

Numerosity adaptation partly depends on the allocation of implicit numerosity-contingent visuo-spatial attention

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Like other perceptual attributes, numerosity is susceptible to adaptation. Nevertheless, it has never been fully investigated whether adaptation to numerosity is fully perceptual in nature or if it stems from the mixed influence of perception and attention. In the present work, we addressed this point throughout three separate experiments aiming at investigating the potential role played by visuo-spatial attentional mechanisms in shaping numerosity perception and adaptation. In Experiments 1 and 2, we showed that the magnitude of numerosity adaptation can be strongly influenced by the distribution of numerosity-contingent visuo-spatial attentional resources during the adaptation period. Results from Experiment 1 revealed a robust reduction of adaptation magnitude whenever a second numerical stimulus was presented in a diametrically opposite location from that of the adaptor, despite this second adapter being neutral as matched in numerosity with the following stimulus displayed in that location. In Experiment 2, we showed that this reduction in adaptation did not occur in cases where the second stimulus was not numerical, suggesting that attentional resources specifically related to numerosity information accounts for the results of Experiment 1. Finally, in Experiment 3, we showed that uninformative visuo-spatial cues shape numerosity discrimination judgments both at baseline and during adaptation. Taken together, our results seem to indicate that visuo-spatial attention plays a relevant role in numerosity perception and that adaptation to numerosity is actively influenced by this cognitive process.

Introduction

The ability to achieve an approximate but rapid and reliable estimate of the quantity of items in a

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set appears to be ubiquitous across different animal species (Dehaene, 2011) and, like other perceptual attributes (e.g. motion, size, color, and orientation), this ability has found to be susceptible to adaptation. In their seminal study, Burr and Ross reported that a prolonged exposure to a set with numerous items induced a robust underestimation of the numerosity of stimuli subsequently presented in the same spatial location, with the opposite effect (overestimation) being a consequence of adaptation to low numerosities (Burr & Ross, 2008). This result has been widely replicated by a series of studies (e.g. Fornaciai, Cicchini, & Burr, 2016; Liu, Zhang, Zhao, Liu, & Li, 2013; Soltész & Szucs, 2014). However, on the one hand, the idea that adaptation reveals the existence of a specific system dedicated to the analysis of numerosity has been challenged by other studies claiming that numerosity adaptation acts via low-level texture-like mechanisms (Dakin, Tibber, Greenwood, Kingdom, & Morgan, 2011; Durgin, 1995; Durgin, 2008; Leibovich, Katzin, Harel, & Henik, 2017; Tibber, Greenwood, & Dakin, 2012). On the other hand, numerosity adaptation has been found to act across different modalities (i.e. vision, audition, or even actions) and presentation formats (i.e. simultaneous or sequential) suggesting that, at a given stage of the information processing hierarchy, perception of numerical quantities become independent from the features of the stimuli (Anobile, Arrighi, Togoli, & Burr, 2016; Anobile, Domenici, Togoli, Burr, & Arrighi, 2019; Arrighi, Togoli, & Burr, 2014; Burr, Anobile, & Arrighi, 2018; Maldonado Moscoso, Cicchini, Arrighi, & Burr, 2020).

Interestingly enough, whether numerosity adaptation is fully perceptual in nature or, rather, reflects a mixture of perceptual and attentional processes have been poorly investigated so far. Conversely, the impact of attention on adaptation to other perceptual attributes

has received much more interest from the scientific community, although the reported results turned out in being rather mixed. For instance, studies about the effects of attention on motion aftereffects provided results both in favor (e.g. Chaudhuri, 1990; Rezec, Kregelberg, & Dobkins, 2004) and against (e.g. Morgan, 2012; Morgan, 2013) a critical role for the attentional mechanisms (for a meta-analysis on motion adaptation and attention see Bartlett, Graf, Hedger, & Adams, 2019). Similarly, studies on adaptation to size showed that the presentation of a demanding central task during adaptation did not affect its magnitude (Tonelli, Pooresmaeili, & Arrighi, 2020) while explicitly moving attention in the direction of the adaptor stimulus was found to even enhance the aftereffect (Kreutzer, Fink, & Weidner, 2015). Within a higher level of the visual processing hierarchy, attention has been reported to consistently affect the adaptation to stimuli such as faces (Rhodes et al., 2011) or body size (Stephen, Sturman, Stevenson, Mond, & Brooks, 2018).

However, in the field of numerosity perception, no study thoroughly investigated the impact of attention on numerosity adaptation although various works revealed a tight relationship between perception of quantities and attention. For example, it is known that when numbers are within the subitizing range (~ 1 to 4) require the integrity of attentional mechanisms (Olivers & Watson, 2008; Railo, Koivisto, Revonsuo, & Hannula, 2008), then attentional demands remain stable over the estimation range (i.e. the range in which the items in the set are still efficiently segregable from each other) and increase again in the texture-density range when items are so cluttered together to yield a texture pattern (Anobile, Tomaiuolo, Campana, & Cicchini, 2020; Anobile, Turi, Cicchini, & Burr, 2012; Pomè, Anobile, Cicchini, Scabia, & Burr, 2019).

