The Road to Success: Necessary and Unnecessary Visual Features in Parallel Individuation

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The Road to Success: Necessary and Unnecessary Visual Features in Parallel Individuation

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The Road to Success: Necessary and Unnecessary Visual Features in Parallel Individuation

Abstract

Each day, we interact with and make judgments about objects we see in the visual field. These interactions depend on the perceptual segmentation of figure from ground, and the subsequent processing of the segmented representations. In order to survive in our increasingly complex world, it is not enough to know what is object and what is background; we must be able to rapidly infer information about sets of objects, such as their identity, in what direction are they moving, and how many are there. Parallel individuation is the rapid selection of multiple targets for precise and rapid processing. One of the hallmarks of parallel individuation behavior is the ability to report the number of items in small sets with extreme speed and accuracy; this behavior is called 'subitizing'. Previous research has suggested that subitizing, and other tasks dependent on parallel individuation, rely on targets that are spatially separate from each other: objects rather than object parts. In this thesis, we explored what visual features, like connectivity, interfere with or are necessary for parallel individuation to occur. We first demonstrated that both connected and unconnected targets can be subitized. In order to ensure the same neural mechanism was responsible for the behavior observed in both stimulus conditions, we used functional magnetic resonance imaging to compare the neural responses to connected and unconnected stimuli. We targeted two regions in the parietal lobe, the inferior and superior intraparietal sulci, which have been previously associated with individuation and identification, respectively. Activity in both regions was modulated by the numerosity of targets in the connected and unconnected conditions. While multi-voxel pattern analyses revealed that the two regions additionally held representations of number, only the inferior IPS could discriminate connected from unconnected stimuli. We concluded from these results that individuation in the inferior IPS does not depend on spatially separate targets, but rather can flexibly select a level from the object hierarchy of a scene within which to define figure and ground. We then investigated the role of other visual features in parallel individuation, working from a condition of failure to pinpoint visual characteristics that are necessary for subitizing to occur. Resolving line ownership, providing unique centers of mass, and removing bounding enclosure information all did not prove sufficient for subitizing to occur in concentrically arranged squares. Changing the arrangement of the squares in space however did demonstrate that subitizing occurs over overlapping targets, with no effect of amount of overlap. Manipulating the presentation time of overlapping targets showed that parallel individuation can operate over both unresolved and completed amodal representations of a scene. We proposed that successful parallel individuation is dependent upon the constraints of three stages of processing: segmentation, individuation, and task specific demands. We suggest that the individuation stage is dependent upon each target occupying a unique location in space, occurring outside the border of all other targets. Finally we discussed the generalization of this model to other tasks involving parallel individuation.

Contents

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1

General Introduction

1.1 Introduction to object individuation

As humans interact with the world, we are constantly selecting different subsets of the visual field for further and more detailed processing. Many different visual processes depend on an ability to pick out information at a particular location in a scene. These include but are not limited to: the maintenance of identity across changes in viewpoint (Warrington, 1982) or perceptual conditions such as luminance and color (Kraft & Brainard, 1999; Marr, 1982), the ability to track objects through time and space (Scholl, Pylyshyn, & Feldman, 2001), or enumerate sets of items (Trick & Pylyshyn, 1994). While the objectives of each of these skills are quite varied, they all depend on the ability of the visual system to separate figure from ground and select either a subset or single unit of those figures. The segmentation of the visual world into meaningful units has been studied in many different contexts, but typically referred to as 'object individuation'.

Object individuation refers to a specific component of our dynamic experience with and processing of items in the world. As we scan a room looking for a particular item, object individuation has typically been defined as the selection of objects or units at a particular location; a separate step from the conscious awareness of the conceptual or featural knowledge associated with the item (object identification) (Leslie, Xu, Tremoulet, & Scholl, 1998). This distinction has been characterized as 'which' instead of 'what' (Kanwisher & Driver, 1992; Watson & Maylor, 2006) and is involved in the selection of items without knowledge of its properties, acting as a pointer or bridge to particular locations where attention can be allocated (Pylyshyn, 1989). Lesion and functional magnetic resonance imaging (fMRI) data also suggest that individuation and identification depend on and occur in different cortical space, again supporting their independent roles in visual processing (Mishkin, Ungerleider, & Macko, 1983; Xu & Chun, 2006; Xu, 2009).

One interesting aspect about the individuation of objects is that it seems to occur in parallel, but only for a limited number of items (Pylyshyn & Storm, 1988; Pylyshyn, 1989). These two ideas are demonstrated in several paradigms that are believed to involve individuation. One measure of individuation used in both infant and adult studies is performance on enumeration tasks. For infants, this takes the form of event monitoring or event mapping (Wilcox & Baillargeon, 1998; Xu & Carey, 1996), whereas accuracy and speed are measured in adults. The phenomenon 'subitizing' is observed in these two measures, where subjects rapidly and accurately enumerate small sets of objects without much cost for each additional item (Kaufman, Lord, Reese, & Volkmann, 1949; Trick & Pylyshyn, 1994). This manifests as a substantially smaller increase in RT and error rate between two consecutive numbers within the 'subitizing range' (1 to

~4) than the increase in RT and errors between consecutive numbers in the 'counting range' (about 5 +). This creates an 'elbow' in response functions where a sharp change in slope occurs at ~4 items, depending on the individual's subitizing range (Akin & Chase, 1978), and is believed to represent the limit of parallel individuation. The subjective experience of subitizing, immediately 'knowing' the answer, contrasts to that of counting, where attention is shifted in a serial fashion around the visual field, or that of estimation which shares the same speeded judgment as subitizing, but lacks the confidence and accuracy.

This subitizing range, or number of items individuated in parallel, is limited potentially by general cognitive limitations such as mapping constraints (Franconeri, Alvarez, & Cavanagh, 2013), or the number of internal representations available for assignment to different items in the visual field. These representations have been labeled 'Fingers of Instantiation' (Pylyshyn, 1989), indexes (Leslie et al., 1998), or object files (Kahneman, Treisman, & Gibbs, 1992) in the context of different theories.

1.2 One or two processes?

Within the context of enumeration, small set sizes are labeled as belonging to the subitizing range, whereas larger set sizes are binned into either a counting or estimation range depending on trial duration. While these categorizations are based on behavioral differences in reaction time or accuracy, not all researchers are convinced that subitizing performance is evidence of an individuation mechanism specific to small sets of items. One view is that the rapid enumeration of small sets is merely a result of highly accurate pattern matching (Mandler & Shebo, 1982); this theory has since been expanded to include the element of similarity, with the faster and more accurate responses for lower numbers reflecting the higher within-number similarity and between-number dissimilarity of the different display configurations for set sizes within the subitizing range as compared to large set sizes (Logan & Zbrodoff, 2003). Another single-process model suggests that subitization is merely the result of preverbal magnitude representations, where the judgment of magnitude has less variability the lower the number (Gallistel & Gelman, 1991). These types of theories are somewhat similar to pattern theories, as they reflect the higher similarity and confusability of consecutive larger numerosities than for smaller magnitudes. Ross (2003) investigated enumeration performance based on Weber fractions and noticed that when comparing magnitudes, the key to success was a difference of 25% or more. He suggested that this could predict the effortless discrimination of small numbers, since 2 is 100% more than 1, etc., and performance starts failing around 5 when 6 is only a 20% difference. Unfortunately, a limitation of Ross's 2003 study is that the stimuli consisted of sets of 8 items or more, making it difficult to draw conclusions about behavior in smaller set sizes.

Nonetheless, a significant amount of behavioral research supports separate processes underlying the enumeration of small (1-~4) and large sets (5+) of items. Revkin, Piazza, Izard, Cohen and Dahaene (2008) directly tested estimation in the lower range and found that performance does not respect Weber's law, supporting a two-system theory. One novel way the difference between the lower and higher set sizes has been studied is through the use of afterimages created by a flashgun (Simon & Vashnavi, 1996; Atkinson, Campbell, & Francis, 1976). When tested at multiple timepoints up to 60 seconds, performance remains highly accurate for 1-4 objects, while performance was poor for 5-7 objects. Even with the extended response time (60 s), performance within the counting range did not improve to match the level of that in the subitizing range. Simon and Vashnavi (1996) concluded that subitizing does not require eye movements to precipitate high performance, unlike numerosities in the counting range. Watson, Maylor, and Bruce (2007) also tested the role of eye movements in subitizing, and found that frequency of eye movements increased significantly after 4 items, and the restriction of eye movements did not decrease performance in the subitizing range.

Neural data have also been helpful in distinguishing subitizing as unique from counting or estimation. Estimation and subitizing were contrasted in a study using functional near-infrared spectroscopy (fNIRS), and the two resulted in unique hemodynamic patterns (Cutini, Scatturin, Basso Moro, & Zorzi, 2014). A magnetoencephalography (MEG) study found distinct areas and temporal peaks for the enumeration of sets within the subitizing and counting ranges (Vuokko, Niemivirta, & Helenius, 2013). Furthermore, different lesion sites are associated with deficits in subitizing and counting (Demeyere, Rotshtein, & Humphreys, 2012).

Recent work using electrophysical (EEG) measures has also supported a limited capacity individuation mechanism by comparing the responses of target and overall numerosity. The numerosity of stimuli without distracters modulated a negative evoked potential occurring around 150 ms after presentation (N1), whereas a separate posterior-contralateral component occurring around 200 ms after stimulus onset (N2pc) was modulated with target numerosity regardless of distracter presence, plateauing at 3 items (Ester, Drew, Klee, Vogel, & Awh, 2012; Mazza & Caramazza, 2011; Mazza, Pagano, & Caramazza, 2013). This N2pc component's modulation is correlated with individual behavioral limits (Pagano & Mazza, 2012; Pagano, Lombardi, & Mazza, 2014) and is believed to relate to the precise individuation of items for further processing.

1.3 Theories of individuation

Several theories have been proposed describing the process of parallel individuation. One of the most popular is the 'FINST' theory, named after the 'Fingers of INSTantiation' (now referred to as indices) that point out items, or individuate them, for further processing (Pylyshyn, 1989). This theory suggests that distinctive items in the visual field are selected preattentively and assigned to a limited number (~4) of indices. These indices have no knowledge of the item's identity or features, but mark the location for further processing by attention. Once an index has been assigned, it will maintain its assignment even throughout the motion (Pylyshyn & Storm, 1988) or occlusion (Scholl & Pylyshyn, 1999) of its target.

The FINST theory does not directly compete with the object file theory, but rather complements it. Object files are a nondescript representation of an item at a particular location, where attention can then be allocated and bind feature or identity information to that item's 'file' (Khaneman et al., 1992). While the object file theory makes explicit that it operates over 'objects', objects can be defined at a variety of levels of attentional selection (Feldman, 2003). Like the FINST theory, there are a limited number of object files, that can update their information of perceptual characteristics or location as the object moves or changes. Within this context, the FINST index can be viewed as the object file before any featural information has been recorded.

More recently, a theory of object indexing similar to both the FINST and object file theories has been proposed, linking adult behavior to that of infants (Leslie et al., 1998). They propose that in development, indices are initially assigned only when they occupy spatially separate locations at the same time (Spelke, Kestenbaum, Simons, & Wein, 1995). Only later at 12 months of age do infants start individuating objects based on their features, such as shape or color (Van de Walle, Carey, & Prevor, 2000; Xu, Carey, & Welch, 1999). If we assume that the individuation mechanism in infants is the same as that in adults, then we may also need to speculate that the number of indices available, or the capacity limitations change throughout development as studies of infant individuation normally include or show success with only one to two objects (Carey & Xu, 2001), instead of the ~3-5 typical of adult individuation.

One behavioral study supports the idea set forth in these three theories that individuation is maintained and not affected by featural changes. Subjects were asked to enumerate objects that either flickered on and off over a very short time, or changed in both their color and shape for their second appearance in the flicker. Within small sets (1-3 items) subject reaction times did not significantly differ between conditions where the items changed their shape and color, or maintained their original properties (Trick, 2008).

There has been some skepticism about the nature of the capacity limit described in the previous theories. While the FINST, object-file, and object indexing theories all suggest a fixed number of representations, be they pointers, object-files, or indices, a somewhat contrasting theory suggest that there are a flexible number of indices. The FLEX, or 'FLexibly allocated indEX', model suggests that rather than 4 indices or slots, there is a flexible resource that can be allocated to a variable number of items depending on the magnitude of the demands of each item (Alvarez & Franconeri, 2007). By manipulating the speed of objects in a multiple-object tracking task, they demonstrated that the number of targets successfully tracked could vary from 1 object at a very high speed, and 8 at a very low speed. According to this account the limitations on individuation, or tracking in this particular example, are due to the resolution of attention needed at a particular speed, with either more space or more of the limited attentional resource required between targets moving at faster speeds (Alvarez & Franconeri, 2007; Shim, Alvarez, & Jiang, 2008). Subsequent research suggests that the key limitation is the spacing between items, and not the speed itself, as increased speeds tend to increase the crowding of the objects in the visual field (Franconeri, Lin, Pylyshyn, Fisher, & Enns, 2008; Franconeri, Jonathan, & Scimeca, 2010). This spacing constraint is believed to be due to the competition for cortical space on a 2D neural map of space in the visual field (Franconeri et al., 2013).

Each model discussed here deviates slightly from the others. The FINST model specifies pre-attentive selection of distinctive items (Pylyshyn, 1989), while Leslie et al. (1998) state that the items must be spatially distinct objects. The FLEX account focuses on the attentional quality of the mechanism, and also challenges the idea that there are a set number of representations available for assignment (Alvarez & Franconeri, 2007). However, all theories agree that there is a limit to the number of representations, regardless of whether it is imposed by resource or mapping constraints (Alvarez & Franconeri, 2007; Franconeri et al., 2013), or the number of available indices (Pylyshyn, 1989; Kahneman et al., 1992; Leslie et al., 1998).

It is important to note that we have discussed evidence from both enumeration and multiple object tracking tasks. Here we are making the assumption that the same individuation mechanism underlies performance in both tasks. We will discuss whether this assumption is founded in the context of the findings of this thesis in the conclusion.

1.4 Units of individuation

When thinking about how a parallel individuation mechanism might function, it becomes important to think about over what types of stimuli subitizing does or does not occur. The FINST theory originally did not marry itself to a particular type of stimulus that could be individuated, outside of the fact that it has to be distinguishable from the background (Pylyshyn, 1989). However, later studies seem to have narrowed the space down to the indices operating over separate objects (Trick & Pylyshyn, 1994). In a multiple-object tracking paradigm, Scholl et al. (2001) asked subjects to track boxes among a set of distracters. They varied the perceived and actual connectivity of square boxes to investigate whether the 'unit' of attention could be part of an object, and found that subjects showed successful tracking performance only when the target and distracting ends were perceived as being spatially separate. This suggests that objects must be spatially distinct in order for individuation to occur.

The individuation mechanism seems to maintain its representations even through occlusion in multiple-object tracking (Pylyshyn & Storm, 1988; Scholl & Pylyshyn, 1999), however, stimuli moving like substances cannot be tracked due to the ambiguity of their location (vanMarle & Scholl, 2003). Akin and Chase (1978) investigated the effects of partial occlusion on rapid enumeration, and showed that subjects could subitize line drawings of cubes that were stacked and arranged in different three-dimensional formations. A confound existed in their study however where only for 4 items or greater could a configuration exist with complete occlusion of one of the targets. As a consequence, it is possible that their finding of a subitizing limit of 3 items was biased based on smaller set sizes including dimensions without occlusion. It will be important to further investigate how occlusion affects subitizing using two-dimensional stimuli that don't provide such a disadvantage for larger configurations before concluding that subitizing occurs within the context of occlusion.

Parallel individuation also does not occur over features as entities separate from the object to which they belong. When subjects were asked to enumerate the number of different colors or orientations in a display consisting of more objects than unique features, they could only successfully subitize the feature set when all objects of the same color or orientation were grouped into a location distinct from the other feature groups; subitizing was not evident when the colors or orientations were mixed (Watson, Maylor, & Bruce, 2005). Thus it seems that items grouped by feature similarity (Watson et al., 2005), or proximity (Trick & Enns, 1997) can be enumerated in parallel, but features themselves cannot. Another case where parallel individuation seems to fail is when enumerating concentrically drawn squares (Trick & Pylyshyn, 1994). The authors suggest that this may be due to the incorrect grouping of parallel edges together due to their proximity, instead of grouping the edges into coherent shapes. However, the exact stimulus characteristic responsible for this result is still unknown.

1.5 Proposed contributions

While much has been researched and discovered about the process of visual segmentation, many aspects of individuation need to be solidified. One of the most nagging questions relates to the ambiguity surrounding the type of visual stimulus that can be individuated. While multiple-object tracking and subitizing data have trended toward individuation occurring over objects (Scholl et al., 2001; Watson et al., 2005), objecthood and location are still conflated in the literature. Object features or parts can be spatially distinct in that a cup handle, or two handles on a child's cup, can exist in different locations while being part of the same object. Is objecthood critical to parallel individuation? Or is it sufficient that items, either parts or whole objects, occupy distinct *locations* in space?

The importance of location has been emphasized in both theories that support a fixed number of indices (Leslie et al., 1998), as well as the cortical map account (Franconeri et al., 2013). Mulitiple-object tracking fails when the location of an object is ambiguous due to its substance-like quality (vanMarle & Scholl, 2003), indicating that location is critical for individuation. However, objecthood and location have not yet been disentangled, with the exception possibly of the aforementioned experiment.

We may also see the importance of location if we consider the conditions under which the individuation mechanism fails. The features color and orientation do not intrinsically hold their own space without a shape boundary, yet once unique locations for each feature were established through grouping, subitizing performance was observed (Watson et al., 2005). The concentric squares existed within the space that the outermost object established, making all inner squares hold a non-unique location (Trick & Pylyshyn, 1994). Furthermore, while each end of the stimulus in Scholl et al. (2001) did hold its own location, the connectivity of the ends may have created the perception of a single entity, and the independent motion of each end may have created a percept that was more similar to a substance than that of a rigid object, making the location of the target more ambiguous. Across these experiments, a pattern seems to emerge where when the target items do not occupy a clear, unique, location in space, individuation fails. Connectivity is an interesting stimulus characteristic within this context because it allows for parts of a single object to still maintain their own locations, in contrast to features like color or orientation. If the individuation mechanism does not require objecthood as a necessary condition but instead can function over connected parts of the same object, like the handles on a cup, then we would expect to see parallel individuation of object parts.

Understanding when parallel individuation can and cannot occur and over which visual features will help create a more accurate description of how such a mechanism functions. This is the question driving the current thesis. For the first part of this thesis, we directly tested whether parallel individuation occurs over the individual elements that make up a connected group, or object, and contrasted this to the behavior of displays containing multiple unconnected objects. Since the field of vision does not have a singular clear definition of what an 'object' is (Cavanagh, 2011), we will use the term 'object' to refer to items that are grouped through connectivity, and sets of items that are spatially separate will be referred to as ungrouped by connectivity or 'multiple objects'. As mentioned previously, Akin and Chase (1978) investigated the subitizing of adjacent elements, however we strove to remove all cues for adjacency or occlusion, and maintained stimuli that were perceived as a single grouped element. Davis & Holmes (2005) also investigated the enumeration of colored ends of bars, contrasting when the target ends occurred on the same or separate objects. However in their study they only tested the numerosities 3 and 4, and so could not state with conviction that their results reflected different behavior for the subitizing and counting ranges, only that they observed slight differences in stimulus conditions. Our results from this section will determine whether or not parallel individuation can occur over parts of a single object, or in other words, targets grouped by connectivity.

The second part of this thesis explores whether grouped and ungrouped stimuli are individuated similarly by the same mechanism. To do this we will target regions in the parietal lobe that have previously been implicated in individuation (Xu & Chun, 2006), and contrast the neural responses for connected and unconnected targets. While there have been investigations using fMRI studying the individuation of small sets of unconnected items (Cuitini et al., 2014; Xu & Chun, 2006; Xu, 2009) as well as the processing of connected and unconnected objects (Xu & Chun, 2007), the two manipulations have not been combined until now. How the brain processes the number of connected vs. unconnected targets will provide a novel contribution into how individuation of small sets of items occurs.

Finally, we propose to shed light onto what characteristics of visual stimuli are necessary for individuation to occur. As we discussed previously, the confines and definition of the space of features that can be individuated has not been fully flushed out in the literature. Here we propose to take several steps forward in clarifying what requirements exist for parallel individuation by manipulating both the visual properties of a particular stimulus as well as identifying effects of different presentation durations. The stimulus condition that we will manipulate is the case of concentric square stimuli, which has been demonstrated to show similar increases in reaction time for each additional item in both the subitizing and counting ranges (Trick & Pylyshyn, 1994). This work has the possibility to impact the state of knowledge of any process that requires parsing of the visual field into units.

2

Visual object individuation occurs over object wholes, parts, and even holes [1]

2.1 Abstract

Segmentation of the world into meaningful units has typically been described as *object* individuation, emphasizing the spatially disconnected quality that comes as a result of objecthood. This segmentation can occur rapidly, even in parallel for multiple objects. It remains unclear whether objecthood is a necessary requirement for parallel individuation, or whether target *features* in distinct locations, such as object parts, may

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[1] A version of this work appears in Porter, K. B., Mazza, V., Garofalo, A., & Caramazza, A. (2016). Visual object individuation occurs over object wholes, parts, and even holes. *Attention, Perception, & Psychophysics, 78*(4), 1145-1162, reproduced with permission from The Psychonomic Society, Inc. The final publication is available at Springer via http://dx.doi.org/10.3758/s13414-016-1064-0

also be individuated in parallel. In a series of six experiments, we used a rapid enumeration task to test whether subitizing, a phenomenon believed to result from parallel individuation, occurs over object parts. We found that subitizing and individuation occur over connected object parts as well as physically separate objects of varied shapes and sizes. We also observed subitizing when target items are indents, features intrinsic to the shape of the object, and when cues for occlusion were removed. The results of these studies suggest that parallel individuation is not bound to objecthood, and can occur over object parts existing in separate locations.

2.2 Introduction

The human mind is remarkable; it has the ability to track objects through time and space (Scholl, Pylyshyn, & Feldman, 2001), enumerate sets of items (Trick & Pylyshyn, 1994), calculate the frequency of events (Brase, Cosmides, & Tooby, 1998), and recognize objects while maintaining their identity under variable perceptual conditions (Kraft & Brainard, 1999; Marr, 1982). While the objectives of each of these skills are quite varied, they all share a commonality: they depend on a mechanism that separates figure from ground and parses the visual field into separate entities. The question remains – what are those entities? In most circumstances, this visual segmentation and selection is referred to as individuation, and the nebulous term "object" fills in the blank for "of what?"

Parallel individuation is often measured by performance on an enumeration task. This takes the form of accuracy and speed when measured in adults. The phenomenon "subitizing" is observed in these two measures, where subjects rapidly and accurately enumerate small sets of physically separate objects without much cost for each additional item, seemingly individuating the items in parallel (Kaufman, Lord, Reese, & Volkmann, 1949; Trick & Pylyshyn, 1994). This manifests as a substantially smaller increase in reaction time (RT) and error rate between two consecutive numbers within the "subitizing range" (1 to ~4) than the increase in RT and errors between consecutive numbers in the "counting range" (about 5 +). This creates an "elbow" in response functions where a sharp change in slope occurs at ~4 items, depending on the individual's subitizing range (Akin & Chase, 1978).

Several theories exist as to why there seems to be a processing advantage for small sets of numbers. One view is that the rapid enumeration of small sets is merely a result of highly accurate pattern matching (Mandler & Shebo, 1982; Palomares & Egeth, 2010); this theory has since been expanded to include the element of similarity, with the faster and more accurate responses for lower numbers reflecting the higher within-number similarity and between-number dissimilarity of the different display configurations for set sizes within the subitizing range as compared to large set sizes (Logan & Zbrodoff, 2003).

While the studies described above tend to characterize subitization as a processing advantage due to discriminability or pattern matching, several other theories suggest that a separate mechanism exists for selecting and processing small sets of items. One of the most pervasive is the "FINST" theory, named after the "Fingers of INSTantiation," or indices, that point out or individuate items for further processing (Pylyshyn, 1989). This theory suggests that distinctive items in the visual field are selected preattentively and assigned to a limited number (~4) of indices. These indices have no knowledge of the item's identity or features, but mark the location for further processing by attention. Once an index has been assigned, it will maintain its assignment even throughout the motion (Pylyshyn & Storm, 1988) or occlusion (Scholl & Pylyshyn, 1999) of its target. While the FINST theory originated from studies of multiple object tracking (MOT), subitizing is believed to draw upon the same individuation resource as MOT. Simultaneous MOT and enumeration reflects a shared limit across the two tasks of about four items (Chesney & Haladjian, 2011). Furthermore, both subitizing (Railo, 2014) and MOT (Alvarez & Cavanagh, 2005) demonstrate a bilateral presentation advantage. Both of these findings support the view of a shared parallel individuation mechanism across the two tasks.

To better understand the mechanism underlying parallel individuation, it is important to consider under what conditions individuation can occur. Humans are capable of object individuation early in development (Spelke, Kestenbaum, Simons, & Wein, 1995), and in this context, the definition of "object" is given as "...unitary, bounded, and persisting objects...operating in accord with the principles of cohesion, boundedness, rigidity, and no action at a distance" (Spelke, 1990). Spatiotemporal information (Spelke et al., 1995) and connectivity seem to be the primary cues infants use to individuate objects through 10 months of age (Xu, Carey, & Welch, 1999), and not until they are 12 months old do they start using object kind or featural information to individuate items (Van de Walle, Carey, & Prevor, 2000). At 3 years of age, children seem predisposed to consider disconnected objects as the basic unit for numerosity judgments, even when the task instructions specifically ask for the number of kinds or features (Shipley & Shepperson, 1990). However, a subsequent study determined that 3-year-olds can in fact individuate and count whole objects, parts, and holes (Giralt & Bloom, 2000). This literature suggests that throughout development infants gain the ability to individuate items based on an increasing number of levels of specificity, from discrete objects based on spatiotemporal and connectivity at a few months of age, to the ability to individuate parts of a single object at 3 years. The question remains, however, do whole physically separated objects maintain a special status throughout adulthood as they do in early infancy? The experiments discussed above do not allow us to discriminate between serial or parallel processing; thus the question remains, can adults individuate connected object parts in parallel?

Objects and object parts can be discriminated based on connectivity; the effect of connectivity on individuation has been studied in both MOT and estimation paradigms. In MOT, when target stimuli are perceived as connected to a distracting element, performance is significantly worse than when compared to tracking of spatially disconnected targets (Scholl, Pylyshyn, & Feldman, 2001). The exception in Scholl et al. (2001) was a condition where the target and distractors were connected by lines that criss-crossed in a random fashion – resulting in the perception of two items connected by a substance. Substances cannot be efficiently tracked (vanMarle & Scholl, 2003). Thus connectivity seems to interfere with object tracking except for when the connecting element is one that cannot be tracked, and as such allows for the isolated individuation of one part of the stimulus. Franconeri, Bemis, and Alvarez (2009) found that adding task irrelevant connecting lines between target shapes caused subjects to underestimate the number of targets, suggesting that estimation relies on representations of distinct unconnected objects. A convergent study suggested that connectivity affects the initial individuation of targets to be estimated, rather than influencing the subsequent magnitude judgment (He, Zhang, Zhou, & Chen, 2009). If estimation relies on the same individuation mechanism as observed in subitizing, we would expect that in a rapid enumeration paradigm subjects would underestimate and thus perform poorly when enumerating object parts.

While connectivity has not been thoroughly tested in the context of rapid enumeration, previous work suggests that subitizing seems to occur over spatially separate, disconnected objects, and not features (Trick & Pylyshyn, 1994; Watson & Maylor, 2006). Parallel individuation does not function over features such as color or orientation, unless the items are grouped into distinct locations (Watson Maylor, & Bruce, 2005). While featural information does not seem to be a minimum requirement for object individuation, and distinct locations are emphasized as important in theories that take into account the developmental trend of individuation ability (Leslie et al., 1998) as well as in MOT (vanMarle & Scholl, 2003), location and "objecthood" remain conflated within the context of subitizing. Object features or parts can be spatially distinct in that a cup handle, or two handles on a child's cup, can exist in different locations while being part of the same object. Is objecthood critical to parallel individuation? Or is it sufficient that items, either connected parts or whole physically separate objects, occupy distinct locations in space?

Using the subitizing phenomenon to measure parallel individuation, we explored whether subjects showed evidence of a subitizing "elbow" when enumerating object features, such as object parts. In Experiment 1, we tested whether subitization occurs over protrusions on a single circle. We then added irregularity to the protrusions in Experiment 2 to test the generalization of individuation over different shapes. To reduce the possibility that the parts were viewed as overlapping physically separated objects, we decreased the separability of the protrusions in Experiment 3, and removed any t-junction occlusion cue that might aid individuation in Experiment 4. We tested the performance of subjects with limited presentation time in Experiment 5 by measuring error rate. Lastly, in Experiment 6, we used line stimuli to eliminate any perception of occlusion in our single-object displays. If the individuation mechanism that allows for the simultaneous selection of things-out-there functions over distinct locations without requiring "objecthood," we would expect to see subitization of stimulus parts.

For each experiment, we aimed for 12 to 17 participants, based on a required sample size estimate of 12, computed for a difference between paired means using G*Power software (Faul, Erdfelder, Lang, & Buchner, 2007) with $\alpha = .05$, and power set to .8. Given the prevalence of the subitizing effect in the literature, we expected a large effect, and chose an effect size of 0.8 according to Cohen's effect size index (Cohen, 1988). Variability in the sample size of each experiment reflects the variability of available subjects in the subject pool.

2.3 Experiment 1: Single-object spike protrusions and multi-object displays

2.3.1 Introduction

In Experiment 1, we tested whether individuation functions over connected stimulus parts, as well as over physically separate objects. To do this, we asked participants to perform an enumeration task for both protrusions and objects.

2.3.2 Method

Participants

Fourteen Harvard University students participated for compensation of either US$8 or course credit. All participants provided informed consent, as approved by the Committee on the Use of Human Subjects in Research at Harvard University. All participants were debriefed about the purpose of the study and supplied with supplemental reading after completion of the experiment.

Stimuli

Displays consisted of two types of stimuli: (1) *multi-object* displays consisting of 1–8 physically separate objects as typically used in subitizing tasks, and (2) *single-object displays* consisting of a single object with 1–8 connected target features to be enumerated. Stimuli were created in Adobe Illustrator. Single-object displays consisted of black target shapes overlapping a black circle. The central circle was selected pseudorandomly from two sizes for each display to avoid the overall area correlating directly with the number of protruding shapes. The target shapes or features were selected from two sizes of spikes. Multi-object displays consisted of spatially separate black dots, positioned at the locations corresponding to the ends of the spikes in the test displays to match for location and eccentricity. Four different variants of a display were created for each stimulus type and number. Stimuli were presented against a gray background. All subjects performed the experiment on the same computer and in the same testing room. Visual stimuli subtended a maximum of 14° visual angle, and were presented using Matlab with the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997).

Procedure

Subjects received instructions to report the number of circles or spikes they saw on the screen as quickly and as accurately as possible. Subjects were asked to state their response out loud while pressing the space bar to record their reaction time (Watson et al., 2005). This ensured they would not use an alternate strategy that might bias their response times, such as reliance on after-images. After indicating their response verbally and via space bar press, subjects recorded their response via the number keys on the keyboard. In written and verbal instructions, we avoided using terminology such as "counting" to avoid biasing the subjects' enumeration strategy and instead asked subjects to report "how many" target items were present.

Subjects completed a practice round consisting of two blocks, each consisting of 32 presentations of one display type (multi-object or single-object). The practice round was followed by the full-length experiment consisting of 160 presentations per block (4 variants x 5 presentations x 8 numerosities). Each block contained displays of the same display type, and the order of the blocks was counterbalanced across subjects. The order of the displays within a block was determined pseudorandomly, constrained such that no two identical displays were presented in succession. Each trial consisted of: 1 s fixation, display presentation for 4 s or until the participant pressed the space bar indicating a response, fixation until number key pressed (only possible answers accepted), and 1 s blank. Every 40 trials, the participants were given the option to take a self-timed break before continuing.

Analyses

Incorrect trials, as well as trials more than two standard deviations from each subject's mean correct response reaction time for each numerosity, were removed from analysis (average: 9.4 % of trials). For all subjects, trials for the highest numerosity were discarded to avoid end effects (Trick & Pylyshyn, 1993).

