a second one for the upper range (5,6,7,8 targets). Numerosity nine[4] was excluded due to too many errors (less than 11% correct trials).

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[4] However the same results were obtained when this numerosity was included in the analyses.

2.2.4 Results

The ANOVA on accuracy showed a significant effect of numerosity both for subitizing $F(3,30)= 29.26$, $p<.0001$, and counting, $F(3,30)= 7.03$, $p<.01$. Participants were overall increasingly less accurate as the number of targets increased (Figure 2.5 A). This was confirmed by a significant quadratic trend for the subitizing range $F(1,10)=16.2$, $p<.01$ and a significant linear trend for the counting range $F(1,10)= 11.4$, $p<.01$. Therefore, no end effect was visible in the present behavioral data.

The N2pc amplitude increased up to four targets and then reached a plateau for numerosities larger than four (Figure 2.5 B). This was confirmed by the following statistical analyses. The ANOVA on N2pc in the range between one and four targets revealed a significant effect of numerosity $F(3,30)= 3.7$, $p<.05$ with a significant linear trend $F(1,10)= 6.8$, $p<.05$. In contrast, when testing the range between five and eight targets no effect of numerosity emerged ($p=.20$), indicating that the amplitude of N2pc was not modulated by large numerosities.

The ANOVA on CDA for small target numerosities showed a significant effect of numerosity $F(3,30)=14.01$, $p<.001$. Similar to N2pc, CDA did not show any effect of numerosity in the range between five and eight targets $p=.10$. Again similar to N2pc, the amplitude of CDA increased as a function of target numerosity up to four targets (Figure 2.5 C) as suggested by a significant linear trend in the 1-4 target range $F(1,10)=5.1$, $p<.05$.

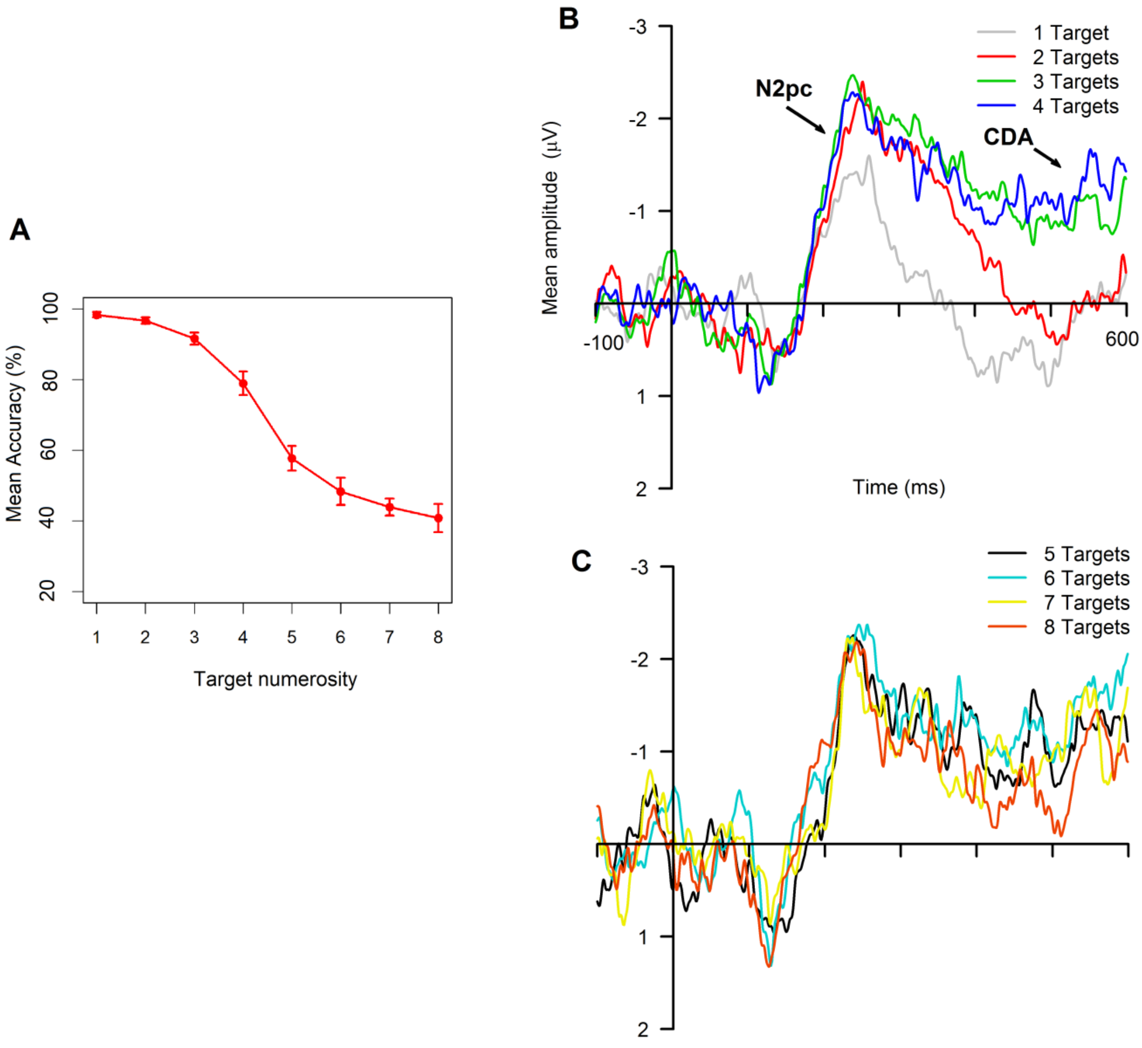

Figure 2.5 Behavioral and ERP results Experiment 2

(A Mean accuracy as a function of target numerosity. (B) Grand-average differential waveforms obtained by subtracting the activity of the contralateral sites from the ipsilateral ones for PO7 and PO8 as a function of numerosity in the range 1-4 and (C) in the range 5-8. Grand averages show that both the N2pc and CDA amplitudes reach an asymptote at four elements

2.2.5 Discussion

The results of Experiment 2 helped disentangling some open issues left from Experiment 1.

Behavioral data showed a significant decrease in accuracy both in the subitizing and in the counting range. As in Experiment 1, and in contrast with some classical findings of subitizing (Trick & Pylyshyn, 1993, 1994a), the decrease in accuracy was more pronounced for the small than for the larger numerosities. Together with Experiment 1, the present results suggest that distractors may significantly affect the way in which targets are enumerated, at least at the behavioral level.

ERP results showed that the N2pc was modulated by target numerosity, as in the previous experiment, as well as other studies (Ester et al., 2012; Mazza & Caramazza, 2011). In addition, N2pc reached a stable plateau starting from approximately four targets, in line with the idea that this component may reflect the neural counterpart of the individuation mechanism.

The results on CDA helped defining the kind of process that is tracked by this component. CDA amplitude was modulated as a function of the number of displayed targets and, similar to the N2pc, reached a clear asymptote at four targets. This result is in line with previous studies (Ikkai et al., 2010; Vogel & Machizawa, 2004) showing that CDA amplitude increases as a function of the items to be recalled in a delayed-match-to-sample task, reaching a plateau around four items. In the light of these previous findings, the present experiment further suggests that CDA represents a visual stage related to working memory that is at the basis of several tasks in which targets must be encoded for further operations, such as the mapping of the set of elements onto a specific numerical value.

2.3 General Discussion

The results of Experiment 1 and 2 helped in understanding the role of individuation and visual working memory related mechanism in visual enumeration.

The behavioral results of the Experiment 1 showed a decrease in performance with increasing numerosities up to five targets and, in line with previous research, an end effect in speed for the largest numerosity (Mandler & Shebo, 1982; Trick, 2008). However, in slight contrast with the classic pattern found in enumeration studies (the so-called subitizing effect), the slope of the RT pattern was more pronounced for smaller (i.e., 1 versus 3) than larger (i.e., 3 versus 5) numerosities. There are several differences between the current experimental paradigm and those used in previous studies that may explain this discrepancy. For instance, it has been shown that the presence of distractors may importantly affect behavioral performance even within the typical subitizing range (Nan et al., 2006). Indeed the results of Experiment 2 in which the decrease in accuracy was steeper for the small than for the larger numerosities suggest that distractors may significantly affect the way in which targets are enumerated, at least at the behavioral level.

The ERP results provided important information on how multiple target individuation occurs in complex scenes during enumeration. First, the N2pc amplitude was modulated in both Experiment 1 and 2 by the number of targets, supporting the idea that feature-to-location binding (as reflected by the N2pc) is a critical process during enumeration of small quantities in cluttered scenes (see also Mazza & Caramazza, 2011; Piazza et al., 2011). Second, the N2pc reached a plateau at about five elements, in line with the limit of simultaneous processing proposed by some models of individuation (Pylyshyn, 1989; Kahneman et al., 1992) and using both a discrete (1, 3, 5, 7) or a continuous (from 1 to 9) range of numerosities. Taken together, these two aspects suggest that visual enumeration of small quantities critically depends on a specific capacity-limited aspect of individuation, the one that finalizes indexes by binding locations to properties.

The present pattern is also in line with previous N2pc findings on multiple object tracking (Drew & Vogel, 2008). The similarity of N2pc patterns between object tracking and enumeration tasks indicates that the present results cannot be interpreted strictly in terms of number-specific processing but that N2pc tracks a mechanism that is common to different tasks. Overall, the present data complement previous work by suggesting a common bottleneck in the capacity of the visual system that limits the number of items that can be simultaneously individuated across different tasks (see also Chesney & Haladjian, 2011; Piazza et al., 2011).

Third, results of the group analysis of Experiment 1 revealed different N2pc asymptotes as a function of the participants' behavioral efficiency in enumeration. Specifically, relative to the high-performance group, the N2pc for the low-performance group reached an asymptote at smaller quantities (i.e., three targets), confirming that participants with lower enumeration efficiency also possess a relatively low limit in the ability to bind properties to locations. This conclusion is further strengthened by the correlation analysis, which shows that the amount of difference in the N2pc amplitudes between large and small numerosities is associated with the individual enumeration efficiency. Interestingly, such results were obtained only for the N2pc component, therefore revealing a specific connection between individuation capacity, as indexed by the N2pc data, and enumeration of quantities.

Two aspects of the present N2pc modulations are worth noting. First, one may wonder whether the present results might not simply reflect effects specifically related to either location-based (e.g. Bichot, Cave, & Pashler, 1999) or feature-based (e.g. Mounts & Melara, 1999) attentional selection alone rather than feature-to-location binding. Although a pure location-based account of N2pc can be ruled out on the basis of previous results (e.g. Woodman et al., 2009) which have shown that the N2pc disappears when a relevant location is not occupied by an object, it could still be the case that the numerosity-related increase of N2pc found in Experiment 1 and 2 is the result of an increase in the area occupied by the targets. While it is not possible to directly rule out this account on the basis of the results reported here, previous research makes such an account highly improbable (Drew & Vogel, 2008). For instance, it was found that the N2pc was not modulated by the target area, suggesting that the spatial extent of the target area cannot be uniquely responsible for the present N2pc effects. Similarly, a pure non-spatial feature-based account of N2pc can be ruled out by the lateralized nature of N2pc, which implies that the locations of the target elements play an important role for the generation of this ERP response. Nonetheless, it is possible to formulate a variant of the feature-based selection account that could explain the numerosity-related modulation of the N2pc as reflecting the overall increase in the "amount" of the target defining features as target numerosity increases. However, recent work has indicated that the occurrence of one versus two features in the same spatial location leads to a modulation in N2pc latency rather than amplitude (Grubert, Krummenacher, & Eimer, 2011). In addition, the results of Experiment 2, showing that N2pc reaches a stable plateau at four targets even when the number of targets increases up to nine elements, further suggest that the modulation of N2pc is more related to a feature-to-location binding stage than to a pure feature-based mechanism. Thus, while additional research is needed to unambiguously disentangle the specific roles of the number of features versus locations in the generation of N2pc modulation, it seems reasonable at this stage to interpret the present modulations of the N2pc amplitudes as reflecting the functioning of a mechanism that integrates both spatial and non-spatial object properties.

Another important aspect of the N2pc modulation is related to an account of this effect in terms of task difficulty. While it is possible that task difficulty may affect the N2pc, the argument that the N2pc modulations are related to task difficulty *per se* actually predicts a number of outcomes contrary to what I and other research groups observed. First, an account strictly based on task difficulty as seen from RTs should predict a reduction of N2pc amplitudes for the seven-target condition, since RTs were faster in this condition. This was not the case in the present data and is in line with our previous findings (Mazza & Caramazza 2011) in which a linear modulation of N2pc amplitudes was visible despite the presence of faster RTs and higher accuracy for the largest numerosity. Second, an account of the present data in terms of an increase of N2pc amplitudes as a consequence of an overall increase of difficulty with larger numerosities would additionally predict that the low-performance group (i.e., for which the task was more difficult as seen from a lower enumeration efficiency) would show the largest N2pc modulations as a function of numerosity. In contrast, I found that the low-performance group showed a difference in N2pc only for one versus 3 targets (see Figure 4). Finally, independent evidence that the N2pc amplitude does not always correlate with behavioral data comes from several studies, using different tasks and paradigms (Drew & Vogel, 2008; Kiss et al., 2008; Mazza et al., 2009b, 2007; Robitaille & Jolicoeur, 2006; Woodman & Luck, 2003).

In contrast with the N2pc findings, and differently from earlier studies (e.g., Hyde & Spelke, 2009 in which no N1 increase was found for numerosities greater than three) the N1 amplitudes showed an overall increasing trend as the number of targets increased. A plausible explanation for the discrepancy with the previous findings is that in the present study target numerosities were not presented along a continuum, thus preventing very fine-grained comparisons (e.g., between 5 and 6 elements). Hyde and Spelke (2009; 2011) proposed that the N1 modulation reflects the functioning of a “parallel individuation system”. In the light of our data, as well as of other recent evidence (Hyde & Spelke, 2011), I can speculate that N1 and N2pc reflect distinct stages of individuation. While the N2pc may reflect the component of individuation that binds relevant properties and locations (as inferred by its lateralized nature and by its numerosity-related modulations), the stage reflected in the N1 may correspond to the initial indexing of a subset of items on the basis of their spatio-temporal properties. This component may be particularly evident when the multiple objects are presented in isolation, namely in the absence of irrelevant elements (as in Hyde & Spelke, 2009), and may be sensitive to the quantity of the overall elements presented in the visual field, rather than to a specific subset of (target) elements. However, given the differences between the paradigms used previously and the present one, future research will need to test this hypothesis directly (see Chapter 3).

The results on the P2p amplitudes showed a linear decrease as a function of target numerosity. Previous research using sequential presentations of different quantities has shown that this pattern reflects the functioning of a mechanism that computes changes in the distance between a specific symbolic or non-symbolic numerosity and a pre-defined number or contrasting numerosities in an adaptation paradigm (Dehaene, 1996; Hyde & Spelke, 2009; Libertus et al., 2007; Szucs & Csépe, 2004; Temple & Posner, 1998). More specifically, P2p amplitudes decrease when the distance between the two numerosities decreases. The present P2p results add to previous research by indicating for the first time that this ERP response may also reflect the ratio between the quantities of the two object sets (namely, targets and distractors) simultaneously presented in a single display. More specifically, given that in our study the overall number of elements in a display was kept constant across the various target numerosities, the ratio between target(s) and distractors decreased as a function of target numerosity (1:31, 3:29, 5:27, 7:25 for one, three, five and seven targets respectively). Accordingly, P2p mean amplitudes increased as this target-distractor ratio decreased.

Finally, CDA amplitudes were modulated by target numerosity in both Experiment 1 and 2, suggesting that the maintenance of the target elements in VWM during the matching of the set to a specific numerical value contributes to quantity enumeration. However, the modulation of CDA in Experiment 1 showed an atypical pattern, with a marked decrease in amplitudes for the largest numerosity in the set (Figure 2). This inverted U-shaped trend invites the inference that participants used different quantity enumeration procedures in assigning numerical values to the smaller versus largest set sizes. It is reasonable to assume that while for the smaller quantities a numerical value was assigned through a process of enumeration that involves individuating all the elements in the set, for the largest quantity a default numerical value may have been assigned on the basis of a rough numerosity estimate of the target elements, a type of “end effect” (Trick & Pylyshyn, 1994; Trick, 2008). The latter procedure would be less taxing on the VWM system, resulting in a smaller CDA amplitude. This interpretation of the CDA pattern is consistent with the RT data of Experiment 1 showing faster numerical enumeration for seven versus five target elements and with the results of Experiment 2 showing that, in the absence of end effect, CDA reaches a plateau at four targets. Taken together these findings confirm that CDA represents a stage related to visual working memory processes that is crucial to maintain the individuated objects for further operations.

In conclusion, Experiment 1 and 2 provide evidence that the feature-to-location binding stage of individuation plays a significant role in visual enumeration of small quantities in complex scenes. This stage has a clear limit in the number of items that can be “bound” simultaneously. Importantly, the results of Experiment 1 further indicate that individual neural differences at this stage of processing are associated with variations in enumeration efficiency. This in turn suggests that differences in feature-to-location binding efficiency are associated with individual skills in enumeration.

Chapter 3

The role of distracting information in multiple object processing

3.1 Experiment 3

Sensitivity to the numerosities of the objects present in the environment seems to be a universal trait of humans, including infants (e.g., Feigenson, Dehaene, & Spelke, 2004), and animals of several species (e.g., monkeys, chicks, fish; Cantlon & Brannon, 2006; Haun, Jordan, Vallortigara, & Clayton, 2010; Nieder, 2005) Accordingly, it has been proposed that apprehension of numerosities represents a basic ability of the brain, like the ones that process color, size, space, or motion (Dehaene, 1997; Ross & Burr, 2010; Walsh, 2003).

Several theories of number processing have drawn a distinction between approximate and exact computation of the number of objects presented in the visual field (Feigenson et al., 2004; Mandler & Shebo, 1982; Piazza, 2010). This distinction captures the contrasting subjective experiences we have in sensing the approximate number of fruits piled up in a stand at the market versus the sense of selecting the several fruits we have chosen to buy. According to these theories, approximate and exact enumeration rely on distinct perceptual processes.

Approximate enumeration is achieved through a system that computes magnitudes in an analog way, as for any other sensory stimulus dimension (Piazza, 2010). While it is not clear yet what physical factors govern this type of computation, previous research (e..g, Dehaene & Changeux, 1993) has suggested that approximate enumeration can be seen as resting on a relatively early perceptual mechanism that appraises at a glance the entire configuration of elements in a display by relying on their status of "spatially" separable entities but with imprecise and coarse featural encoding.