In the present study, we developed three separate experiments, which aimed to shed light on the role of automatic visuo-spatial attentional capture in shaping numerosity adaptation. The aim was to understand whether the amount of numerosity adaptation usually reported in classical discrimination tasks could be, at least partly, explained by the intrusion of uncontrolled visuo-spatial attentional processes. This is because it is known that presenting a stimulus within a given spatial location can temporarily attract or divert the visuo-spatial processing of visual stimuli subsequently presented in the same region of space (e.g. Handy, Jha, & Mangun, 1999; Klein, 2000; Mertes, Wascher, & Schneider, 2016; Müller & Kleinschmidt, 2007; Simons, 2000; Theeuwes & Chen, 2005). In this view, it is possible that the amount of numerosity adaptation is the result of a mixture between perceptual and visuo-spatial attentional mechanisms. To test this hypothesis, in [Experiment 1](#), participants were exposed to two interspersed adaptation conditions, which differed by the presence of one or two adaptors. The

two conditions were theoretically identical in their capability to produce adaptation (because in the double adaptor condition one of the adaptors was always “neutral” to match the numerosity of the stimulus subsequently presented in that location) but differed by the presence of symmetrical versus asymmetrical visuo-spatial numerical percepts during the adaptation period. This simple experimental manipulation allowed us to segregate the contribution of attentional and perceptual processes involved in numerosity adaptation while leaving task execution totally unchanged. In [Experiment 2](#), we used the same paradigm as in [Experiment 1](#), but, in this case, the neutral adaptor was replaced with two bars that had the same aggregate area of the neutral adaptor. So, in the condition of [Experiment 2](#) with two adaptors, we still presented two percepts as in [Experiment 1](#) but, here, one of the adaptors did not contain any numerosity information. With this manipulation, we aimed to investigate whether attentional manipulations obtained in [Experiment 1](#) were induced by attentional resources specifically related to numerical features or generalized to the presence of a stimulus in a given spatial location regardless of it containing numerosity information or not. Finally, in [Experiment 3](#), we used uninformative cues briefly presented before the stimuli for the discrimination task (and, thus, in the adaptation conditions, just after the adaptor offset) to force visuo-spatial attention allocation shifts during the period of time separating adaptor disappearance and the two-alternative choice discrimination judgment. This manipulation allowed us to directly test the influence of involuntary visuo-spatial attentional shifts in both numerosity discrimination and adaptation.

General methods

Participants

Twelve participants (mean age = 29.9 years, SD = 3.04 years; 3 men) took part in [Experiment 1](#), and twelve participants took part in [Experiment 2](#) (mean age = 30.9 years, SD = 3.6 years, 3 men) and twelve participants took part in [Experiment 3](#) (mean age = 30.2 years, SD = 3.1 years, 4 men). Five participants took part in all the experiments. Author Paolo A. Grasso took part in experiments 1, 2, and 3, and Giovanni Anobile took part in [Experiment 2](#), whereas all the other participants were naïve to the purpose of the study. All participants had normal or corrected to normal visual acuity and provided written informed consent. The research was approved by the local ethics committee (“Commissione per l’Etica della Ricerca,” University of Florence, July 7, 2020, n. 111).

Apparatus and stimuli

The experiment was performed in a dimly lit, low-noise environment with participants sitting 57 cm away from the monitor. In all the experiments, stimuli were generated with Psychtoolbox 3 (Kleiner et al., 2007). Numerical stimuli consisted of clouds of not-overlapping random dots (half black and half white; diameter: 0.23 degrees) while non-numerical stimuli (only in Experiment 2) were randomly tilted bars (one black and one white; length = 4.92 degrees; width = 0.10 degrees) presented parallel. All stimuli were inserted in a 7 degree diameter circle with its center spaced 10 degrees left or right from the central fixation point. In all the experiments, adaptor and reference stimuli comprised 48 and 24 dots, respectively, while test stimulus randomly varied across eleven numerosities logarithmically spaced from 12 to 48 dots (12, 14, 16, 18, 21, 24, 28, 32, 36, 42, and 48) with all stimuli being always equated in terms of area of convex hull. These characteristics were chosen with the rationale of using stimuli falling within the numerosity regime. This is because it is thought that the perception of higher numerosities falling within the texture-density regime could rely on the activity of a different system (Anobile, Castaldi, Turi, Tinelli, & Burr, 2016; Anobile, Cicchini, & Burr, 2016). In each experiment, half of the participants received adaptation in the left visual field while the other half received adaptation in the right visual field, with the position of the adaptor being constant across all trials and sessions for each participant.