First we tested for the presence of a subitizing elbow in each display type by comparing the reaction time slopes in the subitizing range and the counting range for each individual. The location of the split between the counting and subitizing ranges was determined using a piecewise linear model from the R library SiZer (Sonderegger, 2012). This models two lines and outputs the slopes and break point between the two lines that best fit the data (see Ester, Drew, Klee, Vogel, & Awh, 2012; Pagano, Lombardi, & Mazza, 2014 for similar analyses). The differences in slopes between individual best-fit counting and subitizing ranges for each display type were entered into one-tailed paired t-tests; the expectation was that compared to the subitizing range the counting slope would be greater, and the difference therefore significantly positive. For these one-tailed paired t-tests we report two-tailed 90 % confidence intervals (CIs) in our results tables, as the lower bound of a two-tailed 90 % CI is mathematically equivalent to a single-tailed 95 % CI.

To ensure that a bilinear model actually best reflected the trends in our data, we compared the adjusted R^2 from the piecewise linear model to the adjusted R^2 of an exponential model (see Balakrishnan & Ashby, 1991) using a two-tailed paired t-test. The modeling was performed following the method of Pagano, Lombardi, & Mazza (2014). The piecewise linear modeling was performed using the R library SiZer (Sonderegger, 2012), and the exponential modeling was performed with a customized R script, derived from the Nelder-Mead optimization algorithm (Nelder & Mead, 1965), that allowed two free parameters to be estimated for each subject: RT = βe^{an} or error = β^{an} depending on dependent measure of interest, where e is the base of the natural logarithm, n is set numerosity, and the two estimated parameters are a and β.

To compare trends in performance across the two display types, we tested the difference between slopes for each of the counting and subitizing ranges with two-tailed paired t-tests. We also tested the difference in subitizing ranges (break points) between the two display types with two-tailed paired t-tests.

For all tests, we calculated two effect sizes: Cohen's d for a paired design ($d = \frac{M_{diff}}{s_{av}}$), and an unbiased estimate of Cohen's d ($d_{unb} = (1 - \frac{3}{4df-1})\ x\ d$) (Cummings, 2012).

2.3.3 Results

We first tested for evidence of subitization by comparing slopes between the counting and subitizing ranges (see Table 2.1 for all Experiment 1 statistics.) We observed the subitizing elbow, represented by significantly higher counting slopes than subitizing slopes, in both the multi-object and the single-object displays. The mean difference in slopes for both conditions had large effect sizes greater than 2. We also tested that a bilinear model, demonstrating the presence of subitizing in the lower numerosities and lack of subitizing in higher numerosities, would best fit the data. While both the bilinear (multi-object: mean adjusted $R^2 = .99$, single-object: mean adjusted $R^2 = .98$) and exponential (multi-object: mean adjusted $R^2 = .89$, single-object: mean adjusted $R^2 = .91$) models fit the data fairly well, a statistical comparison showed that the bilinear model better accounted for the data observed with effect sizes over 1 for both display types.

Table 2.1: Statistical results testing the presence of subitizing and effects of display type. For the one-tailed t-tests examining the presence of a subitizing elbow, we report a two-tailed 90 % CI. For all other tests we report a 95 % CI. See analyses of Experiment 1 for more details. d-unb = d-unbiased, as calculated from Cohen's-d

Statistical results from Experiment 1								
	df	T-value	p-value	Mean Difference	SD	CI	Cohen's D	d-unb
Presence of Subitizing:								
Subitizing Elbow: Difference in slope (Counting-Subitizing)						*90 % CI*		
Multi-Object	13	6.56	<.001	309.44 ms	176.40	[225.95, 392.93]	2.87	2.71
Single-Object	13	7.00	<.001	226.34 ms	120.98	[169.08, 283.60]	2.33	2.20
Best Fit Model: Bilinear-Exponential R2-adjusted						*95% CI*		
Multi-Object	13	2.89	.013	0.10	0.13	[0.02, 0.17]	1.08	1.01
Single-Object	13	3.71	.003	0.07	0.07	[0.03, 0.11]	1.30	1.23
Effects of Display Type:								
Difference in subitizing range (multi-object – single-object)						*95% CI*		
Subitizing Range	13	0.69	>.250	0.17 items	0.93	[-0.37, 0.71]	0.18	0.17
Difference in slope (multi-object – single-object)						*95% CI*		
Subitizing	13	-2.11	.055	-28.81 ms	51.06	[-58.30, 0.67]	-0.69	-0.65
Counting	13	1.48	.164	54.29 ms	137.64	[-25.18, 133.76]	0.39	0.37

We then investigated the effects of display type on performance. The average best-fit subitizing range for the single-object displays was 3.68 spikes, and 3.85 circles for the multi-object displays. There was no significant difference and a small effect size for the mean difference in subitizing range across the two display types. There was also no significant difference in slope across display types for either the subitizing range or the counting range. See Table 2.2 for slopes for each condition, and Figure 2.1 for RT and error rates.

Table 2.2: Average individual slopes for the subitizing and counting ranges as determined by the bilinear model. For Experiments 1–4 and Experiment 6, the slope reflects the increase in RT in ms for each additional item enumerated. For Experiment 5, the slope reflects the increase in error rate for each additional item enumerated. RT = reaction time, MO = multi-object display, SO = single-object display

Average individual subitizing and counting slopes		
	Subitizing	Counting
Measure of interest: RT		
Exp 1 MO: Circles	9.4 ms	318.8 ms
Exp 1 SO: Spikes	38.2 ms	264.6 ms
Exp 2 MO: Shapes	28.0 ms	270.2 ms
Exp 2 SO: Protrusions	36.6 ms	237.5 ms
Exp 3 SO: Outdents	42.4 ms	290.4 ms
Exp 3 SO: Indents	55.7 ms	312.2 ms
Exp 4 MO: Shapes	5.3 ms	305.3 ms
Exp 4 SO: Protrusions	50.3 ms	234.9 ms
Measure of interest: Error Rate		
Exp 5 MO: Shapes	1.4 %	16.0 %
Exp 5 SO: Protrusions	1.5 %	19.3 %
Measure of interest: RT		
Exp 6 MO: Outline Shapes	13.3 ms	246.0 ms
Exp 6 SO: Outline Protrusions	55.0 ms	268.3 ms

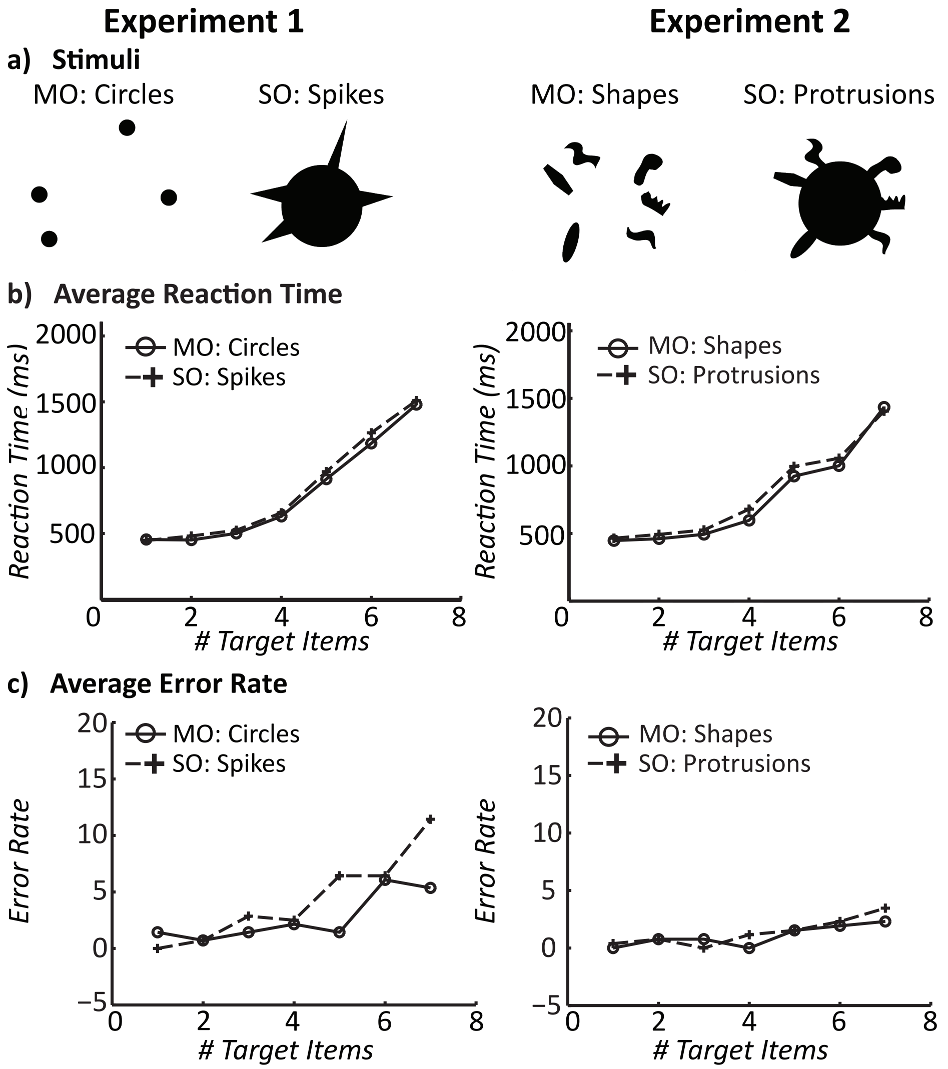

Figure 2.1: Stimuli, average reaction times and error rates for Experiments 1 and 2. Results for Experiments 1 and 2 showing (a) example stimuli, (b) average reaction times, and (c) average error rates. Average reaction time data is reflected in milliseconds, and average error rates are reflected in percent. MO = multi-object display, SO = single-object display

2.3.4 Discussion

These results demonstrate that subitizing occurs over object parts, such as spikes on a circle.

2.4 Experiment 2: Single-object varied protrusions and multi-object displays

2.4.1 Introduction

To control for the possibility that the single feature "spikiness" could be easily selected and used to aid individuation, we varied the shapes of the protrusions.

2.4.2 Method

Participants

Thirteen Harvard University students participated for compensation of either US$8 or course credit. All participants provided informed consent, as approved by the Committee on the Use of Human Subjects in Research at Harvard University. All participants were debriefed about the purpose of the study and supplied with supplemental reading after completion of the experiment.

Stimuli

In this experiment, we varied the shape of the single-object features ("protrusions") to control for the possibility that a single feature such as spikiness can aid selection early in processing, in contrast to the curvature of the central object (Figure 2.1). The stimuli were thus created in the same manner as Experiment 1, with the exception that the target shapes were selected from ten shapes of varied form. Multi-object displays were created by removing the central circle and slightly rotating the protruding shapes to avoid the percept of a circular illusory contour. Four different variants of a display were created for each stimulus type and number. Visual stimuli subtended a maximum of 11.5° visual angle. Presentation of the stimuli was identical to Experiment 1.

PROCEDURE

The same procedure was used as in Experiment 1, except subjects were now instructed to report the number of *shapes* or *protrusions* they saw on the screen as quickly and accurately as possible.

ANALYSES

The same data trimming procedure (average: 7.2 % of trials) and analyses were used as in Experiment 1.

2.4.3 RESULTS

We first tested for evidence of subitizing by comparing slopes between the counting and subitizing ranges (see Table 2.3 for all Experiment 2 statistics). We observed the subitizing elbow, represented by significantly higher counting slopes than subitizing slopes, in both the multi-object and single-object displays. The mean difference in slopes for both conditions had large effect sizes greater than 2.5. We also tested that a bilinear model, demonstrating the presence of subitizing in the lower numerosities and lack of subitizing in higher numerosities, would best fit the data. While both the bilinear (multi-object: mean adjusted $R^2 = .95$, single-object: mean adjusted $R^2 = .94$) and exponential (multi-object: mean adjusted R^2 = .90, single-object: mean adjusted R^2 = .90) models fit the data fairly well, a statistical comparison showed that the bilinear model better accounted for the data observed with effect sizes over 1 for both display types.

We then investigated the effects of display type on performance. The average best-fit subitizing range for the single-object displays was 3.74 protrusions, and 3.88 shapes for the multi-object displays. There was no significant difference and a small effect size for the mean difference in subitizing range across the two display types. There was also no significant difference in slope across display types for either the subitizing range or the counting range (see Table 2.2 for slopes for each condition, and Figure 2.1 for reaction time and error rates).

Table 2.3: Statistical results testing the presence of subitizing and effects of display type. 'd-unb' stands for d-unbiased, as calculated from Cohen's-d. For the one-tailed t-tests examining the presence of a subitizing elbow, we report a two-tailed 90% confidence interval. For all other tests we report a 95% confidence interval. See analyses of Experiment 1 for more details.

Statistical results from Experiment 2								
	df	T-value	p-value	Mean Difference	SD	CI	Cohen's D	d-unb
Presence of Subitizing:								
Subitizing Elbow: Difference in slope (Counting-Subitizing)						*90 % CI*		
Multi-Object	12	7.73	<.001	242.25 ms	112.95	[186.42, 298.08]	2.76	2.59
Single-Object	12	8.95	<.001	200.88 ms	80.91	[160.88, 240.87]	2.97	2.78
Best Fit Model: Bilinear-Exponential R2-adjusted						*95% CI*		
Multi-Object	12	2.83	.015	0.05	0.07	[0.01, 0.09]	1.29	1.21
Single-Object	12	4.90	< .001	0.04	0.03	[0.02, 0.06]	1.31	1.22
Effects of Display Type:								
Difference in subitizing range (multi-object – single-object)						*95% CI*		
Subitizing Range	12	0.50	> .250	0.14 items	1.02	[-0.47, 0.76]	0.14	0.13
Difference in slope (multi-object – single-object)						*95% CI*		
Subitizing	12	-1.04	> .250	-8.64 ms	29.87	[-26.70, 9.41]	-0.31	-0.29
Counting	12	1.16	> .250	32.73 ms	102.15	[-29.00, 94.46]	0.31	0.29

2.4.4 Discussion

Despite the varied shapes of the protrusions, we observed subitization in both display types. This suggests the behavior observed does not result from one simple feature ("spikiness") aiding selection of the object parts.

2.5 Experiment 3: Single-object indent and outdent displays

2.5.1 Introduction

To explore whether the previous data resulted from participants viewing the parts as separable objects occluding the central circle, we decreased the separability of the parts in two single-object displays. We reduced the size of the protrusions in "outdent" displays, and created features intrinsic to the object in "indent" displays.

2.5.2 Method

Participants

Twelve Harvard University students participated for compensation of either US$8 or course credit. All participants provided informed consent, as approved by the Committee on the Use of Human Subjects in Research at Harvard University. All participants were debriefed about the purpose of the study and supplied with supplemental reading after completion of the experiment.

Stimuli

Two types of single-object displays were created to reduce the possibility of participants viewing the parts as separable objects occluding the central circle (Figure 2.2).

The displays consisted of black circles overlapped with either black semicircle "outdents" that were smaller and more difficult to separate from the central stimuli, or gray semicircle "indents" intrinsic to the central object and the same color as the background. The locations of the single-object display target features were generated randomly for each stimulus and each participant, constrained such that no two features could overlap. The stimuli subtended a maximum of 7.5° visual angle and were created in Matlab using the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner et al, 2007; Pelli, 1997).

Procedure

The same procedure as in Experiment 1 was used, with the exception of a change in instruction and experiment length. Subjects were asked to report how many indents or outdents were in each display, and each block consisted of 240 trials (30 variants x 8 numerosities). Since participants could have still viewed the indent condition as small physically separate objects overlapping the larger circle we controlled for this confound by asking each participant after the experiment how they perceived the indent condition. They were provided with the following options with verbal descriptions and example drawings: (a) bites out of a cookie, (b) half moons overlapping a circle, (c) small circles overlapping a large circle, or (d) other.

Analyses

The same analyses were performed as in Experiments 1 and 2. The average percent of trials removed in trimming per numerosity was 6.6 %.

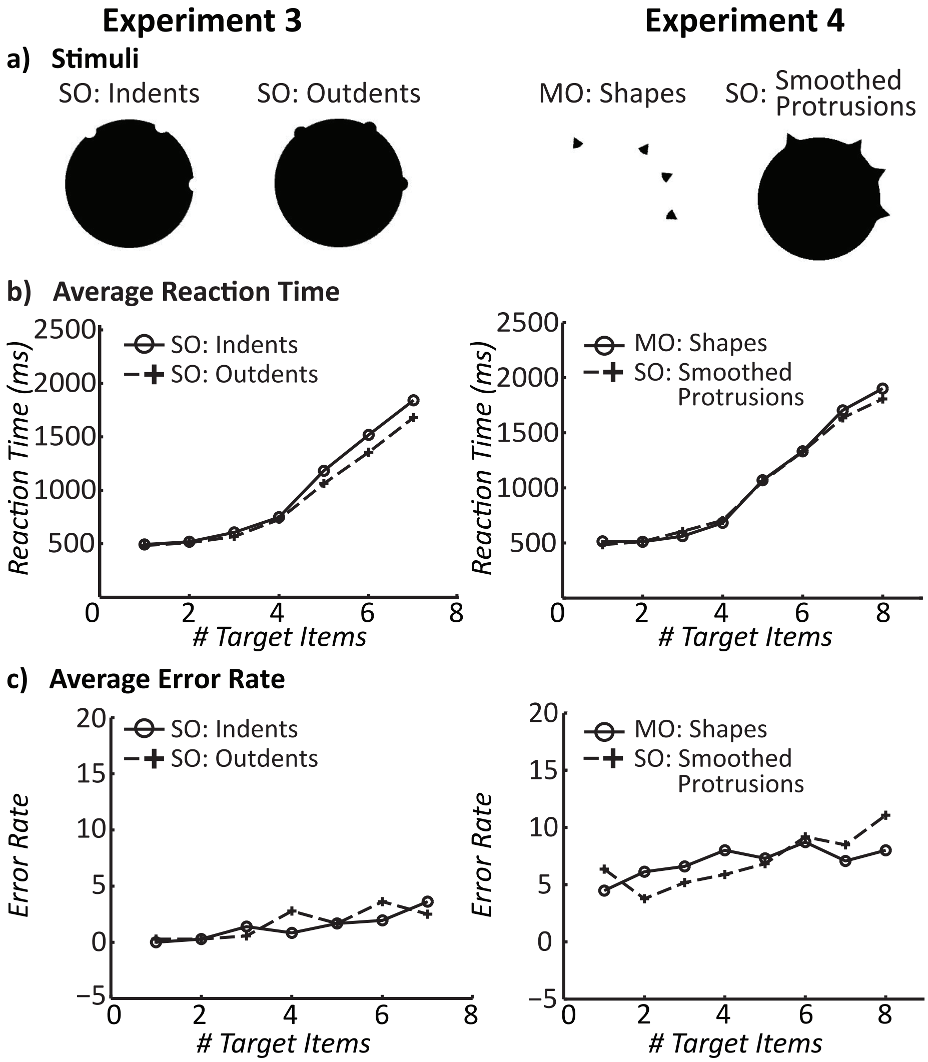

Figure 2.2: Stimuli, average reaction times and error rates for Experiments 3 and 4. Results for Experiments 3 and 4 showing (a) example stimuli, (b) average reaction times, and (c) average error rates. Average reaction time data is reflected in milliseconds, and average error rates are reflected in percent. MO = multi-object display, SO = single-object display

2.5.3 RESULTS

We first tested for evidence of subitizing by comparing slopes between the counting and subitizing ranges (see Table 2.4 for all Experiment 3 statistics). We observed the subitizing elbow, represented by significantly higher counting slopes than subitizing slopes, in both variants of the single-object displays (indents and outdents). The mean difference in slopes for both conditions had large effect sizes greater than 2. As in Experiments 1 and 2, both the bilinear (indent: mean adjusted $R^2 = .98$, outdent: mean adjusted $R^2 = .99$) and exponential (indent: mean adjusted $R^2 = .94$, outdent: mean adjusted $R^2 = .95$) models fit the data well. However, the bilinear model better accounted for the data observed for both testing conditions, with effect sizes greater than 1 for both display types.

Table 2.4: Statistical results testing the presence of subitizing and effects of display type. 'd-unb' stands for d-unbiased, as calculated from Cohen's-d. For the one-tailed t-tests examining the presence of a subitizing elbow, we report a two-tailed 90% confidence interval. For all other tests we report a 95% confidence interval. See analyses of Experiment 1 for more details.

Statistical results from Experiment 3								
	df	T-value	p-value	Mean Difference	SD	CI	Cohen's D	d-unb
Presence of Subitizing:								
Subitizing Elbow: Difference in slope (Counting-Subitizing)						*90 % CI*		
Indent	11	6.74	< .001	256.47 ms	113.87	[188.10, 324.83]	2.57	2.39
Outdent	11	9.62	< .001	247.92 ms	89.24	[201.65, 294.18]	4.04	3.76
Best Fit Model: Bilinear-Exponential R2-adjusted						*95% CI*		
Indent	11	5.07	< .001	0.04	0.03	[0.02, 0.06]	1.61	1.50
Outdent	11	5.30	< .001	0.04	0.02	[0.02, 0.05]	1.57	1.46
Effects of Display Type:								
Difference in subitizing range (multi-object – single-object)						*95% CI*		
Subitizing Range	11	-0.58	> .250	-0.08 items	0.46	[-0.37, 0.22]	-0.12	-0.11
Difference in slope (multi-object – single-object)						*95% CI*		
Subitizing	11	1.25	.239	13.25 ms	36.86	[-10.17, 36.67]	0.50	0.46
Counting	11	1.00	> .250	21.80 ms	75.67	[-26.27, 69.88]	0.19	0.18

We then investigated the effects of display type on performance. The average best-fit subitizing range for each display type was 3.67 outdents, and 3.59 indents. There was no significant difference and a small effect size for the mean difference in subitizing range across the two display types. There was also no significant difference in slope across display types for either the subitizing range or the counting range. See Table 2.2 for slopes for each condition, and Figure 2.2 for reaction time and error rates.

In response to our poll about how participants viewed the indent condition, 8 of the 12 participants responded "bites out of a cookie" or "valleys." One participant was contacted via email 6 days after completing the task, and did not view the drawings. However, the participant responded with an unprompted vivid description, so it seems the drawings were not needed in that case. To test whether the four participants who perceived the indents as separable objects affected the results, we carried out the analyses using only the eight subjects who perceived the indents as "bites." No difference was observed in the results.

2.5.4 Discussion

Subitization occurred for both indents and outdents, suggesting that the individuation mechanism can function over stimuli difficult to separate, or intrinsic to, the central object.

2.6 Experiment 4: Single-object smoothed protrusions and multi-object displays

2.6.1 Introduction

While Experiment 3 decreased the separability of the object parts, it did not eliminate possible cues for occlusion. The presence of t-junctions along a contour is a major cue when determining whether an image is one object or multiple objects with partial occlusion (Rubin, 2001). Here, we created protrusions with smoothed contours to eliminate this cue.

2.6.2 METHOD

PARTICIPANTS

Nineteen Harvard University students participated for compensation of either US$8 or course credit. All participants provided informed consent, as approved by the Committee on the Use of Human Subjects in Research at Harvard University. All participants were debriefed about the purpose of the study and supplied with supplemental reading after completion of the experiment. Two participants were excluded for poor task performance with more than 30 % of trials from multiple numerosities removed according to the trimming procedure described in the method for Experiment 1.

STIMULI

In order to avoid participants viewing the single-object displays as partially occluding shapes, we removed any t-junctions from the stimuli. Single-object displays consisted of a black circle with overlapping arcs, and the junctions between the arcs and the central circle were smoothed to form a continuous contour. Multi-object displays consisted of the arcs with the central circle removed (Figure 2.2). The locations of the single-object display target features were generated randomly for each stimulus and each participant, constrained such that no two features could overlap. The arc orientation in the multi-object displays was randomly selected from a set of angles (-20°, -10°, 0°, +10°, +20°) to avoid the illusory percept of a circle. Visual stimuli subtended a maximum of 9° visual angle, and were presented in the same manner as Experiment 3.

PROCEDURE

The same procedure as in Experiment 1 was used, with the exception of a change in instruction and experiment length. Subjects were asked to report how many protrusions or shapes were in each display, and each block consisted of 215 trials (25 variants x 8 numerosities, 15 variants x 9th numerosity).

ANALYSES

The same analyses were performed as in Experiments 1 and 2. The average percent of trials removed in trimming per numerosity was 13.5 %.

2.6.3 RESULTS

We observed the subitizing elbow, represented by significantly higher counting slopes than subitizing slopes, in both the multi-object and the single-object displays (see Table 2.5). The mean difference in slopes for both conditions had large effect sizes greater than 2.5. We also tested that a bilinear model, demonstrating the presence of subitizing in the lower numerosities and lack of subitizing in higher numerosities, would best fit the data. While both the bilinear (multi-object: mean adjusted $R^2 = .97$, single-object: mean adjusted $R^2 = .96$) and exponential (multi-object: mean adjusted $R^2 = .93$, single-object: mean adjusted $R^2 = .92$) models fit the data fairly well, a statistical comparison showed that the bilinear model better accounted for the data observed with a large effect size for the multi-object displays. The bilinear model also showed statistically better performance for single-object displays, but with a small effect size.

Table 2.5: Statistical results testing the presence of subitizing and effects of display type. 'd-unb' stands for d-unbiased, as calculated from Cohen's-d. For the one-tailed t-tests examining the presence of a subitizing elbow, we report a two-tailed 90% confidence interval. For all other tests we report a 95% confidence interval. See analyses of Experiment 1 for more details.

Statistical results from Experiment 4								
	df	T-value	p-value	Mean Difference	SD	CI	Cohen's D	d-unb
Presence of Subitizing:								
Subitizing Elbow: Difference in slope (Counting-Subitizing)						*90 % CI*		
Multi-Object	16	10.84	< .001	299.94 ms	114.13	[251.62, 348.27]	4.25	4.05
Single-Object	16	7.47	< .001	184.61 ms	101.90	[141.46, 227.75]	2.93	2.79
Best Fit Model: Bilinear-Exponential R2-adjusted						*95% CI*		
Multi-Object	16	9.66	< .001	0.04	0.02	[0.03, 0.05]	1.29	1.23
Single-Object	16	6.89	< .001	0.03	0.02	[0.02, 0.04]	0.47	0.45
Effects of Display Type:								
Difference in subitizing range (multi-object – single-object)						*95% CI*		
Subitizing Range	16	-1.10	>.250	-0.22 items	0.81	[-0.63, 0.20]	-0.28	-0.26
Difference in slope (multi-object – single-object)						*95% CI*		
Subitizing	16	-2.82	.012	-44.99 ms	65.82	[-78.83, -11.15]	-1.03	-0.98
Counting	16	3.53	.003	70.35 ms	82.18	[28.10, 112.60]	0.84	0.80

We then investigated the effects of display type on performance. The average best-fit subitizing range for the single-object displays was 3.58 smoothed protrusions, and 3.37 shapes for the multi-object displays. There was no significant difference and a small effect size for the mean difference in subitizing range across the two display types. The difference in slopes across display types was significant in both the subitizing range and the counting range. See Table 2.2 for slopes for each condition, and Figure 2.2 for reaction time and error rates.

2.6.4 Discussion

To remove occlusion cues from the stimuli, we smoothed the junctions between the central object and the protrusions. While there were significant differences in slope across display types, the presence of a bilinear elbow supports subitizing in both cases. While these results support parallel individuation of both stimulus types, it is possible that the differences in slope observed reflect a less efficient individuation of the smoothed protrusions than the shapes. Nonetheless, these data together with Experiment 3 suggest the participants did not view the protrusions as physically separate objects, but instead can individuate object parts without visual cues supporting separability.

2.7 Experiment 5: Speeded presentation of single-object and multi-object displays

2.7.1 Introduction

The long presentation in previous experiments allowed subjects to accurately count the higher numerosities. To test for subitizing under more pressured conditions, we forced estimation by limiting the presentation time to 200 ms.

2.7.2 Method

Participants

Thirteen Harvard University students participated for compensation of either US$8 or course credit. One participant was removed from analysis for accuracy below 80 % for all numerosities. All participants provided informed consent, as approved by the Committee on the Use of Human Subjects in Research at Harvard University. All participants were debriefed about the purpose of the study and supplied with supplemental reading after completion of the experiment.

STIMULI

The same stimuli as described in Experiment 4 were used.

PROCEDURE

The same procedure was used as in Experiment 4, except instructions only emphasized accuracy and not speed since the presentation time of the stimuli was fixed at 200 ms. Subjects recorded how many items they believed were in each display via keypress after each stimulus presentation. Each block consisted of 250 trials (30 variants x 8 numerosities, 10 variants x 9th numerosity).

ANALYSES

The analyses performed were the same as described in Experiment 1, with one exception: instead of testing for the presence of a subitizing elbow in reaction times, we compared slopes and subitizing ranges for the error rates of each display type. [2]

2.7.3 RESULTS

We first tested for evidence of subitization by comparing error rate slopes between the counting and subitizing ranges (see Table 2.6 for all Experiment 5 statistics). We observed the subitizing elbow, represented by significantly higher counting slopes than subitizing slopes, in both the multi-object and the single-object displays. The mean

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[2] While analyzing error rates is typical in the subitizing literature, in the case of short presentation times we can also investigate differences in display type based on underestimation in average responses. We saw no underestimation or differences in average responses across conditions until the counting range, which is consistent with our findings in Table 2.6 investigating effects of display type. See Appendix Figure A.1 for graph.

difference in slopes for both conditions had large effect sizes greater than 1. We also tested that a bilinear model, demonstrating the presence of subitizing in the lower numerosities and lack of subitizing in higher numerosities, would best fit the data. While the bilinear model fit the data moderately well for the multiple object displays (mean adjusted $R^2 = .76$) and quite well for the single object displays (mean adjusted $R^2 = .93$) the exponential model performed moderately worse across both display types (multi-object: mean adjusted $R^2 = .67$, single-object: mean adjusted $R^2 = .88$). A statistical comparison showed that the bilinear model better accounted for the data observed with effect sizes over .3 for both display types.

Table 2.6: Statistical results testing the presence of subitizing and effects of display type. 'd-unb' stands for d-unbiased, as calculated from Cohen's-d. For the one-tailed t-tests examining the presence of a subitizing elbow, we report a two-tailed 90% confidence interval. For all other tests we report a 95% confidence interval. See analyses of Experiment 1 for more details.

Statistical results from Experiment 5								
	df	T-value	p-value	Mean Difference	SD	CI	Cohen's D	d-unb
Presence of Subitizing:								
Subitizing Elbow: Difference in slope (Counting-Subitizing)						*90 % CI*		
Multi-Object	11	3.54	.002	14.60 % err.	16.19	[7.18, 22.02]	1.45	1.35
Single-Object	11	5.48	< .001	17.72 % err.	11.70	[11.91, 23.53]	2.1	1.96
Best Fit Model: Bilinear-Exponential R2-adjusted						*95% CI*		
Multi-Object	11	4.01	.002	0.09	0.25	[0.04, 0.13]	0.38	0.36
Single-Object	11	6.71	< .001	0.05	0.14	[0.04, 0.07]	0.64	.59
Effects of Display Type:								
Difference in subitizing range (multi-object – single-object)						*95% CI*		
Subitizing Range	11	0.75	.469	0.28 items	1.09	[-0.55, 1.12]	0.22	0.20
Difference in slope (multi-object – single-object)						*95% CI*		
Subitizing	11	-0.23	> .250	0.15 % err.	2.07	[-1.54, 1.25]	-0.07	-0.07
Counting	11	-0.96	> .250	-3.27 % err.	13.70	[-10.75, 4.21]	-0.25	-0.23

We then investigated the effects of display type on performance. The average best-fit subitizing range for the single-object displays was 5.18 spikes, and 5.47 circles for the multi-object displays. There was no significant difference and a small effect size for the mean difference in subitizing range across the two display types. There was also no significant difference in slope across display types for either the subitizing range or the

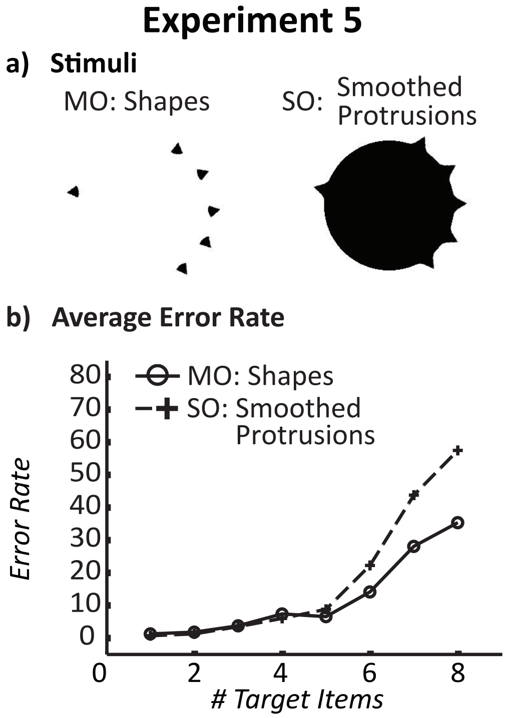


Figure 2.3: Stimuli, average error rates for Experiment 5. The results for Experiment 5 are reflected here with (a) example stimuli, and (b) average error rates. Average error rates are reflected in percent. MO = multi-object display, SO = single-object display

counting range. See Table 2.2 for slopes for each condition, and Figure 2.3 for plotted error rates.