In contrast, exact computation of numerosity requires the selective marking of each individual element of the set to be enumerated, to ensure that each element is counted once and only once. In exact enumeration, a distinction has been drawn between the way small (i.e., up to about four elements) and large numerosities are processed (Ansari, Lyons, van Eimeren, & Xu, 2007; Trick & Pylyshyn, 1993). The distinction is thought to reflect the special status of small numerosities that accrues to them in virtue of the cognitive system's ability to exploit a basic property of the visual perceptual system: the ability to individuate simultaneously 3-4 objects in a scene (Pylyshyn, 2001). Individuation is the ability to process each element of a set as possessing specific features and as being separated from other elements. While its processing structure remains to be fully determined, individuation can result in a set of more robust representations of the isolated objects (for instance, as a consequence of feature binding; e.g., Kahneman et al., 1992), making them ready for further processing (and eventually leading to full object identification). As such, it seems to be the logical prerequisite for exact enumeration, as well as for the execution of other tasks that require multiple object processing, such as multiple object tracking and memory tasks. Early proposals argued that visual object individuation operates separately from attention (Trick & Pylyshyn, 1993) but recent research has suggested that simultaneous indexing of relevant items in a scene is tightly related to attention (Ansari et al., 2007; Cavanagh & Alvarez, 2005; Vetter, Butterworth & Bahrami, 2011; Xu & Chun, 2009). Indeed, it is widely assumed that individuation is a key function of attention (for a discussion, see Cavanagh, 2011). Because simultaneous object individuation is limited to 3-4 items, exact enumeration of larger numerosities must rely on the repeated and successive application of the individuation mechanism over the array of objects to be enumerated.

The distinction I have just described does not imply that the mechanisms underlying approximate and exact enumeration are incompatible with one another. For instance, both mechanisms may be at work during visual enumeration of small numbers of objects, as recent results on humans and monkeys seem to suggest (e.g. Burr, Anobile, & Turi, 2011; Nieder & Miller, 2004). However, I hypothesize that the representations over which exact and approximate computation take place are different, being more detailed in the former case, and that only those formed during individuation are a key factor in exact enumeration of objects.

Crucially, the individuation mechanism should operate not only when the elements to be enumerated are presented in isolation but also when they are presented in cluttered scenes (i.e., together with distracting objects, see Trick & Pylyshyn, 1993).

The functioning of this mechanism should in turn be reflected in a neural response pattern with the following characteristics. First, it should be affected by the number of the specific elements whose quantity needs to be determined (i.e., the targets) and, second, because of its limited ability to process simultaneously only a small subset of target individuals, it should reach a plateau at 3-4 elements. The profile of this neural pattern of response should be present both when the targets are presented in isolation and when they are presented together with irrelevant elements (distractors).For these reasons, in the present ERP study I focus specifically on the exact enumeration of small quantities by manipulating the presence of distractors presented together with the to-be-enumerated targets. On the assumption that the perceptual component that underlies exact enumeration is modulated by the number of relevant elements (with a limit in simultaneous processing at approximately 3-4 elements) I would expect an effect of target numerosity both when the target elements are shown in relative isolation and when they are presented with distractors.

Previous studies on enumeration in humans have not given a definitive answer to the questions raised here. Most studies typically presented the target elements in isolation (i.e., without distractors) or did not manipulate the presence/absence of distractors within a single experiment (e.g., Trick & Pylyshyn, 1993). Furthermore, it has proven difficult to distinguish between the functioning of different perceptual subcomponents involved in computing object quantity on the basis of behavioral measures alone. While fMRI studies have identified regions in frontal, parietal and temporal cortical areas that seem to be associated with a neural distinction between exact and approximate enumeration (for reviews see Hyde, 2011; Nieder & Dehaene, 2009), the brain circuitry involved in enumeration of targets among distractors has not been addressed. Here I adopted an ERP approach that, given its excellent temporal resolution, represents the best neuroimaging technique to isolate the effects taking place at different stages of analysis in terms of their underlying temporal brain dynamics. In the context of the present research question, this approach is well-suited to help uncover the crucial perceptual stage that forms the basis for exact enumeration.

In Experiment 3, I specifically focused on two components of the ERP signal, the N1 and the N2pc. Both these components have been traditionally examined in a wide range of tasks for the study of attentional functions. For instance, several results obtained with spatial cueing paradigms show enhanced amplitudes on the N1 (a negative component peaking at approximately 150 ms) for attended versus unattended elements, inviting the inference that this ERP component reflects the spatial distribution of attention in the visual field (e.g. Mangun, Hillyard, & Luck, 1993) The N2pc is a lateralized posterior response occurring after the N1 (with an onset latency of approximately 180 ms) that typically occurs in visual search paradigms, whenever a relevant object is presented in one hemifield together with distractors (Eimer, 1996; Luck & Hillyard, 1994). The N2pc has typically been interpreted as the neural correlate of attention selection in the visual field, either through distractor suppression (see Luck et al., 1997) or through target enhancement (see Eimer, 1996; Mazza et al., 2009b). Given that N1 and N2pc have been associated with attentional functions (albeit in the context of different experimental paradigms), and on the assumption that attention is intrinsically related to individuation, both these components are ideal candidates for testing the neural underpinnings of exact enumeration. Indeed, recent studies have started to investigate the role of these ERP components in tasks related to object numerosity processing.

Previous ERP studies on number-related tasks (Hyde & Spelke 2009; 2011; Libertus, et al., 2007; Nan et al., 2006) have found modulations in the N1 as a function of item numerosity. In particular, Hyde & Spelke (2009; 2001) found that the N1 increases in amplitude as a function of item numerosity up to 3 elements, and proposed that it reflects multiple object individuation. However, in these (as well as in the previous) studies no explicit enumeration task was required; in addition, only one type of elements were always presented (with the exception of Nan et al., 2006), thus leaving unexplored whether or not the observed electrophysiological pattern is related to a specific target-related individuation mechanism or to a more general encoding of the overall amount of items presented.

By contrast, other recent studies on multiple targets presented among distractors (during multiple object tracking, see Drew & Vogel, 2008; or during exact enumeration, see Ester et al., 2012; Mazza & Caramazza, 2011; Pagano & Mazza, 2012) show that the amplitude of the N2pc is sensitive to target numerosity (when these are presented in one hemifield only), increasing up to approximately 3-4 elements[1]. However, given that distractors were always presented on the target side (but for Experiment 2 of Ester et al., 2012), it is not clear whether this response is directly involved in the individuation of target elements per se or whether it simply reflects the effort of separating the targets from distractors (for instance, by suppressing the irrelevant objects presented on the target side).

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[1] Pagano & Mazza (2012) found an N2pc asymptote at 5 targets. However, in this study we used a limited rather than a continuous range of numerosities, making it difficult to estimate the exact numerosity of the N2pc plateau. Moreover, the data in that study additionally suggested that while good performers reached an N2pc asymptote at 5 elements, this asymptote was set at 3 elements for poor participants.

3.2 General Methods

3.2.1 Participants

Twelve volunteers (6 female, aged 20-31 years) with normal or corrected vision participated in the experiment, after providing written informed consent. The study was approved by the University of Trento Ethics Committee.

3.2.2 Stimuli and procedure

Equiluminant red and green diamonds (17 cd/m^2) were presented on a black background (1 cd/m^2). Each diamond (0.6°x 0.8°) had a 0.4° corner trimmed on the left or right side (Figure 3.1). On each trial, the display (duration: 150 ms) contained a variable number of diamonds, distributed to the left and right side of the fixation circle (0.2°); 1, 2, 3 or 4 diamonds (targets) had a unique color (either red or green) relative to distractors. On multiple target trials, all targets were presented on the same side (either left or right). The color of the target(s) and of the distractors was counterbalanced across participants. The crucial manipulation concerned the presence of distractors in the target field. On no-distractor trials, no distractors were presented on the target(s) side. On distractor-present trials, distractors were always intermingled with targets on the target side. To avoid sensory imbalance, which would make it difficult to disentangle the interpretation of any lateralized neural effect as being related to the processing of relevant elements from an interpretation in terms of asymmetries in the sensory responses, I always presented an equal number of items in each hemifield. For the no-distractor condition, this resulted in a variable number of overall elements as a function of target numerosity (e.g., 2 elements- 1 target and 1 distractor in opposite hemifields- were presented in the one-target trials; see Figure 3.1). In the distractor condition, a fixed number of 16 elements, 8 in each hemifield, were presented. Given that in the no-distractor condition distractor numerosity was the same as target numerosity, participants could have relied on either distractors or targets in order to respond correctly. To discourage the adoption of such a strategy, I introduced catch trials, in which there was a mismatch between the number of distractors and the number of targets. Given the low proportion of these catch trials in the experiment, they were not included in the ERP analyses. Participants reported as fast as possible the number of targets presented on each trial by pressing one of four keys on a computer keyboard with their index or middle fingers of both hands. Response assignment was counterbalanced across participants. Maximum time for responding was 1500 ms. The inter-trial interval was 1500 ms. Participants performed 1 training block of 40 trials and 10 experimental blocks with 144 trials per block (64 no-distractor trials; 64 distractor trials; 16 catch trials; an equal number of trials were delivered for each target numerosity).

3.2.3 EEG recording and data analysis

EEG was recorded from 25 electrodes (including PO7, PO8, O1 and O2) and from a left earlobe electrode, with a right-earlobe reference, and then re-referenced offline to the average of the left and right earlobe sites (bandpass filter: 0.01-40 Hz,

A/D rate: 1000 Hz). Horizontal EOG (HEOG) was recorded from electrodes positioned on the outer canthi of both eyes. Impedance was kept below 6 kΩ for all electrodes. Trials with horizontal eye movements (HEOG exceeding ± 30 μV), eye blinks and other artifacts (any electrode exceeding ± 80 μV) were excluded.

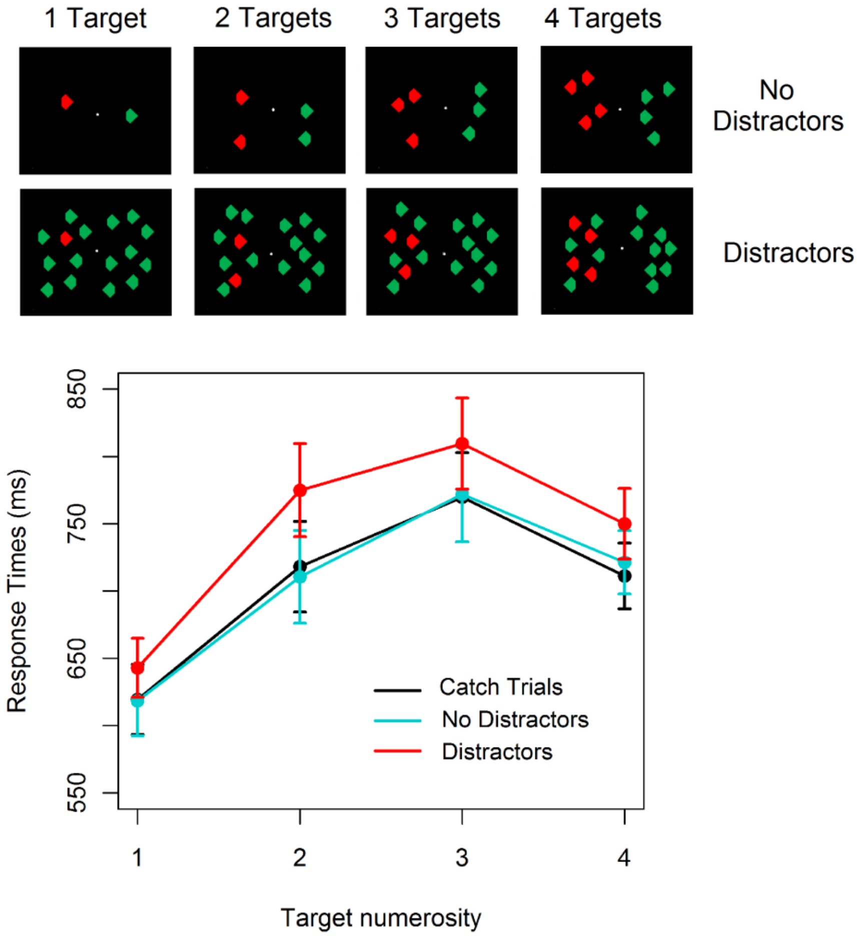

Figure 3.1 Example displays and behavioral results Experiment 3

Top: Examples of stimulus displays with one, two, three and four targets, on both no-distractor (first row) and distractor (second row) trials. Bottom: Behavioral results indicate an increase in RTs as a function of target numerosity followed by an end effect in all three conditions (distractors, no distractors, and catch trials).

Averages for correct responses were computed relative to the 100 ms interval preceding the display onset, separately for each condition and target side (left, right). Statistical analyses for the non-lateralized activation (N1, 120-180 ms; the time window was approximately centered around the N1 peak as visible from the grand-average waveform of all conditions) were conducted on mean amplitude and peak latency values at posterior electrode sites (PO7, PO8, O1, O2) collapsed across target side. The analysis of the mean amplitudes and peak latencies of the lateralized activity (N2pc, 180-300 ms; the time window was approximately centered around the N2pc peak of the grand-average waveform) was conducted on difference amplitudes, obtained by subtracting ERP waveforms at ipsilateral posterior electrodes (i.e., PO7 and O1 for left targets; PO8 and O2 for right targets) from those recorded at contralateral sites (i.e., PO8 and O2 for left targets; PO7 and O1 for right targets), collapsed across target side. These values (as well as behavioral data) were submitted to a repeated-measures ANOVA with numerosity (one, two three, four), distractor presence (distractor, no distractor, and catch trials – for behavioral data only) and ERP component (N1, N2pc; for ERP data only) as factors. When appropriate, Greenhouse-Geisser corrections for sphericity violations were applied, and corrected p-values are reported. Significant effects were further explored by means of contrast analysis.

3.3 Results

3.3.1 Behavioral results

Two ANOVAs were conducted on response times (RTs) for correct responses between 200 and 1500 ms and on the percent of correct responses.

Both ANOVAs on RTs and correct responses showed significant effects of numerosity and distractors, both Fs>9.3, all ps<.001, while a significant interaction emerged for RTs only, F(6,66)=5.6, p<.001. Participants were overall faster and more accurate on no-distractor and catch trials, relative to distractor trials, all ps<.006, with no difference between catch and no-distractor trials (Figure 3.1). In all the conditions, numerosity has the same quadratic pattern, all ps<.003, indicating that participants were increasingly slower and less accurate for numerosities up to three targets, while an end effect was visible for the largest target numerosity in the set (i.e., four elements).

3.3.2 ERP results

ERP results point to two main modulations of electrophysiological activity. First, the early non-lateralized response (N1, 120-180 ms) was modulated by target numerosity but only when no distractors were presented on the target side (Figure 3.2). In contrast, the N2pc amplitudes (180-300 ms) increased as a function of target numerosities (up to three targets) in both conditions (Figure 3.3).

The two overall ANOVAs on mean amplitudes and peak latencies with numerosity, distractor and ERP components indicated a significant three-way interaction, both Fs>8.6, both ps<.001. Therefore, I explored the effects of numerosity and distractor separately for each ERP response.

3.3.2.1 N1

The ANOVA on mean amplitudes indicated significant effects of distractor, $F(1,11)=9.3$, $p=.01$, of numerosity, $F(3,33)=14.2$, $p<.001$, and of their interaction, $F(3,33)=14.0$, $p<.001$. Separate ANOVAs showed no effect of numerosity in the distractor condition, while a significant effect was found in the no-distractor condition ($F(3,33)=17.5$, $p<.001$ and with significant quadratic trend ($p<.005$)), with increasing amplitudes as a function of numerosities up to three targets (i.e., six elements overall; see Figure 3.2 and 3.4 right)

The ANOVA on peak latencies showed the same significant effects, all *F*s>24.3, all *p*s<.001. Latencies were overall earlier in the distractor condition. Crucially, no significant effect of numerosity emerged for the distractor condition, while this was significant (*F*(3,33)=55.2, *p*<.001) and with a significant quadratic trend (*p*<.002) in the no-distractor condition. The N1 occurred progressively earlier for increasing numerosities, reaching a plateau at three targets[2].

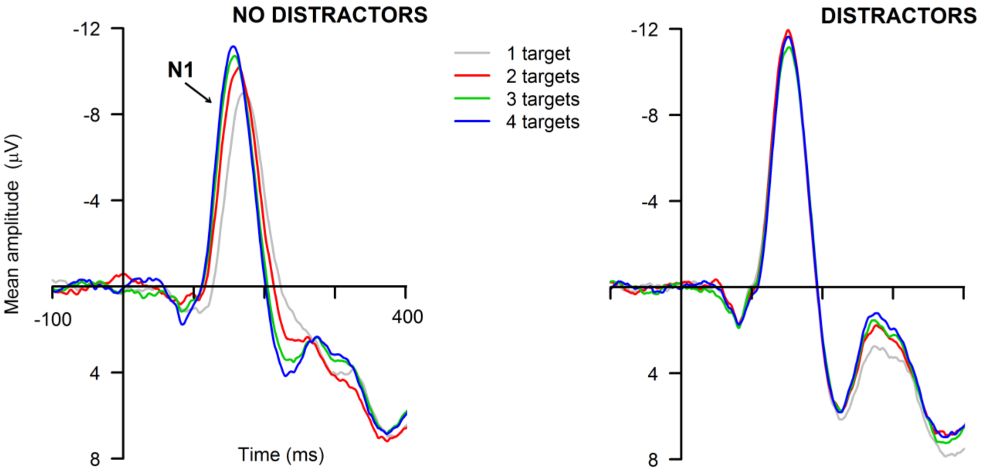

Figure 3.2 N1 modulations Experiment 3

Grand-average non-lateralized ERP waveforms obtained in the 400 ms post-stimulus interval at posterior electrode PO7/PO8 and O1/O2 in the no-distractors (left) and distractors (right) conditions. The N1 component was modulated in amplitude by target numerosity only on no-distractor trials.

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[2] According to previous studies (e.g., Hyde & Spelke, 2009; Libertus et al., 2007; Temple & Posner, 1998) a positive component occurring at approximately 200-250 ms (P2p) may correlate with approximate computation, being sensitive to the ratio difference between successive arrays. However, here I was interested in enumeration of items that are simultaneously presented. Moreover, the ANOVA on this component in our experiment showed a significant distracter x numerosity interaction, *F*(3,33)=15.0, *p*<.001, with the same pattern found for the N1. Therefore, similarly to the N1, the neural representations reflected by the P2p are not sufficient for exact enumeration.