Experiment 1

In Experiment 1, we aimed to investigate the influence of automatic attentional capture produced by symmetrical versus asymmetrical visuo-spatial numerical information during the adaptation period. Most of the numerosity adaptation paradigms consisted of a unilateral presentation of the adaptor stimulus followed by the discrimination of bilaterally presented clouds of dots. This procedure could potentially lead to a mixed influence of perceptual and attentional processes both contributing to shape the reported numerosity adaptation magnitude. Indeed, it is known that presenting a given stimulus in a specific spatial location can temporarily bias subsequent processing of visuo-spatial perceptual information within the same region of space (e.g. Klein, 2000; Mertes, Wascher, & Schneider, 2016; Müller & Kleinschmidt, 2007; Simons, 2000; Theeuwes & Chen, 2005). With the present experiment we, therefore, aimed at disentangling pure perceptual adaptation processes from attentionally

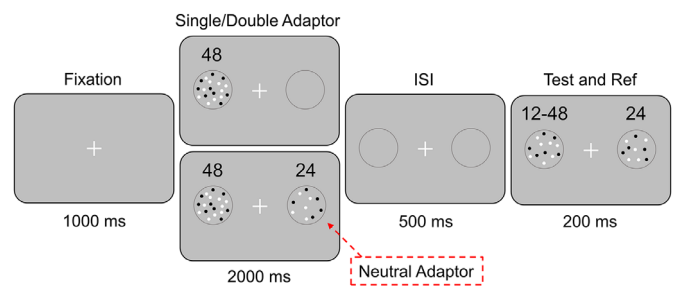


Figure 1. General trial's structure. Adaptor and ISI were not presented during the baseline phase, whereas the initial fixation was not presented during the adaptation phase.

mediated ones. We addressed this issue by comparing adaptation magnitude produced by a unilaterally presented adaptor with those obtained by two bilaterally presented adaptors, one of which being “neutral” as numerically matched to the stimulus subsequently presented in that location.

Experimental paradigm

In the adaptation phase, each trial began with an adaptation period (2000 ms) where the adaptor stimulus could be presented unilaterally (single adaptor condition) or bilaterally (double adaptor condition). In the double adaptor condition, one of the two adaptors was neutral (i.e. having the same numerosity as the reference) and so not expected to affect subsequent numerosity judgements (Aagten-Murphy & Burr, 2016; Burr & Ross, 2008). The two adaptation conditions were randomized on a trial-by-trial basis and were followed by an ISI (500 ms) followed by a simultaneous presentation of test and reference (200 ms). Participants were asked to report which of the two stimuli was more numerous by pressing the left or the right arrow of the keyboard. Baseline consisted in simple discrimination trials between the test and reference with the presentation of these stimuli not being preceded by any adaptation phase (Figure 1). For each numerosity and adaptation condition, 10 trials were collected both in the baseline and in the adaptation phase. Trials with reaction times exceeding three standard deviations from the individual mean were discarded as assumed to reflect a condition of reduced focusing on task execution (mean excluded trials on baseline: 1.5%; single adaptor condition: 1.5%; and double adaptor condition: 2%).

In order to confirm that presenting an adaptor stimulus having the same numerosity of the reference would not influence subsequent numerosity judgments (Aagten-Murphy & Burr, 2016; Burr & Ross, 2008), a control condition was run on a subgroup of participants (i.e. 6). The control condition was identical to the main