2.7.4 Discussion

We explored subitization performance when presentation time was limited so high accuracy for large numerosities was impossible. We saw evidence of subitizing in error rates for both display types, without significant differences in slopes or subitizing range across types. Interestingly, the subitizing ranges for both display types were larger than those observed in the previous experiments, which may result from participants performing at ceiling for the lower numerosities.

2.8 EXPERIMENT 6: SINGLE-OBJECT AND MULTI-OBJECT OUTLINE DISPLAYS

2.8.1 INTRODUCTION

To eliminate any perception of the protruding targets in our single-object display as multiple objects occluding a central circle, we performed an additional experiment using line stimuli. (See Figure 2.4)

2.8.2 METHOD

PARTICIPANTS

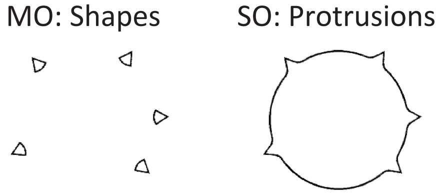
Twelve Harvard University students participated for compensation of either US$8 or course credit. All participants provided informed consent, as approved by the Committee on the Use of Human Subjects in Research at Harvard University. All participants were debriefed about the purpose of the study and supplied with supplemental reading after completion of the experiment.

STIMULI

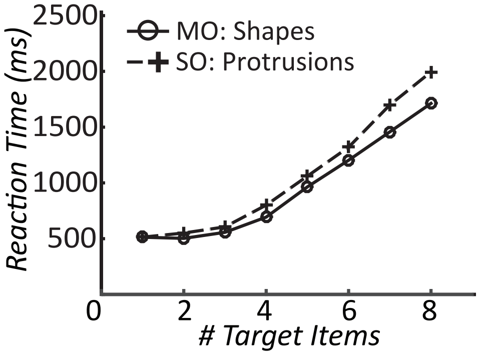
Single-object displays consisted of a black outline of a circle with protruding arcs. Multi-object displays consisted of outline arcs (Figure 2.4). The locations of the single-object display target features were generated randomly for each stimulus and each participant, constrained such that no two features could overlap. The arc orientation in the multi-object displays was randomly selected from a set of angles (-20°, -10°, 0°,

Experiment 6

a) Stimuli



b) Average Reaction Time



c) Average Error Rate

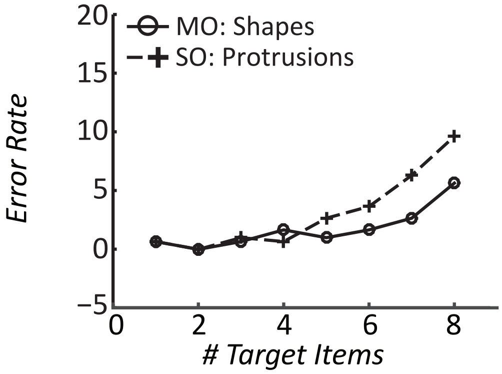


Figure 2.4: Stimuli, average reaction times and error rates for Experiment 6. Results for Experiment 6 showing (a) example stimuli, (b) average reaction times, and (c) average error rates. Average reaction time data is reflected in milliseconds, and average error rates are reflected in percent. MO = multi-object display, SO = single-object display

+10°, +20°) to avoid the illusory percept of a circle. Visual stimuli subtended a maximum of 9° visual angle, and were presented in the same manner as Experiment 3.

PROCEDURE

The same procedure as in Experiment 1 was used, with the exception of a change in instruction and experiment length. Subjects were asked to report how many protrusions or shapes were in each display, and each block consisted of 225 trials (25 variants x 9 numerosities).

ANALYSES

The same analyses were performed as in Experiments 1 and 2. The average percent of trials removed in trimming per numerosity was 7.9 %.

2.8.3 RESULTS

We observed the subitizing elbow, represented by significantly higher counting slopes than subitizing slopes, in both the multi-object and the single-object displays (see Table 2.7 for Experiment 6 statistics). The mean difference in slopes for both conditions had large effect sizes greater than 3. We also tested that a bilinear model, demonstrating the presence of subitizing in the lower numerosities and lack of subitizing in higher numerosities, would best fit the data. While both the bilinear (multi-object: mean adjusted $R^2 = .99$, single-object: mean adjusted $R^2 = .98$) and exponential (multi-object: mean adjusted $R^2 = .95$, single object: mean adjusted $R^2 = .96$) models fit the data well, a statistical comparison showed that the bilinear model better accounted for the data observed with a large effect size for both display types.

Table 2.7: Statistical results testing the presence of subitizing and effects of display type. 'd-unb' stands for d-unbiased, as calculated from Cohen's-d. For the one-tailed t-tests examining the presence of a subitizing elbow, we report a two-tailed 90% confidence interval. For all other tests we report a 95% confidence interval. See analyses of Experiment 1 for more details.

Statistical results from Experiment 6

	df	T-value	p-value	Mean Difference	SD	CI	Cohen's D	d-unb
Presence of Subitizing:								
Subitizing Elbow: Difference in slope (Counting-Subitizing)						*90 % CI*		
Multi-Object	11	7.10	< .001	232.71 ms	121.56	[173.84, 291.57]	3.37	3.14
Single-Object	11	11.27	< .001	213.22 ms	82.95	[179.24, 247.19]	3.95	3.68
Best Fit Model: Bilinear-Exponential R2-adjusted						*95% CI*		
Multi-Object	11	6.45	< .001	0.03	0.02	[0.02, 0.04]	1.92	1.78
Single-Object	11	5.14	< .001	0.02	0.02	[0.01, 0.03]	1.66	1.54
Effects of Display Type:								
Difference in subitizing range (multi-object – single-object)						*95% CI*		
Subitizing Range	11	-0.97	>.250	-0.31 items	1.10	[-1.01, 0.39]	-0.39	-0.36
Difference in slope (multi-object – single-object)						*95% CI*		
Subitizing	11	-2.28	.044	-41.75 ms	59.49	[-82.12, -1.39]	-0.93	-0.87
Counting	11	-1.01	>.250	-22.26 ms	70.83	[-71.01, 26.49]	-0.30	-0.28

We then investigated the effects of display type on performance. The average best-fit subitizing range for the single-object displays was 3.48 smoothed protrusions, and 3.79 shapes for the multi-object displays. There was no significant difference and a small effect size for the mean difference in subitizing range across the two display types. The difference in slopes across display types was significant in the subitizing range only. See Table 2.2 for slopes for each condition, and Figure 2.4 for reaction time and error rates.

2.8.4 DISCUSSION

We created these outline stimuli to avoid any percept of our single-object condition as multiple objects occluding a central circle. While there was a significant difference in subitizing slope across display types, the presence of a bilinear elbow supports subitizing in both cases. These data together with Experiments 3 and 4 suggest the participants did not view the protrusions as physically separate objects, but instead can individuate connected object parts.

2.9 SECONDARY ANALYSES

We performed two sets of post-hoc secondary analyses, to further investigate our data.

2.9.1 SECONDARY ANALYSIS 1: SECONDARY MEASURES

We performed a 2 x 7 repeated measures ANOVA (stimulus type x number) to investigate any effects present in the secondary measures of each experiment (Table 2.8). For experiments measuring reaction time as the measure of interest (Experiments 1–4 and 6), error rates were analyzed as the secondary measure, and vice versa for Experiment 5 which measured error rate as the primary measure. We consider these measures to be secondary, since the experimental paradigm of each experiment focused on variability of one measure. In experiments focused on reaction time, subjects were instructed to respond as quickly and accurately as possible, resulting in error rates at or close to ceiling. In Experiment 5, stimulus presentation time was limited to force errors, and subjects were allowed to respond at their own pace. This limits the amount of information available in the reaction time data.

Table 2.8: Statistical results of a 2x7 repeated measures ANOVA performed over the secondary measures of each experiment. A Greenhouse-Geisser correction was applied when conditions of sphericity were not met.

Secondary Analysis 1			
	df	F	p-value
Experiment 1: Circles | Spikes (Error Rate)			
Stimulus Type	(1,13)	2.94	.11
Numerosity	(1.68,21.79)	5.29	.017
Stimulus Type x Number	(1.88,24.40)	1.77	.193
Experiment 2: Shapes | Protrusions (Error Rate)			
Stimulus Type	(1,12)	.526	>.250
Numerosity	(2.71,32.53)	3.64	.026
Stimulus Type x Number	(3.03,36.32)	.598	>.250
Experiment 3: Outdents | Indents (Error Rate)			
Stimulus Type	(1,11)	.306	>.250
Numerosity	(2.60,28.55)	3.73	.027
Stimulus Type x Number	(2.80,30.77)	1.13	>.250
Experiment 4: Shapes | Protrusions (Error Rate)			
Stimulus Type	(1,16)	.34	>.250
Numerosity	(2.94,47.0)	3.53	.022
Stimulus Type x Number	(7,112)	2.72	.012
Experiment 5: Shapes | Protrusions (Reaction Time)			
Stimulus Type	(1,11)	122.70	<.001
Numerosity	(1.37,15.12)	1.64	.225
Stimulus Type x Number	(7,77)	1.91	.080
Experiment 6: Outline Shapes | Protrusions (Error Rate)			
Stimulus Type	(1,11)	2.31	.157
Numerosity	(1.66,18.20)	5.87	.014
Stimulus Type x Number	(2.11,23.22)	1.52	.239

Discussion

Overall, the results for Experiments 1–4 and 6 indicate a decrease in accuracy for the larger numerosities, although the accuracy was quite high for all numerosities and experiments. This is in line with previous studies showing that enumeration in the subitizing range is characterized by highly fast and accurate performance, whereas counting tends to be slower and more difficult (Trick & Pylyshyn, 1994). Experiment 4 also showed a moderate interaction between stimulus type and number, although there was no significant effect of stimulus type. Experiment 5 only showed a main effect of stimulus type. This suggests that subjects tended to respond at different paces for the two stimulus types, although this is hard to interpret since the subjects were under no time explicit pressure when entering their responses.

2.9.2 Secondary Analysis 2: Effects of slope and stimulus type

We performed a 2 x 2 repeated-measures ANOVA to investigate potential interactions between stimulus type and the slope within each numerosity range (subitizing, counting) using 2 x 2 ANOVAs (Table 2.9).

Table 2.9: Results of a 2x2 Repeated measures ANOVA, with stimulus type and slope of the two ranges (subitizing, counting) as factors. A Greenhouse-Geisser correction was applied when conditions of sphericity were not met.

Secondary Analysis 2			
	df	F	p-value
Experiment 1: Circles | Spikes (Reaction Time)			
Stimulus Type	(1,13)	.376	>.250
Number Range	(1,13)	55.39	<.001
Stimulus Type x Range	(1,13)	5.10	.042
Experiment 2: Shapes | Protrusions (Reaction Time)			
Stimulus Type	(1,12)	.686	>.250
Number Range	(1,12)	94.75	<.001
Stimulus Type x Range	(1,12)	1.91	.192
Experiment 3: Outdents | Indents (Reaction Time)			
Stimulus Type	(1,11)	1.99	.186
Number Range	(1,11)	69.48	<.001
Stimulus Type x Range	(1,11)	.130	>.250
Experiment 4: Shapes | Protrusions (Reaction Time)			
Stimulus Type	(1,16)	4.49	.050
Number Range	(1,16)	147.39	<.001
Stimulus Type x Range	(1,16)	11.46	.004
Experiment 5: Shapes | Protrusions (Error Rate)			
Stimulus Type	(1,11)	.965	>.250
Number Range	(1,11)	24.15	<.001
Stimulus Type x Range	(1,11)	.824	>.250
Experiment 6: Outline Shapes | Protrusions (Reaction Time)			
Stimulus Type	(1,11)	7.09	.022
Number Range	(1,11)	111.17	<.001
Stimulus Type x Range	(1,11)	.353	>.250

Discussion

As expected, we observed significant main effects of number range in all experiments, reflecting different slopes in the subitizing and counting ranges. In Experiments 4 and 6 there was a significant effect of stimulus type, indicating different slopes across stimulus types. The ANOVA in Experiments 1 and 4 also indicated a significant interaction, suggesting that the stimulus types can have differential effects on the slope of the subitizing and counting ranges. However, stimuli were different in both the multi-object and single-object conditions; a more pointed investigation of the effects of protrusion or stimulus type on individuation is needed to interpret these results.

2.10 General discussion

Studies of individuation have typically focused on *object* individuation. While most theories of object individuation agree that items must occupy separable locations in order to be indexed (Leslie et al., 1998), it is unclear whether objecthood and parallel individuation are exclusively linked, or whether individuation can function over other categories of stimulus properties. In Experiment 1 we showed that subitization occurs over object parts that are connected to a central circle. In Experiment 2 we added irregularity to the protrusions to ensure participants did not use a single feature such as spikiness to facilitate selection. In Experiment 3 we explored whether subjects used a strategy that allowed them to visualize the protrusions as objects disconnected from the central circle. To do this, we decreased the separability of the features and added slight indents or outdents to the circle. To further ensure that subjects did not perceive the stimuli as partially occluding shapes, in Experiment 4 we removed the t-junction occlusion cue, and still observed subitization. We conclude that even when targets are perceived as parts of a whole object, subjects can individuate and enumerate the targets using the same strategy as with distinct objects. The subitization of indents in Experiment 3 is particularly interesting, as most subjects saw them as contour discontinuities and not occluding shapes. This indicates that object features do not have to appear detachable to observe subitizing behavior and for the individuation mechanism to function. We also investigated the performance of subjects when confronted with a limited presentation time in Experiment 5, and observed error rates consistent with subitization and parallel individuation for both connected object parts and physically separate objects.

One potential argument with our conclusion that parallel individuation occurs over connected object parts is that it is difficult to state unequivocally that the subjects perceived the protrusions and holes as parts of a single entity. While the majority of subjects reported seeing the target holes in Experiment 3 single-object condition as features of a single object, some perceived the targets as objects occluding the central circle. To remove the possibility that the results discussed here were a result of subjects perceiving the stimuli as many small shapes occluding a central distractor circle, we ran an experiment using line stimuli (Figure 2.4). Since the targets in the single-object condition were merely deformations of a single contour, it would be very difficult for the subjects to perceive the targets as occluding a central shape. The results of Experiment 6 show evidence of subitizing and parallel individuation for the single-object and multi-object outline stimuli, and support our conclusion that parallel individuation can occur over connected object parts.

Importantly our results suggest that the connectivity in our single-object stimuli does not eliminate the subitizing effect. This is in contrast to previous studies where connectivity interfered with estimation (Franconeri, Bemis, & Alvarez, 2009; He et al.,

2009) or multiple object tracking performance (Scholl et al., 2001). However, subitizing differs from estimation in both quantitative range and accuracy, and neural data suggests that separate mechanisms underlie the two processes (Cutini, Scatturin, Basso Moro, & Zorzi, 2014), suggesting that connectivity may have a different impact on exact enumeration and estimation. Our results may differ from those from the MOT literature (Scholl et al., 2001) due to different task requirements. Connectivity may compete with or influence processing demands that occur later than individuation and may not be crucial for a simple enumeration task, such as the maintenance of representations over time or through space or ignoring of distractors.

While connectivity may not interfere with individuation in the case of our single-object stimuli, connectivity plays an important role in the parsing and selection of items in the visual field. Connectivity is a strong cue when segmenting the visual field into units, and has been proposed as the cue resulting in the initial organization of visual field, after which other grouping or parsing can occur (Palmer & Rock, 1994). This theory has since garnered support, with segmentation of units based on uniform connectedness (Palmer & Rock, 1994) occurring faster than grouping by similarity, and as fast as grouping by proximity (Han, Humphreys, & Chen, 1999). Connectivity also has shown to be a very important cue with regards to perception and how attention is allocated, as evidenced by Balint's syndrome. Merely adding a connecting line between two shapes allows patients to perform a task comparing features of the shapes, which was otherwise impossible (Humphreys & Riddoch, 1993, p. 158). For these reasons we believe that our finding that parallel individuation does occur over connected object parts is not trivial, and is somewhat unexpected given the interference present in other tasks (Franconeri, Bemis, & Alvarez, 2009; He et al., 2009; Scholl et al., 2001).

While we successfully showed that objecthood, as defined by lack of connectivity, is not a necessary requirement for individuation, we still do not have a precise definition of the limitations on the segmentation process. The target items in our stimuli all occupied non-overlapping locations in space, however the exact influence of crowding or overlap on the subitization process is still relatively unknown. Atkinson, Campbell, and Francis (1976) found that manipulating the spatial frequency of objects affected the subitizing limit. In a task requiring subjects to track the featural changes of two gabors overlaid in the same space, subjects were not able to successfully attend to and track the features of both gabors (Blaser, Pylyshyn, & Holcombe 2000). It thus seems as though overlapping stimuli cannot be individuated and tracked in parallel, consistent with the hypothesis that occupying a distinct location in space is critical for individuation to occur. Parallel individuation may require a minimum distance between targets, but not require the targets to be disconnected in the context of rapid enumeration. Furthermore, some feature elements other than connectivity may facilitate or inhibit the individuation process more than others, which could explain the difference in subitizing slope across display types we observed in Experiments 4 and 6. Further investigations directed at investigating the modulation of the subitizing effect will help clarify the effect of other features on the individuation process.

While we have emphasized the importance of targets occupying separate locations, one study suggests that intermixed and spatially overlapping groups of targets can be enumerated in parallel (Halberda, Sires, & Feigenson, 2006). This study presented displays consisting of colored dots to participants, and asked them to enumerate subsets of the dots based on their color. Participants successfully enumerated up to three sets of dots, and the authors suggested that groups of dots, as defined by color, could be selected as individuals, with numerosity stored as a feature of those individuals. The overlapping quality of stimuli may or may not interfere with numerosity processing, depending on whether the task requires exact enumeration or estimation. The numerosites stored as features for the stimulus sets in Halberda et al. (2006) fell outside of the subitizing range, making it most probable that the numerosity features stored for each set were obtained using estimation. Overlapping stimuli may affect performance in parallel individuation but not in estimation.

In order to reconcile how parallel individuation could occur over parts of a single connected object, we must consider how the selection of targets could occur. All targets could also be selected as deviations from a frame of reference on some dimension. In the multi-object condition, each object differed in luminance from the background. In the single-object condition, all targets were deviations from the circular form. The more specific frame of reference in the single-object condition may have changed the critical dimension from "deviation from background" to "deviation from circle," or "deviation in color" to "deviation in curvature."

"Deviating from X frame of reference" may be described in terms of discriminability – both spatial and perceptual. The results reported here support an individuation mechanism functioning over items that are both unique in location and perceptually discriminable from a flexible frame of reference. The constraints on this discriminability are still undefined. We know that when distracters are present, the target items must deviate on a single dimension rather than be selected through a conjunction – such as color AND orientation (Trick & Pylyshyn, 1993). What constitutes a single dimension however, remains ambiguous; are indents and outdents on opposing ends of the same scale, or separate dimensions?

The idea of a flexible frame of reference directly relates to the issue of "objecthood" at various hierarchical stages of a scene. Feldman (2003) suggests that strong cues for objecthood result from non-accidental relationships existing at a level one step below a more global parsing of the scene where only accidental relationships exist between parsed units. According to Feldman's theory, the strength of objecthood depends upon the disparity between the number of non-accidental relationships at adjacent levels of the scene hierarchy (2003). The single-object stimuli used in our study has one more level in its hierarchical structure than the multi-object condition. However, the difference in non-accidental properties between the object parts and the whole object still seems to be significant enough to allow for parallel individuation to occur.

Within the broader context of the subitizing literature, parallel individuation has already been shown to occur over several levels of a scene hierarchy. Trick and Enns (1997) demonstrated that both grouped dots located at the vertices of invisible shapes and line-drawn shapes can be subitized. Our experiment expanded their results to show that not only can subitization occur over groups and distinct objects, but it can also occur over parts of a single object.

Simply because parallel individuation can occur over multiple levels of a hierarchical tree does not require each level to be processed equally well in all contexts. When distracting elements were added to the grouped stimuli, subitizing was no longer present (Trick & Enns, 1997). Our results do not speak to how individuation occurs over connected object parts in the context of distractors. We also limited our investigation to identifying the presence of subitizing in different stimulus types, and did not directly manipulate or test the effectiveness of individuating different stimulus types or protrusions. We investigated potential interactions between stimulus type and numerosity range in our data post-hoc using 2 x 2 ANOVAs (Secondary Analysis 2) and observed a significant main effect of stimulus type in Experiments 4 and 6, and significant interactions in Experiments 1 and 4, suggesting that various stimulus features can have a differential effect on the slope, either for both ranges, or more so on one numerosity range. The effect of different features on the subitizing slope is an important question that begs further study. In the present study, we observed a range of slopes within the experiments presented here. However, we feel confident that the variation in slope does not reflect a lack of parallel individuation. In fact, a variance in slope is typically reported in the subitizing literature. In subitizing "...each additional item may add 40–100 ms. When there are more than 4 items, the slope jumps to 250–350 ms/item." (Trick & Pylyshyn, 1994, p. 80). All of our results fall nicely within those ranges.

An investigation into how different object parts may affect subitizing performance would relate to the pattern-matching theory of subitizing (Mandler & Shebo, 1982), where targets form vertices of shapes that can then be matched to a number concept. A recent study showing that subitizing performance cannot be explained by the probability of detecting target items supports this theory (Palomares & Egeth, 2010). The importance of the overall shape has also been emphasized in a study of the effects of the medial axis or skeletal structure of a shape on the perception of texture (Harrison & Feldman, 2009). Harrison and Feldman's results suggest that when the skeleton of a shape is consistent with internal local features, perception of those local features is enhanced. For the single-object stimuli used in the present study, the type of uniform connectivity added by the central circle would not dramatically affect the skeleton of the shape, since the protruding targets define the skeleton shape. Thus a theory of subitizing that relies on pattern-matching would suggest equal performance for both multi-object and single-object stimuli. However, altering the skeleton or gestalt of the single-object stimuli may affect the individuation of the target parts differently than the multi-object stimuli. For example, if the protruding stimuli were manipulated to be misaligned with the internal structure, then we could observe worse performance than similarly rotated targets in a multi-object display. This is an open question.

Further investigations such as the ones described above will help winnow out different theories of parallel individuation. A careful manipulation of object parts could provide results that speak to the validity of pattern-matching theories. The type of object part could also affect ease of selection. Requiring a target to have certain qualities on a particular dimension affords some tension with theories that describe individuation of an item as occurring without knowledge of its features (Leslie et al., 1998; Pylyshyn, 1989). If an item is selected as "unique," how does that occur without identifying what dimension reflects the difference? It may be useful to consider our stimuli and those of future experiments within the framework of "textons." Textons are visual stimuli that can be discriminated preattentively without knowledge of the relevant positioning of the items (Julesz, 1984). It is possible that the individuation mechanism may be the joint result of information from a perceptual texton detector and spatial location discriminator. If we combine our emphasis on location with the discriminability of textons, we may have a working definition of individuation that does not rely on objecthood.

Previously, parallel individuation has been nearly synonymous with parallel object individuation. While objecthood clearly provides important information that many tasks depend upon, such as multiple-object tracking, it does not appear to be a necessary requirement in all situations. Within the context of subitizing, we showed that deviations occupying distinct locations on a single connected object provide enough information for parallel individuation to occur. These results are unexpected given the behavioral results of other tasks relying on individuation. Future investigations on how parallel individuation occurs and is influenced by different task demands should consider individuation as not necessarily bound to objecthood or connectivity, and allow for the possibility of individuation functioning over different locations merely on the basis of local discontinuity.

3

Flexible object individuation occurs over connected and unconnected objects in inferior intraparietal sulcus

3.1 Abstract

Object identification, tracking, and enumeration all rely heavily on the ability to segment, or individuate, objects from the background. The role of connectivity in this segmentation is still under debate. While previous fMRI experiments suggest that connectivity affects the processing and enumeration of objects, recent behavioral work has demonstrated that parallel individuation occurs over both connected and unconnected targets. Using univariate and multivariate measures, we explored the role of connectivity in object individuation in the parietal cortex; object individuation and identification have been previously linked to activity in the inferior and superior intraparietal sulci, respectively. We report that the connectivity of target items does not affect the modulation of neural activity by number in the lateral occipital complex and both inferior and superior intraparietal sulci. Multi-voxel pattern analyses reveal that while all three regions hold representations of number that can generalize across stimulus type, only the inferior IPS can discriminate connected and unconnected stimuli. Our results are consistent with an individuation mechanism that operates and selects targets over a flexible object hierarchy. We propose that the selection of task relevant figure and background, and subsequently the appropriate targets, occurs in the inferior IPS. The representations computed in this region may then be passed on to the superior IPS, where further processing such as identification can occur. These findings contribute to a multi-stage theory of object processing in the parietal lobe.

3.2 INTRODUCTION

On a daily basis, humans rely heavily on the ability to distinguish objects from the background. This ability to select a subset number of items to be available for further processing, such as enumeration or tracking, is quite important. When a mother is shooing her children out the front door, it is useful for her to be able to see, at a glance, that all three children are present and accounted for. However, in that moment, it is only critical for her to know that there are three beings; she does not need to identify who each child is. Only if her tally comes up short does she need to identify each individual, and name the missing child.

Many theories support the differentiation of these two stages in object processing. The first stage is object individuation, consisting of the selection of items at a particular location without specific knowledge of their features, which is followed by object identification, when a feature-rich representation becomes accessible (Kahneman, Treisman, & Gibbs, 1992; Leslie, Xu, Tremoulet, & Scholl, 1998; Pylyshyn, 1989; Xu, 2009, Xu & Chun, 2009). The individuation stage has the unique characteristic of being able to select multiple items in parallel without a behavioral cost. This has been demonstrated in the ability to track multiple moving targets at once (Pylyshyn & Storm, 1988; Howe, Cohen, Pinto, & Horowitz, 2010), as well as in the rapid enumeration of targets (Trick & Pylyshyn, 1994). Lesion and fMRI data also suggest that individuation and identification depend on and are processed in different cortical space, supporting their distinct roles in visual processing (Mishkin, Ungerleider, & Macko, 1983; Xu & Chun, 2006; Xu, 2009).

Parallel individuation has been studied extensively using behavioral methods. In the context of an enumeration task, parallel individuation is characterized by near zero errors, and short reaction times (RTs). Performance on these two measures changes dramatically based on the target set size. Within the 'subitizing range' (~1-4), errors and RTs show little increase for each additional target, whereas there is a much larger cost for each additional target in the 'counting range' (~5+) (Kaufman, Lord, Reese, & Volkmann, 1949). The different response profiles across these two ranges creates an 'elbow' as the slopes in error rates or RT change at ~4 items, depending on the individual's subitizing range (Akin & Chase, 1978). Thus there is a limit to how many items can be individuated in parallel, which can be defined behaviorally for each individual. Perhaps if Kevin's mother in the film 'Home Alone' only had 4 children instead of 5, she wouldn't have erred so many times when enumerating the number of children accounted for.

Neural measures have also supported the existence of a limited capacity individuation mechanism. Recent work in EEG compared the responses to target and overall numerosity; a posterior-contralateral component occurring around 200 ms after stimulus onset (N2pc) was modulated by target numerosity regardless of distracter presence, plateauing at 3 items (Ester, Drew, Klee, Vogel, & Awh, 2012; Mazza & Caramazza, 2011; Mazza, Pagano, & Caramazza, 2013). The location of the plateau was found to correlate with individual behavioral limits (Pagano & Mazza, 2012; Pagano, Lombardi, & Mazza, 2014) and is believed to relate to the precise individuation of items for further processing. Similar results have been observed in multiple-object tracking, again with modulation of the N2pc by target numerosity (Drew & Vogel, 2008).

In cortical space, fMRI studies have targeted the parietal lobe as the probable location of this limited capacity individuation mechanism (Todd & Marois, 2004; Mitchell & Cusack, 2008). Activity in the inferior intraparietal sulcus (inferior IPS) is modulated by the number of objects existing in unique locations regardless of their features (Xu, 2009), and has a limit of about four objects (Todd & Marois, 2004; Xu & Chun, 2006). This is in contrast to the superior intraparietal cortex (superior IPS), where activity is modulated only by the number of objects with different features suggesting it is involved in object identification (Xu, 2009). Studies on number also converge on the parietal lobe, demonstrating activity modulated by target set size in neural regions also involved in spatial relations (Hubbard, Piazza, Pinel, & Dehaene, 2005). This overlap is consistent with an individuation mechanism tracking the number of items and their locations.

Previously, the large majority of functional neuroimaging experiments using an enumeration paradigm (Ansari, Lyons, van Eimeren, & Xu, 2007; Cutini, Scatturin, Moro, & Zorzi, 2014; Damarla, Cherkassky, & Just, 2016; Knops, Piazza, Sengupata, Eger, & Melcher, 2014; Sathian, Simon, Peterson, Patel, Hoffman, & Grafton, 1999) and studying parallel individuation (Xu & Chun, 2006; Xu, 2009) have asked subjects to individuate separate, unconnected target items. However, connectivity plays an important role when segmenting the visual field into separate units, and has been proposed to be the cue resulting in the initial organization of visual field (Palmer & Rock, 1994). Connectivity also plays an important role in the allocation of attention (Driver & Baylis, 1998), and has been demonstrated to aid or interfere with different tasks. Balint's syndrome is an example where connectivity aids performance. Whereas patients suffering from Balint's syndrome are normally only able to visually apprehend a single object, adding a connecting line between two objects allows their attention to spread to include both objects and successfully compare the features of the two items (Humphreys & Riddoch, 1993). Connectivity has been shown to affect parallel individuation negatively in a behavioral multiple object tracking task with typical participants. When target stimuli were manipulated so that they were perceived as either connected to a distracting element or independently moving and disconnected from any distractors, performance suffered in the connected conditions (Scholl, Pylyshyn, & Feldman, 2001).

Whether connectivity has a negative effect on parallel individuation is still under debate. Recent behavioral work repeatedly showed the presence of subitizing for the enumeration of both connected (single-object, with target features) and unconnected (multi-object targets) sets of stimuli (Porter, Mazza, Garofalo, & Caramazza, 2016). This is somewhat contradictory to prior studies indicating an effect of connectivity on individuation performance (He, Zhou, Zhou, He, & Chen, 2015; Scholl et al., 2001). Neuroimaging studies have also suggested that connectivity could affect the individuation of targets. An fMRI adaptation study found that connecting target dots with lines in an enumeration task caused a shift in the adaptation curves in IPS, suggesting a decrease in the encoded numerosity for those displays (He et al., 2015). Another study has investigated the effects of grouping on neural activity in the inferior IPS, and reported that grouped displays resulted in lower levels of activity than ungrouped displays (Xu & Chun, 2007). However, while He at al. (2015) found effects of connectivity within the subitizing range behaviorally, they only investigated neural effects of connectivity for 5+ targets. Xu & Chun (2007) also found neural effects of connectivity, but did not manipulate numerosity. Thus, the neural effect of connectivity on the individuation of items within the subitizing range remains unexplored.

In the current experiment, we will investigate the effects of connectivity on individuation in the parietal cortex, specifically including set sizes within the range of parallel individuation. We will contrast activity for multi-object (unconnected targets) and single-object (connected targets) displays with set sizes within the subitizing range in order to help us understand the role of connectivity and objecthood in parallel individuation. We will expand upon the past literature by using both univariate and multi-voxel pattern analysis methods to gain a better understanding of the representation of individuated items in the parietal cortex. If the IPS is sensitive to connectivity, as is hinted by He et al. (2015) and Xu & Chun (2007) then it is possible that we will see different response patterns to connected and unconnected sets of targets. The most extreme outcome would be that there would be no modulation by target number for the connected items, as all set sizes will be viewed as one object. In contrast, if the role of the inferior IPS were to individuate target items across different frames of reference and definitions of figure and ground, then we would predict similar modulation by set size for both unconnected and connected targets. A previous study has shown some evidence of cross-classification of number across tasks in the posterior parietal cortex, indicating there is some ability to generalize number across stimulus types (Knops et al., 2014). Consequently we also expect to see above-chance classification of numerosity in the IPS for both display types, as well as cross-display type classification.