3.3.2.2 N2pc

A different pattern emerged in the analysis of the N2pc data (Figure 3.3 and 3.4 left). As for the N1, there were significant effects of distractor, *F*(1,11)=52.7, *p*<.001, of numerosity, *F*(3,33)=39.0, *p*<.001, and of their interaction, *F*(3,33)=6.7, *p*<.001. However, separate ANOVAs on both distractor and no-distractor conditions showed a significant effect of numerosity (both *F*s>5.4, both *p*s<.005), both with a significant quadratic trend (*p*<.025). The N2pc amplitudes increased as a function of target numerosities in both conditions, reaching an asymptote at three targets[3] (see Figure 3.3).

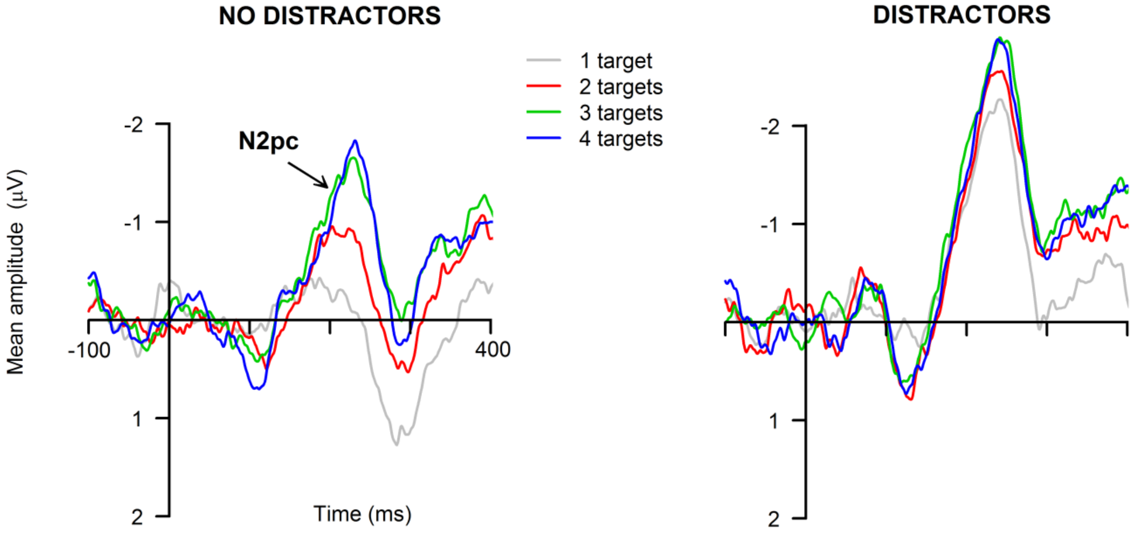

Figure 3.3 N2pc modulations Experiment 3

The grand-average lateralized ERP difference waveforms, obtained by subtracting the ipsilateral activations from contralateral activations at posterior sites PO7 (and O1) and PO8 (and O2), show a modulation of the N2pc amplitudes as a function of target numerosity for both no-distractors (left) and distractors (right) trials.

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[3] To compare these results with those from previous studies (e.g., Hyde & Spelke, 2009), I additionally specifically tested for a significant linear trend only in the 1-3 numerosity range for both the N1 and N2pc amplitudes. The results confirmed our main analyses showing the presence of a significant linear trend in the N2pc for both distractor and no distractor conditions (both ps<.001), and a significant linear trend in the N1 for the no distractor condition only (p<.001).

The ANOVA on the N2pc peak latencies revealed significant effects of distractor, *F*(1,11)=25.4, *p*<.001, of numerosity, *F*(3,33)=7.6, *p*<.001, and of their interaction, *F*(3,33)=7.9, *p*<.001. Separate ANOVAs revealed no significant effect of numerosity in the distractor condition, while this was significant in the no-distractor condition, *F*(3,33)=8.8, *p*<.001, with later latencies for larger numerosities, as indicated by a significant linear trend (*p*<.004). Notably, this pattern was in the opposite direction compared to the N1 component, which showed earlier latencies for larger numerosities.

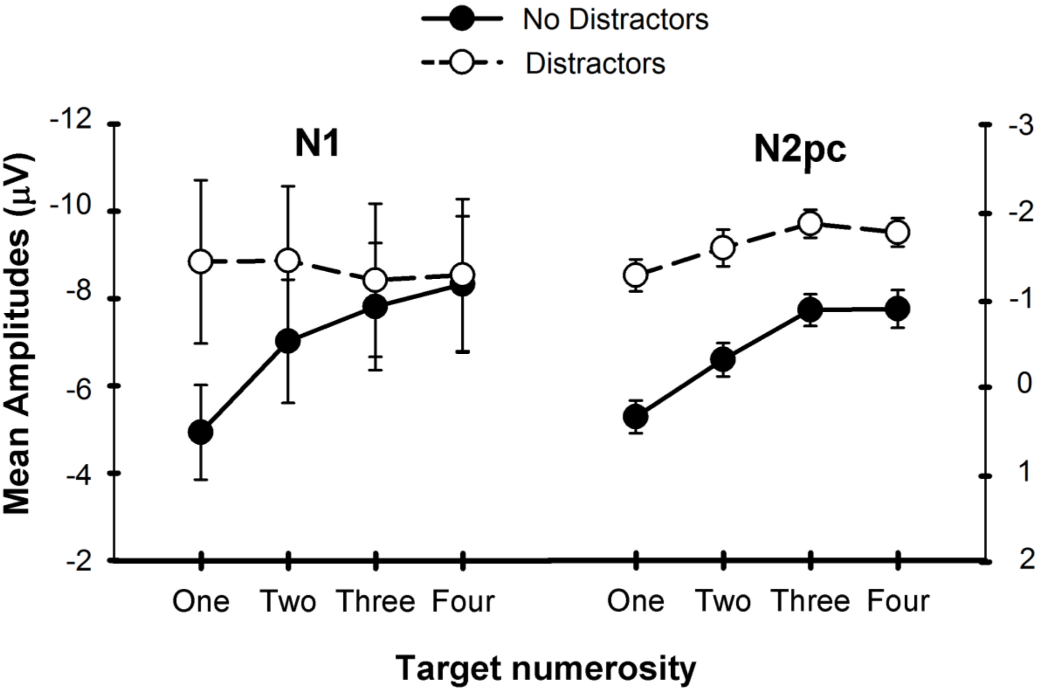

Figure 3.4 N1 and N2pc modulations Experiment 3

Mean amplitudes and standard errors of N1 (120-180 ms) and N2pc (180-300 ms) as a function of distracter presence and target numerosity.

3.2.2.3 Control analysis

To control for the presence of sensory effects related to the increase in target numerosity (especially for the no-distractor condition), I conducted an additional ANOVA on the P1 mean amplitudes (60-100 ms post-stimulus) with numerosity and distractor as factors. Neither the effect of numerosity nor the interaction was significant, both *ps*>. 78.

3.3 Discussion

I used electrophysiological recordings during an exact enumeration task to address whether the specific computation of multiple relevant objects can be dissociated from mechanisms that may only be sensitive to the overall (target and distractor) quantity of objects in the visual field. The results suggest that this may in fact be the case.

Behavioral data showed an overall increase of RTs for the distractor condition, suggesting that distractors interfere with the process of individuating multiple targets for exact enumeration. Target numerosity led to the same pattern of results in all conditions (distractors, no distractors, catch trials), with larger RTs for larger target sets and an end effect for the largest numerosity. Importantly, the fact that no difference in RTs was visible between no-distractor and catch trials indicates that participants did not rely on specific strategies based on distractor numerosity to infer the correct answer.

ERP results indicated that target numerosity had similar effects on the N2pc both with and without distractors, providing novel information on the mechanism involved in computing exact object numerosity. Specifically, the N2pc amplitudes were modulated by target numerosity in both the target only and target plus distractor conditions. The fact that the N2pc modulation was visible even when no distractors were presented on the target side reasonably dismisses the possibility that this pattern is exclusively related to distractor suppression and, in line with very recent findings (Ester et al., 2012; Pagano & Mazza, 2012) indicates that this electrophysiological response reflects the functioning of a processing stage that is tightly associated with the exact computation of the relevant quantities. In particular, I propose that it reflects the selective and simultaneous individuation of a subset of target elements in the visual field by means of a mechanism that binds featural properties and locations. This interpretation is substantiated by the lateralized nature of the N2pc (a proxy for location coding), by its asymptote at 3 targets (an index of capacity limit in simultaneous processing), and by the fact that it is found both when distractors are present and when they are absent (a proxy for selective individuation of the target elements). In line with this interpretation, the overall longer latencies observed in the N2pc for the distractor condition relative to the no distractor condition indicate, as would be expected if this response were sensitive to relevant rather than irrelevant numerosities, that extracting targets from a visual display may take longer when they are spatially intermingled with distractors.

In contrast, the N1 pattern was differentially modulated by target numerosity as a function of distractor presence. In line with previous findings (e.g., Hyde & Spelke, 2009; 2011), in the no-distractor condition the amplitude of the N1 was modulated by target numerosity, being progressively larger for the larger target sets up to a limit of 3 targets (6 elements). N1 latencies in the no-distractor condition were also modulated by target numerosity, with progressively earlier latencies for the larger target sets. In the distractor condition, in which the total number of elements (always 16) was larger than in the no distractor condition, the N1 was overall larger and earlier. However, no differences in the N1 emerged among the target numerosities.

It is important to note that in Experiment 3 (as well as in previous studies, e.g., Hyde & Spelke, 2009; Nan et al., 2006), the increase in item numerosity is confounded with increases in other continuous variables (such as total area and luminance). This leaves open the possibility that sensitivity to sensory properties, rather than to item numerosity per se, may account for the N1 pattern found for both conditions, and especially for the no-distractor condition (see Libertus et al., 2007 for such an account). For this reason, and under the assumption that sensory properties should influence the earliest stages of stimulus processing, such as the one reflected by the P1 component (see Johannes, Münte, Heinze, & Mangun, 1995 for the specific case of luminance), I conducted an additional analysis on this component. Unlike the N1 component, no numerosity-related effect was found for the P1 component. Therefore, it is difficult to explain the N1 pattern found in the present study directly and exclusively in terms of sensory effects, although I acknowledge that future research will need to address this issue more deeply.

According to Hyde and Spelke (2011), the N1 numerosity modulation reflects “the distribution and maintenance of attention to particular locations in space evoked by particular items.” Interestingly, they interpreted the occurrence of earlier N1 latencies for larger compared to smaller sets of elements by assuming that in the former case the group of elements is treated and selected as one item, while multiple items are selected in parallel for smaller numerosities. As a consequence, selection is slower in the case of multiple items (small numerosities) relative to the selection of the group of elements (large numerosities). While the present results may be partially explained in these terms, they add novel information on the way numerosities are computed by indicating that these “locations” in space are selected with no reference to the relevance for the task at hand. In other terms, our findings indicate that while the N1 may be sensitive, at least to some degree, to the number of elements presented in the visual field, it does not discriminate between relevant and irrelevant quantities. These results resonate with the idea that the N1 reflects the functioning of a perceptual mechanism that extracts the information of the overall amount of elements in a display by relying on their status of “spatially” separable entities but with imprecise and coarse featural encoding, but they also indicate that this mechanism alone does not provide sufficient information for exact enumeration.

The present results provide significant constraints on theories of numerosity representation and of multiple object processing in general.

First, the fact that the N2pc pattern shows the same inflection point in neural activation (at around three targets) as a function of target elements, both with and without distractors, and that this inflection point is not obtained because of a ceiling effect (as might otherwise be the case for the N1 component), makes me infer that the representation generated by the neural structures underlying the N2pc contains the fine-grained information required for exact enumeration. This conclusion is in line with recent proposals (see Ester et al., 2012) arguing for a neural fixed-capacity model of enumeration, in which small target quantities are enumerated via a multiple object individuation mechanism. More generally, the present findings converge with previous studies (e.g., Drew & Vogel, 2008) in suggesting the existence of a perceptual mechanism that provides separate representations of a subset of the objects in the visual field that are then further elaborated and used for the execution of several tasks involving multiple objects, such as enumeration, multiple object tracking and memory tasks. Importantly, our results provide evidence that only the representation generated at the stage of the N2pc is sufficient for generalized exact enumeration.

Second, the N1 pattern found in our study suggests that the stage of processing reflected in this component does not distinguish between target versus non-target quantities. On the basis of this result, I speculate that the representation captured in the neural structures generating N1 may provide the basic information required for approximate enumeration, as it reflects the overall number of items in the visual map. One could argue that given that the maximum number of elements presented in our study was only 16, and that Hyde & Spelke (2009; 2011) did not find modulations for arrays larger than 3 (but see Libertus et al, 2007; Nan et al 2006), our N1 data do not directly speak to the issue of approximate enumeration. However, because no target-related N1 modulations were found in the distractor condition, the modulations visible in the no-distractor condition cannot be directly related to the processing of the exact numerosities of the targets, but rather to a more approximate and relatively imprecise coding of quantities. Our results do not exclude the possibility that the representations formed at the N1 stage could be used for exact enumeration (as proposed by the object-individuation account of the N1 in Hyde and Spelke, 2009; 2011), but this would only be possible for the special case where the elements to be enumerated do not have to be distinguished from each other on the basis of some perceptual features (e.g., color). More generally, as hypothesized for the mechanism of individuation, these representations are not specifically related to enumeration/estimation tasks, but are common to several tasks requiring multiple object processing. Indeed, the existence of early-level structural representations of the scene layout (proto-objects) can explain why, contrary to the sparse (fully) conscious representation indicated by phenomena like change blindness, we usually have the feeling of being able to see all the things out there (Rensink, 2004).

In conclusion, the results reported here show that the selection of multiple relevant elements can be dissociated from the processing of the general (target and distractor) quantity of objects in the visual field. Expanding upon previous interpretations (e.g, Ester et al., 2012; Mazza & Caramazza 2011; Pagano & Mazza, 2012), I propose that the stage reflected in the N2pc may reflect the component of individuation that binds relevant properties and locations, as inferred from its lateralized nature and from its target numerosity-related modulations both with and without distractors. As a result of this operation, a more stable representation of the relevant objects becomes available, making them ready for further processing, including exact enumeration.

Chapter 4

The role of semantic information in multiple object processing

4.1 Experiment 4

Humans are usually very fast and accurate in enumerating small numerosities of objects (up to approximately three-four) compared to larger ones, a phenomenon known in the literature as subitizing (Kaufman et al., 1949). According to an influential account (Trick & Pylyshyn, 1994a) subitizing is the consequence of a capacity-limited mechanism that indexes up to four objects simultaneously and represents them as separate entities. This first stage of multiple object processing – individuation – was initially conceived of as pre-attentive, but recent research has provided evidence that indexing elements as separate entities is a key aspect of attention (Cavanagh & He, 2011). Importantly, this perceptual stage is considered as pre-numeric, being “blind” to the quantity value of the numerosity of the objects. Quantity values would become available only after objects have been individuated and are the result of a mapping between the indexed objects and the numerical magnitude of the elements (Trick & Pylyshyn, 1994).

Recent ERP studies (Ester et al., 2012; Mazza & Caramazza, 2011; Pagano & Mazza, 2012) have shown that subitizing is associated with amplitude modulations of the N2pc component, a lateralized response arising at approximately 200 ms at posterior sites contralateral to the hemifield in which a target is presented together with distractors (Luck & Hillyard, 1994). These studies have indicated that during enumeration the amplitude of N2pc increases as a function of target numerosity, reaching an asymptote at 3-4 elements. This result is interpreted as evidence that N2pc reflects an individuation mechanism that indexes up to 3-4 objects simultaneously, making them ready for further operations (such as the assignment of a numerical value to the target set in the case of enumeration). However, it is still unclear whether or not in the context of enumeration the representation generated at the stage of processing reflected by the N2pc already contains the quantity value of the individuated targets. This question is relevant also in the light of previous studies showing that some semantic aspects of the objects, such as their identity or category, can be extracted relatively early during stimulus processing (Thorpe, Fize, & Marlot, 1996) and that the semantic relationship between a target and a distractor can modulate the N2pc amplitudes (Dell’Acqua, Pesciarelli, Jolicoeur, Eimer, & Peressotti, 2007; Telling, Kumar, Meyer, & Humphreys, 2010).

To investigate whether individuation, as reflected by the N2pc, is affected by target identity during subitizing we used a variant of the numerical Stroop task (Francolini & Egeth, 1980). Participants were required to enumerate a variable number of target digits whose identity could either match their numerosity (congruent condition; e.g., the digit “3” was presented three times) or not (incongruent condition; e.g., the digit “3” was presented twice). Previous behavioral research has shown the occurrence of a Stroop-like interference, wherein response times are higher for incongruent than congruent trials. Such interference is due to the semantic processing of digit identity and the automatic retrieval of the associated digit magnitude (Pavese & Umiltà, 1998). Thus, if semantic information is inherently bound to the individuation of multiple targets, we expect that N2pc should be modulated by the congruency between target identity and target numerosity. In contrast, if the individuation process reflected in N2pc variations is mainly based on low-level rather than high-level target information, there should be little or no effect of congruency on the N2pc amplitudes.

To evaluate whether number-related semantic information might instead affect later stages of processing, we additionally tested for the effect of congruency on a second sustained lateralized activity (Contralateral Delayed Activity, CDA, see Vogel & Machizawa, 2004; also called Sustained Posterior Negativity, SPCN; Jolicœur, Sessa, Dell’Acqua, & Robitaille, 2006), which has been associated with the active maintenance of lateralized visual information when deeper analyses are required. CDA/SPCN is modulated by the number of targets and also reaches an asymptote at 3-4 elements during the execution of a variety of tasks, ranging from short-term memory to multiple object tracking and enumeration tasks (Drew & Vogel, 2008; Pagano & Mazza, 2012; Vogel & Machizawa, 2004). Interestingly, the CDA/SPCN likely reflects the activity of specific portions of the intraparietal sulcus (Robitaille et al., 2010). Given that these neural structures are also involved in the semantic representation of numerical magnitude (e.g., Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004), we may expect modulations of this ERP response as a function of congruency in the present study.

4.2 Methods

4.2.1 Participants

Twenty-four participants (mean age: 21.5 years; 14 females) volunteered to participate in the present study after providing written informed consent. The study was approved by the local ethics committee.