3.3 METHODS

3.3.1 fMRI METHODS

PARTICIPANTS

14 participants between the ages of 20 and 26 (10 female) were scanned at the University of Regensburg and compensated for their participation. One participant was excluded from analyses due to incomplete data collection as a result of computer failure. All participants were right-handed, and had normal or corrected-to-normal vision. The study was approved by: the Committee on the Use of Human Subjects in Research at Harvard University, the Ethics Committee for Experimentation with Human Beings at the University of Trento, and the Faculty of Medicine Ethics Committee at the University of Regensberg.

MAIN EXPERIMENT

There were 12 stimulus conditions (6 numerosities x 2 display types); the two display types were grouped (single-object) and ungrouped (multi-object) targets. The grouped targets consisted of a black outline of a circle with protruding arcs. Multi-object displays consisted of outline closed arcs (Figure 3.1). The locations of the single-object display target features were generated randomly for each stimulus and each participant, constrained such that no two features could overlap. The orientation of each arc in the multi-object displays was randomly selected from a set of angles (-20°, -10°, 0°, +10°, +20°) to avoid the illusory percept of a circle. The goal of the use of outline stimuli instead of filled shapes was twofold: to eliminate any possible percept of the protruding arcs as separate shapes occluding the central circle in the single-object condition, and

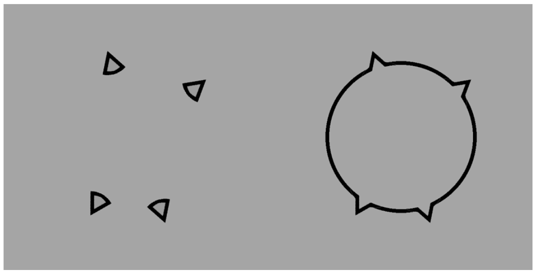


Figure 3.1: An example of the matched stimuli for the two stimulus display types. Note that the ungrouped arcs in the mult-object display (left) were jittered slightly in their rotation to avoid the perception of an illusory circle.

to better match the low-level visual properties of the two display types. A unique stimulus set was created in advance and presented for each participant using Matlab with the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997); no stimulus was presented twice. However, the locations of the targets to be enumerated were controlled across display types, such that for each unique grouped stimulus, a matched ungrouped stimulus also existed (Figure 3.1). Data from a previous study (Porter et al., 2016) demonstrated that the grouped and ungrouped outline stimuli showed behavioral evidence of parallel individuation.

Each run was presented as a mini-block design, with 5 stimulus presentations per block. Subjects performed an oddball detection task, pressing a button when they saw a numerosity that was different from that previously established by the stimuli in the block (Figure 3.2). Each block was 5.5 s long, with 500 ms presentation, 600 ms inter-stimulus-interval, followed by a 2.5 second inter-block-interval, resulting in 8 seconds between the onset of each block (Figure 3.3).

Forty-seven blocks were presented per run: 36 'pure' blocks without oddball stimuli (3 repetitions x 6 numerosities x 2 display types), 7 blocks containing an oddball trial, and 4 fixation blocks (8 s long). An additional 8 seconds of fixation was added

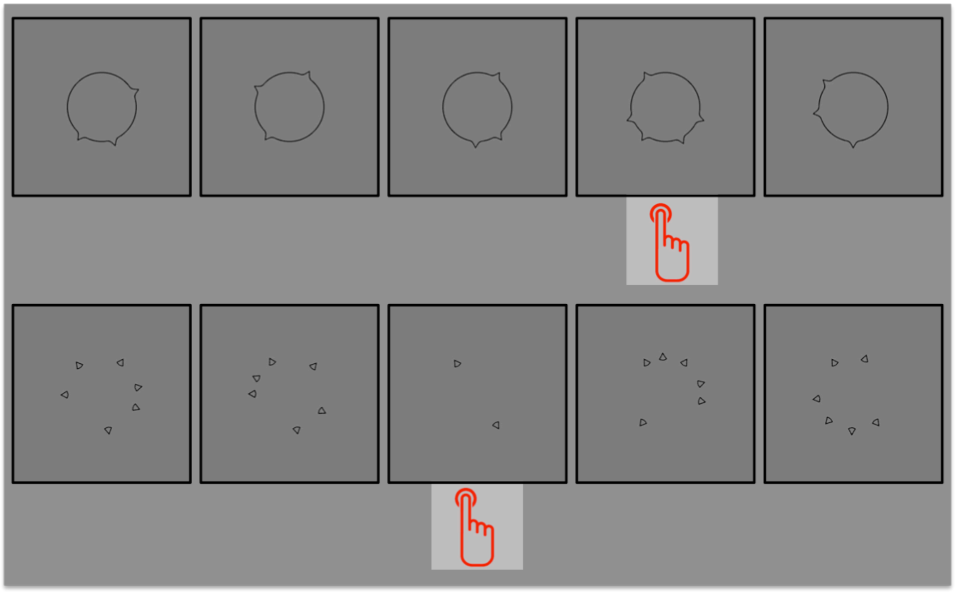


Figure 3.2: Examples of oddball blocks, and the expected response point, for each display type.

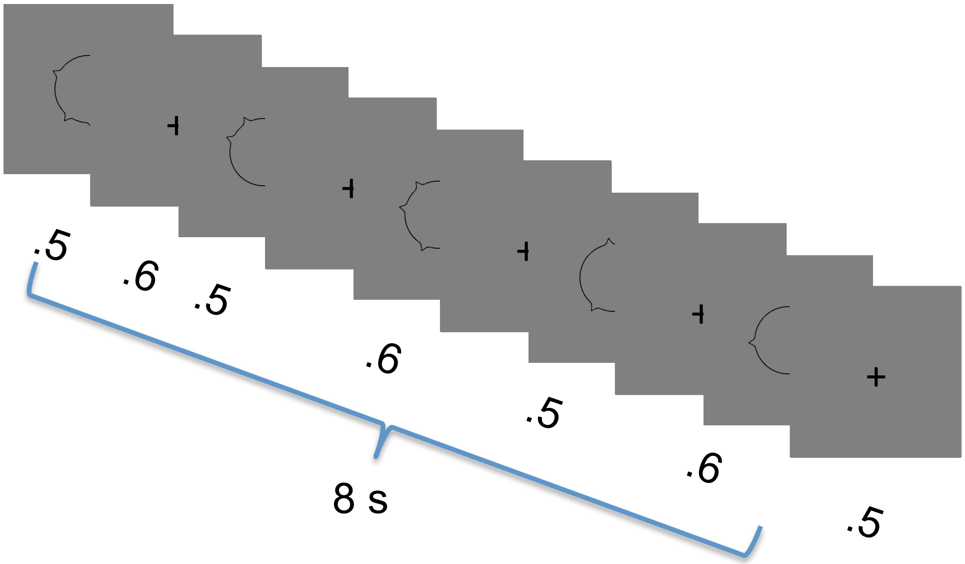


Figure 3.3: Diagram demonstrating the time sequence for one block for the main experiment.

at the beginning and end of each run. This organization resulted in fixation for 12.2% of the run, and 14.9% of the blocks including an oddball trial. Six runs were collected for each participant, resulting in 18 blocks per stimulus condition. Since the number of oddball blocks did not divide evenly into the number of stimulus types, we pseudorandomly determined the stimulus type in the following manner: over the 42 possible oddball blocks in all 6 of the runs, 3 repetitions occurred for each stimulus condition; the remaining 6 blocks were split into 1 block per numerosity, with the display type (grouped, ungrouped) determined randomly for each block. These oddball blocks were excluded from all analyses.

The order of the blocks in each run was pseudorandomly determined in the following manner for each subject. First, the position of the 4 fixation blocks and 7 oddball blocks were determined randomly, with the constraint that fixation could not occur in the first or last block of the run. The pure stimulus blocks were then inserted into the remaining available positions: the twelve stimulus conditions were randomly shuffled, and then inserted into the first 12 available slots. This was repeated two more times to fill the remaining block positions.

Localizers

Two localizer tasks were used to identify regions of interest. To define the LOC and iIPS, we used a localizer from Xu & Chun (2006) and Xu (2009). This localizer consisted of blocks of displays consisting of six black shapes on a gray background, and then blocks of noise images (Figure 3.4). Each image was presented for 500 ms with an inter-stimulus-interval (ISI) of 200 ms. Subjects performed a motion detection task. Each subject performed 2 runs, each 4.67 minutes long. We decided to not modify the shapes used in this localizer to reflect the stimuli used in our main experiment since

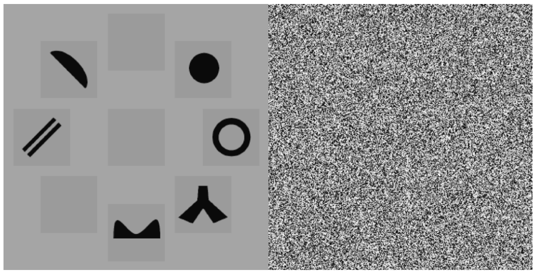


Figure 3.4: Example stimuli for the LOC, iIPS localizer. Object displays (left) and noise.

there were not enough black pixels in the outline shape to generate noise images.

To define the sIPS, we used the main experiment visual working memory task from Xu (2009) with the exclusion of the identical shape trials; all shapes presented in each display were unique. One, 2, 3, 4, or 6 black shapes were presented around fixation for 200 ms, creating a display very similar to those used as the shape stimuli from the first localizer (Figure 3.4), followed by a 1 s blank, after which a test shape was presented at fixation, and the subject pressed the a button to indicate whether the shape had been present in the display (index finger), or absent from the previous display (middle finger). Subjects had 2.5s to respond before receiving feedback for that trial. A feedback display was shown for 1.3 s, indicating whether the subject's response was correct (smiley face presented at fixation) or incorrect (sad face). Each subject performed 2 runs of this task, each lasting 7.97 minutes. We also decided not to use our outline stimuli as the shapes in the VSTM task, since they are so visually similar we expected it would be too difficult for subjects to perform.

Scanning Parameters

Functional and anatomical data were collected using a 3-Tesla Allegra scanner (Siemens, Erlangen, Germany) at the University of Regensburg with a single channel head coil.

Functional data were collected using ascending interleaved slice acquisition with a T2*-weighted gradient echo planar imagine (EPI) sequence (image matrix: 64 x 64 with 34 axial slices, repetition time = 2000 ms, echo time (TE) = 30 ms; flip angle (FA) = 90°, field of view (FOV) = 192 x 192 mm^2, slice thickness = 3 mm, gap = 0.30 mm, with 3 x 3 mm in-plane resolution). Structural data were acquired using a high-resolution scan (160 sagittal slices, 1 x 1 x 1 mm^3) with a T1-weighted MP-RAGE sequence (TR = 2.25 s, TE 2.6 ms, FA = 9°, FOV = 240 x 256 mm). The sequence was optimized for the differentiation of gray and white matter by using parameters from the Alzheimer's Disease Neuroimaging Initiative project (http://adni.loni.ucla.edu/). Stimuli were generated using Psychophysics toolbox for MATLAB and projected onto a screen inside the bore with a LCD projector (JVC, DLA-G20, Yokohama, Japan), which was viewed by a mirror attached to the head coil.

3.3.2 fMRI Analyses

The fMRI data were analyzed using SPM8 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8) and MARSBAR (Brett, Anton, Valabregue, & Poline, 2002) as well as custom Matlab software. Data preprocessing consisted of slice timing correction, spatial realignment, removal of the first four volumes of each run, coregistration, segmentation of gray and white matter, and normalization. The two localizer scans also underwent spatial smoothing with a 6 mm FWHM kernel.

Localizers

To localize the inferior IPS and LOC, we performed a general linear model with two regressors: objects and noise. The two ROIs were defined individually for each participant based on a contrast of objects > noise. The superior IPS was localized based on a general linear model with each set size of the VSTM task weighted by the Cowan's K estimate for that set size for that participant (Cowan, 2001). The K-value was calculated as K = (HR+CR-1)*N where K = number of items encoded, HR = hit rate, CR = correct rejection rate, and N = set size. All three regions of interest were defined individually for each participant. For each region, a peak voxel was selected based on Talairach coordinates previously reported for these regions (Todd & Marois, 2004; Xu, 2009) which were converted into MNI space for use in SPM (Lancaster et al., 2007; Laird et al., 2010). A 5.5 mm radius sphere was then build around the peak voxel, resulting in ~27 voxels selected, to approximate the same size as previously used in the literature (Xu, 2009). The center of the sphere was adjusted ~2mm when the built cluster extended outside of the brain.

Main Experiment

We performed a general linear model on our main task with one regressor for each stimulus type (6 numerosities x 2 display types). We first investigated the effect of the different stimulus types on the level of activity in each ROI based on peak percent signal change. The percent signal change was calculated as: [timecourse intensity / average fixation intensity] * 100 – 100. The peak TR was selected as follows: for each subject, all conditions of interest were collapsed and averaged, and then the TR with the peak average percent signal change was selected within the timeframe of 10s post trial onset (each trial was 8s long). The peak time point was then averaged across subjects, and the resulting TR was used to select the percent signal change for analysis. This was repeated for each ROI. We performed a 2x6 repeated-measures ANOVA to investigate potential main effects and interactions between display type and number. A multiple-comparisons correction was performed, defining a more stringent α as α/k, where k = the number of repeated tests or the number of ROIs. As a result our significance threshold is considered .0167 instead of .05. To ensure that low-level factors were not driving our results, we replicated the GLM and analyses with number of black pixels in each image presented as a regressor of non-interest. To investigate the point at which activity plateaued in each region, we performed paired two-tailed t-tests comparing percent signal change between the largest three numerosities.

Our second analysis consisted of training a linear support vector machine (SVM) classifier to discriminate patterns of activity for our stimulus types, using the MATLAB functions "svmtrain" and "svmclassify". In order to remove amplitude effects of the different conditions, we standardized the data using the following z-transformation: $z = (x - \mu)/\sigma$, where x represents the multi-voxel pattern, or vector of beta weights, for one stimulus condition, in one ROI of one subject, μ is the mean response of that pattern, and σ the standard deviation. Using this method we performed three different classifications. First, we looked at the classification accuracy within each ROI when generalizing across stimulus type to discriminate number. The classifier was trained to categorize number on one display type and tested on the other for two iterations (e.g. train = grouped, test = ungrouped, and vice versa). Chance for this classifier was 16.7%, as there were 6 numerosities. We then investigated classification accuracy decoding display types across number. The classifier was trained to discriminate display type (grouped, ungrouped) on 5 out of the 6 numerosities, and tested on the remaining numerosity. This was iterated 6 times, leaving out each numerosity once, with chance performance of 50%. The performance of both classifiers was compared to their respective chance level using paired two-tailed t-tests. To better interpret the results of these two classifications, we performed a split-half reliability measure for each ROI within each subject. This was accomplished by correlating two halves of the data (odd and even runs) and correcting for test length using the Spearman-Brown prediction formula.

The final classification was done to create a pairwise discrimination matrix: a classification was performed for each pair of stimuli, training the classifier to discriminate the two types on 5 out of the 6 runs, testing on the data from the final run, and iterating the classification 6 times, with chance at 50% for each classification, and significant performance above chance assessed with t-tests. The neural discrimination matrix for each subject was then correlated with model discrimination matrices based on behavioral results and theoretical predictions. These correlations were then contrasted against chance performance using two-tailed paired t-tests. Chance performance was represented by a random model generated for each ROI by selecting random values for each matrix cell from the range of values within that ROIs discrimination performance. In order to assess whether the magnitude rather than the direction of the correlation was significant, negative correlations were contrasted against a negative random model, and positive correlations against a positive random model. Correlation coefficients were Fisher transformed before statistical tests. Behavioral model matrices included average behavioral reaction time and accuracy reported from a behavioral task. Theoretical model matrices included two difference measures, one based on the different number of targets between each pair, and another on the difference in average number of pixels in each stimulus pair. Both differences were calculated using Weber Fractions ($(N_{larger} - N_{smaller}) / N_{smaller}$). The final model represented performance of stimulus type without knowledge of number.

3.3.3 BEHAVIORAL METHODS

To compare neural classification performance to models based on behavioral performance, we collected data on a behavioral discrimination task similar to the task performed in the scanner.

PARTICIPANTS

13 Harvard University students participated for compensation of either $10 or course credit. One participant was removed from analysis due to poor performance indicative of not attending to or performing the task. All participants provided informed consent, as approved by the Committee on the Use of Human Subjects in Research at Harvard University. All participants were debriefed about the purpose of the study and supplied with supplemental reading after completion of the experiment.

STIMULI

The same stimuli were used as in the fMRI experiment, with new unique stimulus sets created for each participant.

PROCEDURE

Participants performed a number discrimination task consisting of trials with pairs of stimuli. They received instructions to report as quickly and as accurately as possible whether the second stimulus presented in each trial had the same or different number of shapes OR arcs as the first stimulus presented. Responses were recorded by keypress, with one key representing 'same' responses, and another 'different'.

Subjects completed a short practice round followed by the full-length experiment consisting of 468 trials (pairs of 6 numerosities x 2 display types with 6 presentations per pair). When a pair consisted of different display types, one multi-object and one single-object, the presentation order was counterbalanced with each stimulus taking the first presentation slot 3 times. The order of presentation was randomized for each subject.

Each trial consisted of: 1 second fixation, display first stimulus of pair for 500 ms, 600 ms blank gray screen, presentation of second stimulus for 500 ms or until a response was recorded via buttonpress. The presentation timing was designed to mimic the experience of the participants in the fMRI experiment, with the same stimulus duration and inter stimulus interval as the mini-block presentation. Every 40 trials, the participants were given the option to take a self-timed break before continuing.

3.3.4 BEHAVIORAL ANALYSIS

We recorded reaction times and accuracy for each trial. For each pair type, we calculated the median RT and entered it into a 12 x 12 matrix (6 numerosities x 2 display types). We collapsed the matrix across the identity line, such that there were 6 trials contributing to each cell. We created a similar matrix representing the percent correct for each pair type. We then averaged the matrices across subjects to create two models, reaction time and accuracy, to correlate with the neural pairwise discrimination classifier performance.

3.4 RESULTS

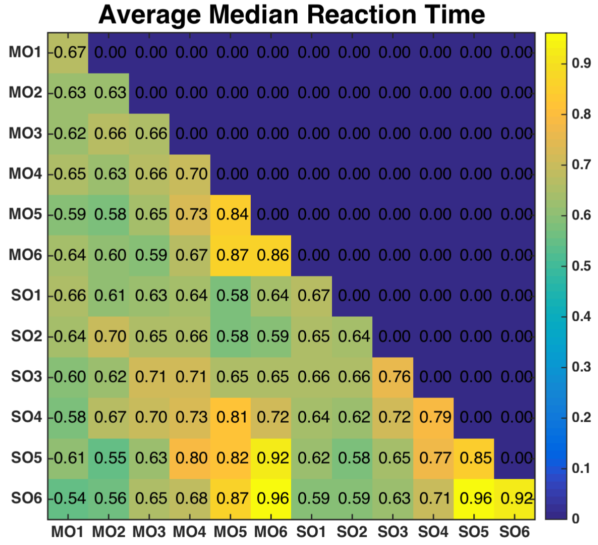
3.4.1 BEHAVIORAL RESULTS

SCANNER TASKS

For our main experiment and inferior IPS/LOC localizer (objects vs. noise) participants performed a task to ensure they remained attentive and alert throughout the course of the experiment. Within the main experiment, subjects performed an oddball detection task; all participants demonstrated adequate performance, with a range of 71.4% to 97.6% correct averaging across the 6 runs. In the localizer, all participants performed well at a motion detection task with greater than 90% correct detection for all runs. We also collected behavioral data for the VSTM superior IPS localizer. The behavioral results and estimated Cowen's K were comparable to those previously reported in the literature (Todd & Marois, 2004; Xu, 2009), indicating that our subjects were successfully attending to and performing the task (Table 3.1).

Table 3.1: Results from the VSTM localizer. K represents Cowen's K estimate for number of items encoded for each set size.

Behavioral Performance: VSTM Localizer					
Set Size	1	2	3	4	6
Mean K	0.97	1.84	2.24	2.51	2.34
SEM K	0.02	0.06	0.12	0.20	0.37
RT (correct, ms)	633.97	722.23	773.43	856.18	962.92
SEM RT	59.71	63.39	65.64	79.85	96.75
# Correct Trials (N = 13)	317	308	280	261	219
# Trials Total	321	321	321	321	320
% Correct	98.75%	95.95%	87.23%	81.31%	68.44%

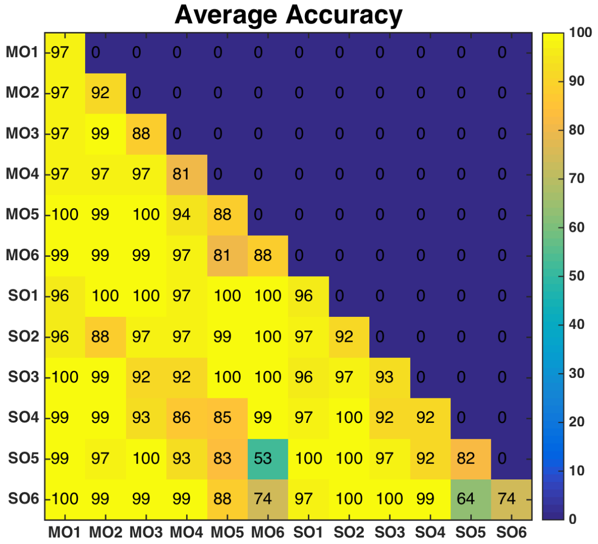


	MO1	MO2	MO3	MO4	MO5	MO6	SO1	SO2	SO3	SO4	SO5	SO6
MO1	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO2	0.63	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO3	0.62	0.66	0.66	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO4	0.65	0.63	0.66	0.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO5	0.59	0.58	0.65	0.73	0.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO6	0.64	0.60	0.59	0.67	0.87	0.86	0.00	0.00	0.00	0.00	0.00	0.00
SO1	0.66	0.61	0.63	0.64	0.58	0.64	0.67	0.00	0.00	0.00	0.00	0.00
SO2	0.64	0.70	0.65	0.66	0.58	0.59	0.65	0.64	0.00	0.00	0.00	0.00
SO3	0.60	0.62	0.71	0.71	0.65	0.65	0.66	0.66	0.76	0.00	0.00	0.00
SO4	0.58	0.67	0.70	0.73	0.81	0.72	0.64	0.62	0.72	0.79	0.00	0.00
SO5	0.61	0.55	0.63	0.80	0.82	0.92	0.62	0.58	0.65	0.77	0.85	0.00
SO6	0.54	0.56	0.65	0.68	0.87	0.96	0.59	0.59	0.63	0.71	0.96	0.92

Figure 3.5: Model of discrimination matrix based on behavioral reaction time. The median reaction time for each cell was calculated for each subject, then averaged. MO = multi-object, SO = single-object

BEHAVIORAL EXPERIMENT

The average median reaction times for the discrimination task are provided in Figure 3.5, and average accuracy is provided in Figure 3.6. While participants were asked to respond both as quickly and as accurately as possible, there appears to be more variability in reaction time, with a 400 ms difference between the fastest average median response (comparing multi-object 1, and single-object 6), and the slowest average medium responses (comparing multi-object 6 and single-object 6, as well as comparing single-object 5 and 6). While the accuracy for most comparisons was close to ceiling, performance suffered when adjacent numerosities were compared. The lowest accuracy was 53%, when comparing single-object 5 and multi-object 6.



	MO1	MO2	MO3	MO4	MO5	MO6	SO1	SO2	SO3	SO4	SO5	SO6
MO1	97	0	0	0	0	0	0	0	0	0	0	0
MO2	97	92	0	0	0	0	0	0	0	0	0	0
MO3	97	99	88	0	0	0	0	0	0	0	0	0
MO4	97	97	97	81	0	0	0	0	0	0	0	0
MO5	100	99	100	94	88	0	0	0	0	0	0	0
MO6	99	99	99	97	81	88	0	0	0	0	0	0
SO1	96	100	100	97	100	100	96	0	0	0	0	0
SO2	96	88	97	97	99	100	97	92	0	0	0	0
SO3	100	99	92	92	100	100	96	97	93	0	0	0
SO4	99	99	93	86	85	99	97	100	92	92	0	0
SO5	99	97	100	93	83	53	100	100	97	92	82	0
SO6	100	99	99	99	88	74	97	100	100	99	64	74

Figure 3.6: Model of discrimination matrix based on behavioral accuracy. The accuracy for each cell was calculated for each subject, then averaged. MO = multi-object, SO = single-object

3.4.2 fMRI Results

Regions of Interest

Using the procedure detailed in the analyses, we localized the LOC and inferior IPS in all 13 subjects. The superior IPS could only be identified in 11 of the 13 participants included in the analyses. The three regions progressed appropriately from ventral to dorsal locations, and shared no overlapping voxels in any participant. The regions of interest for one subject are shown in a standard brain in Figure 3.7.

Percent Signal Change

We calculated the peak signal change for each condition above the baseline activity of fixation. The peak percent signal change for each condition and ROI is plotted

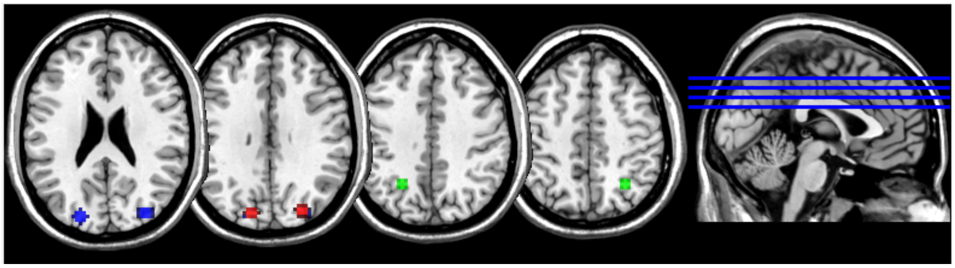


Figure 3.7: Individually defined spherical regions of interest for one participant. LOC (blue), inferior IPS (red), superior IPS (green)

in Figure 3.8. A 2 x 6 (display type x number) repeated-measures ANOVA showed a significant main effect of number in all three regions (Table 3.2). While there was a significant interaction in LOC between display type and number, it did not survive multiple comparison correction. These results suggest that all three regions are modulated by target number in both the multiple object and single-object conditions, with no statistically significant difference between display types. Removing the number of pixels from the regression did not affect the pattern of results, and so are not reported.

We also investigated the point at which the increase in percent signal change for each additional target plateaued. Comparisons of the difference in activity from 4 targets to 5, and 5 to 6 in both numerosities demonstrated a plateau was established by 5 targets in both multi-object and single-object displays (Table 3.3). While the increase between 4 and 5 targets was technically not significant according to our more stringent alpha for multi-object displays in the inferior and superior IPS, and for single-object displays in the LOC and inferior IPS, the effects were trending toward significance. Therefore while the true plateau may occur between 4 and 5 targets, we consider a strong plateau to be established by 5 targets in this dataset.

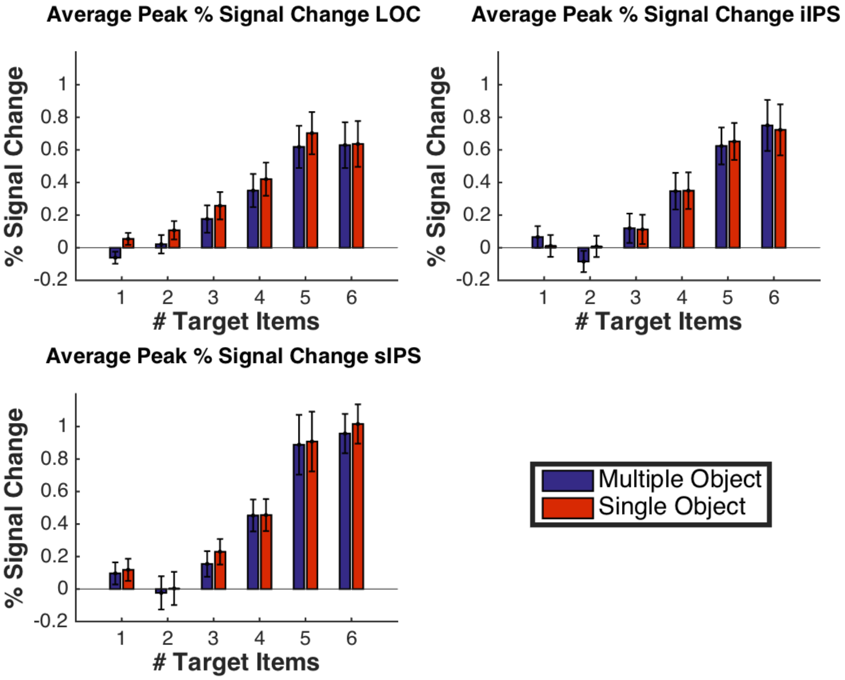


Figure 3.8: Average peak signal change above fixation for each ROI. In all three regions, number significantly modulates neural activity with no main effect of stimulus type.

Table 3.2: Results from a repeated-measures ANOVA of percent signal change in each region. The final column indicates whether the reported p-values survive multiple comparison correction (MCC), with ⍰ defined as .0167. Only a main effect of numerosity survived multiple comparison correction in all three regions of interest.

Repeated-Measures ANOVA: % Signal Change				
	df	F	p-value	p-value <.0167 (MCC)
LOC				
Stimulus Type	(1, 12)	3.60	.082	
Numerosity	(1.58, 18.92)	22.79	< .001	*
Stimulus Type x Number	(5, 60)	0.29	.024	
inferior IPS				
Stimulus Type	(1, 12)	0.11	.749	
Numerosity	(1.67, 20.01)	17.70	< .001	*
Stimulus Type x Number	(3.06, 36.67)	0.43	.738	
superior IPS				
Stimulus Type	(1, 10)	4.73	.055	
Numerosity	(1.43, 14.32)	18.94	< .001	*
Stimulus Type x Number	(5, 50)	0.13	.984	

Linear SVM Classification

Linear SVM classifications were performed to investigate representations of stimulus type and number in the patterns of activity in each ROI. Patterns were normalized to remove differences in magnitude of activity between the regions. The LOC, inferior IPS, and superior IPS all showed classification above chance for target number, generalizing across stimulus type (Figure 3.9, Table 3.4). This suggests all three regions can discriminate number, abstracting across the visual differences between multi-object and single-object displays. Only the inferior IPS performed above chance classifying stimulus type, discriminating between multi-object and single-object trials while generalizing across numerosity significantly above chance (Figure 3.10). The inferior IPS thus seems

Table 3.3: Results of paired t-tests investigating the point at which the increase in percent signal change for each additional target plateaued. A strong plateau is established at 5 targets in all three regions. A * indicates that the result survives multiple-comparison correction.

Increase in Response Magnitude					
	df	T	p-value	sd	95% CI
Increase in % signal change: 4 to 5 targets					
multi-object displays					
LOC	12	4.10	< .01 *	0.24	[0.13, 0.41]
inferior IPS	12	2.65	.021	0.38	[0.05, 0.51]
superior IPS	10	2.76	.020	0.52	[0.08, 0.79]
single-object displays					
LOC	12	2.77	.017	0.37	[0.06, 0.50]
inferior IPS	12	2.73	.018	0.40	[0.06, 0.54]
superior IPS	10	4.03	< .01 *	0.37	[0.20, 0.70]
Increase in % signal change: 5 to 6 targets					
multi-object displays					
LOC	12	0.26	.797	0.15	[-0.08, 0.10]
inferior IPS	12	1.60	.136	0.18	[-0.05, 0.30]
superior IPS	10	0.77	.461	0.30	[-0.13, 0.27]
single-object displays					
LOC	12	-0.85	.412	0.28	[-0.24, 0.10]
inferior IPS	12	0.98	.348	0.26	[-0.09, 0.23]
superior IPS	10	1.17	.269	0.31	[-0.10, 0.31]

to be able to represent the difference of single-object and multi-object stimuli, ignoring the perceptual differences occurring due to changes in numerosity.

To better interpret the difference between significant and non-significant classification performance, we must consider the reliability of the neural multi-voxel patterns for each of our classifications in the ROIs. It could be that the varying reliability of neural patterns is driving the results we report here instead of differences in the information represented in each region. The reliability of multi-voxel representations of stimulus type was constant across regions (Figure 3.11). A two-sample t-test between su-

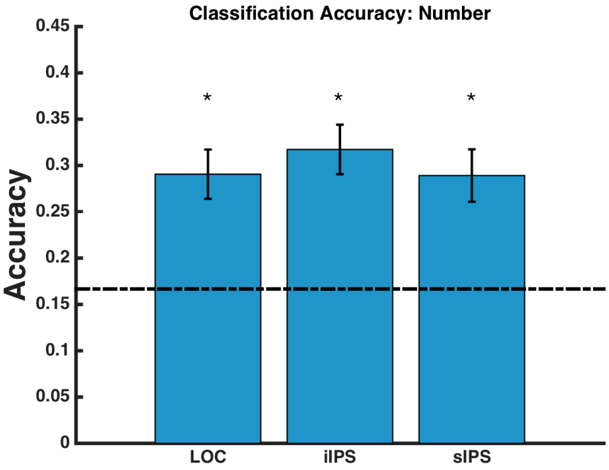


Figure 3.9: Average accuracy of the SVM classifier when discriminating number. The classifier successfully decoded number while generalizing across stimulus type in all three ROIs. Chance (.167) is represented by the dotted line.

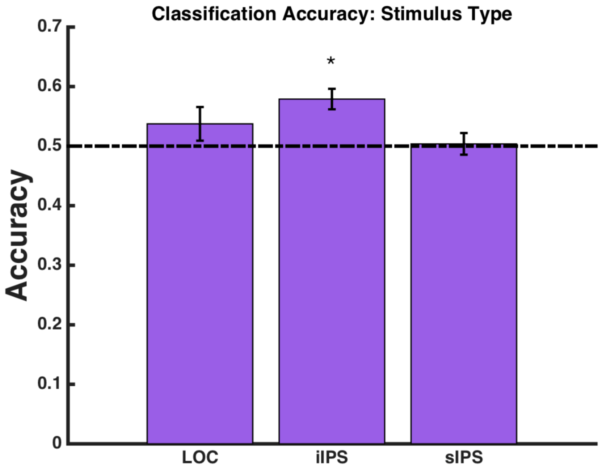


Figure 3.10: Average classification accuracy of the SVM classifier when discriminating stimulus type. The classifier successfully decoded stimulus type while generalizing across number in the inferior IPS only. Chance (.5) is represented by the dotted line.

Table 3.4: Classification accuracy for stimulus type and number in each ROI. A * indicates that the performance survives multiple-comparison correction. While all three regions successfully discriminate target number when generalizing across stimulus type, only the inferior IPS successfully discriminates multi-object and single-object displays, generalizing across numerosity.

Classification Accuracy						
	df	T	p-value	Mean Accuracy	sd	95% CI
Classification of Stimulus Type				*Chance = 50%*		
LOC	12	1.32	.211	53.7%	10.2%	[47.6,59.9]
inferior IPS	12	4.60	< .001 *	57.9%	6.2%	[54.2,61.7]
superior IPS	10	0.21	.839	50.4%	6.0%	[46.3,54.4]
Classification of Target Number				*Chance = 16.7%*		
LOC	12	4.66	< .001 *	29.1%	9.6%	[23.3,34.9]
inferior IPS	12	5.64	< .001 *	31.7%	9.6%	[25.9,37.6]
superior IPS	10	4.33	< .01 *	28.9%	9.4%	[22.6,35.2]

perior IPS and inferior IPS for split-half correlations in the multi-object condition was not significant (t(22) = -0.36, p = 0.72). Thus, despite comparable reliability in multi-voxel patterns across regions, the inferior IPS was the only region to perform above chance when classifying stimulus type. The neural patterns for number showed low reliability that varied across ROI and numerosity (Figure 3.12). Despite these noisy representations, the classifier was able to discriminate number significantly above chance in all three ROIs.

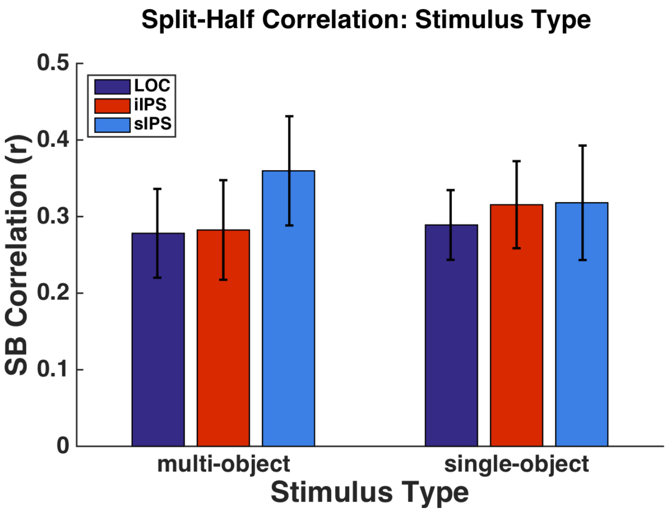


Figure 3.11: Split-half correlations as a measure of multi-voxel pattern reliability in each ROI. Spearman-Brown prediction correlations are reported for neural patterns of each stimulus type. The reliability of neural patterns representing multi-object and single-object displays appears to not differ between regions of interest.

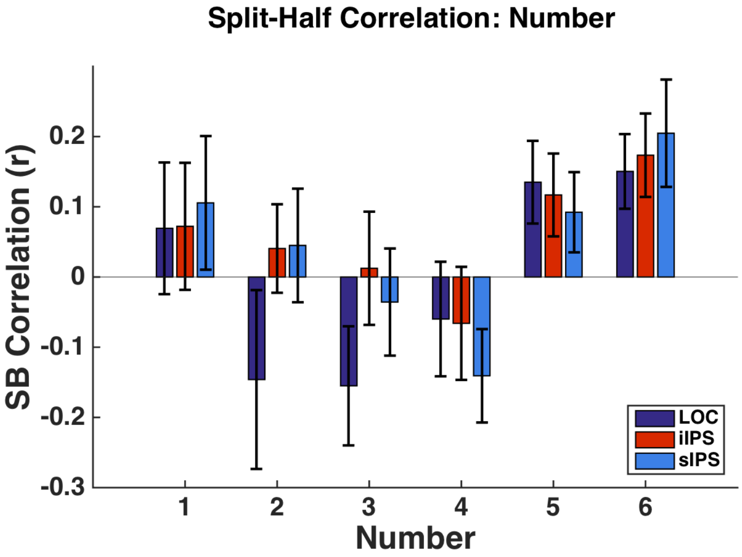
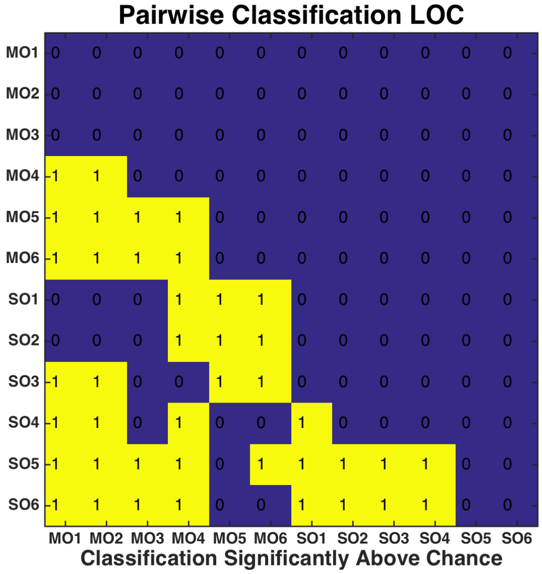


Figure 3.12: Split-half correlations as a measure of multi-voxel pattern reliability in each ROI. Spearman-Brown prediction correlations are reported for neural patterns of each numerosity. Reliability of the neural patterns varies across number and regions.



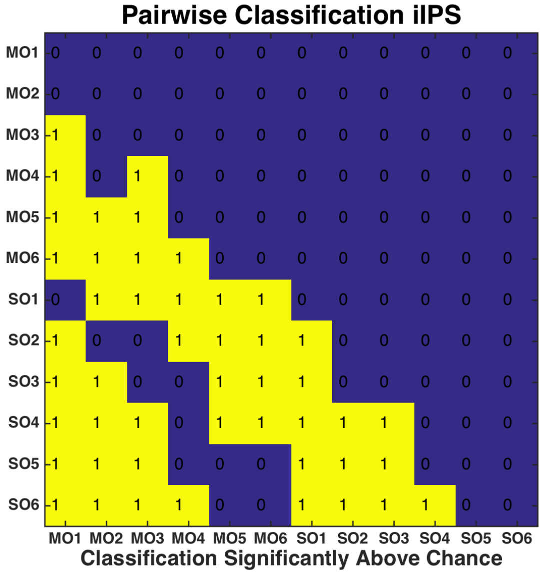
	MO1	MO2	MO3	MO4	MO5	MO6	SO1	SO2	SO3	SO4	SO5	SO6
MO1	0	0	0	0	0	0	0	0	0	0	0	0
MO2	0	0	0	0	0	0	0	0	0	0	0	0
MO3	0	0	0	0	0	0	0	0	0	0	0	0
MO4	1	1	0	0	0	0	0	0	0	0	0	0
MO5	1	1	1	1	0	0	0	0	0	0	0	0
MO6	1	1	1	1	0	0	0	0	0	0	0	0
SO1	0	0	0	1	1	1	0	0	0	0	0	0
SO2	0	0	0	1	1	1	0	0	0	0	0	0
SO3	1	1	0	0	1	1	0	0	0	0	0	0
SO4	1	1	0	1	0	0	1	0	0	0	0	0
SO5	1	1	1	1	0	1	1	1	1	1	0	0
SO6	1	1	1	1	0	0	1	1	1	1	0	0

Figure 3.13: Statistical performance of pairwise linear SVM classification for each stimulus condition in LOC. Classification accuracy significantly above chance is represented with a value of 1. MO = multi-object, SO = single-object

Pairwise Classification

To investigate the representations driving the classification in each ROI, we created a matrix representing the ability of a linear SVM classifier to discriminate each possible pair of stimulus conditions (see statistical results Figures 3.13 - 3.15, classification values Appendix Figures A.2 - A.4). The pattern of performance does not seem to vary dramatically across regions; the most successful classification occurs when comparing large and small numbers in all three ROIs, and decreases as numerosities become closer in magnitude. Performance additionally does not appear to differ when discriminating numbers within the same stimulus type (multi-object vs. multi-object) compared to across stimulus types (multi-object vs. single-object).

To assess how well the pattern of performance in each region could be represented

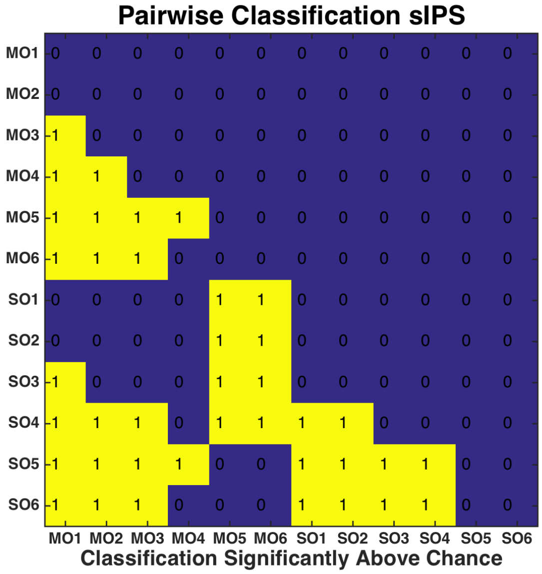


	MO1	MO2	MO3	MO4	MO5	MO6	SO1	SO2	SO3	SO4	SO5	SO6
MO1	0	0	0	0	0	0	0	0	0	0	0	0
MO2	0	0	0	0	0	0	0	0	0	0	0	0
MO3	1	0	0	0	0	0	0	0	0	0	0	0
MO4	1	0	1	0	0	0	0	0	0	0	0	0
MO5	1	1	1	0	0	0	0	0	0	0	0	0
MO6	1	1	1	1	0	0	0	0	0	0	0	0
SO1	0	1	1	1	1	1	0	0	0	0	0	0
SO2	1	0	0	1	1	1	1	0	0	0	0	0
SO3	1	1	0	0	1	1	1	0	0	0	0	0
SO4	1	1	1	0	1	1	1	1	1	0	0	0
SO5	1	1	1	0	0	0	1	1	1	0	0	0
SO6	1	1	1	1	0	0	1	1	1	1	0	0

Figure 3.14: Statistical performance of pairwise linear SVM classification for each stimulus condition in inferior IPS. Classification accuracy significantly above chance is represented with a value of 1. MO = multi-object, SO = single-object

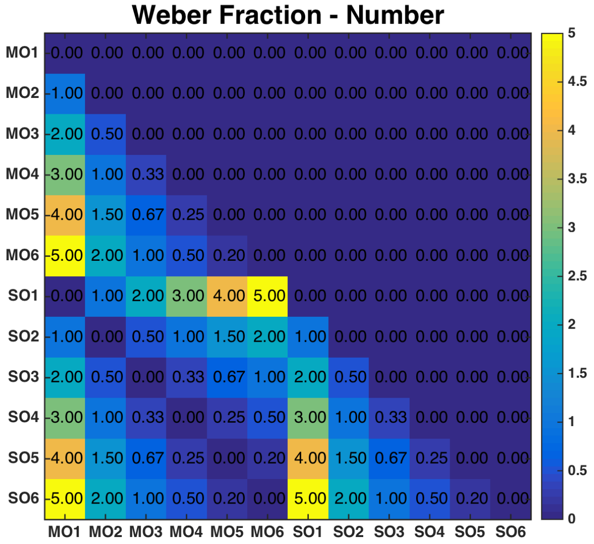
by different kinds of information, we correlated the neural discrimination matrix for each region with several different model matrices. We first compared how similar the neural discrimination matrix was to behavioral measures from a discrimination task designed to be similar to the task performed in the scanner. We built models using both reaction time data (Figure 3.5) and accuracy (Figure 3.6). We also created matrices based on the numerical and perceptual difference between each stimulus pair. Numerical difference is represented by a Weber Fraction calculated from target number (Figure 3.16), and perceptual difference is represented by a Weber Fraction calculated from the number of pixels in each stimulus (Figure 3.17). The final model represents performance based on information about stimulus type but not number (Figure 3.18)

The average correlation between each participant's neural discrimination matrices and each model are represented in Figure 3.18 and reported in Table 3.5. The largest



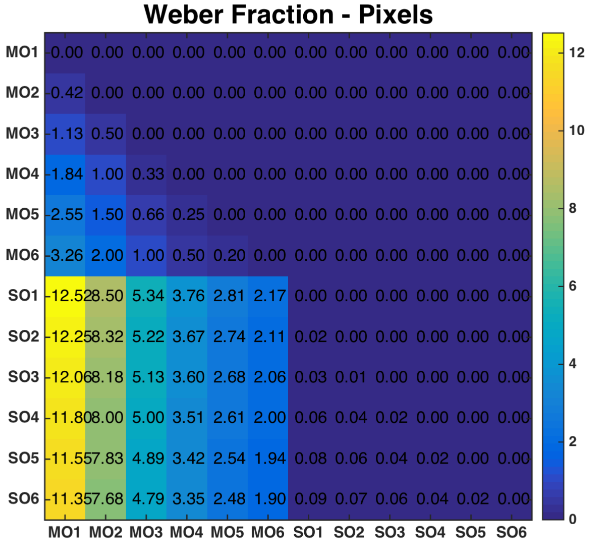
	MO1	MO2	MO3	MO4	MO5	MO6	SO1	SO2	SO3	SO4	SO5	SO6
MO1	0	0	0	0	0	0	0	0	0	0	0	0
MO2	0	0	0	0	0	0	0	0	0	0	0	0
MO3	1	0	0	0	0	0	0	0	0	0	0	0
MO4	1	1	0	0	0	0	0	0	0	0	0	0
MO5	1	1	1	1	0	0	0	0	0	0	0	0
MO6	1	1	1	0	0	0	0	0	0	0	0	0
SO1	0	0	0	0	1	1	0	0	0	0	0	0
SO2	0	0	0	0	1	1	0	0	0	0	0	0
SO3	1	0	0	0	1	1	0	0	0	0	0	0
SO4	1	1	1	0	1	1	1	1	0	0	0	0
SO5	1	1	1	1	0	0	1	1	1	1	0	0
SO6	1	1	1	0	0	0	1	1	1	1	0	0

Figure 3.15: Statistical performance of pairwise linear SVM classification for each stimulus condition in superior IPS. Classification accuracy significantly above chance is represented with a value of 1. MO = multi-object, SO = single-object



	MO1	MO2	MO3	MO4	MO5	MO6	SO1	SO2	SO3	SO4	SO5	SO6
MO1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO2	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO3	2.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO4	3.00	1.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO5	4.00	1.50	0.67	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO6	5.00	2.00	1.00	0.50	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SO1	0.00	1.00	2.00	3.00	4.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00
SO2	1.00	0.00	0.50	1.00	1.50	2.00	1.00	0.00	0.00	0.00	0.00	0.00
SO3	2.00	0.50	0.00	0.33	0.67	1.00	2.00	0.50	0.00	0.00	0.00	0.00
SO4	3.00	1.00	0.33	0.00	0.25	0.50	3.00	1.00	0.33	0.00	0.00	0.00
SO5	4.00	1.50	0.67	0.25	0.00	0.20	4.00	1.50	0.67	0.25	0.00	0.00
SO6	5.00	2.00	1.00	0.50	0.20	0.00	5.00	2.00	1.00	0.50	0.20	0.00

Figure 3.16: Model of discrimination performance driven by the difference between stimulus number represented by Weber Fractions. MO = multi-object, SO = single-object



	MO1	MO2	MO3	MO4	MO5	MO6	SO1	SO2	SO3	SO4	SO5	SO6
MO1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO2	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO3	1.13	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO4	1.84	1.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO5	2.55	1.50	0.66	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO6	3.26	2.00	1.00	0.50	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SO1	12.52	8.50	5.34	3.76	2.81	2.17	0.00	0.00	0.00	0.00	0.00	0.00
SO2	12.25	8.32	5.22	3.67	2.74	2.11	0.02	0.00	0.00	0.00	0.00	0.00
SO3	12.06	8.18	5.13	3.60	2.68	2.06	0.03	0.01	0.00	0.00	0.00	0.00
SO4	11.80	8.00	5.00	3.51	2.61	2.00	0.06	0.04	0.02	0.00	0.00	0.00
SO5	11.55	7.83	4.89	3.42	2.54	1.94	0.08	0.06	0.04	0.02	0.00	0.00
SO6	11.35	7.68	4.79	3.35	2.48	1.90	0.09	0.07	0.06	0.04	0.02	0.00

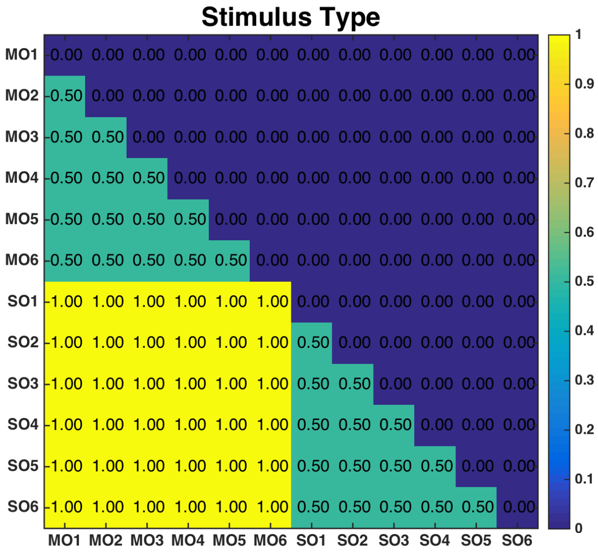
Figure 3.17: Model of discrimination performance driven by the difference between number of pixels in each stimulus as represented by Weber Fractions. MO = multi-object, SO = single-object

average correlations for each region were between the neural classification performance and the models based on behavioral reaction time, and difference in number.

Table 3.5: Average Fisher transformed correlation coefficients between the neural pairwise classification matrix and other matrix models within each ROI. WF = Weber Fraction

Correlation SVM Classification and Models												
	Reaction Time		Accuracy		Number (WF)		Pixels(WF)		Stimulus Type		Random	
	$\bar{r}$	SEM	$\bar{r}$	SEM	$\bar{r}$	SEM	$\bar{r}$	SEM	$\bar{r}$	SEM	$\bar{r}$	SEM
LOC	-.370	.070	.262	.064	.398	.059	.059	.035	-.018	.025	-.139	.028
iIPS	-.469	.042	.370	.036	.488	.046	.037	.039	-.043	.026	-.121	.027
sIPS	-.398	.086	.343	.078	.404	.055	-.015	.044	-.068	.024	-.127	.027

The correlations between each model and the neural classification performance matrix were compared against the correlation between the neural matrix and a randomly generated matrix to use as a baseline measure of chance. The statistical results of t-test comparisons against the performance of the random model are detailed in Table 3.6.



Stimulus Type

	MO1	MO2	MO3	MO4	MO5	MO6	SO1	SO2	SO3	SO4	SO5	SO6
MO1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO2	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO3	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO4	0.50	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO5	0.50	0.50	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MO6	0.50	0.50	0.50	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SO1	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
SO2	1.00	1.00	1.00	1.00	1.00	1.00	0.50	0.00	0.00	0.00	0.00	0.00
SO3	1.00	1.00	1.00	1.00	1.00	1.00	0.50	0.50	0.00	0.00	0.00	0.00
SO4	1.00	1.00	1.00	1.00	1.00	1.00	0.50	0.50	0.50	0.00	0.00	0.00
SO5	1.00	1.00	1.00	1.00	1.00	1.00	0.50	0.50	0.50	0.50	0.00	0.00
SO6	1.00	1.00	1.00	1.00	1.00	1.00	0.50	0.50	0.50	0.50	0.50	0.00

Figure 3.18: Model of discrimination performance driven only by information about stimulus type, and not number. Performance would be perfect when the pair included one multi-object stimulus and one single-object stimulus, but would be at chance when forced to discriminate number within stimulus type. MO = multi-object, SO = single-object

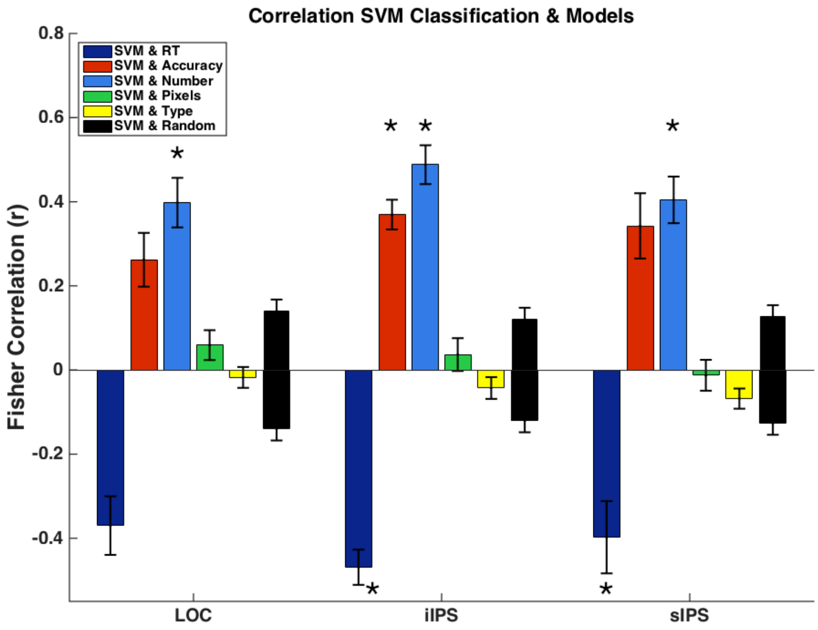


Figure 3.19: Fisher transformed correlation coefficents representing the relationship between the SVM classifier pairwise discrimination matrix and matrices based on behavioral and theoretical models in each ROI. A * indicates that the comparison of the model correlation to that of the random matrix survives multiple-comparison correction. SVM = Support Vector Machine pairwise classification performance, RT = behavioral reaction time model, Accuracy = behavioral accuracy model, Number = Difference in number as Weber Fraction model, Pixels = Difference in number of pixels as Weber Fraction model, Type = stimulus type model, Random = randomly generated matrix representing a baseline chance correlation.

The model representing differences in number was significantly more correlated with classification performance than the random matrix in all three regions of interest. The behavioral model of reaction time was also significantly more correlated than chance in the inferior and superior IPS, with trending significance in the LOC. The behavioral model for accuracy was significant in the inferior IPS only. The model for the perceptual difference as measured by number of pixels, and the model based on information about stimulus type both were less correlated with the neural discrimination performance than a chance matrix in all three ROIs. The classification performance in the LOC seems to be best represented by a model of difference in number. In the inferior IPS, the model based on difference in number was significantly more correlated than the model based on behavioral accuracy (t(12) = 2.75, p = .018), however the strength of the correlation was not significantly different between behavioral reaction time and difference in number (t(12) = 0.50, p = 0.628). The same was true for the superior IPS (t(10) = 0.12, p =0.904). Therefore the strength of relationship between the neural discrimination matrix and the models based on difference in number and behavioral reaction time seem to be equal in magnitude in both the inferior and superior IPS. However, the correlation between the neural classification performance and difference in number is a positive one, whereas behavioral reaction time has a negative relationship with classification performance.

Table 3.6: Results from two-tailed paired t-tests comparing the strength of correlation between each model and the neural discrimination matrix, against the correlation of the neural discrimination matrix and the random model. A * indicates that the result survives multiple-comparison correction.

Comparison of Model Performance					
	df	T	p-value	sd	95% CI
Reaction Time vs. Random					
LOC	12	-2.70	.019	0.31	[-0.42, -0.04]
inferior IPS	12	-6.45	< .001 *	0.19	[-0.47, -0.23]
superior IPS	10	-3.14	.0105 *	0.29	[-0.46, -0.08]
Accuracy vs. Random					
LOC	12	1.53	.153	0.29	[-0.05, 0.30]
inferior IPS	12	5.03	< .001 *	0.18	[0.14, 0.36]
superior IPS	10	2.72	.022	0.26	[0.04, 0.39]
Number Weber Fraction vs. Random					
LOC	12	3.76	< .01 *	0.25	[0.11, 0.41]
inferior IPS	12	7.55	< .001 *	0.18	[0.26, 0.47]
superior IPS	10	5.13	< .001 *	0.18	[0.16, 0.40]
Pixel Weber Fraction vs. Random					
LOC	12	-1.94	.077	0.15	[-0.17, 0.01]
inferior IPS	12	-1.72	.111	0.18	[-0.19, 0.02]
superior IPS	10	-2.55	.029	0.18	[-0.26, -0.02]
Stimulus Type vs. Random					
LOC	12	2.73	.018	0.16	[0.02, 0.22]
inferior IPS	12	1.71	.113	0.14	[-0.02, 0.18]
superior IPS	10	2.06	.067	0.09	[-0.005, 0.12]

3.5 Discussion

In this experiment, we aimed to test the effect of connectivity on individuation in three regions of interest: LOC, inferior IPS, superior IPS. We showed that the number of targets, regardless of connectivity, modulates activity in all three of these regions. Multi-voxel pattern analyses investigating the representation of information within these regions showed that while all three regions hold representations of number that can be generalized across stimulus type, only the inferior IPS performed above chance when discriminating multi-object and single-object displays. Further investigation of the neural representation of our stimulus types suggests that pairwise classification performance may be related to the difference between numerosities as measured by a Weber fraction, and is unlikely to be driven solely by perceptual differences such as number of pixels in the image.

It is surprising that we did not observe a univariate main effect of stimulus type in inferior IPS, as previous studies have demonstrated effects of grouping and connectivity in this region. One study reported that when shapes were grouped by a common background, they evoked smaller response magnitudes than a similar display with each shape occurring on its own background (Xu & Chun, 2007). Another study showed that connecting a subset of dots in a display caused underestimation in behavioral judgments, as well as a shift in the neural adaptation curves in IPS indicative of underestimation (He et al., 2015). Based on these results, we would have expected the response of each numerosity in the single-object displays to be lower than that of the comparable multi-object display. The lack of this univariate effect in the current study could be the result of different selection demands. Grouping in Xu & Chun's (2007) study was performed by placing objects within one of several dark fields present in the gray display, thus even when all targets were grouped within the same field, other black fields were still visible against the gray background. The selection of figure could shift between the larger object, the dark field, or the smaller feature, the target shape. This was also true of the displays used in He et al. (2015). Their task required participants to make judgments about the number of dots in a display. These displays also included irrelevant lines, which could sometimes be oriented so that they connected some of the dots. In their connected condition, the same display would thus contain two possible definitions of figure and ground, both of which were necessary to accurately perform the task. By contrast, our single-object stimuli only contained one relevant definition of figure and ground to perform the task – the protruding arcs were the target figures against a circular ground. Therefore the decrease in activity previously observed in the inferior IPS to connected and grouped items may have resulted from competing levels of selection within the same task, with a bias toward figure as defined by a lack of connectivity. In contrast, when connectivity had a uniform effect on the selection of targets, as in our study, connected targets could be treated as separate objects.

We observed modulation of neural activity by number in all three ROIs for both stimulus types. We expected this result in the inferior IPS as previous studies have demonstrated that it is sensitive to the number of items in different locations (Naughtin, Mattingley, & Dux, 2014; Xu, 2009; Xu & Chun, 2006). However, those same studies have shown that the superior IPS and LOC are modulated by the number of unique features, or identities, in the display as opposed to the number of overall targets. We predicted that the number of targets in both of our stimulus conditions would not modulate activity in these two areas given their identical shapes (either arcs or protruding arcs) and that they would be processed in these areas as a single feature or identity. The modulation we observe could reflect that the rotated orientations of the arcs in our multi-object displays and arc protrusions in our single-object displays made each target unique enough to be considered as a unique feature. Alternatively, these results could demonstrate differences in task demands; our task required participants to focus specifically on the number of targets, whereas the working memory task used in earlier studies placed emphasis on identity (Naughtin, et al., 2014; Xu, 2009; Xu & Chun, 2006). In a working memory task, a display containing one circle could be encoded using the same representation as a display containing four circles – ‘circle’.

The numerosity judgment used in the current experiment instead forced participants to focus on the difference between those two displays – 1 vs. 4. This difference in task demands could explain why we observed modulation by number in the superior IPS and LOC whereas previous studies did not.

The plateau in percent signal change we observed is consistent with those previously reported in studies involving individuation. In working memory, a plateau at 4 objects is common (Todd & Marois, 2004; Xu & Chun, 2006), whereas a functional near-infrared spectroscopy (fNIRS) study that used a simple enumeration task reported a plateau in hemodynamic activity at 5 items (Cutini et al., 2014). Our results indicate a solid plateau established by 5 items for all three ROI, with a trending effect at 4 items. This is consistent with a subitizing limit of ~4 items (Kaufman et al., 1949), but is a bit higher than the plateau of 3 reported in studies using electrophyscial (EEG) measures (Ester et al., 2012; Mazza & Caramazza, 2011; Mazza, Pagano, & Caramazza, 2013). This could be due to the difference in methodology, as the plateaus observed in fMRI tend to be larger.

Multi voxel pattern analysis using a linear SVM classifier allowed us to look at whether neural response patterns in our regions of interest held information about number or stimulus type, with the ability to generalize across the other dimension. While the LOC, and both inferior and superior IPS can significantly classify number, generalizing across multi-object and single-object stimuli, only inferior IPS could classify the two display types collapsing across numerosity. These results have some precedent, with one study showing that voxels in the parietal lobe could classify number generalizing across changes in spatial configurations, as well as modality (Damarla, Cherkassky, & Just, 2016), and another demonstrating that the posterior parietal cortex can classify number in both enumeration and visual working memory tasks (Knops et al., 2014). Additionally, the inferior IPS has been shown to be able to decode both the number of objects in a display as well as discriminate between displays either consisting of multiple objects of the same shape, or unique shapes (Naughtin et al., 2016).

While our results are consistent with previous findings of classification performance in the parietal lobe, we also investigated the reliability of the patterns we used in each region to ensure the pattern of results we observe is not due to varying reliability across regions. The patterns of activity used in our linear SVM classifier varied dramatically in their reliability across the two analyses. While the split-half correlations for each number were quite low, correlations within multi-object displays and single-object displays in contrast were fairly stable across regions and the two stimulus types. The significant results of our classifier when discriminating number is most likely a result of there being more variability across numerosity than within, leading to the robust performance of the classifier despite low reliability of the multi-voxel patterns. The more stable reliability of the representation of stimulus type across regions of interest lends confidence in our interpretation that the inferior IPS holds information about stimulus type whereas the LOC and superior IPS do not.

To explore what kind of information was driving the performance of our classifier, we compared the accuracy of the classifier when discriminating each possible stimulus pair to several different models. The model discriminating stimuli based on difference in number calculated as a Weber Fraction performed best in the LOC. This model also performed very well in the inferior and superior IPS, but was not significantly different in magnitude than the model based on behavioral reaction time. While the current data does not allow us to discriminate whether reaction time or numerical distance is driving the classifier performance in the inferior and superior IPS, we suggest that numerical difference is a likely candidate. The modulation of behavioral reaction time has also been linked to Weber's law (Whalen, Gallistel, & Gelman, 1999) so it is quite possible that both the neural and behavioral performance are being driven by the numerical differences, instead of behavioral reaction time driving neural classification.