4.2.2 Stimuli and procedure

A central white cross was surrounded by 32 equiluminant red and green (8 cd/cm²) digits and letters displayed on a grey background (6 cd/cm²). Stimuli locations were chosen randomly from a 8 (columns) X 10 (rows) invisible grid centered on the fixation cross, with an equal number of items in each hemifield. Targets were one, two, three or four, uniquely colored (green or red) digits ("1", "2", "3", "4") equally presented to the left or right of fixation. The letter A, either green or red, served as distractor (Figure 3.1 A and B). The display duration was 150 ms. Participants' task was to report as fast and accurately as possible the number of targets presented on each trial by pressing one of four buttons arranged vertically. The maximum time for responding was 1500 ms. The inter-trial interval was 1500 ms. Participants completed a total of 1280 experimental trials divided in 10 blocks. In the *congruent* condition (320 trials) the digit magnitude matched the target quantity (e.g. four 4s); in the *incongruent* condition (960 trials) there was a mismatch between digit magnitude and the quantity of targets (e.g. three 4s). An equal number of trials (320) was presented for each target numerosity.

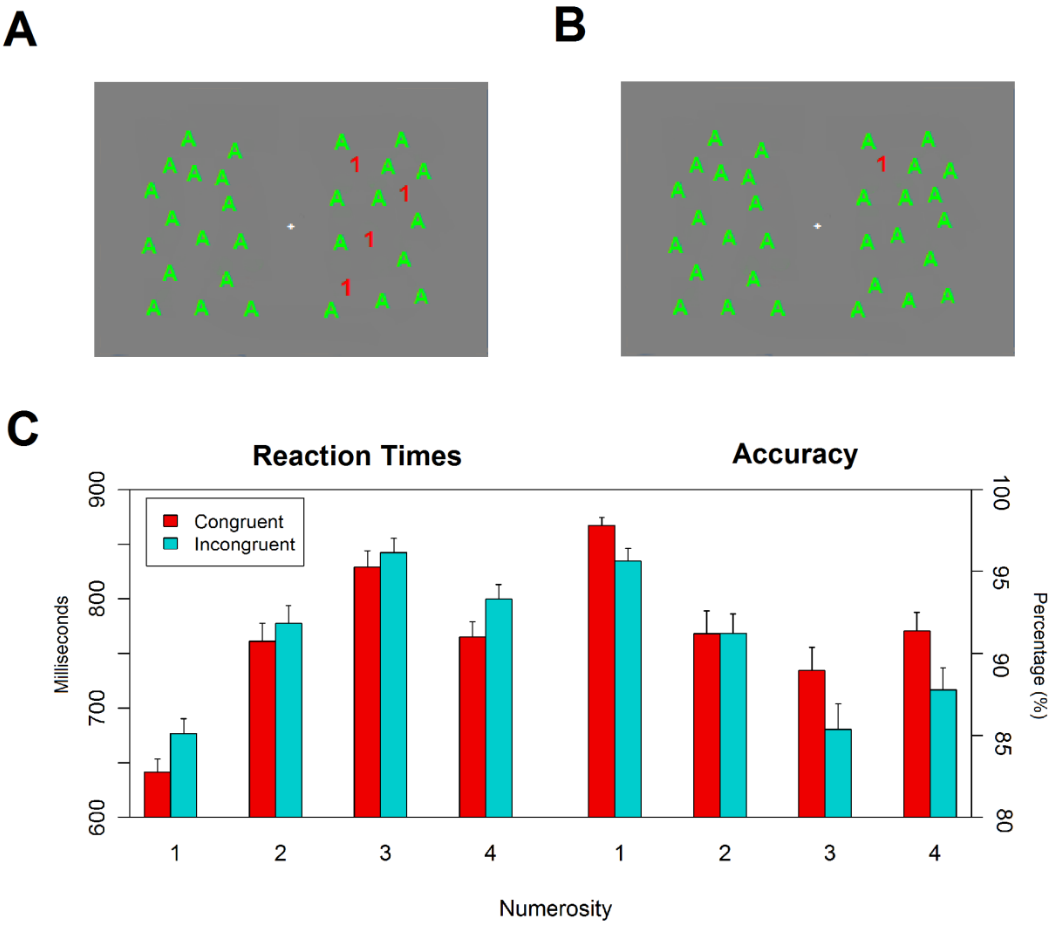

Figure 4.1 Example of displays and behavioral results Experiment 4

(A) Incongruent and (B) congruent displays with four and one target. (C) Mean reaction times and accuracy as a function of target numerosity and congruency.

4.2.3 EEG recordings and data analysis

EEG was recorded from 25 electrodes (including PO7 and PO8) and referenced on-line to the right-earlobe activity (bandpass filter: 0.01-40 Hz; A/D rate: 1000 Hz). The signal was re-referenced offline to the average of right and left earlobes. Horizontal electro-oculogram (HEOG) was recorded from two electrodes placed on the external canthi of both eyes. The impedance was kept below 5 KΩ. Trials with horizontal saccades (HEOG exceeding ± 30 µV), eye-blinks or head movements (any other channel exceeding ± 80 µV) were discarded.

Stimulus-locked averages for correct responses were computed relative to a 700-ms interval starting 100 ms before stimulus onset, separately for each level of numerosity (1, 2, 3, 4) and congruency (congruent, incongruent). Statistical analyses were conducted on mean difference amplitudes obtained by subtracting ERP waveforms at ipsilateral posterior electrodes (e.g., PO7 for left targets) from those recorded at contralateral sites (e.g, PO8 for left targets), collapsed across target side, for the following post-stimulus intervals: N2pc (190-290 ms) and CDA/SPCN (400-600 ms. These amplitude mean values (as well as behavioral data) were submitted to a repeated-measures ANOVA with congruency (congruent, incongruent) and numerosity (1, 2, 3, 4) as factors. Greenhouse-Geisser correction was used when appropriate, and only corrected *p* values are reported. Follow-up analyses were conducted by means of contrast analysis (for any significant effect of numerosity) and t-tests with Scheffè correction (for any significant interaction).

4.3 Results

4.3.1 Behavioral results

The ANOVAs on RTs (for correct responses between 200 and 1500 ms) and error rates revealed a significant effect of numerosity (both *F*s>23, both *p*s<.001), with increasing RTs and errors for larger target numerosities (Figure 4.1 C) and an "end effect" for the largest quantity in the set (i.e., four targets), as indicated by significant quadratic and cubic trends in the contrast analysis (both *ps*<.05)**.** Congruency was significant in both RTs and error rates (both *F*s>26, both *p*s<.001), with higher RTs and errors for incongruent than congruent trials. The numerosity x congruency interaction was also significant (both *F*s>7, both *p*s<.001), with further comparisons (t-tests) indicating a stronger effect of congruency for numerosities one, two and four on RTs (all *p*s≤ .05), and for numerosities three and four on errors (both *p*s<.001).

4.3.2 ERP results [1]

The ANOVA on the N2pc amplitudes revealed a significant effect of numerosity, *F*(3,69)=44.8, *p*<.001, with increasing amplitudes up to three targets, as indicated by a significant quadratic trend, *F*(1,23)=40.8, *p*<.001 (Figure 4.2**).** The numerosity x congruency interaction was also significant, *F*(3,69)=3.6, *p*<.05. However, follow-up comparisons indicated that congruency had no effect at any target numerosity (all *p*s>.18)**.**

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[1] Signal-to-noise ratio was higher in the incongruent condition since incongruent trials were 3/4 of the total trials. To test whether this may have biased the results, I additionally conducted two ANOVAs on the N2pc and CDA mean difference values for the incongruent condition with number of trials (1/4- as in the congruent condition- vs.3/4 of the total trials) and numerosity as factors. Only the main effect of numerosity was significant (both ps<.001), indicating no substantial effect of the difference in signal-to-noise ratio.

In contrast, the effect of congruency was significant in the ANOVA on the CDA/SPCN, $F(1,23)=5.7$, $p<.05$, with more negative amplitudes for incongruent than congruent trials (Figure 4.2). Numerosity was also significant, $F(3,69)=28.6$, $p<.001$, with the CDA showing a similar quadratic pattern as the N2pc, $F(1,23)=33.6$, $p<.001$[2].

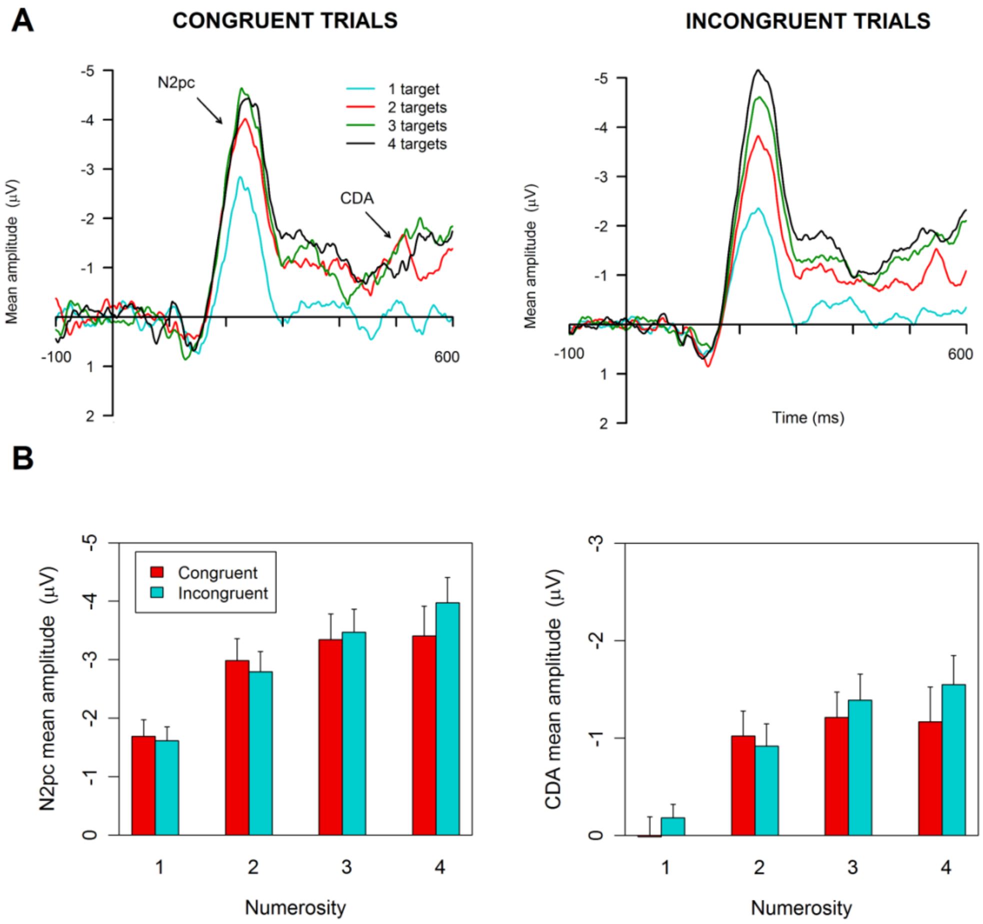

Figure 4.2 ERP results Experiment 4

(A) Grand-average ERPs and difference waveforms (contralateral minus ipsilateral activity) at PO7/PO8 as a function of target numerosity in the congruent (right) and incongruent (left) condition. (B) Mean N2pc (left) and CDA (right) amplitudes (with standard errors) for each level of numerosity and congruency.

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[2] To further evaluate the robustness of the results, we performed a Bayesian analysis (see Masson, 2011). The results supported our main analyses by indicating that congruency had higher probability values for the null hypothesis in the N2pc data ($p(H_0|D)=.65$); the opposite was found for the CDA ($p(H_0|D)=.13$). For both the N2pc and CDA, we found higher probability values associated with the alternative hypothesis for numerosity (both $p(H_1|D)>.97$) and lower values for the numerosityXcongruency interaction (both $p(H_1|D)>.22$).

4.4 Discussion

Behavioral data replicated previous findings on the number-Stroop effect, with overall slower and less accurate responses on incongruent trials. Electrophysiological data complemented behavioral results by providing a fine-grained evaluation of the effect of congruency in processes preceding response execution.

In line with previous findings (Ester et al., 2012; Mazza & Caramazza, 2011; Pagano & Mazza, 2012), the N2pc amplitude was modulated by target numerosity up to three targets, confirming that this component tracks a capacity-limited individuation/selection mechanism involved in the subitizing phenomenon. Congruency had instead no effect on the N2pc, indicating that the semantic interference effect during subitizing does not specifically originate at the perceptual stage reflected by N2pc. This in turn suggests that the identity of the targets and their associated numerical magnitude do not interfere with their individuation. While these results do not exclude the possibility that semantic information can be processed either earlier than or simultaneously with the individuation process reflected by the N2pc (see Thorpe et al., 1996), they also point out that this is not the *crucial* information used for target individuation during enumeration.

In contrast with our results, previous studies with single-target presentations (Dell’Acqua et al., 2007; Telling et al., 2010) have found modulations of the N2pc amplitudes as a function of the semantic relationship between target and distractor during lexical decision and visual search tasks, suggesting that individuation/selection of single targets is crucially affected by objects’ meaning. There is however an important difference in the nature of the stimuli used in those studies (words and objects) compared to ours (digits). According to neuropsychological and neuroimaging research (Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003; Thioux et al., 1998), semantic processing of numbers may have a separate architecture from the one(s) leading to the semantic representation of words and objects. As a consequence, it is possible that number semantics is not a crucial component for the operation of multiple target individuation, either in general or during enumeration. Overall, the present data suggest that the individuation mechanism can flexibly operate over different levels of object features as a function of task demands (see Mazza & Caramazza, 2011).

Finally, the lateralized negativity (CDA/SPCN) associated with later stages of object processing was modulated both by target and congruency for all target numerosities, suggesting that number semantic properties play a crucial role during late stages of object analysis.

In conclusion, the results of the present study complement previous studies on enumeration by highlighting that individuation during subitizing is a perceptual stage whose functioning is mainly based on a set of low-level object features.

Chapter 5

Multiple object processing in the absence of awareness

Imagine yourself while crossing a street or driving a car. It will become clear that we constantly need to perceive several distinct objects simultaneously in order to avoid potential dangers. Theories of multiple object processing (Kahneman et al., 1992; Pylyshyn, 1989; Xu & Chun, 2009) proposed that this ability depends closely on the functioning of both early individuation and late memory-related stages (for a discussion, see Chapter 1). In the present electrophysiological study I asked whether the functioning of these two stages of multiple object processing necessarily requires awareness to operate. More specifically, I seek to investigate whether it is possible to individuate and fully encode multiple objects in conditions of reduced awareness, for instance when part of the visual input is masked. While previous models of multiple object processing (Kahneman et al., 1992; Pylyshyn, 1989; Trick & Pylyshyn, 1993) have focused on the issue of whether attention is needed during individuation and encoding of multiple items, they have failed to specify whether awareness is a crucial component for the successful functioning of these mechanisms (for a discussion, see Chapter 1). The fact that recent research has highlighted a link between individuation and attention should not lead to the misleading conclusion that, at least during individuation, awareness is then necessarily involved too. Although attention and awareness were traditionally considered as coupled (e.g. Posner, 1994; Posner & Rothbart, 1998), recent models of awareness suggest that this may not be the case (see Lamme, 2003 for a review). These models point out that we can be aware of unattended objects without being able to consciously report them (Lamme, 2003) or, alternatively, that we can be unaware of details of attended scenes, like in change blindness or inattentional blindness paradigms (Rensink, 2000; Simons, 2000). Thus, awareness can be conceived of as a complex construct in which attention may or may not play a role, depending on the method used to manipulate awareness.

One way to assess whether and how the various stages of processing involved in multiple object analysis are related to awareness is to use a masking procedure to directly manipulate awareness. Different masking paradigms have been used to reduce or eliminate awareness of a stimulus by adding perceptual noise (Mitchell, 1972) or by adding a surrounding contour like in metacontrast masking (e.g. Debner & Jacoby, 1994). Combining a masking procedure with a target enumeration task here I investigated the functioning of individuation and working memory in the presence versus absence/reduction of awareness. Among the different types of masking procedures, the four-dot masking (Di Lollo, Enns, & Rensink, 2000; Enns & Di Lollo, 1997) is particularly suitable for the implementation of experimental contexts that involve multiple object processing. Four-dot masking (also known as object-substitution masking or delayed-offset masking Di Lollo, Enns, & Rensink, 2000; Enns, 2004; Enns & Di Lollo, 1997) is a form of backward masking that occurs when a four-dot pattern displayed around a target is delayed in time with respect to the to-be-masked target.

In their seminal study, Enns and Lollo (1997) presented a display with multiple diamonds trimmed either to the left or to the right. One diamond (the target) was surrounded by a four-dot pattern that cued the position of the object to be focused on. Participants' task was to report the side of the diamond that was trimmed. When the four-dot pattern offset together with the targets, participants were very accurate. By contrast, when the offset of the four-dot pattern was delayed with respect to the target display, participants' accuracy dropped, indicating the presence of a masking effect. Four-dot masking has several peculiar characteristics. First, masking is more effective when multiple items are displayed (Enns & Di Lollo, 1997). Enns and Di Lollo directly compared the amount of the masking effect (i.e. the number of errors) when a single target was displayed, with a condition in which the target was presented together with two distractors. The masking effect was maximized in the latter condition, indicating that splitting attention towards several objects increase the efficacy of four-dot masking. Second, the masking effect is achieved without altering the critical stimulus, but only by varying the temporal delay of the four small dots that represent the masking configuration. This is a substantial difference with respect to other, more "invasive", forms of masking in which the stimulus is rendered invisible by superimposing a noise pattern on it or by masking the stimulus contours (Debner & Jacoby, 1994; Mitchell, 1972).

In the four-dot masking procedure the perceptual differences between the masking and non-masking conditions are minimal. This is particularly important when one wants to use EEG measures, since differences in the physical parameters of the stimuli may result in modulations of various components of the EEG signal; for this reason they should be avoided if they are not the main focus of an EEG study. Together with the fact that four-dot masking has proved to be effective with multiple objects (Enns, 2004; Enns & Di Lollo, 1997), this form of masking is particularly suitable to study the ERP correlates of multiple object processing.

In this study I combined a four-dot masking paradigm with a visual enumeration task of targets presented among distractors while recording the two ERP components - N2pc and CDA- that have been so far associated with early and late stages of multiple object processing (see also Drew & Vogel, 2008; Luck & Hillyard, 1994; Mazza & Caramazza, 2011; Vogel & Machizawa, 2004).