One open question is whether the representation of number in parietal cortex is a result of information about numerosity or a result of sensory cues, such as area, (Gebuis, Gevers, & Kadosh, 2014). Our model based on the difference in number of pixels in each display allows us to investigate this in our data. The pixel-based model was not strongly correlated with neural performance, suggesting that solely the amount of 'stuff' on the screen could not be driving our results. Two other pieces of converging evidence from this study include: the addition of number of pixels in our GLM as a regressor of no interest did not affect the pattern of results, and variability within each stimulus condition was such that the average visual representation, a blurred circle, was very similar across conditions (Figure 3.20). Considering the poor performance of our pixel based model, and given that our stimuli were presented in blocks of 5 varied images forcing an averaged visual representation, it is difficult to explain how successful classification based on retinotopic information would arise.

Another consideration is whether the modulation by number and pairwise classification we observe is merely a result of task difficulty. We believe this is unlikely as previous research has suggested that activity in the inferior IPS is modulated by the number of targets even when conditions were matched for task difficulty (Cusack, Mitchell, & Duncan, 2010). Furthermore, in our multi-voxel pattern analysis all three regions successfully classified number based on patterns of activity that had been standardized to account for differences in amplitude across conditions.

The pattern of results we report here are consistent with a neural individuation mechanism that exists in the inferior IPS. While the LOC, inferior IPS, and superior

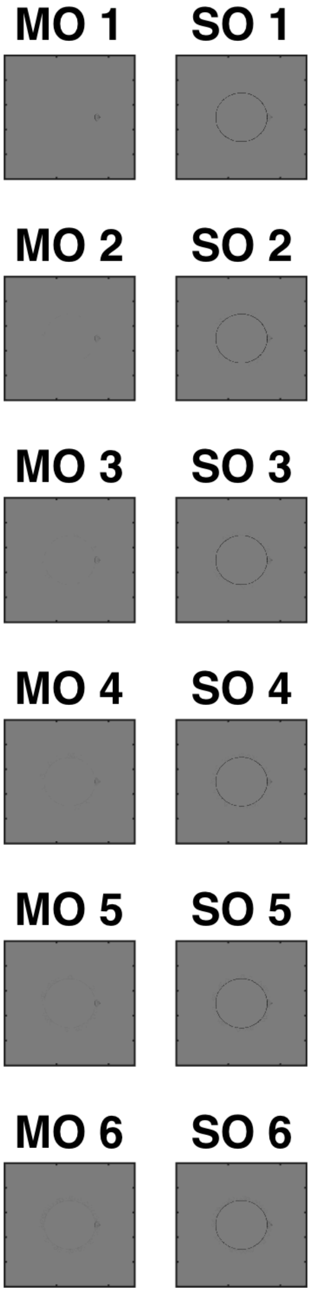


Figure 3.20: Average images for each stimulus condition. All of the images used for one participant were averaged to represent the retinotopic footprint of each stimulus condition. MO = multi-object, SO = single-object.

IPS all hold univariate and multivariate representations of numerosity, only the inferior IPS holds information about stimulus type generalizing across number. Information about stimulus type is relevant when selecting the figure and ground for the selection and individuation of target items. We propose that the inferior IPS holds information about the visual features in a scene for the purpose of selecting targets at the task-relevant level of the visual hierarchy. Once individuated, the selected targets are passed on to the superior IPS for further processing, such as identification. Thus, we would not expect information about stimulus type to be relevant to the superior IPS unless it was related to the task demands, as in visual working memory. This explains why previous studies showed sensitivity in the superior IPS to stimulus identities (Xu, 2009) whereas the current task did not. The LOC also did not successfully classify stimulus type, even though it has been shown to be able to categorize different objects and exemplars across viewpoints and size changes (Eger, Ashburner, Haynes, Dolan, & Rees, 2008). It may be that whereas classification of stimulus type in inferior IPS is driven by a representation of the visual hierarchy, the LOC holds more of a precise representation of identity within the displays, making it difficult to generalize from one arc to six arcs. Another alternative is that the LOC is sensitive to task demands (Xu & Chun, 2007) and thus does not hold the irrelevant information about stimulus type.

Previous studies have suggested that grouping and connectivity can affect the neural individuation and enumeration of items (He et al., 2015; Xu & Chun, 2007). Here we suggest that this is not a direct result of connectivity, but rather the addition of a second and confounding figure/ground within the same display. Our results are consistent with the neural object file theory proposed in Xu & Chun 2009, suggesting that the inferior IPS is the location of object individuation, followed by identification in superior IPS. We propose to add to the neural object file theory the specification that the inferior IPS can operate over a flexible definition of field and ground. When figure and ground are not confounded, connectivity does not have a detrimental effect on individuation performance.

4

Constraints on parallel individuation: overlapping targets allow for successful subitizing of both unresolved and amodal representations

4.1 ABSTRACT

Subitizing, the rapid and accurate enumeration of small sets of objects, depends on a mechanism that can rapidly separate figure from ground. This selection is so efficient and rapid that it has been characterized as occurring in parallel. While previous research has shown that not all visual representations can be efficiently individuated in parallel, the visual features necessary for parallel individuation are still unknown. In three experiments, we used a subitizing paradigm to test several hypotheses as to why parallel

individuation fails in the stimulus test case of concentric squares. We found that line ambiguity, shared center of mass, and bounded enclosure do not explain participant failure to subitize concentric shapes. We further demonstrate that parallel individuation does occur over two dimensional overlapping targets, with no effect of degree of overlap or presentation duration. We propose a three stage model for subitizing, with successful parallel individuation relying on each target occupying a unique space in the visual field.

4.2 INTRODUCTION

The human visual system has the remarkable ability to rapidly separate figure from ground in the visual field. This process of establishing distinct visual units, or objects, seems to occur very quickly, even in parallel (Pylyshyn, 1989; Pylyshyn & Storm, 1988). While multiple visual targets can be selected, or individuated, with perceived ease, there is a limit to the number of items individuated in parallel, which varies across participants (Akin & Chase, 1978). This limit can be measured behaviorally using both enumeration and multiple-object tracking tasks. In enumeration, rapid reaction times and low error rates characterize the 'subitizing range', which is believed to result from parallel individuation (Kaufman, Lord, Reese, & Volkmann, 1949). In multiple-object tracking (MOT), performance is measured through the accurate tracking of target items in the presence of identical distractors (Pylyshyn & Storm, 1988).

The conditions under which parallel individuation will and will not function has been a topic of study for quite some time. Previously it was assumed that parallel individuation occurs over unconnected objects (Scholl, Pylyshyn, & Feldman, 2001; Watson, Maylor, & Bruce, 2005). Recent work has demonstrated that connectivity does not interfere with parallel individuation in the context of rapid enumeration, and connected object parts can be subitized (Porter, Mazza, Garofalo, & Caramazza, 2016). Other types of visual grouping have also resulted in successful parallel individuation. Groups of dots organized by similar color have been successfully subitized (Watson et al., 2005) as well as grouped dots that formed shapes by marking the position of corners (Trick & Enns, 1997).

All of the stimulus conditions where subitizing succeeds include targets that occur in spatially unique locations, whether they are connected, unconnected, or grouped. When the spatial constraints of each stimulus are not well defined, performance begins to suffer. The enumeration of features such as number of colors fails when the items are not grouped, but rather are intermixed (Watson et al., 2005). When the spatial frequency of arranged dots becomes too high, the number of items individuated in parallel decreases (Atkinson, Campbell, & Francis, 1976). Items that did not maintain their structure but rather flowed like a substance, not clearly occupying defined location, were not successfully individuated and tracked in a MOT task (vanMarle & Sholl, 2003). Another MOT task demonstrated that parts of targets that were connected to a distracting element could not be tracked unless the connecting element was perceived as a substance (Scholl et al., 2001), thus reducing the percept of connectivity and allowing the target and distracting end to be perceived as independent entities.

While the spatial arrangement of targets seems to influence subitizing performance, what visual features or stimulus characteristics are critical for parallel individuation to occur is still unknown. One additional condition where subitizing fails is when items are presented concentrically (Saltzman & Garner, 1948; Trick & Pylyshyn, 1993). Trick & Pylyshyn (1993) investigated whether the proximity of the contours or variety in target size inherent in concentric stimuli could be the cause of the failure. They concluded that neither proximity nor variance in size interfered with subitizing, but rather the shared center of focus interfered with parallel individuation. Here we will continue their work in an attempt to identify necessary visual features for parallel individuation. To do so, we will manipulate the concentric squares stimulus condition to test different hypotheses as to why concentric squares cannot be subitized, and what visual characteristics may be required for parallel individuation.

There are many reasons as to why concentric shapes could not allow for individuation. As Trick & Pylyshyn (1993) mentioned, concentric shapes all share a center of mass. Additionally when the shapes are identical, as in stimuli previously used (Trick & Pylyshyn, 1993), the line ownership is ambiguous; for example a group of two circles can either be perceived as two outlines or a single doughnut shape. Furthermore, since the outer square encompasses all other squares, only one item occupies its own location in space.

In our first experiment, we compared within-subject performance for the rapid enumeration of three different stimulus conditions. We included concentric squares as a baseline condition, and added two test stimuli. The first test stimulus addressed whether a shared center of mass interfered with parallel individuation. To remove this factor, we jittered the locations of the squares such that their centers were misaligned. The second test stimulus in the first experiment tested whether removing line ambiguity would result in subitizing performance. To resolve line ownership, we introduced motion to the display, such that each square would 'jitter' back and forth in a unique direction.

Our second and third experiments explored the importance of the space owned or occupied by each item in individuation. There are two components to the ownership of space in the concentric stimuli. First, the stimuli are all enclosed within each other, with the boundary of the largest square defining the area relevant for the task. While the removal of boundary closure has been demonstrated to not remove same-object advantages in a spatial cuing task, the same study also reported that they observed much larger effects with complete enclosure (Marino & Scholl, 2005). In Experiment 2, we investigated whether boundary enclosure interferes with parallel individuation by removing one of the line segments from each square to create concentrically arranged arches. We created two test conditions with incomplete enclosure: one with the bottom border of each square removed, matching the concentric square control in all other ways, and another with the sides of each square extended to a common plane, to remove the potential percept of depth / a hallway when the edge termination was not matched.

The third experiment investigated the effects of competing ownership of space. Studies using MOT have shown that object individuation and tracking is affected by the spacing between targets; closer items are more difficult to track (Franconeri, Jonathan, & Scimeca, 2010; Shim, Alvarez, & Jiang, 2008). This effect has been linked to anatomical constraints based on how information is processed neurally (Carlson, Alvarez, & Cavanagh, 2007) and developed into a theory where selected items compete for cortical space (Franconeri, Alvarez, & Cavanagh, 2013). A second theory of individuation also suggests that the mechanism underlying parallel individuation can only select targets if they occupy distinct locations in space (Leslie, Xu, Tremoulet, & Scholl, 1998). In Experiment 3 we explored whether the degree of overlap and competition for ownership of space would affect parallel individuation. If the amount of unique space occupied by each target affects how well it can be selected, then we would expect that less overlap would result in better performance, and more overlap would result in worse performance.

The effect of overlap on individuation has been investigated via the enumeration of

Figure 4.1: Example stimuli for 3-dimensional occlusion, as used in Akin & Chase (1978). **a)** All possible combinations of three blocks. Cube faces lying on a single dimension without occlusion are highlighted in blue. **b)** An example stimulus consisting of four blocks, with one block completely occluded.

three-dimensional structures. Akin & Chase (1978) demonstrated a subitizing limit of 3 for displays of arranged adjacent cubes. However, a confound intrinsic to their stimuli may have affected the enumeration of four or more blocks. Figures composed of three blocks always have one dimension where the face of all blocks line up on the same plane without occlusion; subjects could have just identified the relevant dimension and then subitized the stimuli as non-occluded 2D adjacent shapes (Figure 4.1a). As soon as the stimuli consist of four blocks however, configurations exist where blocks can be completely occluded (Figure 4.1b). As a consequence, it is possible that the results were biased toward a subitizing elbow, and individuation may have actually failed in the case of occlusion – starting at 4 items.

Here we will use two-dimensional squares, with both small and large amounts of overlap to test the effect of shared space on individuation. We will also add a manipulation of presentation time. Overlapping stimuli force the visual system to perform amodal completion to resolve the hidden portion of each object. The amount of time required for the complete representation of the occluded object to resolve varies depending on the size of the occluded area (Rauschenburger & Yantis, 2001), with some studies reporting a time range of 100 to 200 ms to resolve an occluded object (Sekuler, Palmer, & Flynn, 1994). In Experiment 3, we presented no overlap, small overlap, and large overlap squares for two presentation durations. The short presentation time we selected (100 ms) falls within the time frame where amodal representations are still being processed, and the long presentation time falls outside of this range (250 ms) after most occluded objects have been amodally completed. If parallel individuation operates best over the resolved representations of the occluded objects, we would expect to see typical subitizing performance for all three stimulus types when presented for 250 ms, but modulation of performance at a presentation time of 100 ms with better performance for the no overlap and small overlap conditions. By manipulating concentrically arranged stimuli in Experiment 1 and 2, we will narrow the hypotheses space as to what visual feature is causing subitizing to fail, as well as expand the current knowledge about what visual features may be necessary for parallel individuation. Additionally, our manipulation of overlap in Experiment 3 will reveal the effect of targets occupying shared space in individuation. Finally, by varying the presentation time, we will examine how the process of resolving overlapping representations affects subitizing performance.

4.3 Experiment 1

4.3.1 Introduction

In Experiment 1, we tested whether the lack of parallel individuation observed in the concentric square stimuli is due to ambiguity in the perceived line ownership, or due to a shared center of mass. To remove the ambiguity of line ownership, we created stimuli where each square moved slightly over the course of the presentation, in order to establish each square as its own entity. To vary the center of mass, we jittered the location of each square.

4.3.2 Method

Participants

Twelve Harvard University students participated for compensation of either $10 or course credit. All participants provided informed consent, as approved by the Committee on the Use of Human Subjects in Research at Harvard University. All participants were debriefed about the purpose of the study and supplied with supplemental reading after completion of the experiment.

Stimuli

Displays consisted of three types of stimuli: concentric squares, motion jitter squares, and center of mass jittered squares (Figure 4.2). The number of squares present in each display for all three conditions ranged from 1 to 7. Each stimulus was uniquely created for each subject. Concentric square stimuli consisted of black squares presented centrally with a shared center point. The set of squares for each trial was randomly selected without replacement from 10 possible square sizes. The 10 sizes were generated randomly for each subject, within the range of 24 x 24 pixels to 340 x 340 pixels. The difference between each square size within a set ranged from 24 to 34 pixels, resulting in a minimum distance between any two edges of 12-17 pixels, about 3 cycles/degree. Previous work has shown that subitizing performance is only affected at a spatial frequency of greater than 8 cycles/degree (Atkinson et al., 1976). The squares were drawn with a line width of 3 pixels. Motion jitter squares were created in a similar manner to the concentric squares. Each set of squares was selected randomly without replace-

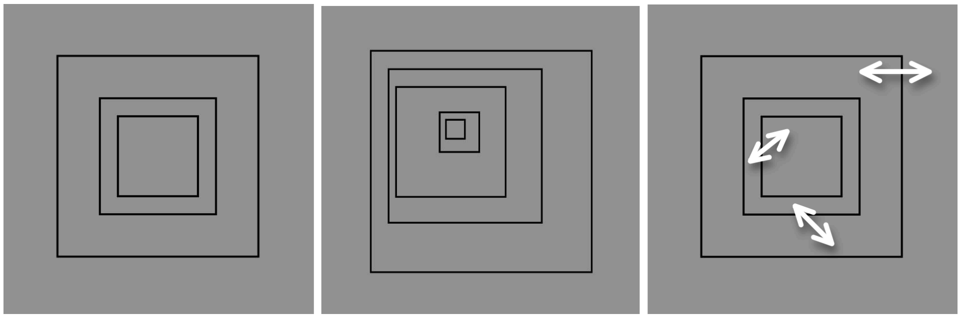


Figure 4.2: Example stimuli for Experiment 1. Figures represent a subset of the screen. *left* concentric squares, *center* center of mass jitter, *right* schematic of motion jitter – see link to movie in method.

ment from 10 possible square sizes, created as described above. Each square was then randomly assigned without repetition a direction of motion, from the set of 8 possible motions (N, S, E, W, NE, NW, SE, SW). Each square moved one pixel in its assigned direction, reversing direction each frame for the duration of the presentation. The frame rate on the testing computer was 60 hz. Center of mass squares were created in a similar manner as the concentric squares, except the size of the squares ranged from 34 x 34 pixels to 440 x 440 pixels. The difference in square sizes ranged from 34 to 44 pixels. Square placement for each display was such that the largest square was presented centrally, and then each additional inner square in order of size was moved off center in a random direction and amount with the constraint that the minimum distance between any two edges had to be at least 10 pixels. Participants performed the experiment on the same computer and in the same testing room. All stimuli were created in Matlab using the Psychophysics Toolbox extensions and were presented against a gray background (Brainard, 1997; Pelli, 1997; Kleiner et al, 2007). Videos of example trials can be found as supplementary information here: `https://www.dropbox.com/sh/oklv8emwjcq2s5k/AACjKlE1Oq5WHoP8LbCpolDsa?dl=0`

PROCEDURE

Subjects received instructions to report the number of squares they saw on the screen as quickly and as accurately as possible. Subjects recorded their response via the number keys on the keyboard. In written and verbal instructions, we avoided using terminology such as 'counting' to avoid biasing the subjects' enumeration strategy and instead asked subjects to report 'how many' target items were present. To reduce end effects we did not inform subjects as to the maximum number of squares possible.

The experiment was presented in 3 blocks, one for each stimulus type. Subjects completed a short practice before starting the experiment consisting of 14 trials per block. The full experiment included 210 trials per block (30 presentations x 7 numerosities). Each block contained displays of the same display type, and the order of the blocks was counterbalanced across subjects. The order of the displays within a block was determined randomly. Each trial consisted of: 1000 ms fixation cross, 200 ms presentation, grayscale noise mask until response. Every 50 trials, the participants were given the option to take a self-timed break before continuing.

4.3.3 ANALYSES

The analyses performed were similar to those used in Porter et al. (2016). These consisted of first testing for the presence of a subitizing elbow in each condition by comparing the error slopes in the subitizing range and the counting range for each individual. To identify the point of the subitizing elbow in each individuals error rates, we used a piecewise linear model from the R library SiZer (Sonderegger, 2012). The differences in slopes between individual best-fit counting and subitizing ranges for each display type were entered into 1-tailed paired t-tests; the expectation was that compared to the subitizing range the counting slope would be greater, and the difference therefore significantly positive. For these 1-tailed paired t-tests we report two-tailed 90% confidence intervals in our results tables, as the lower bound of a two-tailed 90% confidence interval is mathematically equivalent to a single-tailed 95% confidence interval. For all tests, we calculated two effect sizes: Cohen's d for a paired design ($d = \frac{M_{diff}}{s_{av}}$), and an unbiased estimate of Cohen's d ($d_{unb} = (1 - \frac{3}{4df-1}) * d$) (Cummings, 2012).

To compare trends in performance across the three display types, we performed a repeated-measures ANOVA. A Greenhouse-Geisser correction was applied when conditions of sphericity were not met.

4.3.4 Results

We first tested for evidence of subitization by comparing slopes between the counting and subitizing ranges. (See Table 4.1 for Experiment 1 statistics.) None of our conditions exhibited a subitizing elbow, indicating the slope within the counting range was not statistically significantly steeper than the slope in the subitizing range.

We then investigated the effects of display type on performance with a repeated-measures ANOVA. There was no significant main effect of display type (F(2,22) = 0.42, *p* = .665). There was a significant main effect of number (F(2.09,22.98) = 40.21, *p* < .001) and no significant interaction between number and stimulus type (F(12,132) = 0.65, *p* = .796). See Figure 4.3 for error rates.

4.3.5 Discussion

We proposed two hypotheses as to why performance indicative of subitizing does not occur for concentrically presented squares. First, we suggested that the ambiguity

Table 4.1: Statistical results testing the presence of subitizing best fit models. '$d - unb$' stands for d-unbiased, as calculated from Cohen's-d. For the one-tailed t-tests examining the presence of a subitizing elbow, we report a two-tailed 90% confidence interval. See analyses of Experiment 1 for more details.

Statistical Results: Experiment 1								
	df	T	p	$\overline{difference}$	sd	90% CI	Cohen's d	$d - unb$
Subitizing Elbow: Difference in slope (Counting - Subitizing)								
Concentric	11	-1.68	.939	-0.29	0.60	[-0.83, 0.25]	-0.74	-0.69
Motion Jitter	11	-1.73	.944	-0.26	0.53	[-0.74, 0.21]	-0.81	-0.75
Center Jitter	11	-0.66	.738	-0.078	0.41	[-0.45,0.29]	-0.32	-0.30

of line ownership could interfere with parallel individuation. We added motion to each square in the display to help establish line ownership, and did not observe a subitizing elbow in the error rates of our participants. Second, we hypothesized that the individuation mechanism may depend upon unique centers of mass. To remove this factor, we jittered the location of the squares so that they did not share a center, and still did not observe subitizing. These results suggest that the parallel mechanism is not failing in the case of concentric squares due solely to line ownership ambiguity or a shared center of mass.

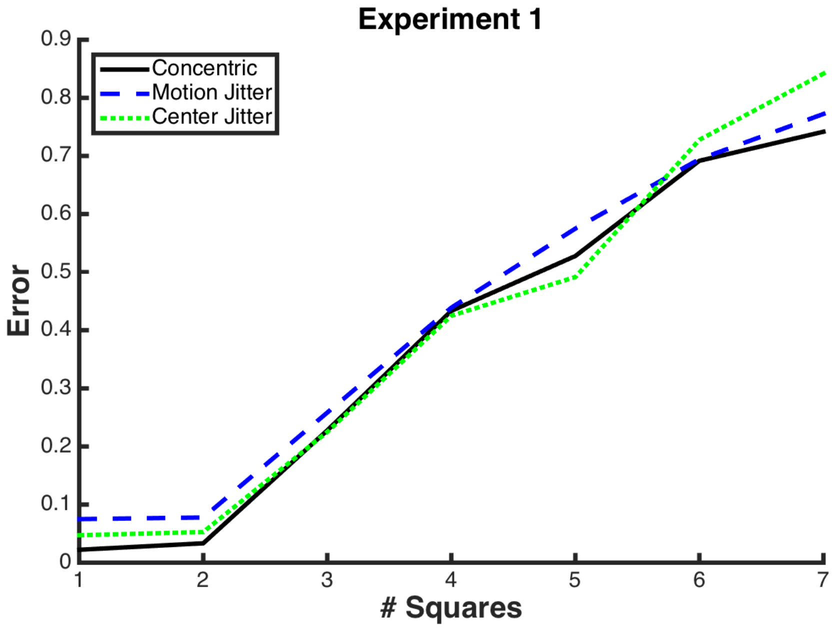


Figure 4.3: Error rates for Experiment 1. Results for Experiment 1 showing average error rates.

4.4 EXPERIMENT 2

4.4.1 INTRODUCTION

In Experiment 2, we tested whether the lack of parallel individuation observed in the concentric square stimuli is due to the inner squares being completely enclosed within the outer squares. It could be that the parallel individuation mechanism selects items based on the enclosed border; if the exterior square 'owns' the space occupied by the inner squares, the inner squares may not be able to be individuated. To test this, we removed one side of the squares to create open squares that were identical to the concentric stimuli, except for the lack of bounding enclosure. We removed the bottom side to create stimuli that were more realistic: arches. We created a third condition with the lines of each arch extended to a common termination line, to further break the percept of complete enclosure and eliminate the potential percept of depth.

4.4.2 METHOD

PARTICIPANTS

Twelve Harvard University students participated for compensation of either $10 or course credit. All participants provided informed consent, as approved by the Committee on the Use of Human Subjects in Research at Harvard University. All participants were debriefed about the purpose of the study and supplied with supplemental reading after completion of the experiment.

STIMULI

Displays consisted of three types of stimuli: concentric squares, open squares, and even-bottom squares (Figure 4.4). The number of squares present in each display for all three conditions ranged from 1 to 7. Each presented stimulus was uniquely created for each subject. Concentric square stimuli were created using the same procedure as Experiment 1. Open Squares were created the same way as concentric squares, with the subtraction of the bottom side. The even-bottom squares were created the same way as well, except the left and right sides of each square were extended to match the bottom of the largest square. Participants performed the experiment on the same computer and in the same testing room. All stimuli were created in Matlab using the Psychophysics Toolbox extensions and were presented against a gray background (Brainard, 1997; Pelli, 1997; Kleiner et al, 2007). Videos of example trials can be found as supplementary information here: `https://www.dropbox.com/sh/oklv8emwjcq2s5k/AACjKlE1Oq5WHoP8LbCpolDsa?dl=0`

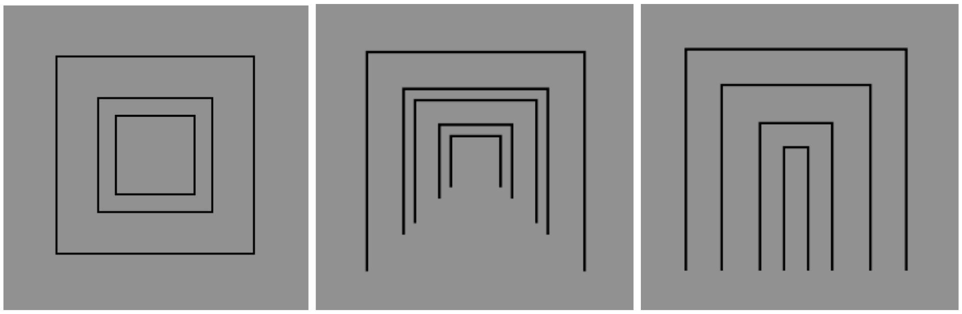


Figure 4.4: Example stimuli for Experiment 2. Figures represent a subset of the screen. *left* concentric squares, *center* open arches, *right* even-bottom arches

Procedure

The procedure of Experiment 1 was repeated, only changing the stimulus conditions.

4.4.3 Analyses

The same analyses were performed as detailed in Experiment 1.

4.4.4 Results

We first tested for evidence of subitization by comparing slopes between the counting and subitizing ranges. (See Table 4.2 for Experiment 2 statistics.) None of our conditions exhibited a subitizing elbow, indicating the slope within the counting range was not statistically significantly steeper than the slope in the subitizing range.

We then investigated the effects of display type on performance with a repeated-measures ANOVA. There was no significant main effect of display type (F(2,22) = 1.45, p = .250). There was a significant main effect of number (F(2.64,29.13) = 48.25, p < .001) and no significant interaction between number and stimulus type (F(12,132) = 0.96, p =

.490). See Figure 4.5 for error rates.

Table 4.2: Statistical results testing the presence of subitizing best fit models. '$d - unb$' stands for d-unbiased, as calculated from Cohen's-d. For the one-tailed t-tests examining the presence of a subitizing elbow, we report a two-tailed 90% confidence interval. See analyses of Experiment 1 for more details.

Statistical Results: Experiment 2								
	df	T	p	$\overline{difference}$	sd	90% CI	Cohen's d	$d - unb$
Subitizing Elbow: Difference in slope (Counting - Subitizing)								
Concentric	11	-0.63	.728	-0.07	0.37	[-0.40, 0.27]	-0.34	-0.31
Open	11	-1.92	.959	-0.19	0.35	[-0.50, 0.12]	-1.05	-0.98
Even-Bottom	11	-0.23	.589	-0.02	0.35	[-0.34,0.29]	-0.13	-0.12

4.4.5 Discussion

In this experiment we tested whether removing the feature of complete enclosure from the concentric square stimuli would allow for parallel individuation to occur. Neither removing the bottom edge of the squares nor extending the vertical sides to a common edge resulted in subitizing. These results suggest that removing the bounded enclosure is not sufficient for parallel individuation.

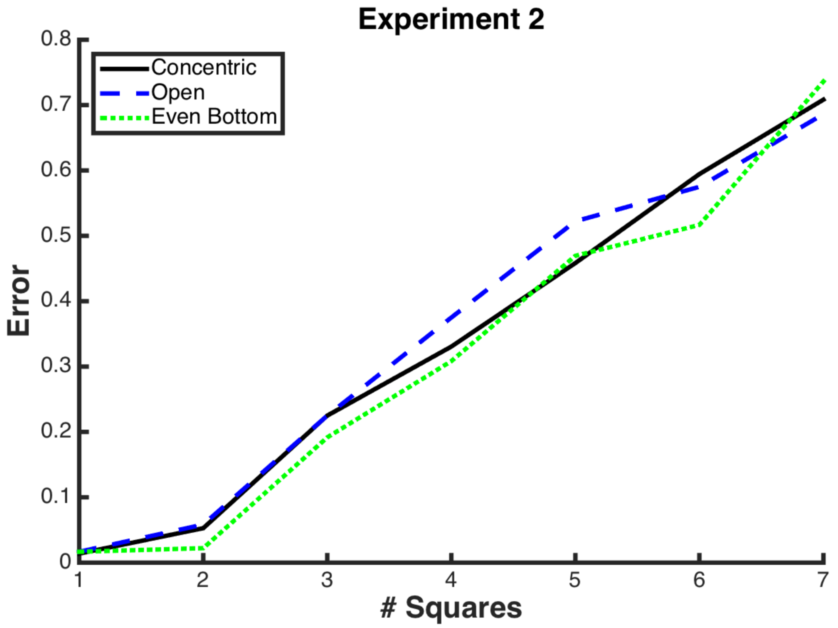


Figure 4.5: Error rates for Experiment 2. Results for Experiment 2 showing average error rates.

4.5 EXPERIMENT 3

4.5.1 INTRODUCTION

In Experiment 2, we tested whether subitizing would occur over concentrically arranged arches, without a bounded enclosure. In Experiment 3, we expanded on this idea of the outer square, or arch, 'owning' the inner space and causing difficulty for the individuation mechanism to separate different targets. We hypothesized that the amount of space each square shared would affect how efficiently they could be individuated. We created three sets of stimuli, consisting of non-overlapping squares, squares overlapping a small amount, and squares overlapping a large amount. We predicted that the amount of overlap would modulate the efficacy of the individuation mechanism; more overlap would decrease the number of items individuated and increase error rates. As overlap increases however, the image becomes more complex and the different items become more difficult to resolve. Previous work with overlapping objects has shown that in visual search shorter presentation times result in better performance than longer presentation times; pre-amodal representations of the partially hidden object are easier to operate over in the search task (Raushenberger & Yantis, 2001). We presented our stimuli for two different durations, 100 ms and 250 ms to represent pre-amodal and amodal representations as in Raushenberger & Yantis (2001), to investigate whether a representation holding a resolved relationship of the overlap in the display helps or hinders parallel individuation.

4.5.2 METHOD

PARTICIPANTS

17 Harvard University students participated for compensation of either $10 or course credit. One participant was removed from analyses for poor performance in the lower numerosities indicative of inattention and no attempt to perform the task. The number of participants was increased compared to Experiments 1 and 2, since the high number of experimental conditions forced us to decrease the number of trials per condition. All participants provided informed consent, as approved by the Committee on the Use of Human Subjects in Research at Harvard University. All participants were debriefed about the purpose of the study and supplied with supplemental reading after completion of the experiment.

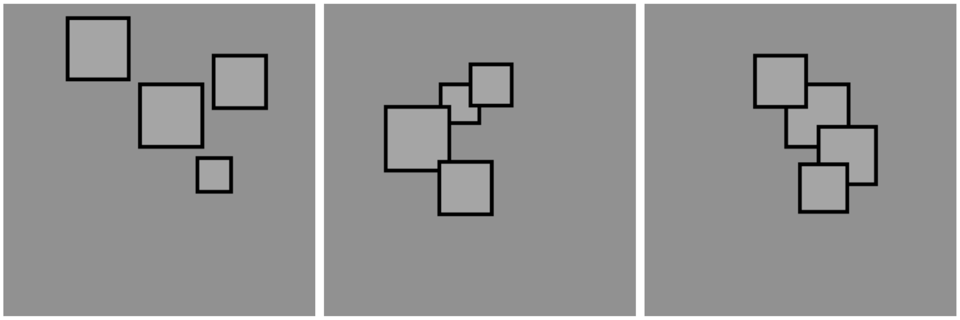


Figure 4.6: Example stimuli for Experiment 3. Figures represent a subset of the screen. *left* no overlap, *center* small overlap, *right* large overlap

STIMULI

Stimulus sets were created for each subject, in advance, and loaded in at the time of data collection. Three types of stimuli were created: no overlap, small overlap, large overlap (Figure 4.6).