Importantly for the purpose of this study, N2pc for single targets has been previously investigated in experimental conditions of reduced/absent awareness, such as change blindness and four-dot masking. While in the first case N2pc is not elicited on trials where a change is missed (Eimer & Mazza, 2005), suggesting that this attentional component is closely linked to awareness, different results were found using four-dot masking. In the studies by Woodman and Luck (2003) and by Prime et al. (2011) an N2pc was visible independently of the presence of masking, although participants' performance was impaired during masking trials. While these two different results may be attributed to the difference in the methodology used, they also point out that there is currently no clear answer as to whether individuation can operate in the absence of awareness.

The studies employing the four-dot masking procedure (Prime et al., 2011; Woodman & Luck, 2003) showed that the selection/individuation mechanism survived to four-dot masking and suggested that is a mechanism dissociable from awareness. However, in both these studies only a single target was presented, thus leaving unexplored the role of awareness when multiple targets have to be processed. Only one of these studies (Prime et al., 2011) additionally focused on the CDA. This study found that, similar to N2pc, CDA was visible during four-dot masking, but was elicited only on masked trials when masking was ineffective (i.e. when participants were able to provide the correct response despite the effect of masking), disappearing when masking was effective (i.e. when participants were unable to provide the correct response).

On the basis of these results, I expect that in the context of multiple object presentation, the N2pc will be elicited both with and without awareness (i.e. masked trials) and that its amplitude will be modulated as a function of the number of displayed targets. As for the CDA, the only existing study indicated that this component is more sensitive than N2pc to four-dot masking, disappearing when participants are unaware of the target presence (Prime et al., 2011). Therefore, I may expect that the numerosity-related modulations of CDA may disappear when awareness is reduced.

As discussed earlier, previous studies on four-dot masking focused on the processing of a single target during discrimination or detection tasks (Enns & Di Lollo, 1997; Prime et al., 2011; Woodman & Luck, 2003). To combine a task that requires the selection and encoding of multiple targets with the four-dot masking procedure I first conducted three behavioral studies in order to find a suitable paradigm that combined visual enumeration with four-dot masking. The first experiment (Experiment 5a) was conducted using a modified version of the task by Woodman and Luck (2003), in which the target defining feature was shape. Experiment 5b investigated whether four-dot masking effects could be achieved using color as target feature. Experiment 5c combined the conditions used in the experiment by Woodman and Luck (2003) with the paradigm used in Experiment 5b. These experiments are presented in the following sections.

5.1 Experiment 5a: Masking shapes

In the attempt to combine an enumeration task with a four-dot masking procedure, I used a modified version of the paradigm by Woodman and Luck (2003). In the Woodman and Luck (2003) study, two different target shapes, one in each hemifield, were presented together with homogeneous distractors. In separate blocks of trials, a specific shape was defined as the target and participants had to report whether the target was presented or not. Two four-dot patterns were presented around two objects, cueing the potential target positions. The four-dot patterns could either offset together with the stimulus or with a delay, eliciting a masking effect in the latter condition.

The paradigm used in Experiment 5a differs from the one of Woodman and Luck (2003) in the following aspects. First, I presented a variable number of targets all in the same hemifield. Second, participants were asked to enumerate the targets. Third, to obtain a baseline enumeration performance, in half of the trials the four-dot patterns were not presented.

5.1.2 Participants

Five (3 females, aged 18-26) participants were tested after providing informed consent. All had normal or corrected-to-normal vision.

5.1.3 Stimuli and Procedure

Stimuli consisted of 32 black (8 cd/m²) circles and triangles equally displayed to the left and right of a white (12 cd/m²) fixation cross on a grey background (6 cd/m²).Targets and distractors appeared within an invisible grid of 8 columns X 10 rows, centered on the fixation cross. In each trial one, two, three or four targets appeared randomly and with equal probability either on the left or on the right of fixation. Targets neither occurred in the extreme columns and rows, nor in the columns closest to fixation (see figure 5.1 A). In half of the blocks circles were defined as targets and triangles served as distractors; the opposite was done in the remaining blocks (the order was counterbalanced across participants). In 50% of the trials (masking trials) a black four-dot pattern was displayed around one target in the target hemifield, and around one distractor in the opposite hemifield. In the other half of the trials (no masking trials) the four-dot patterns were not presented. Display duration was 80 ms, followed by a 1500 ms time interval for response. In masking trials the four-dot pattern remained on screen for 600 ms after stimulus offset. An intertrial interval of 1500 ms was used. Participants reported the number of uniquely shapes regardless of the presence of a four-dot pattern. Response was provided using the index and middle fingers of both hands by pressing one of four buttons arranged vertically. After a practice session participants completed a total of 512 experimental trials divided in 4 blocks (64 trials for each numerosity and masking condition).

Given that the focus of the study was on the masking effect, and that masking influences mainly accuracy, only accuracy data were considered. Mean percent of correct responses were submitted to a repeated measures ANOVA with target numerosity (4 levels: one, two, three or four targets) and masking (2 levels: masking trials and no-masking trials) as factors.

5.1.4 Results and discussion

Accuracy decreased as a function of the number of targets, but there was no difference between the mask and no-mask conditions. This was confirmed by the results of the ANOVA, indicating a significant effect of numerosity *F*(3,12)=5.8, *p*<.05 but no significant effect of masking, *F*<1, *p*=.75, or interaction *F*(3,12)=1.2, *p*=.29. Overall, e performance was very poor, with mean accuracy values ranging between 62% and 21% (see figure 5.1 B).

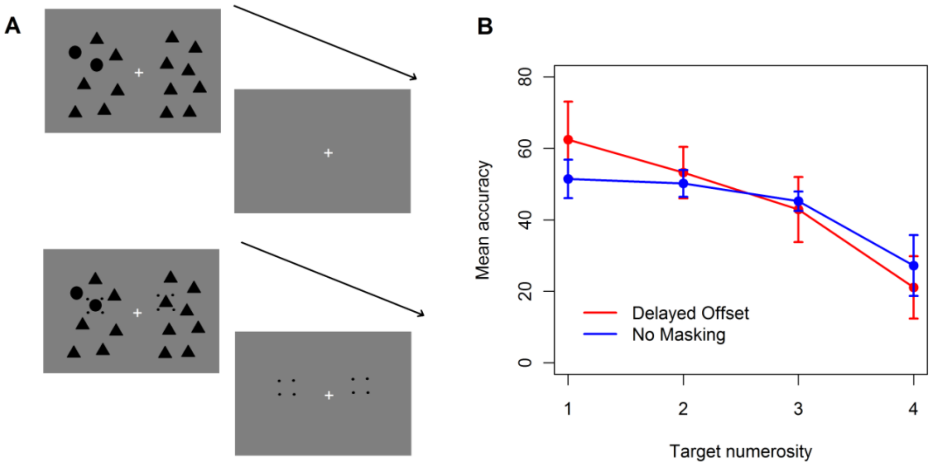

Figure 5.1 Example of display and results Experiment 5a

(A) Display with two targets in the no masking (top) and masking condition (bottom). Example displays are simplified with respect to the original ones having only 16 items in total.

(B) Mean accuracies as a function of target numerosity and masking. Notice how accuracy decreases as a function of target numerosity but no effect of masking is present.

These results suggest that enumeration of target shapes using short display duration is a difficult task. As a consequence, there might be no room for a further decreasing in performance on masking trials, leading to a sort of “floor effect”. The difficulty of the present task can be ascribable to two factors: the use of shape as target defining feature and/or the brief stimulus presentation. For this reason, in Experiment 5b I used color (instead of shape) as target feature, on the assumption that the use of a more salient feature, such as color, should improve the overall performance. This is important to obtain a consistent masking effect, while having at the same time an adequate number of trials for which target numerosity can be reported consciously (i.e. correct trials).

5.2 Experiment 5b: Masking colors

Previous studies have shown that color can be masked during four-dot masking when only one target is presented (Gellatly, Pilling, Cole, & Skarratt, 2006). In the present study I tried to replicate these effects using multiple targets.

5.2.1 Participants

Nine participants (7 females, aged 19-25), all with normal or corrected vision, volunteered for this experiment after providing informed consent.

5.2.2 Stimuli and Procedure

The first difference with respect to Experiment 5a was that the stimuli were 32 black and white circles. Colors were adjusted so that differences in luminance were minimized (white: 10 cd/m^2 , black: 8 cd/m^2). The second difference was the color of the four-dot pattern. In order to make the four-dot pattern less salient than the targets, the masking pattern consisted of two black and two white dots placed at the opposing vertexes of an illusory square formed by the four-dot pattern (figure 5.2 A). Previous research has shown that masking occurs also when dots are not homogeneously colored (Kahan & Enns, 2010; Kahan & Mathis, 2002); hence, the use of a double colored four-dot mask should not affect the efficacy of masking.

5.2.3 Results and discussion

The ANOVA showed a significant main effect of masking *F*(1,8)=131.4 *p*<.001, with participants less accurate in the masking condition (mean accuracy 58.8 %) with respect to the no-masking condition (mean accuracy 83%). Accuracy also decreased as a function of numerosity, *F*(3,24)=3.08, *p*<.05. A significant numerosity X masking interaction was found, *F*(3,24)=3.04, *p*<.05, due to the presence of an “end effect” for the no-masking condition (accuracy for four targets was the same as for two targets *p*=.40).

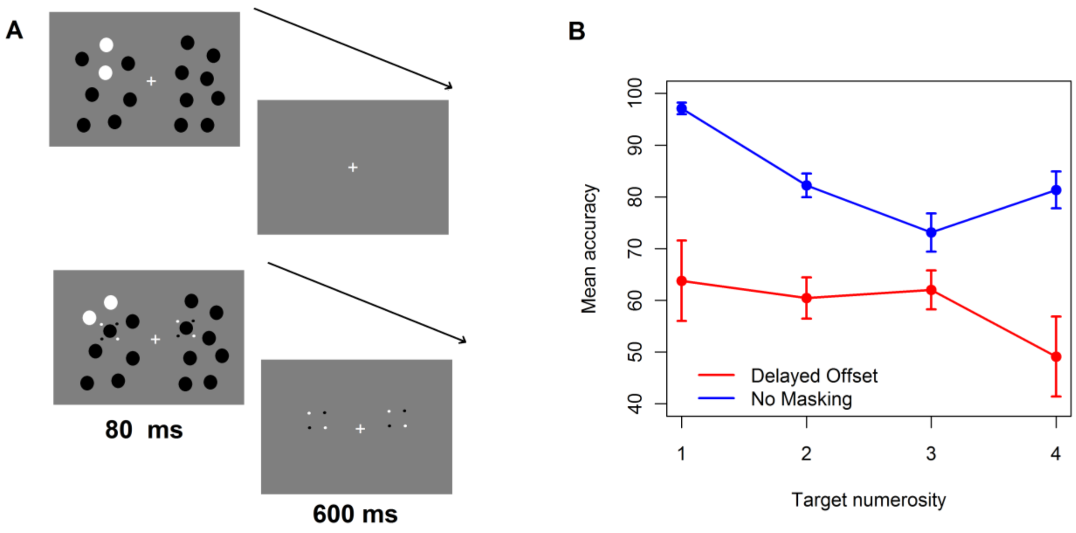

Figure 5.2 Example of display and results Experiment 5b

(A) Display with two targets in the no masking (top) and masking condition (bottom). (B) Mean accuracies as a function of target numerosity and masking. Notice how accuracy decreases as a function of target numerosity but no effect of masking is present.

These results indicated that a four-dot pattern elicited a significant masking effect when the masked feature is color (see Gellatly et al., 2006). Importantly, the masking effect was present for all numerosities, suggesting that four-dot masking can reduce target awareness when multiple targets are processed.

5.3 Experiment 5c: The final paradigm

In the previous experiment I demonstrated that it is possible to elicit a masking effect using multiple targets defined by color. However, the conditions used in the previous experiment were very different in terms of sensory information, due to the fact that the four-dot patterns were present on some trials, while absent on others. As sensory confounds represents an important issue for EEG measurements, in this experiment the four-dot pattern was presented both on masking and no masking trials. As in the original versions of the object-substitution paradigm, the four-dot configuration could offset simultaneously with the other stimuli or after a temporal delay.

5.3.1 Participants

Twelve volunteers (9 females, aged 18-22), all with normal vision, participated in the present pilot experiment, after providing informed consent.

5.3.2 Stimuli and Procedure

Stimuli were identical to the previous experiment except for the following changes. In all trials a four-dot pattern was displayed around one target and one distractor in the opposite hemifield. In the *common offset* condition (50% of trials), the four-dot pattern disappeared together with the other objects (overall display duration: 80 ms). In the *delayed offset* condition (50% of trials) the four-dot pattern remained on the screen for a prolonged interval (600 ms) with respect to the other items (80 ms). Participants completed a total of 512 trials divided in 4 block, with 64 trial for each condition.

5.3.3 Results and discussion

Participants' accuracy decreased as a function of the target numerosity, *F*(3,33)= 9.1, *p*<.001. Participants were also generally less accurate in the delayed offset condition with respect to the common offset condition, *F*(1,11)=15.7, *p*<.01.

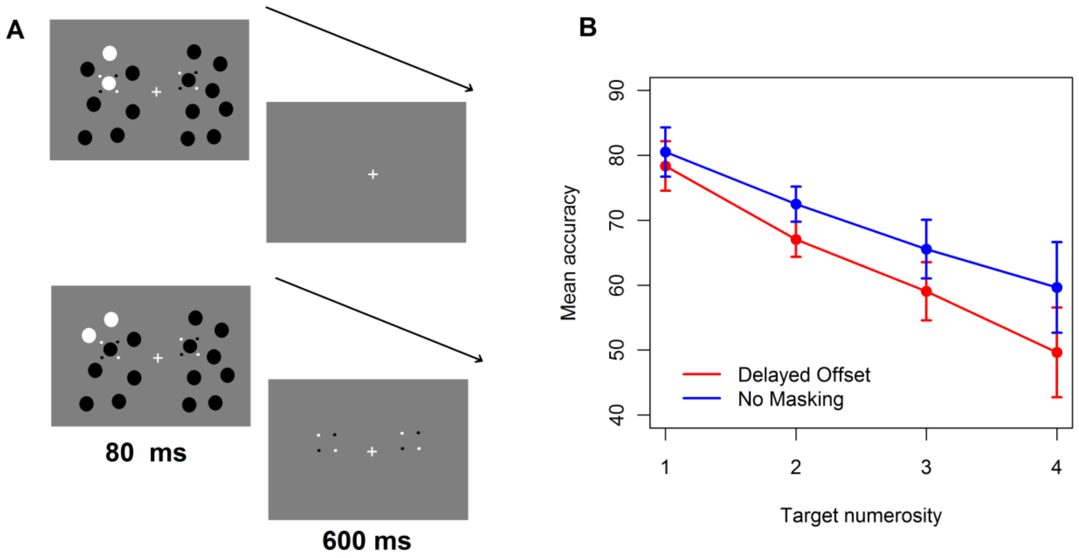

Figure 5.3 Example of display and behavioral results Experiment 5c

(A) Example of displays representing the common offset (top) and delayed offset condition (bottom). The same stimuli have been used in the subsequent EEG experiment. (B) Accuracy as a function of target numerosity and masking.

The present experiment showed that even when sensory differences between the masking and no-masking condition are minimized, a significant masking effect for colored target can be elicited. For this reason, this paradigm was chosen for the subsequent EEG experiment.

5.4 Experiment 6: Electrophysiological correlates of multiple object processing in the absence of awareness

This EEG study addressed whether the various stages of multiple object processing, as indexed by N2pc and CDA modulations, require awareness to operate. Here I combined a four-dot masking procedure (Di Lollo et al., 2000; Trick & Enns, 1997) with a task requiring to enumerate the uniquely colored targets presented among distractors.

5.4.1 Participants

Twenty healthy participants (12 females, aged 18-28), with normal or corrected-to-normal vision, volunteered for the study after providing written informed consent. The study was approved by the local ethics committee.

5.4.2 Stimuli and procedure

The stimuli and paradigm were the same as in Experiment 5c, except for one difference: in the present experiment, the range of target numerosity varied from zero to three targets. This was done in order to avoid the use of a strategy (different from enumeration) to respond to one target numerosity in the delayed-offset condition. Indeed, when 1 to 4 targets are used, participants might correctly guess that, even when they do not consciously perceive a target within the four-dot pattern, but there is no other target element in the display, one target was presented. Thus, I added a zero-target condition in which the four-dot pattern was displayed around two distractors, one in each hemifield.

After a practice session with 32 trials, participants completed 10 blocks of 160 trials each (20 trials for combination of numerosity and masking condition).

5.4.4 EEG recordings and analysis

EEG recordings were the same as in Experiment 4 . The average number of retained trials for each participant after artifact rejection was %. ERP averages were computed relative to a 700 ms time interval starting 100 ms before stimulus onset. ERP averages for target-present trials were computed separately for each target numerosity (one, two and three), target side (left and right) masking condition (common and delayed offset) and accuracy (correct and incorrect trials). Statistical analysis for the lateralized activities (N2pc:180-300 ms; and CDA: 350-600 ms) were carried out on mean amplitude differences at posterior sites (PO7 and PO8) obtained by subtracting activity in the ipsilateral electrode relative to target side (e.g. PO7 for left targets) from the corresponding activity at the contralateral site (e.g. PO8 for left targets). Contralateral and ipsilateral activities were obtained by collapsing electrodes across target side.

In a first analysis, a repeated measures ANOVA was carried out on N2pc and CDA mean amplitudes with component (two levels: N2pc and CDA), target numerosity (three levels: one, two three), and masking (two levels: common offset, delayed offset) as factors. This analysis was done to explore the masking effects on both components regardless of accuracy. A second analysis was carried out on delayed offset trials only in order to explore more in detail the effects of masking on N2pc and CDA. Here we wanted to test whether the numerosity-related modulations of N2pc and CDA could be modulated by the level of participants' awareness. For this reason, we additionally include accuracy (correct, incorrect responses) as factor. Common offset trials could not be included in this analysis as there were not enough incorrect responses. For all analyses Greenhouse-Geisser correction was applied when sphericity assumption was violated; only corrected *p* values are reported. Post hoc analysis were performed using t tests corrected with the Tukey HDS correction for multiple comparisons.