Each square size was randomly selected from a range of 30 to 55 pixels in length. The amount of overlap varied by condition, with a fixed gap between two adjacent squares of 5 pixels for the no-overlap condition, an overlap of 11 pixels for the small overlap condition, and an overlap of 20 pixels for the large overlap condition. Within the overlap stimuli, there was a minimum distance required between any two square sides of 10 pixels, to avoid line ownership ambiguity. Additionally, only two squares could exist in any one location, such that each pixel could only contain one instance of overlap. The location of each square was determined as follows. The available space for stimulus creation was constrained to a 250 x 250 pixel window at the center of the screen. The first square was required to exist within center half of this creation window. The location of each additional square was randomly chosen from the set of possible locations that would result in an overlap of the designated amount (either 11 or 20 pixels between

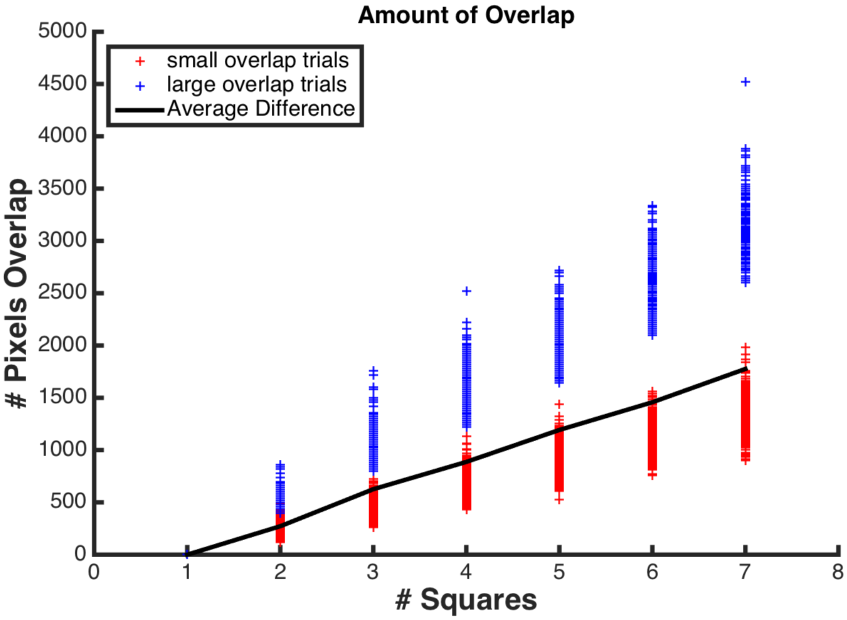


Figure 4.7: Area of overlap in small and large overlap trials. The number of pixels containing overlap in each trial are plotted in blue for large overlap trials, and red for small overlap trials. The average difference in overlap between the large and small overlap conditions for each numerosity is represented as a black line.

square sides, depending on the condition). The amount of overlap was defined based on the x-axis, thus the actual area of overlap could vary depending on the relationship of overlapping stimuli on the y-axis. To ensure our two overlap conditions did differ in the area of overlap, we calculated the area of overlap in each trial for all subjects, and calculated the difference in average area, as measured by number of pixels, for each number between the large and small overlap conditions (Figure 4.7).

Participants performed the experiment in two testing rooms with identical computer setups and similar lighting conditions. All stimuli were created in Matlab using the Psychophysics Toolbox extensions and were presented against a gray background (Brainard, 1997; Pelli, 1997; Kleiner et al, 2007). Stimuli were filled with a gray slightly lighter than the background to enhance the percept of opacity. Complete stimulus sets for each subject can be viewed as supplementary information here: `https://www.dropbox.com/sh/lcorfh3sslhj75l/AACFRyaX-1jr1njs4xIdqloIa?dl=0`

Procedure

Subjects received instructions to report the number of shapes they saw on the screen as quickly and as accurately as possible. We did not use the term 'squares' to avoid biasing subjects toward amodal completion when performing the task. Subjects recorded their response via the number keys on the keyboard. In written and verbal instructions, we avoided using terminology such as 'counting' to avoid biasing the subjects' enumeration strategy and instead asked subjects to report 'how many' target items were present. To avoid end effects we did not inform subjects as to the maximum number of shapes possible.

The experiment was presented in two halves, each with three blocks. Each block consisted of one stimulus type (no overlap, small overlap, large overlap) and each experiment half consisted of one presentation type (100 ms or 250 ms). Subjects completed a short practice before starting the experiment consisting of 7 trials per block. Due to the increased number of experimental conditions, we had to decrease the number of presentations per condition so the experiment was a tolerable length for subjects. There were six possible stimulus conditions (2 presentation times x 3 overlap variants). For each stimulus condition, ten trials were presented in each block for stimuli that contained only one square, and thus no overlap. Other numerosities were presented for 15 trials per block. The full experiment included 600 trials per block. The order of the blocks, and experiment halves, was counterbalanced across subjects, however within each experiment half the block order remained constant. The order of the displays within each block was determined randomly. Each trial consisted of: 1000 ms fixation cross, either 100 or 250 ms presentation, grayscale noise mask until response. Every 50 trials, the participants were given the option to take a self-timed break before continuing.

4.5.3 ANALYSES

We first tested for the presence of a subitizing elbow in each condition by comparing the error slopes in the subitizing range and the counting range for each individual using a piecewise linear model from the R library SiZer (Sonderegger, 2012). Since we were forced to have fewer observations per condition in this experiment, the individual data were too noisy to fit bilinear models. (See results) We therefore used the average data to report adjusted R^2 from the piecewise linear model as well as the adjusted R^2 of an exponential model and linear model. The exponential modeling was performed in Python using the numpy.exp exponential function and the scipy optimization curve fitting function curve_fit (van der Walt, Colbert, & Varoquaux, 2011) with three parameters estimated: $error = ae^{-b*x} + c$, where x is set numerosity, e is the base of the natural logarithm, and the three estimated parameters are a, b, and c.

To compare trends in performance across the three degrees of overlap, two presentation times, and number, we performed a repeated-measures ANOVA. A Greenhouse-Geisser correction was applied when conditions of sphericity were not met. We further explored the effects of each independent variable using post-hoc pairwise comparisons, using Bonferroni correction for multiple comparisons. We also performed a post-hoc repeated-measures ANOVA only including errors within the subitizing range (1-4) to investigate whether the results seen in the complete ANOVA were driven by errors in the counting range.

We additionally plotted the average responses for each number, to identify whether overlap caused underestimation in number as reported for connected stimuli in some instances (He, Zhang, Zhou, & Chen, 2009; He, Zhou, Zhou, He, & Chen, 2015) or whether overlap would not affect response judgments of connected stimuli as reported in Porter et al. (2016).

4.5.4 RESULTS

Our first test of subitization by comparing slopes between the counting and subitizing ranges demonstrated that the data was too noisy for this analysis at the individual participant level. Noisy data from some participants resulted in bilinear fits that did not characterize the behavior present in the data (Figure 4.8) A complete set of figures with the bilinear fit for each individual for each condition can be found here: https://www.dropbox.com/sh/hlnmeacs41yrzeq/AAAVBN8ugK7pkFECbTRjcvrqa?dl=0

Instead, we fit the bilinear function to the average error rates for each condition, and observed that the slope in the counting range was larger than that of the subitizing range in all six conditions, and the break point of the bilinear fit for each condition was between 3 and 6, performance typical of subitizing. Furthermore, the adjusted R^2 from the bilinear fit and exponential models were larger than the R^2 for the linear model in all six conditions. While the exponential model performed better than the bilinear model in the small overlap 100 ms presentation condition, it is difficult to determine whether this is a significant difference. The overall pattern of results suggests a better fit of the bilinear function across the conditions. See Figure 4.9 for average error rates for each condition, and Table 4.3 for results from each model.

We then investigated the effects of display type on performance with a repeated-measures ANOVA (Table 4.4). There were significant main effects of the amount of

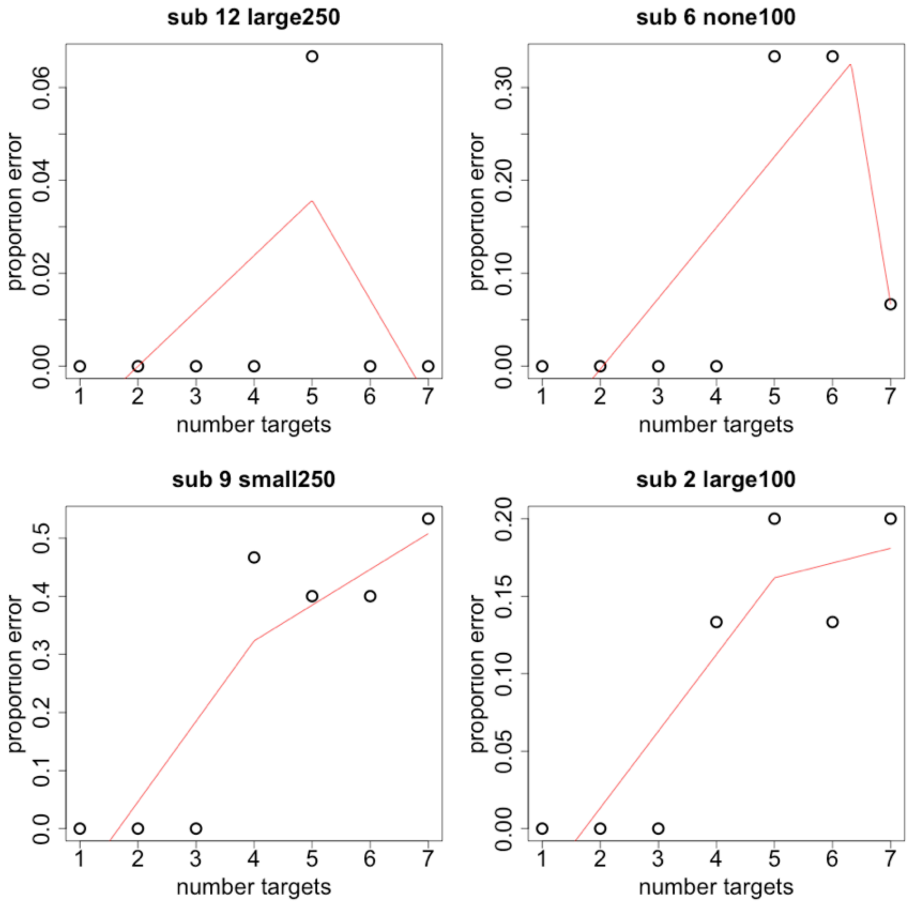
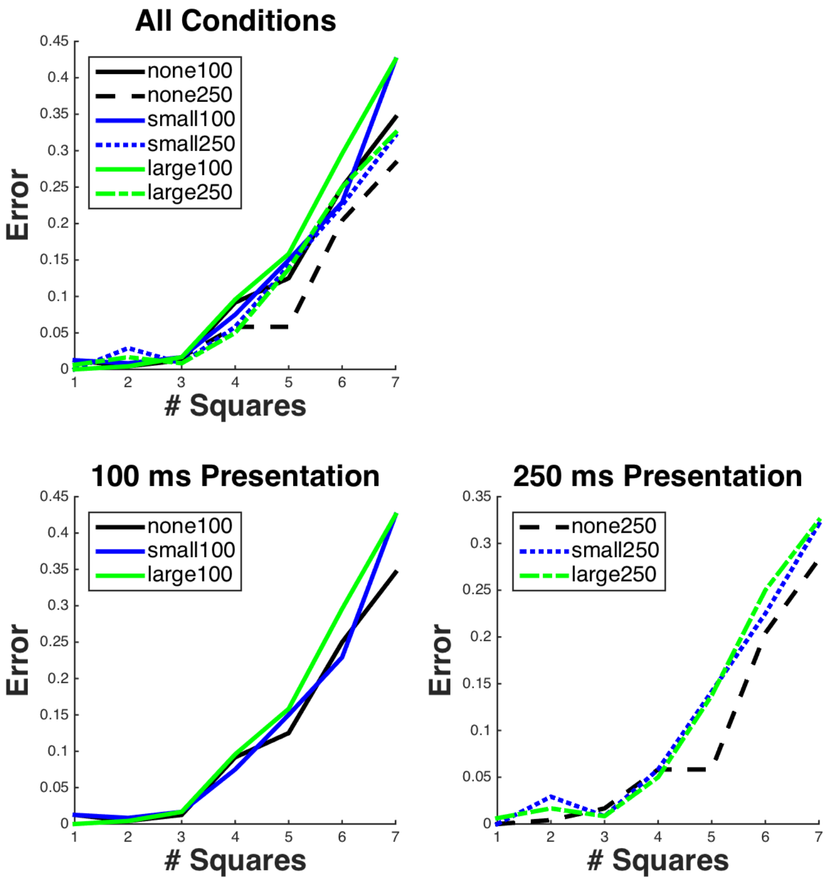


Figure 4.8: Examples of bilinear fit functions for four participants. Note that the bilinear fit does not seem to characterize the behavioral performance.



All Conditions

100 ms Presentation

250 ms Presentation

Figure 4.9: Average error rates for each stimulus condition. top All six stimulus conditions. bottom Data split by presentation time. None, small, and large refer to the amount of overlap.

Table 4.3: Results from bilinear, exponential, and linear models for average error rates. Slopes represent change in proportion errors.

Model Results - Average Data					
	bilinear fit		adjusted R^2		
	diff. slope (C-S)	break point	bilinear	exponential	linear
100 ms presentation					
no overlap	0.089	3.32	0.975	0.960	0.848
small overlap	0.075	5.54	0.966	0.987	0.793
large overlap	0.128	3.51	0.986	0.981	0.865
250 ms presentation					
no overlap	0.079	4.97	0.977	0.925	0.776
small overlap	0.096	3.58	0.992	0.959	0.850
large overlap	0.092	3.60	0.996	0.939	0.833

overlap, presentation time, and number. No interactions between the three manipulations were significant.

Table 4.4: Results from repeated-measures ANOVA investigating the effects of overlap, presentation time, and number on error rates.

Repeated-Measures ANOVA 1-7			
	df	F	*p*
Main Effects			
overlap	(2,30)	3.55	.041
time	(1,15)	7.29	.016
number	(2.05,30.79)	33.12	$< .001$
Interactions			
overlap*time	(2,30)	0.56	.577
overlap*number	(4.27,64.03)	1.74	.149
time*number	(2.09,31.39)	1.79	.182
overlap*time*number	(5.59,83.89)	.689	.649

To investigate the differences in error rates driving the main effects for each condition, we performed post-hoc pairwise comparisons (results in Appendix Tables A.1-A.3). The main effect of overlap seemed to be driven by a significant difference in error rate between the no overlap and large overlap conditions ($p = .027$), with the large overlap resulting in more errors. There was no significant difference between small overlap and either no overlap or large overlap. There also was a significant difference in presentation time, with 100 ms displays resulting in greater errors than 250 ms displays (*p* = .016). The main effect of number of squares seems to be driven by differences in error rates between the large and small numerosities (Figure 4.10). No significant differences between displays including 1 to 4 squares were observed, whereas there were significant differences between displays containing 5, 6, and 7 squares. This pattern is consistent with a near flat slope observed in the subitizing range, and larger costs for each additional square in the counting range. In each pairwise comparison, the mean error rate was always larger for the larger numerosity.

Given the insignificant pairwise comparisons between displays containing 1-4 squares, we performed a second repeated-measures ANOVA to test whether the main effects we reported were driven by differences in the counting range. We observed a significant main effect of number (*p* = .01) but no significant main effects of overlap, or presentation time. There were no significant interactions (Table 4.5). This suggests that the main effects observed in Table 4.4 were driven by the higher numerosities.

Finally, we observed no evidence in underestimation in responses within the subitizing range for overlapping stimuli or any of the stimulus conditions (Appendix Figure A.5). Some underestimation was observed for displays containing 6 or 7 squares with a presentation time of 100 ms, and this existed for all three overlap conditions.

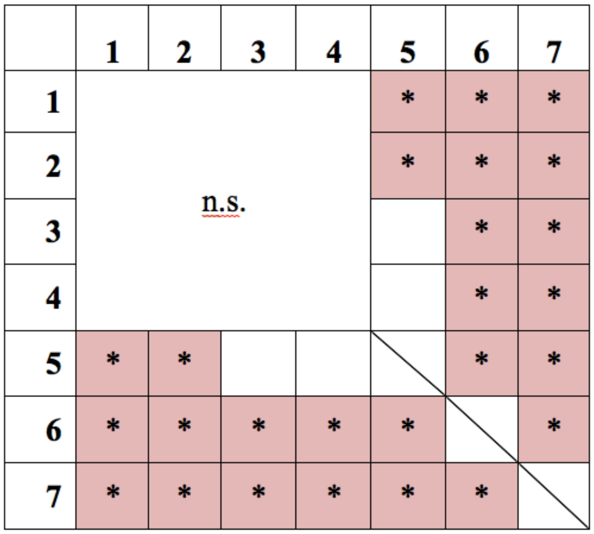
4.5.5 DISCUSSION

In this experiment we tested whether the amount of space shared between items to be individuated would affect parallel individuation performance, by manipulating the area of overlap existing between target squares. We additionally manipulated pre-

Table 4.5: Results from repeated-measures ANOVA investigating the effects of overlap, presentation time, and number on error rates for displays containing only 1 to 4 squares.

Repeated-Measures ANOVA 1-7			
	df	F	*p*
Main Effects			
overlap	(1.46,21.92)	0.04	.961
time	(1,15)	1.72	.210
number	(1.11,16.67)	8.14	.010
Interactions			
overlap*time	(1.76,26.42)	0.22	.777
overlap*number	(2.48,37.26)	0.42	.706
time*number	(1.13,19.67)	2.81	.101
overlap*time*number	(2.84,42.53)	0.70	.551

sentation time, to investigate whether individuation would be more efficient over a representation including resolved amodal completion. A bilinear model best fit the average data, suggesting the presence of a subitizing elbow in all six conditions. However, we found that a large amount of overlap resulted in statistically more errors than no overlap, and that performance was significantly worse in the 100 ms than 250 ms presentation condition. Given the lack of statistically significant differences in the post-hoc pairwise comparisons for errors in displays containing 1-4 squares, we performed a post-hoc repeated-measures ANOVA to investigate effects of overlap and time solely in the subitizing range. Within the smaller set sizes, no significant effects of overlap or presentation time were observed. This suggests that parallel individuation can occur even in the presence of overlapping targets, and over representations that do and do not include amodal completion. For the larger numerosities however, we believe that performance is better with less overlap and a longer presentation time that allows for amodal completion. This conclusion is also consistent with the underestimation observed in the 100 ms presentation time (Appendix Figure A.5).



	1	2	3	4	5	6	7
1	n.s.				*	*	*
2					*	*	*
3						*	*
4						*	*
5	*	*				*	*
6	*	*	*	*	*		*
7	*	*	*	*	*	*	

Figure 4.10: Statistical results for pairwise comparisons of average error rates for each numerosity. A * indicates a comparison that was statistically significant. A Bonferroni correction for multiple comparisons was applied. See Appendix Table A.3 for detailed results.

4.6 General Discussion

Despite the long history of subitizing within the context of parallel individuation, the features necessary for this highly accurate and rapid selection and enumeration of objects is still unknown. Over three experiments, we attempted to narrow the hypothesis space of possible stimulus features that could be required for parallel individuation to occur. In Experiments 1 and 2, we manipulated a known case of failure, concentric squares, to eliminate potential reasons for a lack of parallel individuation. In Experiment 1, we provided evidence that resolving line ambiguity and creating unique centers of mass are not sufficient for subitizing to occur. In Experiment 2, we showed that removing the feature of bounded enclosure is also not adequate for concentrically organized stimuli to be subitized. In Experiment 3, we investigated whether increasing the amount of overlap between targets would affect subitizing performance, and found no effect of overlap in the subitizing range. We also manipulated presentation time to identify whether parallel individuation operates over pre-amodal representations or whether a longer presentation time allowing for resolution of occluded areas would improve performance. We found no effect of presentation time within the subitizing range, suggesting that the parallel individuation mechanism can operate over both pre-amodal and completed amodal representations.

Our initial hypothesis was that the increased competition between target squares caused by overlap would affect subitizing performance negatively as the amount of unique space occupied by each item decreased, as several studies have emphasized the importance of space in individuation (Atkinson et al., 1976; Franconeri et al., 2010; Shim et al., 2008). While we demonstrated a lack of competition from overlap in Experiment 3, we maintain that the spatial arrangement of targets is important for parallel individuation. We propose that successful subitizing is observed when targets can be selected based on attention guiding features (Wolfe & Horowitz, 2004) as well as occupy a unique location in space. We define a 'unique' location as occurring outside the border, whether literal or inferred closure, of any other target. We suggest that subitizing performance results from three stages of processing that selectively depend on these constraints. We will outline and provide evidence for this model below (Figure 4.11).

In order for parallel individuation to occur, items must first be segmented from the background. We suggest that for successful individuation, items must be discriminable from the background, any distractors, and each other, without the need for attention demanding processing. The visual features that guide attention as opposed to demanding attention have been listed in reference to visual search (Wolfe & Horowitz, 2004) and align nicely with evidence from subitizing. Wolf and Horowitz describe color and orientation as features that "undoubtedly" guide the allocation of attention. Subitizing

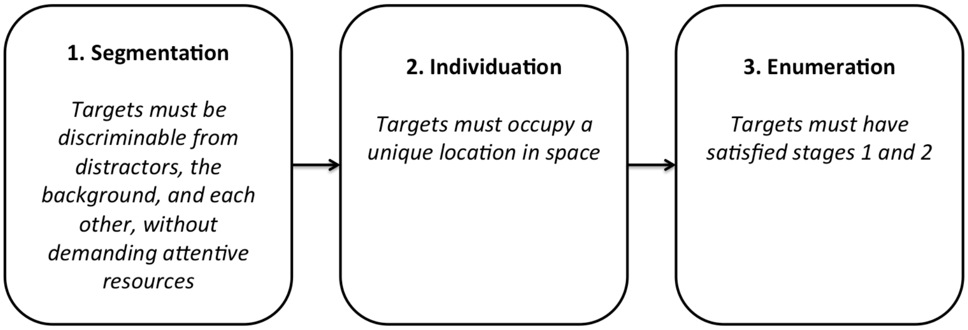


Figure 4.11: Three stage model of parallel individuation leading to subitizing performance.

has been demonstrated when target stimuli differ from distractors by color or orientation (Trick & Pylyshyn, 1993), as well as groups of targets defined by color (Watson et al., 2005). Furthermore, shape, curvature, luminance polarity, and pictorial depth cues are listed as "probable" attributes guiding attention (Wolf & Horowitz, 2004). Evidence of subitizing has been demonstrated when items are grouped by shape, or differ in shape from distractors (Trick & Enns, 1997; Trick & Pylyshyn, 1993). Changes in curvature also lead to evidence of subitizing, even when part of a single object (Porter et al., 2016). Subitizing also occurs when there is enough luminance between target and background for detection, with no change in subitizing limit as the contrast in luminance is modulated past the initial detection (Palomares & Egeth, 2010). In the current study we demonstrated that the pictorial depth cue of overlap also allows for subitizing. Efficiency of visual search also depends on a substantial enough difference between target and distractor that the search does not become demanding of attentional resources (Duncan & Humphreys, 1989). When the identification of targets for enumeration requires a conjunction of features, or the difference between target and distractor is not significant, subitizing performance disappears (Trick & Pylyshyn, 1993).

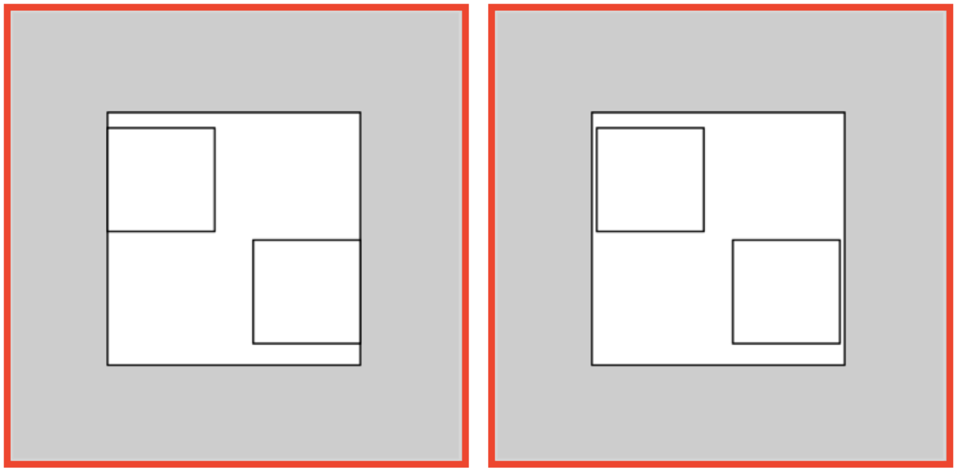


Figure 4.12: Two examples of stimuli that should not result in subitizing due to a failure of individuation but not segmentation. In both cases all three squares can be easily segmented, however two of the squares do not occupy unique locations outside the border of the third square.

It is not enough for items to be segmentable for rapid enumeration to occur. An excellent example of this is the concentric square condition, and the other stimulus conditions used in Experiments 1 and 2. These stimuli lead us to suggest a limitation to the process of individuating each target: the items must occupy a unique location in space. We define this as occurring outside the border of any other target, whether the border is closed or not. All of our stimuli in Experiments 1 and 2 fail this requirement. Even in the arch stimuli, inferred closure of the shape causes the inner arches to exist within the space of the outer arch. Closure could no longer be inferred if a second side was removed, making the arches corners. Trick & Pylyshyn (1993) tested this condition, and indeed observed subitizing. Figure 4.12 demonstrates two examples of easily segmentable stimuli that do not occupy unique locations; we predict parallel individuation would fail in both cases.

If however the stimuli were shifted just slightly so that the smaller two squares exist outside the border of the larger square (Figure 4.13), we would predict subitizing

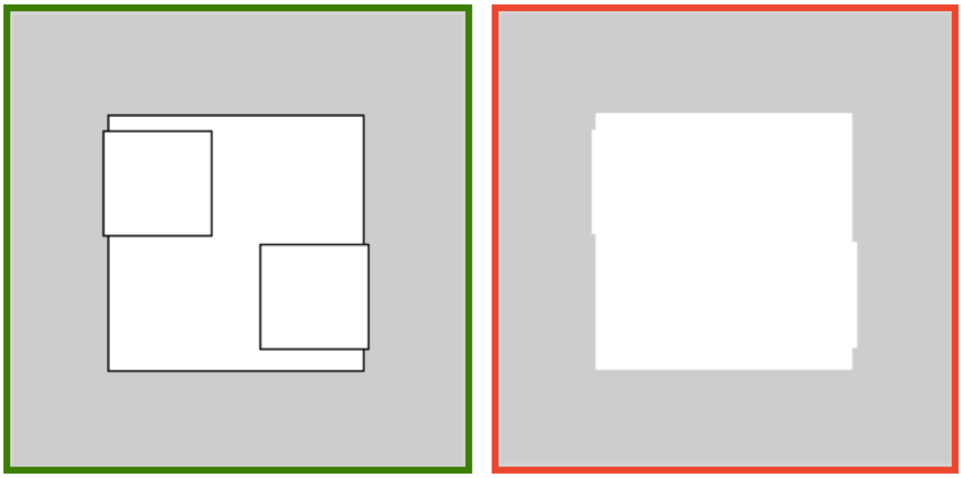


Figure 4.13: Two examples of stimuli that we predict will and will not result in subitizing behavior. *left* Stimulus that satisfies both segmentation and individuation demands *right* Stimulus that satisfies individuation but not segmentation demands.

performance. This minimal amount of unique space cannot drive subitizing behavior alone however; if the contrasting borders are removed and with it pictorial depth, the squares are no longer segmentable.

We believe our definition of unique space may correlate with configural processing such as parts related segmentation based on local minima cues (Barenholtz, Cohen, Feldman, & Singh, 2003; Cohen, Barenholtz, Singh, & Feldman, 2005; Xu & Singh, 2002), or a shape skeleton (Feldman & Singh, 2006). As the smaller squares were moved outside of the larger square in Figure 4.13, the shape skeleton would have changed, with new branches growing toward the two smaller squares. While the skeleton of a shape is processed accurately without awareness (Firestone & Scholl, 2014), the limitations on individuation need to be empirically tested. For example, we predict the no-border stimulus in Figure 4.13 will not be individuated, but larger differences in skeleton paths such as those in Figure 4.14 may be enough for segmentation and then individuation to occur.

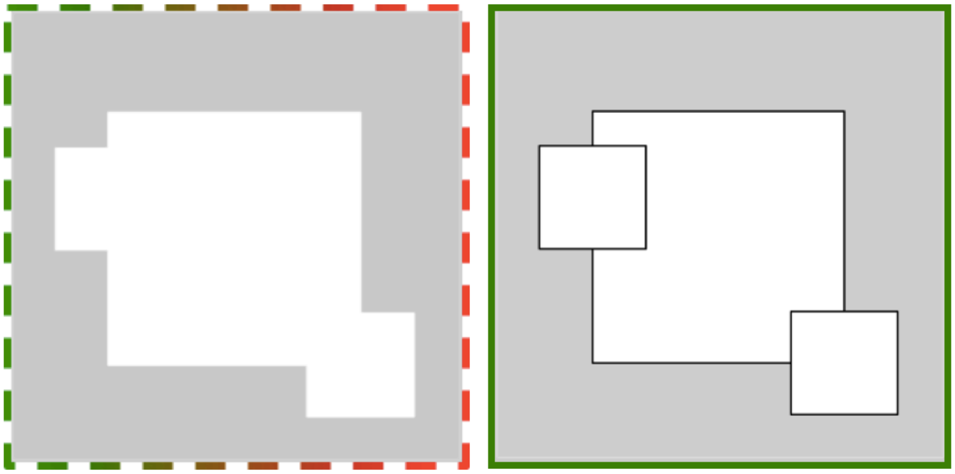


Figure 4.14: Stimulus examples that pass the individuation requirement of occupying a unique location. *left* Information about local minima and the shape skeleton may be enough to drive segmentation in this case, even without border information *right* Same stimulus with border, as used in Experiment 3.

A few more examples demonstrate how a lack of unique space hinders parallel individuation. When participants are asked to enumerate the number of colors in a display, if the dots are intermixed subitizing fails, but if they are grouped according to color subitizing behavior is present (Watson et al., 2005). When items are too close together, such as at a spatial frequency of greater than 8 cycles / degree, the number of items that can be individuated decreases (Atkinson et al., 1976).

The third stage, assignment of a numerosity to the individuated target set, is difficult to disentangle from the individuation process itself. While several studies suggest that multiple tasks draw upon the same individuation mechanism (Anderson, Vogel, & Awh, 2013b; Chesney & Haladjian, 2011; Knops, Piazza, Sengupta, Eger, & Melcher, 2014), it is difficult to separate limitations on individuation from limitations on enumeration. One open question is why there is a slope, albeit shallow, in the subitizing range. The commonly used term ‘parallel individuation’ implies that the individuation stage is not responsible for additional response time or error with increasing set sizes within the subitizing range. Additionally, smaller slopes in studies with fewer options of numerosities to choose from have led to the conclusion that the slope is due to response choice and assignment of a number term rather than individuation (Trick & Pylyshyn, 1994). Before including range of response options in our model, we will await further evidence.

The visual requirements for parallel individuation have yet to be clearly defined. Here we provided evidence that concentrically arranged stimuli cannot be subitized, even when line ambiguity, shared center of mass, and complete enclosure are removed. We further demonstrated that parallel individuation does occur over partially occluded shapes, with temporal presentation times that include both amodal and non-amodal representations. Lastly, we outlined a three stage model with testable predictions for failure and success at the level of segmentation and individuation. We believe that future investigations testing this model will help elucidate the constraints and requirements of the process of parallel individuation.

5

General Discussion

The goal of this thesis was to study the contexts in which parallel individuation does and does not occur, in order to better understand how this mechanism functions. We have shown that object parts, or items grouped by connectivity, can be individuated in parallel as well as items that are ungrouped and do not share a contour. This is contrary to previous evidence suggesting that only spatially separate items could be individuated (Scholl et al., 2001; Watson et al., 2005). Using a similar stimulus set in the context of fMRI, we demonstrated that the number of targets in both connected and unconnected stimuli modulates activity in the inferior and superior IPS. These regions have been implicated in the individuation and identification of objects, respectively (Xu, 2009; Xu & Chun, 2006; Xu & Chun, 2009), suggesting that visual targets need not be disconnected to be treated as separate individuals. Results from multi-voxel pattern analysis indicate that while the inferior IPS holds distinct representations for connected and unconnected stimuli, it functions and individuates items over a flexible definition of figure and ground.