5.4.5 Results

5.4.5.1 Accuracy

Participants' accuracy was lower in the delayed offset than common offset condition, as confirmed by a significant main effect of masking *F*(1,19)=88.5, *p*<.001. Accuracy decreased also as a function of target numerosity, being higher for one than two and three targets (see figure 5.4 C). This resulted in a significant main effect of target numerosity *F*(2,38)=20.6, *p*<.001. Finally, the effect of masking increased as a function of numerosity leading to a significant numerosity X masking interaction, *F*(2,38)=42.5 *p*<001. The interaction was due to the different effect of target numerosity in each masking condition. While in the delayed offset condition accuracy decreased linearly from one to three targets (all *p*s<.001), in the common offset condition numerosity one and three were enumerate equally accurately (*p*=.15), a sort of "end effect" (Mandler & Shebo, 1982).

5.4.5.2 ERP components

Both N2pc and CDA mean amplitudes increased as a function of target numerosity. However the effect of numerosity on each ERP component depended on the masking condition.

The overall ANOVA indicated significant effects of target numerosity *F*(2,38)=23.04, *p*<.001, target numerosity X component, *F*(2,38)=4.11 *p*<.0.5, masking X component *F*(1,19)=10.4, *p*<.01, and numerosity X masking X component, *F*(2,38)=3.3, *p*=.05. To further explore the significant three-way interaction we conducted two analyses separately on N2pc and CDA mean amplitudes, with target numerosity (three levels) and masking (two levels) as factors.

5.4.5.2.1 N2pc

N2pc mean amplitude increased as a function of target numerosity in both common offset and delayed offset conditions, as indicated by the significant effect of numerosity *F*(2,38)=27.72, *p*<0001. N2pc was also slightly smaller in the delayed offset condition relative to common offset trials, resulting in a significant effect of masking *F*(1,19)=5.09, *p*<.05 (5.4 A and B).

5.4.5.2.2 CDA

The ANOVA on CDA amplitudes indicated significant effects of numerosity *F*(2,38)= 12.33, *p*<.001, and of the numerosity X masking interaction, *F*(2,38)=3.4, *p*=.05, indicating that the effects of numerosity were different in the two masking conditions. Further analyses (pairwise comparisons) for the common offset condition indicated that the CDA was larger in three-target trials than in two-target or one-target trials (both *p*s<.01); CDA was also larger for two targets than one target (p<.05). In the delayed offset condition, no difference emerged between two and three targets (p=.99), but trials with one target were different from two- or three-target trials (both ps<.01).

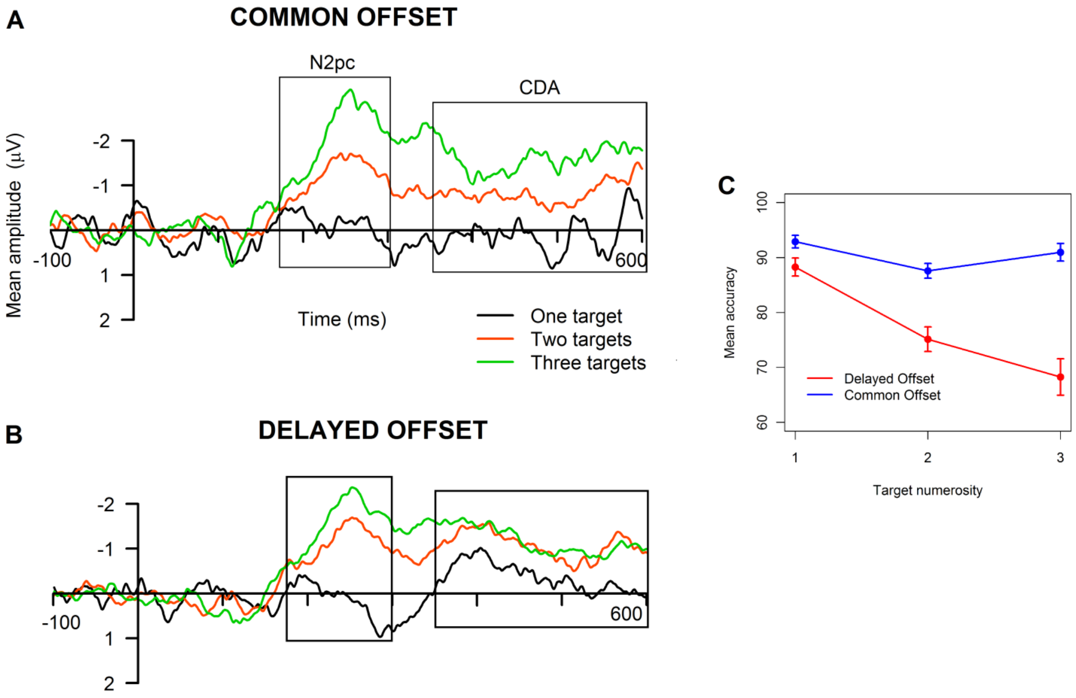

Figure 5.4 Behavioral and ERP results Experiment 6

Grand averages obtained by subtracting ipsilateral from contralateral activity at PO7/8 as a function of target numerosity in the common offset (A) and delayed offset (B) conditions. N2pc increases as a function of target numerosity in both masking conditions whereas CDA shows this effect only in the common offset condition. Notice that these plots represent the average of correct and incorrect trials (C) Mean accuracy as a function of target numerosity and offset, behavioral results replicate the masking effect found in Experiment 5c.

5.4.5.3 Analysis of error trials

This analysis focused on delayed-offset trials and assessed the effect of numerosity separately for each component (N2pc and CDA) and accuracy level (correct versus incorrect trials).

5.4.5.3.1 N2pc

An effect of target numerosity emerged for both correct, *F*(2,38)=19.32, *p*<.001, and incorrect trials, *F*(2,38)= 8.11, *p*<.001.

5.4.5.3.2 CDA

In contrast with the N2pc results, the effect of numerosity was significant only for correct trials, *F*(2,38)=11.15, *p*<.001.

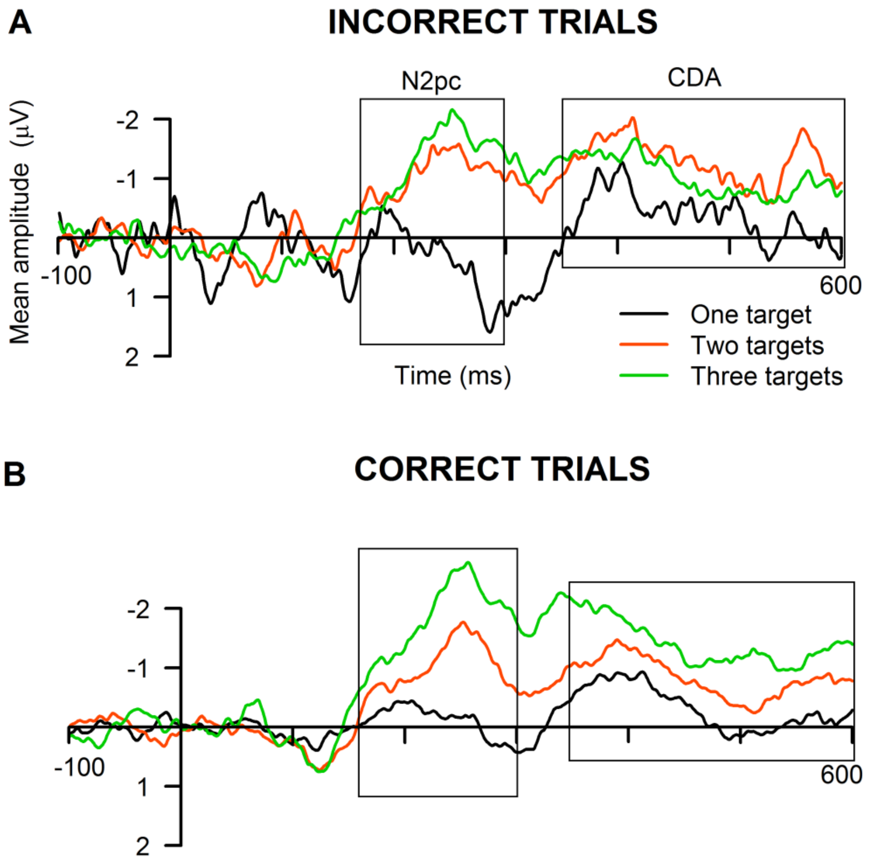

Figure 5.5 ERP results in the delayed offset trials as a function of accuracy

N2pc and CDA modulations as a function of target numerosity in the delayed offset condition split in incorrect (A) and correct (B) trials. CDA amplitude modulation disappears in incorrect trials.

5.4.6 Discussion

In line with previous findings (e.g., Woodman & Luck, 2003), the N2pc was modulated by the number of displayed targets independently of masking. By contrast, CDA showed a differential pattern of numerosity-related modulations as a function of masking. In addition, the analysis on delayed-offset trials showed that while N2pc was modulated by target numerosity both in correct and incorrect trials, the CDA modulations were present only in correct trials. Taken together, these results suggest that while individuation of multiple targets does not require awareness to operate, awareness is needed to maintain multiple object representations active and available for further operations.

There is however an important caveat. In the paradigm used in the present experiment, participants might have used a guessing strategy to respond correctly to numerosities two and three. It should be noted that (on target-present trials) multiple targets were always presented in one side, and that the four-dot pattern always surrounded one target. As a consequence, the presence of one and two targets outside the four-dot pattern configurations was always predictive of the presence of, respectively, two and three targets (one of which occurred inside the four-dot configuration). Therefore, especially for the “more difficult” delayed-offset condition, it is possible that participants relied on the number of targets presented outside the four-dot configurations in order to infer the correct numerosity of the target set. While this strategy could not possible for one-target trials, as the overall absence of targets outside the four-dot configuration could be associated either with the presence of one target or with zero-target trials, it remains a viable option for numerosities two and three.

The next behavioral experiment was conducted in order to examine whether such a strategy was used in this experiment and, if so, how it may affect participants' performance.

5.5 Experiment 7

In this Experiment the use of a guessing strategy based on the visible (i.e. non-masked) information was discouraged by adding a condition in which only distractors were masked. This in turn made the number of visible targets in the delayed-offset condition non predictive of the total number of displayed targets. In this new condition (distractor masking condition), one, two or three targets were presented but none of them was masked. The four-dot pattern was presented around two distractors (one for each hemifield), as for the zero-target condition.

If participants were using a guessing strategy in Experiment 6, I expected to find a different behavioral performance when the strategy is discouraged, as in the present experiment.

5.5.1 Participants

Eight participants (5 females, aged 18-22) were tested in this experiment. All of them reported normal or corrected to normal vision. Participants took part to the experiment after giving their informed consent.

5.5.2 Stimuli and procedure

Stimuli were identical to the ones used in the EEG experiment except for one aspect. In half of the trials (distractor-masked trials) the four-dot patterns appeared around two distractors, one in the side where targets were displayed and one in the opposite side (see figure 5.6 A); in the remaining half of the trials (target-masked trials) stimuli were identical to the ones used in Experiment 6. For each of the four target numerosities used in the present experiment there were four types of trials: distractor-masked/delayed offset trials, distractor-masked/common offset trials, target-masked/delayed offset trials, and target-masked/common offset trials (16 conditions in total). For each condition there were 32 trials, for a total of 512 trials divided in four blocks. Target color (white, black) and response assignment were counterbalanced across participants.

In the result section I will focus on the analysis of target-masked trials only, as these trials are identical to the ones presented in Experiment 6. Mean accuracies were submitted to a repeated measures ANOVA with target numerosity (three levels: one, two and three) and masking (two levels: delayed and common offset) as factors.

5.5.3 Results and Discussion

Results were virtually identical to the ones of Experiment 6 (see figure 5.6 B and 5.4 C). The ANOVA showed that accuracy decreased as a function of target numerosity in both common and delayed offset trials $F(2,14)=4.7$, $p<.05$. In addition participants were less accurate in the delayed offset with respect to the common offset trials leading to a significant effect of masking $F(1,7)=19.3$, $p<.01$.

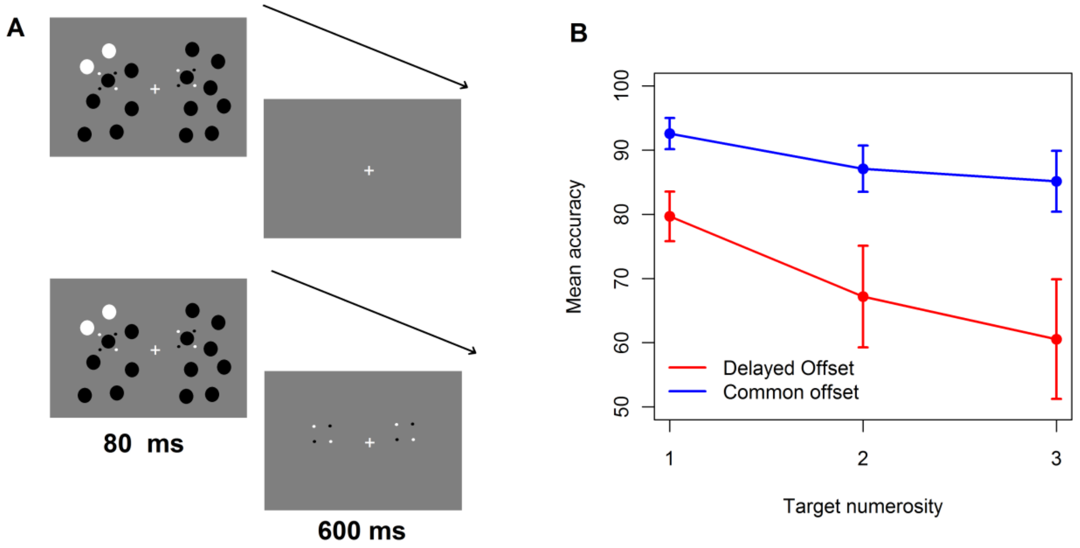

Figure 5.6 Example of displays and behavioral results Experiment 7

(A) Example of the distractor-masked/common-offset condition (top) and distractor-masked/delayed off-set condition (top). (B) Behavioral results in the target-masked condition as a function of target numerosity and offset. Results are identical to the ones of Experiment 6

Overall, the presence of a behavioral pattern that closely matches the one in Experiment 6 reasonably rules out the possibility that in the previous experiment participants relied on the number of targets presented outside the four-dot configurations in order to infer the correct numerosity of the target set.

5.6 General discussion

In the experiments presented in this chapter I investigated the role of awareness in multiple object processing. More in detail, I wanted to address whether it is possible to individuate and maintain multiple objects when part of the visual information is masked. Two main aspects emerged from this study.

The first aspect is related to the methodology used in the present experiments. To my knowledge this is the first time a four-dot masking procedure is adapted to an enumeration task or, more generally, to multiple object processing. The behavioral findings of Experiments 5, 6, and 7 overall suggests that by masking a single target, it is possible to manipulate the overall perception of multiple objects, leading to impairments in the ability to report the numerosity of a set of objects.

The second and more important aspect is related to the EEG results. These finding clearly showed a dissociation between the effects of four-dot masking on N2pc and on CDA when multiple targets must be processed.

In line with previous studies (Drew & Vogel, 2008; Ester et al., 2012; Mazza & Caramazza, 2011; Pagano & Mazza, 2012), the N2pc amplitude was modulated by the number of targets; moreover, and again in line with previous findings (Prime et al., 2011; Woodman & Luck, 2003), the N2pc was overall visible in both the unmasked and masked conditions (although it was slightly reduced in the masked condition). Crucially, the data indicated that the modulation of N2pc as a function of target numerosity was present independently of masking, suggesting that the individuation mechanism can operate when awareness is reduced. This interpretation is further strengthened by the results of the analysis considering correct and incorrect responses. Here I found that N2pc amplitude was modulated by target numerosity regardless of whether participants could infer correctly the target numerosity. In other words, the individuation mechanism could track multiple objects also when awareness was likely absent, namely in incorrect trials. Taken together, these findings indicate that the functioning of the first stage of multiple object processing, individuation, is independent from the observer’s state of awareness.

A surprising and quite unexpected result additionally emerged in the present study. When one-target trials were considered, no clear N2pc was visible for this numerosity in both the delayed and common offset conditions . Although this effect was not expected on the basis of the Woodman and Luck (2003) study, it is partially in line with the findings of Prime et al. (2011) that indicated no N2pc in the common offset condition. These authors argue that in the common offset condition participants were able to individuate the target by maintaining a “diffused attentional state” that allowed for the selection of potentially relevant elements in both hemifield, therefore eliminating the N2pc (Prime et al., 2011). Similarly, one possible explanation of the present results is that the masking of one target was not very effective in my experiments, therefore leaving some extra resources for the selection of the two elements surrounded by the four-dot configurations in both hemifields, both in the mask and no no-mask conditions.

A second interesting result was provided by the analyses on the CDA. The results showed that CDA was elicited both in delayed and common offset trials; crucially, however, the amplitude of CDA was clearly modulated by target numerosity only during the no-masking condition. On the assumption that CDA represents the functioning of a mechanism that encodes multiple targets in greater detail and maintain them for further operations, the present result suggest that maintenance and/or deep encoding of multiple objects is impaired during masking.

This interpretation is supported by the results of the analysis based on correct and incorrect responses. This analysis showed that CDA was elicited during delayed offset trials, being modulated by target numerosity, when participants provided the correct response. Conversely, CDA was not modulated by target numerosity in delayed offset trials with incorrect responses. Interestingly, these results suggest that when awareness is reduced (i.e. in masked incorrect trials) the mechanism that maintains multiple representations for further operations fails to operate successfully.

To conclude in the present Chapter I presented a series of experiment whose aim was to investigate the role of awareness during multiple object processing. The results showed that this issue can be successfully investigated using a paradigm in which a masking procedure and enumeration are combined. Moreover, the EEG results showed that the individuation stage of multiple object processing, as indexed by N2pc modulation, operates also when awareness is consistently reduced and/or absent. By contrast, the results on the CDA modulations indicated that the functioning of the late stages of multiple object analysis is strongly linked to awareness. This in turn suggests that awareness is progressively required to establish detailed representations of multiple objects.

Chapter 6

Conclusions

In this thesis I presented a series of studies aimed at examining the ability to process multiple relevant objects. This topic brings together several areas of research, such as attention selection, working memory, numerosity representation and object recognition, and for this reason it has recently become one of the most investigated topics in cognitive neuroscience (for reviews see Hyde, 2011; Piazza, 2010; Xu & Chun, 2009). Using a novel approach based on electrophysiological measures, these studies provide new information on the involvement of early selection/individuation stages and late working-memory procedures in the computation of quantities during visual enumeration tasks.