Lastly we explored whether several different candidate visual features are necessary for parallel individuation to occur. Working backward from a condition of subitizing failure, we provided evidence that resolving line ownership, providing distinct centers of mass, and removing complete border enclosure do not result in subitizing performance for concentrically arranged stimuli. We further showed that parallel individuation can occur over two-dimensional overlapping stimuli, and subitizing behavior is not altered by the amount of overlap. Performance within the subitizing range for these stimuli additionally was not affected by presentation time; longer durations allowing for amodal completion of the overlapping shapes did not improve subitizing performance. Using evidence from these experiments and those previously reported in the literature, we proposed a model for parallel individuation that involves three separate stages: visual segmentation, individuation, and enumeration. This model suggests that successful segmentation relies on targets that are discriminable without demanding attention, and that individuation relies on targets occupying a unique location in space.

5.1 Generalization of the individuation mechanism

The model we described in the last paper of this thesis included a separate stage involving enumeration, thus allowing for task specific constraints. While we have cited evidence from several tasks believed to be dependent upon parallel individuation, we have yet to argue that multiple tasks actually depend on the same individuation mechanism. We have been preferentially discussing evidence from multiple-object tracking tasks and rapid enumeration (subitizing) tasks, because they share the most supporting evidence of a shared mechanism. First, there is some evidence that both subitizing and multiple-object tracking demonstrate a processing advantage for stimuli presented bilaterally. Alvarez and Cavanagh (2005) concluded that multiple-object tracking relies on independent resources for the left and right hemifields, allowing for better performance than for stimuli presented unilaterally. Railo (2014) also demonstrated that subitizing results in better performance and faster reaction times for stimuli that are presented bilaterally. Not all evidence supports a bilateral advantage for subitizing however (Delvenne, Castronovo, Demeyerre, & Humphreys, 2011), forcing us to only tentatively accept this as potential support for similar mechanism underlying the two tasks.

There have been some skeptics as to the parallel nature of individuation within the context of multiple-object tracking. Yantis (1992) suggested that rather than there being a limited number of indices that can be selected and attended independently, small sets of objects can be tracked by expanding the scope of attention and perceiving the objects as vertices of a single, non-rigid shape. With this account, attention would be directed to a single grouped object instead of multiple disparate entities, an idea that is similar to the pattern matching theory put forth by Mandler and Shebo (1982) to explain subitizing behavior. However, one could argue that within the case of multiple-object tracking the constantly changing form of the shape would require independent updating of the location of each corner. More recent work has argued for a parallel account of multiple-object tracking, in contrast to rapid and serial shifts of attention (Howe, Cohen, Pinto, & Horowitz, 2010). This is further supported by evidence using event-related potentials (ERP), showing that attention can be allocated in parallel to multiple objects with independent time courses measured for each attended object (Elmer & Grubert, 2014).

The common behavioral limitations observed across tasks have also been used as an argument for a common individuation mechanism. Several tasks have shown an ability to efficiently process about 4 items. Behavioral subitizing limits (Kaufman et al., 1949) tend to match up with those reported in multiple-object tracking (Pylyshyn & Storm, 1988; vanMarle & Scholl, 2003) and visual working memory tasks (Todd & Marois, 2004), at 4 or 5 items. However, when we look at studies using EEG, the number of items processed in parallel is nearly always 3, for both multiple-object tracking tasks (Drew & Vogel, 2008) as well as rapid enumeration tasks (Anderson, Vogel, & Awh, 2013a; Ester, Drew, Klee, Vogel, & Awh, 2012; Mazza, Pagano, & Caramazza, 2013; Pagano & Mazza, 2013). This is consistently a smaller individuation range than observed in behavioral (Trick & Pylyshyn, 1994) or functional neuroimaging measures (Cutini et al., 2014). One potential reason for this is that the number of items individuated is measured using the N2pc component, which is a contralateral measure. Thus, the target items are always presented in one hemifield. This fact could indirectly support a mechanism that benefits from bilateral presentation, as does multiple-object tracking (Alvarez & Cavanagh, 2005). We see even further evidence for a common limiting mechanism in the simultaneous representations of action plans (Gallivan, Chapman, Wood, Milne, Ansari, Culham, & Goodale, 2011). There is some evidence that within multiple-object tracking the number of items tracked in parallel can increase to 8 targets, if the targets are spaced far enough apart (Alvarez & Franconeri, 2007). This increased limit could result from the decreased precision with which targets need to be represented. If target locations are more likely to be stable over time due to the larger spacing between other targets and distractors, it may be more possible for shifts of attention to occur, extending the limit of items tracked overall while individuating a subset at any one time.

If multiple tasks do have a common limited capacity mechanism, they should draw upon the same resource. One study has directly investigated whether subitizing and multiple-object tracking share a mechanism. Chesney and Haladjian (2011) employed the logic that if two tasks share a mechanism and limited amount of resources, executing both tasks at the same time would limit performance on the secondary task. Using this dual-task paradigm they found that as the number of objects tracked increased, the number of items enumerated with subitizing-like performance decreased, resulting in an overall aggregate of about 4 objects accurately tracked and enumerated in each subject. Similar results were also found when contrasting enumeration and visual working memory, with performance indicative of a shared mechanism trading off between the two tasks (Piazza, Fumarola, Chinello, & Melcher, 2011). Work investigating competition between visual working memory and multiple-object tracking suggests that the two tasks compete for resources only when the visual working memory task involves spatial information (Fougnie & Marois, 2006; Zhang, Xuan, Fu, & Pylyshyn, 2010).

The above evidence suggests that the parallel mechanism may be used by multiple tasks involving spatial perception. This is in contrast to the possibility that the subitizing and multiple-object tracking limits observed are due to a general resource limitation. This is in line with results from Atkinson et al. (1976) who found that manipulating the spatial frequency of the objects affected the subitizing limit, but varying the temporal presentation of afterimages did not, suggesting that the limits on individuation are perceptual rather than a limit in a general memory resource. Following this line of reasoning, we would expect only tasks drawing on perceptual resources to show evidence of parallel individuation. Subitizing does seem to occur over tactile stimuli in blindfolded sighted subjects (Plaisier, Bergmann Tiest, & Kappers, 2009), and blind subjects also show performance comparable to that of sighted subjects (Ferrand, Riggs,

& Castronovo, 2010). However, a study asking subjects to enumerate different pitches suggests that subitization does not occur in audition (McLachlan, Marco, & Wilson, 2012). One could argue that the generalization from visual to tactile information suggests a general resource responsible for individuation, however the tactile stimuli are also discriminated based on their location in space. Therefore it is possible that the cortical map (Franconeri, et al., 2013), or indexing system (Pylyshyn, 1989) is not restricted to visual input, but can process any input that exists in a spatial layout.

5.2 Individuation in the brain

Converging evidence from fMRI suggests that the parietal lobe is a good candidate for a parallel individuation mechanism operating over multiple tasks. Activity in the posterior parietal cortex (PPC) is modulated by the number of items held in visual short-term memory (VSTM), plateauing at 4 items (Todd & Marois, 2004). However, the same region that was modulated by VSTM is also modulated by tasks not involving memory, suggesting the modulation of the PPC was not memory specific and rather reflected the selection and processing of a limited number of targets (Mitchell & Cusack, 2008). Data from multiple-object tracking also suggests that the PPC is involved in selecting targets for attention rather than processing the features of each object in detail; the PPC was modulated by the number of targets overall, and not by the speed of the tracked objects (Shim, Alvarez, Vickery, & Jiang, 2010). Regions in the PPC have also been shown to be involved in processing number (Santens, Roggeman, Fias, & Verguts, 2010). One study contrasted visual working memory and enumeration, finding that the PPC had some ability to decode numerosity across tasks, supporting the theory of a shared mechanism for representing sets of individual objects (Knops, Piazza, Sengupta, Eger, & Melcher, 2014).

Within the parietal cortex, the distinction has been made between regions that individuate objects vs. those that track identity. Activity in the inferior intraparietal sulcus (IPS) is modulated by the number of items in a display, whereas modulation in the superior IPS is affected by feature information such as object complexity and the number of unique targets in the display (Xu & Chun, 2006; Xu, 2009). The work described in the second paper of this thesis demonstrated that both of these regions are modulated by an enumeration task, with a plateau in activity consistent with the upper limit of the subitizing range. We further showed that the inferior IPS holds information about visual stimuli relevant for individuating items from a flexible definition of a background, whereas the superior IPS does not. These results are consistent with a flexible individuation mechanism functioning within the inferior IPS over a variety of tasks.

A lot of interesting information about the process of parallel individuation comes from studies using EEG. Three distinct components have been identified in the context of individuation: the N1, occurring 100 ms post stimulus onset and responding to the number of items in the display, the N2pc, a contralateral component occurring 200 ms post stimulus onset responding to the number of targets in the display, and the CDA, a lateralized component occurring 300 ms post onset also modulated by target numerosity (Mazza & Caramazza, 2015). The N2pc has been identified as a candidate measure of individuation due to its modulation by the number of targets in multiple-object tracking (Drew & Vogel, 2008), visual search (Mazza, Turatto, & Caramazza, 2009), and working memory tasks (Anderson, Vogel, & Awh, 2011; Anderson, Vogel, & Awh, 2013b) as well as numerosity (Pagano, Lombardi, & Mazza, 2014). While both the N2pc and CDA have been shown to represent a limited number of target stimuli, recent work has disentangled the role each component plays in individuation. Pagano, Lombardi, and Mazza (2014) compared individual differences in enumeration performance to the responses of each component. They found that while activity in the N2pc is correlated with individual differences in the subitizing range, the CDA was not correlated with these differences, suggesting a role more involved in working memory than individuation.

The three components discussed here nicely fall onto the model for parallel individuation described in the third part of this thesis. The N1 component matches up with the first segmentation stage, where items are segmented from the background but have not yet been selected as targets. Stage 2, individuation, matches up with the N2pc component, which has been shown to reflect a limited number of targets. Finally, we will modify the last stage in our model to simply reflect specific task demands. In the context of visual working memory, this would be the CDA. Within the context of enumeration, one study separated the process of individuation from the representation of number. Using a numerical stroop task, the N2pc increased with the number of items on the display regardless of whether the digit the items represented was congruent or incongruent with the number of items overall (Pagano & Mazza, 2013). These results support our conclusion that the judgment of number occurs as a separate, third step occurring after parallel individuation.

5.3 Attention and individuation

It would be remiss of us to not include a discussion about the relationship between attentive resources and parallel individuation, as whether or not parallel individuation occurs preattentively or engages attention has been a subject of debate. The FINST theory originally stated that individuation occurred preattentively (Pylyshyn, 1989).

One study presenting stimuli as afterimages suggested that subitizing did not require attention, as subitizing did not require eye movements and allowing for longer stimulus presentations did not improve performance (Simon & Vaishnavi, 1996). Another experiment used PET to identify regions involved in the enumeration of targets amongst distractors (Sathian, Simon, Peterson, Patel, Hoffman, & Grafton, 1999). Sathian et al. found activity in the occipital extrastriate cortex and concluded that the involvement of earlier visual regions is consistent with a preattentive visual process. However, the bulk of more recent studies have shown that subitizing performance decreases under conditions of high attentional load (Vetter, Butterworth, & Bahrami, 2008). When subjects are placed under attentionally demanding conditions, their behavior becomes more inaccurate and similar to that of estimation, which is unaffected by attentional load (Burr, Turi, & Anobile, 2010). These results suggest that the near perfect performance that is characteristic of subitizing small sets of items requires attention, whereas estimation does not. Attentional demand also negatively impacted accuracy within the subitizing range when attentional resources were modulated with an inattentional blindness task (Railo, Koivisto, Revonsuo, & Hannula, 2008). Three experiments manipulating resources with an attentional blink task also demonstrated that higher attentional load decreased subitizing performance (Egeth, Leonard, & Palomares, 2008; Oliviers & Watson, 2008; Xu & Liu 2008) The seemingly final nail in the preattentive coffin comes from evidence in EEG. The N2pc component is believed to be involved in the attentional selection of target items within the display (Mazza & Caramazza, 2015). Furthermore, work has shown specific and separate components for both the attentive suppressing of distractors and selection of targets, suggesting both parts of the display require attention and that the N2pc is the summation of these two effects (Hickey, Di Lollo, & McDonald, 2009).

Based on this evidence, we can assume that parallel individuation does involve attentional resources. Thinking about which stages of processing require attentional resources can help explain the different behavior seen across tasks. We propose that attention is a limited resource, drawn upon by both stages 1 and 2 of our model: individuation and task specific demands. When task demands are low, such as in the simple enumeration of spatially separate dots, attention can be dedicated more to the selection of items for processing in parallel (Elmer & Grubert, 2014). If the items were presented focally enough, then full attentional resources could be devoted to individuation without the aid of attentional shifts or eye movements, resulting in apparent preattentive behavior (Simon & Vaishnavi, 1996). However, when task demands are high, such as in visual working memory with complex targets, more attentional resources would be allocated toward the task demand stage, resulting in worse individuation performance. This interaction between individuation and task demands in working memory has been supported by neural data (Xu & Chun, 2006).

5.4 Conclusion

Over the course of this thesis, we strove to better understand the mechanism underlying parallel individuation. To do so, we explored what visual features are necessary for parallel individuation to occur by manipulating the presence and absence of candidate features and contrasting results from both behavioral and neural measures. We demonstrated that targets need not be spatially separate and disconnected for parallel individuation to occur, and that both connected and unconnected targets modulate activity in the inferior IPS. We propose that the inferior IPS is the location of a parallel individuation mechanism that can represent and flexibly select a level of the visual hierarchy within which to define figure/ground relations. Forthcoming work also supports this view, demonstrating that the N2pc component associated with individuation responds to both connected and unconnected target stimuli, similar to the stimuli used here (Poncet, Caramazza, & Mazza, in preparation). The final part of this thesis further explored what kind of visual information is necessary for individuation to occur. We narrowed the hypothesis space of candidate features necessary for parallel individuation, and provided a model of individuation dependent on the spatial relations between targets.

Here we can update our model to include our assumptions, argued based on the broader literature, that the same mechanism underlies parallel individuation in multiple tasks involving spatial information, and that both individuation and task specific demands draw upon a limited attentional resource. We have performed these changes in Figure 5.1, and additionally have assigned both temporal (N2pc) and spatial (inferior IPS) markers to the neural individuation mechanism.

While we believe this thesis has made great progress in understanding the limitations of parallel individuation, there are still many areas of uncertainty. Future work is needed to confirm our three-stage processing theory, and identify specific limitations resulting from each of the tasks involving parallel individuation. More study is also needed to verify which tasks do indeed share a common individuation mechanism. We believe a three-pronged approach would best advance understanding of these issues. Combining behavioral evidence with responses from EEG and fMRI for a single task will allow in-depth comprehension of how different stimuli and tasks affect processing in the inferior IPS and the responses of the N2pc component. The results from these studies could have important implications in how attention is divided and allocated in tasks involving multiple targets.

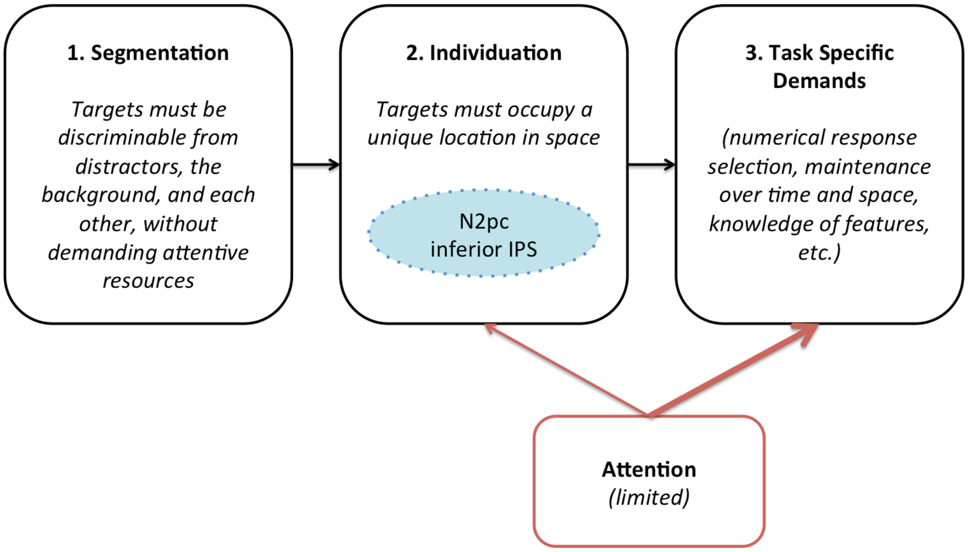


Figure 5.1: Updated task-general three stage model of parallel individuation. Stage 2 is associated with activity in the N2pc electrophysiological component, as well as the inferior IPS neural region. Stage 3 has been generalized to represent task specific demands. Both Stage 2 and 3 draw upon attentional resources; the thickness of the line represents our prediction that Stage 3 may be more attentionally demanding than Stage 2.

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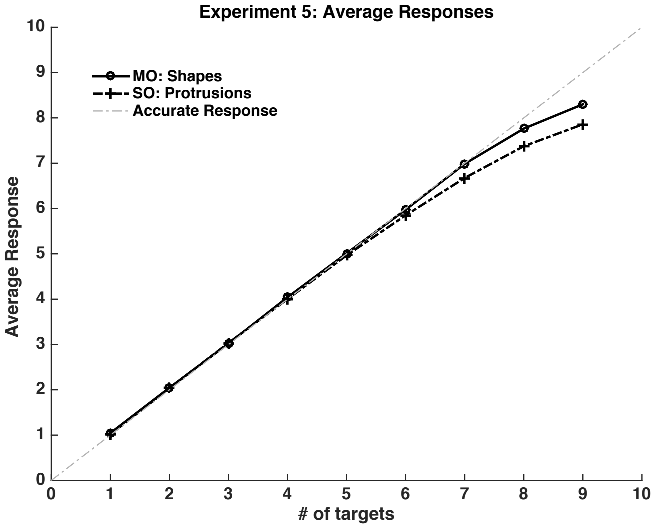
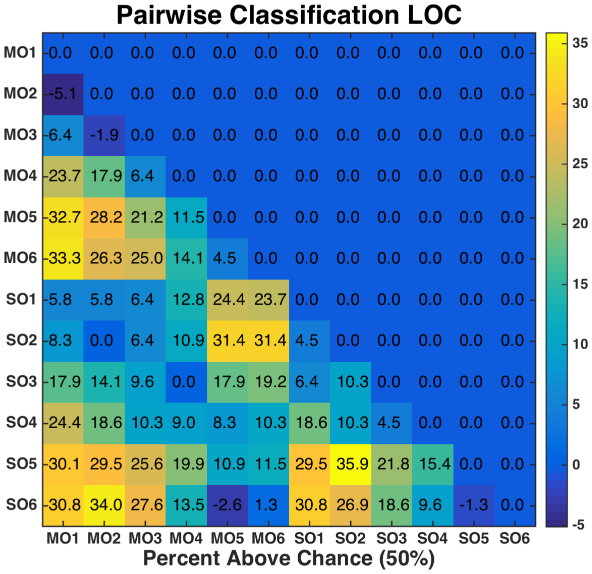
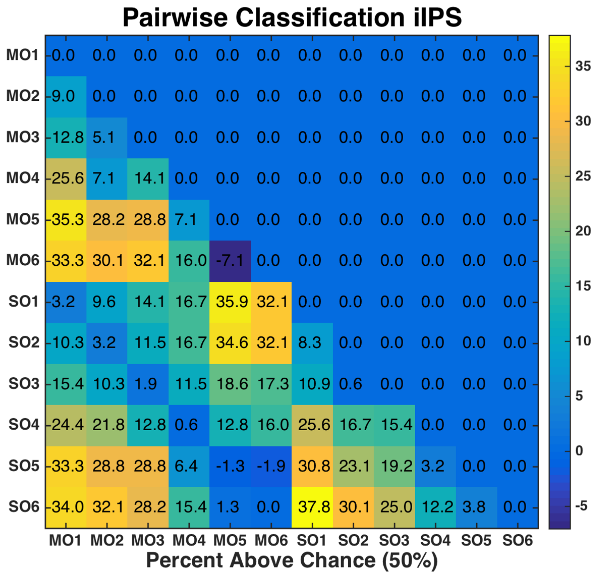


Figure A.1: Chapter 2: Average responses for each display type in Experiment 5. The gray dotted line indicates the correct response. MO = multi-object, SO = single-object



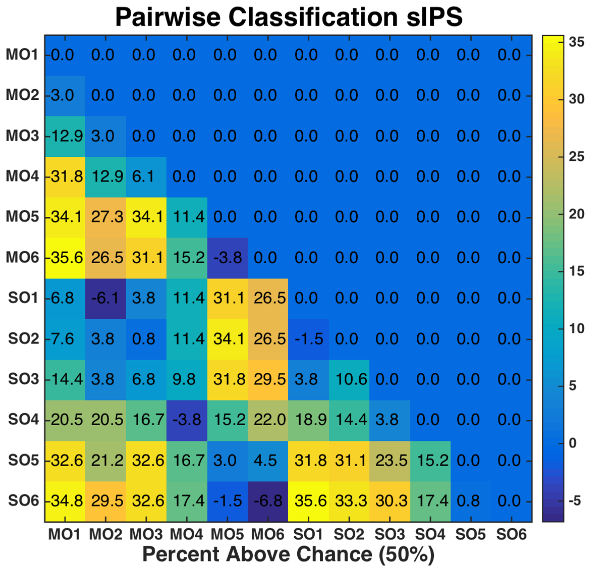
	MO1	MO2	MO3	MO4	MO5	MO6	SO1	SO2	SO3	SO4	SO5	SO6
MO1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO2	-5.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO3	6.4	-1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO4	23.7	17.9	6.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO5	32.7	28.2	21.2	11.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO6	33.3	26.3	25.0	14.1	4.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SO1	5.8	5.8	6.4	12.8	24.4	23.7	0.0	0.0	0.0	0.0	0.0	0.0
SO2	8.3	0.0	6.4	10.9	31.4	31.4	4.5	0.0	0.0	0.0	0.0	0.0
SO3	17.9	14.1	9.6	0.0	17.9	19.2	6.4	10.3	0.0	0.0	0.0	0.0
SO4	24.4	18.6	10.3	9.0	8.3	10.3	18.6	10.3	4.5	0.0	0.0	0.0
SO5	30.1	29.5	25.6	19.9	10.9	11.5	29.5	35.9	21.8	15.4	0.0	0.0
SO6	30.8	34.0	27.6	13.5	-2.6	1.3	30.8	26.9	18.6	9.6	-1.3	0.0

Figure A.2: Chapter 3: Performance of pairwise linear SVM classification for each stimulus condition in LOC. Accuracy reported is percent above chance (50%). MO = multi-object, SO = single-object



	MO1	MO2	MO3	MO4	MO5	MO6	SO1	SO2	SO3	SO4	SO5	SO6
MO1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO2	9.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO3	12.8	5.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO4	25.6	7.1	14.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO5	35.3	28.2	28.8	7.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO6	33.3	30.1	32.1	16.0	-7.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SO1	3.2	9.6	14.1	16.7	35.9	32.1	0.0	0.0	0.0	0.0	0.0	0.0
SO2	10.3	3.2	11.5	16.7	34.6	32.1	8.3	0.0	0.0	0.0	0.0	0.0
SO3	15.4	10.3	1.9	11.5	18.6	17.3	10.9	0.6	0.0	0.0	0.0	0.0
SO4	24.4	21.8	12.8	0.6	12.8	16.0	25.6	16.7	15.4	0.0	0.0	0.0
SO5	33.3	28.8	28.8	6.4	-1.3	-1.9	30.8	23.1	19.2	3.2	0.0	0.0
SO6	34.0	32.1	28.2	15.4	1.3	0.0	37.8	30.1	25.0	12.2	3.8	0.0

Figure A.3: Chapter 3: Performance of pairwise linear SVM classification for each stimulus condition in inferior IPS. Accuracy reported is percent above chance (50%). MO = multi-object, SO = single-object



	MO1	MO2	MO3	MO4	MO5	MO6	SO1	SO2	SO3	SO4	SO5	SO6
MO1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO2	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO3	12.9	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO4	31.8	12.9	6.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO5	34.1	27.3	34.1	11.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MO6	35.6	26.5	31.1	15.2	-3.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SO1	6.8	-6.1	3.8	11.4	31.1	26.5	0.0	0.0	0.0	0.0	0.0	0.0
SO2	7.6	3.8	0.8	11.4	34.1	26.5	-1.5	0.0	0.0	0.0	0.0	0.0
SO3	14.4	3.8	6.8	9.8	31.8	29.5	3.8	10.6	0.0	0.0	0.0	0.0
SO4	20.5	20.5	16.7	-3.8	15.2	22.0	18.9	14.4	3.8	0.0	0.0	0.0
SO5	32.6	21.2	32.6	16.7	3.0	4.5	31.8	31.1	23.5	15.2	0.0	0.0
SO6	34.8	29.5	32.6	17.4	-1.5	-6.8	35.6	33.3	30.3	17.4	0.8	0.0

Figure A.4: Chapter 3: Performance of pairwise linear SVM classification for each stimulus condition in superior IPS. Accuracy reported is percent above chance (50%). MO = multi-object, SO = single-object

Table A.1: Chapter 4: Post-hoc pairwise comparisons of error rates for different amounts of overlap. Values are reported as proportion error.

Pairwise Comparisons - Overlap				
overlap	mean diff.	std. error	*p*	95% CI
small – none	.017	.009	.287	[-0.009,0.042]
large – small	.006	.010	1.00	[-0.020,0.032]
large – none	.023	.008	.027	[0.002,0.044]

Table A.2: Chapter 4: Post-hoc pairwise comparisons of error rates for different presentation times. Values are reported as proportion error.

Pairwise Comparisons - Time				
time	mean diff.	std. error	*p*	95% CI
100ms – 250 ms	.026	0.010	.016	[0.006,0.047]

Table A.3: Chapter 4: Post-hoc pairwise comparisons of error rates for different numbers of squares. Values are reported as proportion error.

Pairwise Comparisons - Number				
number	mean diff.	std. error	*p*	95% CI
2 – 1	.006	.004	1.00	[-0.007,0.019]
3 – 1	.008	.004	1.00	[-0.008,0.024]
4 – 1	.066	.021	.121	[-0.009,0.142]
5 – 1	.123	.031	.027	[0.009,0.237]
6 – 1	.237	.044	.001	[0.078,0.396]
7 – 1	.349	.045	.000	[0.186,0.512]
3 – 2	.002	.005	1.00	[-0.016,0.020]
4 – 2	.060	.022	.294	[-0.019,0.140]
5 – 2	.117	.031	.042	[0.003,0.232]
6 – 2	.231	.044	.002	[0.071,0.391]
7 – 2	.343	.045	.000	[0.178,0.508]
4 – 3	.058	.022	.341	[-0.020,0.137]
5 – 3	.115	.033	.066	[-0.005,0.235]
6 – 3	.229	.044	.002	[0.067,0.391]
7 – 3	.341	.045	.000	[0.178,0.504]
5 – 4	.057	.021	.340	[-0.020,0.134]
6 – 4	.171	.037	.007	[0.036,0.306]
7 – 4	.283	.039	.000	[0.140,0.425]
6 – 5	.114	.031	.044	[0.002,0.226]
7 – 5	.226	.040	.001	[0.081,0.370]
7 – 6	.112	.028	.028	[0.008,0.215]

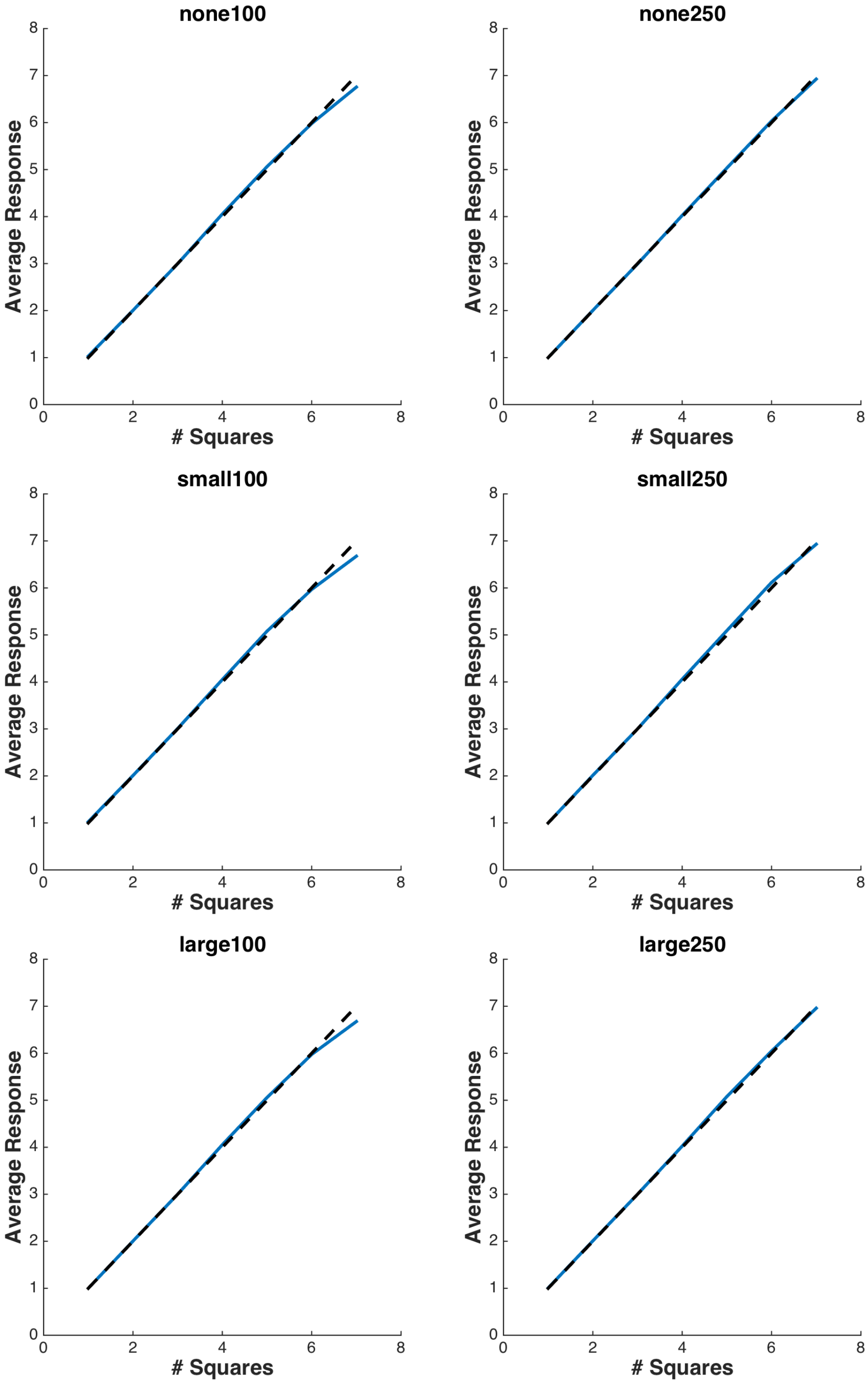
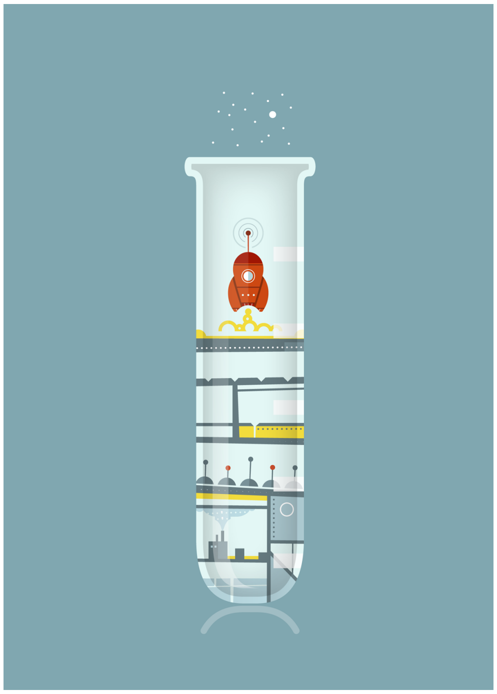


Figure A.5: Chapter 4: Average responses for each numerosity and condition. The dotted line represents perfect performance.



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