The novel approach consists in the use of two lateralized components of the EEG signal – N2pc and CDA – that have previously been associated respectively with attention selection and working memory, in order to test some of the hypotheses concerning multiple object analysis proposed by previous models of visual perception (Kahneman et al., 1992; Pylyshyn, 1989). Until now, the majority of the studies on the N2pc component (Eimer, 1996; Luck et al., 1997; Luck & Hillyard, 1994) have focused on the issue of individuation/selection when only a single target is presented, thus leaving unexplored whether this component is a good candidate for the study of multiple target processing. On the other hand, the CDA component has been associated to the active maintenance of a set of multiple objects in a working memory buffer (Ikkai et al., 2010; Vogel & Machizawa, 2004). However, this interpretation was formulated on the basis of studies in which an explicit memory task was required, thus leaving unexplored whether this component could successfully track memory procedures also in the context of other tasks requiring multiple object processing.

Overall, these two components have not been systematically tested within a general theory of multiple object processing. The only exception is represented by two previous EEG studies (Drew & Vogel, 2008; Mazza & Caramazza, 2011) concerning multiple object tracking and visual enumeration. These studies found modulations of both the N2pc and CDA amplitudes as a function of target numerosity, suggesting that these components track the functioning of, respectively, two mechanisms (individuation/selection and working memory) that are common to the execution of several tasks. However, given the limited range of target numerosities used in these studies, none of them have tested systematically one of the distinctive features of both individuation and working memory, namely their capacity limit in simultaneous analysis (see Cowan, 2001 and Pylyshyn, 1989).

In all the experiments of the present thesis I established that both N2pc and CDA were modulated by the number of relevant items during the execution of an enumeration task. In particular, the issue of the limit in simultaneous processing was the focus of the first EEG study (Chapter 2). In Experiments 1 and 2 I found that the N2pc amplitude was modulated by the number of targets to be enumerated, supporting the idea that individuation (as reflected by the N2pc) is a critical process during enumeration of small quantities in cluttered scenes (see also Mazza & Caramazza, 2011; Piazza et al., 2011). Moreover, the N2pc reached a plateau at about four-five elements, in line with the limit of simultaneous processing proposed by some models of individuation (Pylyshyn, 1989; Kahneman et al., 1992). Together with some recent findings on enumeration (see Ester, Drew, Klee, Vogel, & Awh, 2012) and with previous N2pc findings on multiple object tracking (Drew & Vogel, 2008), these results indicate that N2pc tracks a mechanism that is common to different tasks (Chesney & Haladjian, 2011). This pattern of results was complemented by the group analysis revealing different N2pc asymptotes as a function of the participants' behavioral efficiency in enumeration. This, in turn, suggests that individual neural differences in the individuation capacity can predict enumeration performance.

Experiment 1 and 2 also shed light on the role of working-memory related stages in visual enumeration, as indexed by the CDA. Overall, and similarly to the N2pc pattern, the two experiments indicated that CDA amplitudes were modulated by target numerosity and reached a plateau at approximately four elements, suggesting that the maintenance of the target elements in VWM during the mapping onto a symbolic numerical system also plays a significant role in enumeration.

In contrast with the majority of studies on visual enumeration, in the first study the to-be-enumerated targets were always presented with distractors. While this aspect represents a more realistic approximation of daily life contexts, in which the relevant objects are usually presented in cluttered scenes (i.e., together with distracting information), it nonetheless leaves out the possibility that the results, and in particular the ones concerning N2pc, simply reflect the effort of separating the targets from distractors (for instance, by suppressing the irrelevant objects presented on the target side, see Luck et al., 1997). In the second study (Chapter 3) I directly addressed this issue by systematically manipulating the presence of distractors in the hemifield in which targets were displayed. This manipulation also allowed me to reconcile the apparent contrasting results and interpretations of the N2pc as the neural correlate of “individuation” with those from recent studies, according to which the individuation stage is located at an earlier attention-related ERP component, the N1 (Hyde, 2011; Hyde & Spelke 2009; 2011; Hyde & Woods, 2011).

The results were straightforward. The N2pc amplitudes were modulated by target numerosity in both the target only and target plus distractor conditions. These results reasonably dismiss that this component is exclusively related to distractor suppression and, in line with very recent findings (Ester et al., 2012; Pagano & Mazza, 2012), further confirmed that the N2pc reflects the functioning of a processing stage associated with the exact computation of the relevant quantities, namely the selective and simultaneous individuation of a subset of target elements in the visual field. This interpretation is substantiated by the lateralized nature of the N2pc (a proxy for location coding), by its asymptote at 3 targets (an index of capacity limit in simultaneous processing), and by the fact that it is found both when distractors are present and when they are absent (a proxy for selective individuation of the target elements).

By contrast, the N1 pattern was differentially modulated by target numerosity as a function of distractor presence. While in the no-distractor condition the amplitude of the N1 was modulated by target numerosity (see also Hyde & Spelke, 2009; 2011), no differences in the N1 emerged among the target numerosities in the distractor condition. These findings indicated that while the N1 may be sensitive to the number of elements presented in the visual field, it does not discriminate between relevant and irrelevant quantities. They also suggest that N1 reflects the functioning of a perceptual mechanism that extracts the information of the overall amount of elements in a display by relying on their status of "spatially" separable entities but with imprecise and coarse featural encoding. Overall, these results further strengthen the idea that N2pc can successfully track simultaneous individuation, and that this is a key process for exact enumeration of small quantities. In addition, they indicate that the selection of multiple relevant elements can be distinguished from the computation of the general (target and distractor) numerosity of objects, providing hints about the distinct perceptual mechanisms that may be involved in exact versus approximate enumeration.

As previously discussed in the Introduction (Chapter 1), the issue of the exact contents of the representations produced during individuation has received little investigation. In Experiment 4 (Chapter 4) I specifically focused on whether high-level features (such as semantic information) are incorporated in the representations produced at the stage of individuation. As far as enumeration is concerned, previous models of individuation (Trick & Pylyshyn, 1994) assume that this stage is pre-numeric, in the sense that the semantic information related to the object quantity (i.e., their magnitude values) would become available only after objects have been individuated. Quantity values are the result of a mapping between the indexed objects and the numerical magnitude of the elements. However, previous N2pc studies have showed that this component can be modulated by semantic information (Dell'Acqua et al., 2007; Telling et al., 2010). Using a numerical Stroop paradigm, in this experiment I tried to clarify the contents of the representations produced at the individuation stage during enumeration.

The results showed that N2pc was modulated by target numerosity but not by target congruency, indicating that the interference effect produced by the Stroop task does not originate at the level reflected by N2pc. This in turn suggested that the identity of the targets and their associated numerical magnitude do not interfere with their individuation. While these results do not exclude the possibility that semantic information can be processed either earlier than, or simultaneously with the individuation process reflected by the N2pc (see Thorpe et al., 1996), they also point out that this is not the *crucial* information used for target individuation during enumeration, at least in a number-Stroop paradigm. By contrast, the CDA was modulated by congruency for all target numerosities, suggesting that number semantic properties play a role during late stages of object analysis.

In Chapter 5, I asked whether multiple object processing necessarily requires awareness. While we usually become aware of the multiple objects we need to process, it is not clear whether the early individuation stages or the late working-memory related procedures (or both) can operate in conditions of absent/reduced awareness, for instance when part of the visual input is masked. To address this issue I conducted a series of behavioral studies (Experiments 5a-c and 7) and one EEG study (Experiment 6) based on an object-substitution masking procedure (four-dot masking, Enns & Di Lollo, 1997).

While the results of Experiments 5a-c and 7 indicated that multiple object enumeration can be impaired when a single target is masked, the ERP results of Experiment 6 showed an interesting dissociation between the effect of masking on N2pc and CDA when multiple targets are elaborated. The N2pc showed a significant modulation of its amplitude as a function of target numerosity independently from masking; by contrast, CDA was clearly modulated by target numerosity in the no masking condition only. This suggest that while the individuation mechanism can operate when awareness is reduced, the active maintenance of multiple object representations for further operations (such as the retrieval of the numerosity of a set) is less effective in condition of reduced awareness. This interpretation was supported also by the result that CDA was modulated by target numerosity in those masked trials in which participants were able to provide a correct response. Conversely, the effect of target numerosity on CDA disappeared in masked trials in which participants were not able to report target numerosity. Overall, the results presented in Chapter 5 indicated that although awareness overall affects the functioning of multiple object analysis, multiple target individuation can operate in conditions of reduced/absent awareness. In contrast, detailed encoding procedures on multiple targets are significantly less effective with reduced awareness. This in turn suggests that awareness is progressively required to build a full representation of multiple objects.

In conclusion, the studies presented in this thesis added new important information on the way multiple object processing is achieved. As mentioned in the Introduction, the use of neuroimaging techniques has proven useful for testing the classical cognitive theories of multiple object perception by evaluating its underlying brain dynamics. In analogy with the neuronatomical distinction involved in multiple object processing proposed by Xu and Chun (2009), here I showed that two temporally distinct neural activations are involved respectively in the individuation and maintenance of a set of relevant elements. The analysis of these two separate activations provided new information on the way early individuation and late WM stages interact for successful object perception, as well as on their functional dissociation during multiple object processing.

Unfortunately, the separate use of neuroimaging techniques (such as EEG and fMRI) that largely differ in terms of their spatial and temporal resolution in measuring brain activity, prevents the integration of the resulting information into a unitary description of the spatio-temporal patterns of neural activity. Therefore, a complete picture of the spatial and temporal brain dynamics involved in multiple object processing still lacks. Recent methodological advances have allowed for a successful combination of some of the neuroimaging techniques. This combination, known as “multimodal imaging”, represents a promising tool to get a complete picture of the brain activity supporting a specific cognitive function (Debener, Ullsperger, Siegel, & Engel, 2006; Herrmann & Debener, 2008; Ritter & Villringer, 2006; Thut & Miniussi, 2009). Future research using multimodal imaging will be able to simultaneously address the temporal and spatial features of brain activity involved in multiple-object processing. This integrated approach will establish the diverse functional and neural aspects involved in the perception of multiple objects.

References

Alvarez, G. A., & Cavanagh, P. (2005). Independent resources for attentional tracking in the left and right visual hemifields. *Psychological Science*, *16*(8), 637–43. doi:10.1111/j.1467-9280.2005.01587.x

Alvarez, G. A., & Franconeri, S. L. (2007). How many objects can you track? Evidence for a resource-limited attentive tracking mechanism. *Journal of Vision*, *7*(13), 14.1–10. doi:10.1167/7.13.14

Annan, V., & Pylyshyn, Z. W. (2006). Dynamics of target selection in Multiple Object Tracking (MOT). *Spatial Vision*, *19*(6), 485–504. doi:10.1163/156856806779194017

Ansari, D., Lyons, I. M., van Eimeren, L., & Xu, F. (2007). Linking visual attention and number processing in the brain: the role of the temporo-parietal junction in small and large symbolic and nonsymbolic number comparison. *Journal of Cognitive Neuroscience*, *19*(11), 1845–53. doi:10.1162/jocn.2007.19.11.1845

Bahrami, B., Vetter, P., Spolaore, E., Pagano, S., Butterworth, B., & Rees, G. (2010). Unconscious numerical priming despite interocular suppression. *Psychological Science*, *21*(2), 224–33. doi:10.1177/0956797609360664

Behrmann, M., Geng, J. J., & Shomstein, S. (2004). Parietal cortex and attention. *Current Opinion in Neurobiology*, *14*(2), 212–7. doi:10.1016/j.conb.2004.03.012

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Stastical Society B*, *57*(1), 189–300.

Bettencourt, K. C., & Somers, D. C. (2009). Effects of target enhancement and distractor suppression on multiple object tracking capacity. *Journal of Vision*, *9*(7), 1–11. doi:10.1167/9.7.9.

Bichot, N. P., Cave, K. R., & Pashler, H. (1999). Visual selection mediated by location: feature-based selection of noncontiguous locations. *Perception & Psychophysics*, *61*(3), 403–23.

Burr, D. C., Anobile, G., & Turi, M. (2011). Adaptation Affects Both High and Low (Subitized) Numbers Under Conditions of High Attentional Load. *Seeing and Perceiving*, *24*(10), 141–150.

Burr, D. C., Turi, M., & Anobile, G. (2010). Subitizing but not estimation of numerosity requires attentional resources. *Journal of Vision*, *10*(6), 20. doi:10.1167/10.6.20

Cantlon, J. F., & Brannon, E. M. (2006). Shared system for ordering small and large numbers in monkeys and humans. *Psychological Sciencecience*, *17*(5), 401–6. doi:10.1111/j.1467-9280.2006.01719.x

Carey, S., & Xu, F. (2001). Infants' knowledge of objects: beyond object files and object tracking. *Cognition*, *80*(1-2), 179–213. doi:10.1016/S0010-0277(00)00154-2

Cavanagh, P. (2011). Visual cognition. *Vision Research*, *51*(13), 1538–51. doi:10.1016/j.visres.2011.01.015

Cavanagh, P., & Alvarez, G. A. (2005). Tracking multiple targets with multifocal attention. *Trends in Cognitive Sciences*, *9*(7), 349–54. doi:10.1016/j.tics.2005.05.009

Cavanagh, P., & He, S. (2011). Attention mechanisms for counting in stabilized and in dynamic displays. In E. B. and S. Dehaene (Ed.), *Space Time and Number, Attention & Performance XXIV*. Oxford University Press.

Chesney, D. L., & Haladjian, H. H. (2011). Evidence for a shared mechanism used in multiple-object tracking and subitizing. *Attention, Perception & Psychophysics*, *73*(8), 2457–80. doi:10.3758/s13414-011-0204-9

Cordes, S., Gelman, R., Gallistel, C. R., & Whalen, P. J. (2001). Variability signatures distinguish verbal from nonverbal counting for both large and small numbers. *Psychonomic Bulletin & Review*, *8*(4), 698–707. doi:10.3758/BF03196206

Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, *24*(1), 87–114. doi:10.1017/S0140525X01003922

Debener, S., Ullsperger, M., Siegel, M., & Engel, A. K. (2006). Single-trial EEG-fMRI reveals the dynamics of cognitive function. *Trends in Cognitive Sciences*, *10*(12), 558–63. doi:10.1016/j.tics.2006.09.010

Debner, J. A., & Jacoby, L. L. (1994). Unconscious perception: Attention, awareness, and control. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *20*(2), 304–317.

Dehaene, S. (1996). The Organization of Brain Activations in Number Comparison: Event-Related Potentials and the Additive-Factors Method. *Journal of Cognitive Neuroscience*, *8*(1), 47–68. doi:10.1162/jocn.1996.8.1.47

Dehaene, S. (1997). *The Number Sense: How Mathematical Knowledge Is Embedded in Our Brains*. New York: Oxford University Press.

Dehaene, S., & Changeux, J.-P. (1993). Development of Elementary Numerical Abilities: A Neuronal Model. *Journal of Cognitive Neuroscience*, *5*(4), 390–407.

Dehaene, S., & Cohen, L. (1994). Dissociable mechanisms of subitizing and counting: Neuropsychological evidence from simultanagnosic patients. *Journal of Experimental Psychology: Human Perception and Performance*, *20*(5), 958–975. doi:10.1037/0096-1523.20.5.958

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology*, *20*(3), 487–506. doi:10.1080/02643290244000239

Dell’Acqua, R., Pesciarelli, F., Jolicoeur, P., Eimer, M., & Peressotti, F. (2007). The interdependence of spatial attention and lexical access as revealed by early asymmetries in occipito-parietal ERP activity. *Psychophysiology*, *44*(3), 436–43. doi:10.1111/j.1469-8986.2007.00514.x

Di Lollo, V., Enns, J. T., & Rensink, R. A. (2000). Competition for consciousness among visual events: The psychophysics of reentrant visual processes. *Journal of Experimental Psychology: General*, *129*(4), 481–507. doi:10.1037/0096-3445.129.4.481

Doran, M. M., & Hoffman, J. E. (2010). The role of visual attention in multiple object tracking: evidence from ERPs. *Attention, Perception & Psychophysics*, *72*(1), 33–52. doi:10.3758/APP.72.1.33

Drew, T., Horowitz, T. S., Wolfe, J. M., & Vogel, E. K. (2011). Delineating the neural signatures of tracking spatial position and working memory during attentive tracking. *The Journal of Neuroscience*, *31*(2), 659–68. doi:10.1523/JNEUROSCI.1339-10.2011

Drew, T., & Vogel, E. K. (2008). Neural measures of individual differences in selecting and tracking multiple moving objects. *The Journal of Neuroscience*, *28*(16), 4183–91. doi:10.1523/JNEUROSCI.0556-08.2008

Eger, E., Sterzer, P., Russ, M. O., Giraud, A.-L., & Kleinschmidt, A. (2003). A Supramodal Number Representation in Human Intraparietal Cortex. *Neuron*, *37*(4), 719–726. doi:10.1016/S0896-6273(03)00036-9

Egeth, H. E., Leonard, C. J., & Palomares, M. (2008). The role of attention in subitizing: Is the magical number 1? *Visual Cognition*, *16*(4), 463–473. doi:10.1080/13506280801937939

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, *99*(3), 225–234. doi:10.1016/0013-4694(96)95711-9

Enns, J. T. (2004). Object substitution and its relation to other forms of visual masking. *Vision Research*, *44*(12), 1321–31. doi:10.1016/j.visres.2003.10.024

Enns, J. T., & Di Lollo, V. (1997). Object Substitution: A New Form of Masking in Unattended Visual Locations. *Psychological Science*, *8*(2), 135–139. doi:10.1111/j.1467-9280.1997.tb00696.x

Ester, E. F., Drew, T., Klee, D., Vogel, E. K., & Awh, E. (2012). Neural measures reveal a fixed item limit in subitizing. *The Journal of Neuroscience*, *32*(21), 7169–77. doi:10.1523/JNEUROSCI.1218-12.2012

Feigenson, L., & Carey, S. (2005). On the limits of infants' quantification of small object arrays. *Cognition*, *97*(3), 295–313. doi:10.1016/j.cognition.2004.09.010

Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends in Cognitive Sciences*, *8*(7), 307–14. doi:10.1016/j.tics.2004.05.002

Francolini, C. M., & Egeth, H. E. (1980). On the nonautomaticity of "automatic" activation: evidence of selective seeing. *Perception & Psychophysics*, *27*(4), 331–42. doi:10.3758/BF03206122

Franconeri, S. L., Alvarez, G. A., & Enns, J. T. (2007). How many locations can be selected at once? *Journal of Experimental Psychology: Human Perception and Performance*, *33*(5), 1003–12. doi:10.1037/0096-1523.33.5.1003

Franconeri, S. L., Jonathan, S. V., & Scimeca, J. M. (2010). Tracking multiple objects is limited only by object spacing, not by speed, time, or capacity. *Psychological Science*, *21*(7), 920–5. doi:10.1177/0956797610373935

Gellatly, A., Pilling, M., Cole, G., & Skarratt, P. (2006). What is being masked in object substitution masking? *Journal of Experimental Psychology. Human Perception and Performance*, *32*(6), 1422–35. doi:10.1037/0096-1523.32.6.1422

Grubert, A., Krummenacher, J., & Eimer, M. (2011). Redundancy gains in pop-out visual search are determined by top-down task set: behavioral and electrophysiological evidence. *Journal of Vision*, *11*(14), 1–10. doi:10.1167/11.14.10

Haun, D. B. M., Jordan, F. M., Vallortigara, G., & Clayton, N. S. (2010). Origins of spatial, temporal and numerical cognition: Insights from comparative psychology. *Trends in Cognitive Sciences*, *14*(12), 552–60. doi:10.1016/j.tics.2010.09.006

Herrmann, C. S., & Debener, S. (2008). Simultaneous recording of EEG and BOLD responses: a historical perspective. *International Journal of Psychophysiology*, *67*(3), 161–8. doi:10.1016/j.ijpsycho.2007.06.006

Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, *21*(4), 760–75. doi:10.1162/jocn.2009.21039

Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of Cognitive Neuroscience*, *18*(4), 604–13. doi:10.1162/jocn.2006.18.4.604

Hyde, D. C. (2011). Two systems of non-symbolic numerical cognition. *Frontiers in Human Neuroscience*, *5*(November), 150. doi:10.3389/fnhum.2011.00150

Hyde, D. C., & Spelke, E. S. (2009). All numbers are not equal: an electrophysiological investigation of small and large number representations. *Journal of Cognitive Neuroscience*, *21*(6), 1039–53. doi:10.1162/jocn.2009.21090

Hyde, D. C., & Spelke, E. S. (2011). Spatiotemporal dynamics of processing nonsymbolic number: An event-related potential source localization study. *Human Brain Mapping*, *000*(March). doi:10.1002/hbm.21352

Hyde, D. C., & Wood, J. N. (2011). Spatial attention determines the nature of nonverbal number representation. *Journal of Cognitive Neuroscience*, *23*(9), 2336–51. doi:10.1162/jocn.2010.21581

Ikkai, A., McCollough, A. W., & Vogel, E. K. (2010). Contralateral delay activity provides a neural measure of the number of representations in visual working memory. *Journal of Neurophysiology*, *103*(4), 1963–8. doi:10.1152/jn.00978.2009

Jensen, E. M., Reese, E. P., & Reese, T. W. (1950). The subitizing and counting of visually presented fields of dots. *The Journal of Psychology: Interdisciplinary and Applied*, *30*(2), 363–392.

Johannes, S., Münte, T. F., Heinze, H. J., & Mangun, G. R. (1995). Luminance and spatial attention effects on early visual processing. *Cognitive Brain Research*, *2*(3), 189–205. doi:10.1016/0926-6410(95)90008-X

Jolicoeur, P., Brisson, B., & Robitaille, N. (2008). Dissociation of the N2pc and sustained posterior contralateral negativity in a choice response task. *Brain Research*, *1215*, 160–72. doi:10.1016/j.brainres.2008.03.059

Jolicoeur, P., Sessa, P., Dell'Acqua, R., & Robitaille, N. (2006). On the control of visual spatial attention: evidence from human electrophysiology. *Psychological Research*, *70*(6), 414–24. doi:10.1007/s00426-005-0008-4

Kahan, T. A., & Enns, J. T. (2010). Object trimming: When masking dots alter rather than replace target representations. *Journal of Experimental Psychology. Human Perception and Performance*, *36*(1), 88–102. doi:10.1037/a0016466

Kahan, T. A., & Mathis, K. M. (2002). Gestalt grouping and common onset masking. *Perception & Psychophysics*, *64*(8), 1248–1259. doi:10.3758/BF03194769

Kahneman, D., Treisman, A. M., & Gibbs, B. J. (1992). The reviewing of object files: object-specific integration of information. *Cognitive Psychology*, *24*(2), 175–219. doi:10.1016/0010-0285(92)90007-O

Kaufman, E. L., Lord, M. W., Reese, T. W., & Volkmann, J. (1949). The Discrimination of Visual Number. *The American Journal of Psychology*, *62*(4), 498. doi:10.2307/1418556

Kiss, M., Van Velzen, J., & Eimer, M. (2008). The N2pc component and its links to attention shifts and spatially selective visual processing. *Psychophysiology*, *45*(2), 240–9. doi:10.1111/j.1469-8986.2007.00611.x

Koechlin, E., Naccache, L., Block, E., & Dehaene, S. (1999). Primed numbers: Exploring the modularity of numerical representations with masked and unmasked semantic priming. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(6), 1882–1905. doi:10.1037/0096-1523.25.6.1882

Leslie, A. M., Xu, F., Tremoulet, P. D., & Scholl, B. J. (1998). Indexing and the object concept: developing `what' and `where' systems. *Trends in Cognitive Sciences*, *2*(1), 10–18. doi:10.1016/S1364-6613(97)01113-3

Libertus, M. E., Woldorff, M. G., & Brannon, E. M. (2007). Electrophysiological evidence for notation independence in numerical processing. *Behavioral and Brain Functions*, *3*, 1. doi:10.1186/1744-9081-3-1

Logan, G. D., & Zbrodoff, N. J. (2003). Subitizing and similarity: toward a pattern-matching theory of enumeration. *Psychonomic Bulletin & Review*, *10*(3), 676–82.

Luck, S. J., Girelli, M., McDermott, M. T., & Ford, M. A. (1997). Bridging the gap between monkey neurophysiology and human perception: an ambiguity resolution theory of visual selective attention. *Cognitive Psychology*, *33*(1), 64–87. doi:10.1006/cogp.1997.0660

Luck, S. J., & Hillyard, S. A. (1994). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, *31*(3), 291–308. doi:10.1111/j.1469-8986.1994.tb02218.x

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, *390*(6657), 279–81. doi:10.1038/36846

Mandler, G., & Shebo, B. J. (1982). Subitizing: An analysis of its component processes. *Journal of Experimental Psychology: General*, *111*(1), 1–22. doi:10.1037/0096-3445.111.1.1

Mangun, G. R., Hillyard, S. A., & Luck, S. J. (1993). Electrocortical substrates of visual selective attention. In D. Meyer & S. Kornblum (Eds.), *Attention and performance XIV* (pp. 219–243). MIT Press, Cambridge, MA USA.

Masson, M. E. J. (2011). A tutorial on a practical Bayesian alternative to null-hypothesis significance testing. *Behavior research methods*, *43*(3), 679–90. doi:10.3758/s13428-010-0049-5

Mazza, V., & Caramazza, A. (2011). Temporal brain dynamics of multiple object processing: the flexibility of individuation. *PloS one*, *6*(2), e17453. doi:10.1371/journal.pone.0017453

Mazza, V., Turatto, M., & Caramazza, A. (2009a). Attention selection, distractor suppression and N2pc. *Cortex*, *45*(7), 879–90. doi:10.1016/j.cortex.2008.10.009

Mazza, V., Turatto, M., & Caramazza, A. (2009b). An electrophysiological assessment of distractor suppression in visual search tasks. *Psychophysiology*, *46*(4), 771–5. doi:10.1111/j.1469-8986.2009.00814.x

Mazza, V., Turatto, M., Umiltà, C., & Eimer, M. (2007). Attentional selection and identification of visual objects are reflected by distinct electrophysiological responses. *Experimental Brain Research*, *181*(3), 531–6. doi:10.1007/s00221-007-1002-4

Mitchell, D. C. (1972). Short-term visual memory and pattern masking. *The Quarterly Journal of Experimental Psychology*, *24*(4), 394–405. doi:10.1080/14640747208400298

Mounts, J. R. W., & Melara, R. D. (1999). Attentional selection of objects or features: evidence from a modified search task. *Perception & Psychophysics*, *61*(2), 322–41. doi:10.3758/BF03206891

Nan, Y., Knösche, T. R., & Luo, Y.-J. (2006). Counting in everyday life: discrimination and enumeration. *Neuropsychologia*, *44*(7), 1103–13. doi:10.1016/j.neuropsychologia.2005.10.020

Nieder, A. (2005). Counting on neurons: the neurobiology of numerical competence. *Nature Reviews. Neuroscience*, *6*(3), 177–90. doi:10.1038/nrn1626

Nieder, A., & Dehaene, S. (2009). Representation of number in the brain. *Annual Review of Neuroscience*, *32*, 185–208. doi:10.1146/annurev.neuro.051508.135550

Nieder, A., & Miller, E. K. (2004). A parieto-frontal network for visual numerical information in the monkey. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(19), 7457–62. doi:10.1073/pnas.0402239101

Olivers, C. N. L., & Watson, D. G. (2008). Subitizing requires attention. *Visual Cognition*, *16*(4), 439–462. doi:10.1080/13506280701825861

Pagano, S., & Mazza, V. (2012). Individuation of multiple targets during visual enumeration: new insights from electrophysiology. *Neuropsychologia*, *50*(5), 754–61. doi:10.1016/j.neuropsychologia.2012.01.009

Pavese, A., & Umiltà, C. (1998). Symbolic distance between numerosity and identity modulates Stroop interference. *Journal of Experimental Psychology: Human Perception and Performance*, *24*(5), 1535–1545. doi:10.1037/0096-1523.24.5.1535

Piazza, M. (2010). Neurocognitive start-up tools for symbolic number representations. *Trends in Cognitive Sciences*, *14*(12), 542–51.

Piazza, M., Fumarola, A., Chinello, A., & Melcher, D. (2011). Subitizing reflects visuo-spatial object individuation capacity. *Cognition*, *121*(1), 147–53. doi:10.1016/j.cognition.2011.05.007

Piazza, M., & Izard, V. (2009). How humans count: numerosity and the parietal cortex. *The Neuroscientist*, *15*(3), 261–73. doi:10.1177/1073858409333073

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron*, *44*(3), 547–55. doi:10.1016/j.neuron.2004.10.014

Poiese, P., Spalek, T. M., & Di Lollo, V. (2008). Attentional involvement in subitizing: Questioning the preattentive hypothesis. *Visual Cognition*, *16*(4), 474–485. doi:10.1080/13506280801969676

Posner, M. I. (1994). Attention: The mechanisms of consciousness. *Proceedings of the National Academy of Sciences of the United States of America*, *91*, 7398–7403.

Posner, M. I., & Rothbart, M. K. (1998). Attention, self-regulation and consciousness. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *353*(1377), 1915–27. doi:10.1098/rstb.1998.0344

Prime, D. J., Pluchino, P., Eimer, M., Dell'Acqua, R., & Jolicoeur, P. (2011). Object-substitution masking modulates spatial attention deployment and the encoding of information in visual short-term memory: insights from occipito-parietal ERP components. *Psychophysiology*, *48*(5), 687–96. doi:10.1111/j.1469-8986.2010.01133.x

Pylyshyn, Z. W. (1989). The role of location indexes in spatial perception: a sketch of the FINST spatial-index model. *Cognition*, *32*(1), 65–97. doi:10.1016/0010-0277(89)90014-0

Pylyshyn, Z. W. (2001). Visual indexes, preconceptual objects, and situated vision. *Cognition*, *80*(1-2), 127–158. doi:10.1016/S0010-0277(00)00156-6

Pylyshyn, Z. W. (2004). Some puzzling findings in multiple object tracking: I. Tracking without keeping track of object identities. *Visual Cognition*, *11*(7), 801–822. doi:10.1080/13506280344000518

Railo, H., Koivisto, M., Revonsuo, A., & Hannula, M. M. (2008). The role of attention in subitizing. *Cognition*, *107*(1), 82–104. doi:10.1016/j.cognition.2007.08.004

Rensink, R. A. (2000). Seeing, Sensing, and Scrutinizing. *Vision Research*, *40*, 1469–1487.

Rensink, R. A. (2004). Visual Sensing Without Seeing. *Psychological Science*, *15*(1), 27–32. doi:10.1111/j.0963-7214.2004.01501005.x

Ritter, P., & Villringer, A. (2006). Simultaneous EEG-fMRI. *Neuroscience and Biobehavioral Reviews*, *30*(6), 823–838.

Robitaille, N., & Jolicoeur, P. (2006). Fundamental properties of the N2pc as an index of spatial attention: Effects of masking. *Canadian Journal of Experimental Psychology*, *60*(2), 101–111. doi:10.1037/cjep2006011

Robitaille, N., Marois, R., Todd, J. J., Grimault, S., Cheyne, D., & Jolicoeur, P. (2010). Distinguishing between lateralized and nonlateralized brain activity associated with visual short-term memory: fMRI, MEG, and EEG evidence from the same observers. *NeuroImage*, *53*(4), 1334–45. doi:10.1016/j.neuroimage.2010.07.027

Ross, J., & Burr, D. C. (2010). Vision senses number directly. *Journal of Vision*, *10*(2), 10.1–8. doi:10.1167/10.2.10

Sathian, K., Simon, T. J., Peterson, S., Patel, G. A., Hoffman, J. M., & Grafton, S. T. (1999). Neural evidence linking visual object enumeration and attention. *Journal of Cognitive Neuroscience*, *11*(1), 36–51.

Scholl, B. J., & Pylyshyn, Z. W. (1999). Tracking multiple items through occlusion: clues to visual objecthood. *Cognitive Psychology*, *38*(2), 259–90. doi:10.1006/cogp.1998.0698

Simons, D. J. (2000). Attentional capture and inattentional blindness. *Trends in Cognitive Sciences*, *4*(4), 147–155. doi:10.1016/S1364-6613(00)01455-8

Storm, R. W., & Pylyshyn, Z. W. (1988). Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spatial Vision*, *3*(3), 179–197. doi:10.1163/156856888X00122

Szucs, D., & Csépe, V. (2004). Similarities and differences in the coding of numerical and alphabetical order using acoustic stimulation as revealed by event-related potentials in humans. *Neuroscience Letters*, *360*(1-2), 65–8. doi:10.1016/j.neulet.2004.02.038

Telling, A. L., Kumar, S., Meyer, A. S., & Humphreys, G. W. (2010). Electrophysiological evidence of semantic interference in visual search. *Journal of Cognitive Neuroscience*, *22*(10), 2212–25. doi:10.1162/jocn.2009.21348

Temple, E., & Posner, M. I. (1998). Brain mechanisms of quantity are similar in 5-year-old children and adults. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(13), 7836–41.

Thioux, M., Pillon, A., Samson, D., de Partz, M.-P., Noël, M., & Seron, X. (1998). The Isolation of Numerals at the Semantic Level. *Neurocase*, *4*(4-5), 371–389. doi:10.1080/13554799808410633

Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature*, *381*(6582), 520–2. doi:10.1038/381520a0

Thut, G., & Miniussi, C. (2009). New insights into rhythmic brain activity from TMS-EEG studies. *Trends in Cognitive Sciences*, *13*(4), 182–9. doi:10.1016/j.tics.2009.01.004

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology, 12*(1), 97–136. doi:10.1016/0010-0285(80)90005-5

Trick, L. M. (2008). More than superstition: Differential effects of featural heterogeneity and change on subitizing and counting. *Perception & Psychophysics, 70*(5), 743–760. doi:10.3758/PP.70.5.743

Trick, L. M., & Enns, J. T. (1997). Measuring Preattentive Processes: When is Pop-out Not Enough? *Visual Cognition*, *4*(2), 163–198. doi:10.1080/713756754

Trick, L. M., & Pylyshyn, Z. W. (1993). What enumeration studies can show us about spatial attention: Evidence for limited capacity preattentive processing. *Journal of Experimental Psychology: Human Perception and Performance*, *19*(2), 331–351. doi:10.1037/0096-1523.19.2.331

Trick, L. M., & Pylyshyn, Z. W. (1994a). Why are small and large numbers enumerated differently? A limited-capacity preattentive stage in vision. *Psychological Review*, *101*(1), 80–102. doi:10.1037/0033-295X.101.1.80

Trick, L. M., & Pylyshyn, Z. W. (1994b). Cueing and counting: Does the position of the attentional focus affect enumeration? *Visual Cognition, 1*(1), 67–100. doi:10.1080/13506289408402294

Vetter, P., Butterworth, B., & Bahrami, B. (2008). Modulating attentional load affects numerosity estimation: evidence against a pre-attentive subitizing mechanism. *PloS one, 3*(9), e3269. doi:10.1371/journal.pone.0003269

Vetter, P., Butterworth, B., & Bahrami, B. (2011). A candidate for the attentional bottleneck: set-size specific modulation of the right TPJ during attentive enumeration. *Journal of Cognitive Neuroscience, 23*(3), 728–36. doi:10.1162/jocn.2010.21472

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*(6984), 748–51. doi:10.1038/nature02447

Walsh, V. (2003). A theory of magnitude: common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, *7*(11), 483–488. doi:10.1016/j.tics.2003.09.002

Whalen, P. J., Gallistel, C. R. R., & Gelman, R. (1999). Nonverbal Counting in Humans: The Psychophysics of Number Representation. *Psychological Science*, *10*(2), 130–137. doi:10.1111/1467-9280.00120

Woodman, G. F., Arita, J. T., & Luck, S. J. (2009). A cuing study of the N2pc component: an index of attentional deployment to objects rather than spatial locations. *Brain Research*, *1297*, 101–11. doi:10.1016/j.brainres.2009.08.011

Woodman, G. F., & Luck, S. J. (2003). Dissociations among attention, perception, and awareness during object-substitution masking. *Psychological Science*, *14*(6), 605–11. doi:10.1046/j.0956-7976.2003.psci_1472.x

Xu, Y. (2007). The role of the superior intraparietal sulcus in supporting visual short-term memory for multifeature objects. *The Journal of Neuroscience*, *27*(43), 11676–86. doi:10.1523/JNEUROSCI.3545-07.2007

Xu, Y. (2009). Distinctive neural mechanisms supporting visual object individuation and identification. *Journal of Cognitive Neuroscience*, *21*(3), 511–8. doi:10.1162/jocn.2008.21024

Xu, Y., & Chun, M. M. (2009). Selecting and perceiving multiple visual objects. *Trends in Cognitive Sciences*, *13*(4), 167–74. doi:10.1016/j.tics.2009.01.008

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