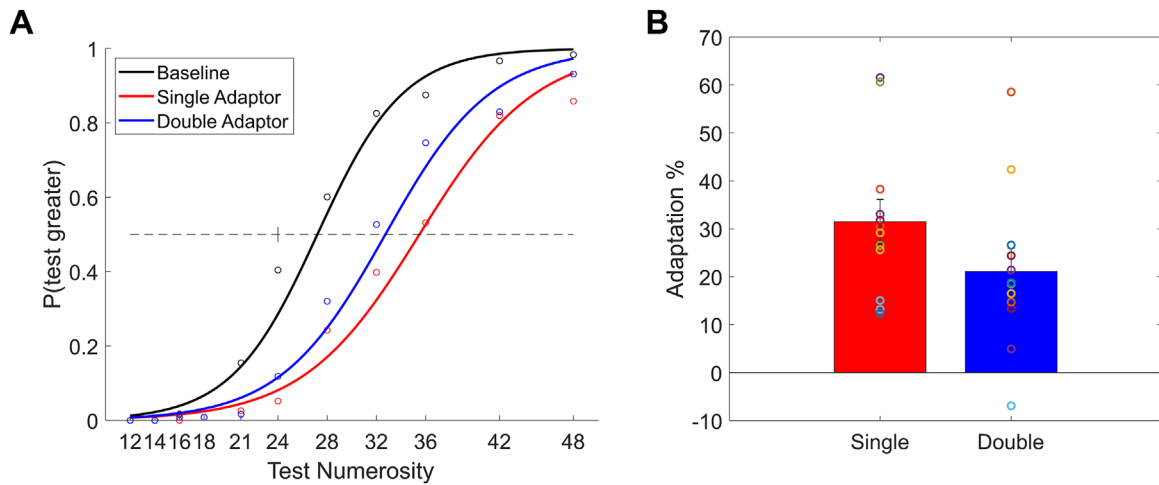


Figure 2. (A) Psychometric fitting of aggregate data for the baseline (black line) and the two adaptation conditions (single adaptor = red line; double adaptor = blue line). (B) Normalized percentage of PSE shift from baseline in the two adaptation conditions. Error bars indicate 1 SEM, whereas circles represent single participants data.

experiment except for the presence of sole neutral adaptors presented both unilaterally and bilaterally.

Results

The proportion of trials in which the test stimulus was perceived as more numerous was plotted as a function of test numerosities and fitted with a cumulative gaussian function to obtain an estimate of the point of subjective equality (PSE). Figure 2A shows the results by aggregating all participants' data together. In the baseline condition (black curve) the PSE was around the physical value of the reference stimulus (24). Under the two adaptation conditions (red and blue curves), the curves shifted rightward, indicating an underestimation of the test stimulus. The fact that the curve corresponding to the single adaptor condition (red) shifted more from the baseline compared to the double adaptor curve (blue) indicates that the adaptation effect was stronger in magnitude when only one adaptor was presented.

To quantify the effects, the PSEs were measured for each participant separately and a one-way ANOVA with the within factor Adaptation (baseline, single adaptor, and double adaptor) was run on the obtained PSE values. Results revealed a main effect of adaptation ($F_{(2, 22)} = 29.881$; $p < 0.001$) and the post hoc analysis (Newman-Keuls method) showed that all the three conditions significantly differed from each other (all p ISI value < 0.017). In particular, the PSE measured in the double adaptor condition (PSE = 32.8) differed significantly from the PSE obtained in the single adaptor condition (PSE = 35.7; $p = 0.01$). To further contrast the effects produced by the two adaptation conditions, adaptation magnitude was measured

for each participant as the normalized percentage shift from the baseline condition (i.e. $[(PSE_{\text{adaptation}} - PSE_{\text{baseline}}) / PSE_{\text{baseline}}] * 100$). Percentage change obtained in the single adaptor condition was compared to percentage change in the double adaptor condition using a two-tailed dependent sample t -test. Results revealed a strong and statistically significant reduction of the adaptation magnitude in the double adaptor condition ($t_{(11)} = 4.553$, $p < 0.001$). The percentage change obtained in the double adaptor condition was roughly one third smaller than that obtained in the single adaptor condition (single = 31%; double = 21%; Figure 2B).

The results of Experiment 1 might be accounted for in two different ways. On one side, it might be the case that, whereas the single adaptor induced an automatic deployment of spatial attention in a single spatial position, in the double adaptor condition, attentional resources are shared among two different locations. In this light, the reduction of adaptation in the double adaptor condition might be accounted for in terms of a reduction of the attentional component being part of the whole magnitude of adaptation aftereffect. However, an alternative interpretation is that even adaptation to a numerosity matching the reference stimulus could induce a significant adaptation aftereffect, and this quantity might be discarded by that triggered by the contralateral high numerosity adaptor. To disentangle between these two possibilities, we ran a control experiment with the same experimental procedures of Experiment 1 but implementing the presentation of sole neutral adaptors. Results from the one-way ANOVA revealed a not statistically significant effect of adaptation ($F_{(2, 10)} = 1.247$; $p = 0.328$). Furthermore, the two-tailed t -test comparing percentage change from baseline in the single and

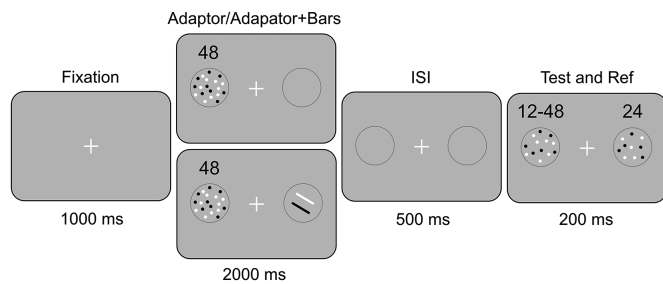


Figure 3. General trial's structure. Adaptor and ISI were not presented during the baseline phase, whereas the initial fixation was not presented during the adaptation phase.

double adaptors conditions revealed no difference ($t_{(5)} = 0.854$, $p = 0.432$). The effects produced by the control adaptation conditions were comparable and very close to a null shift of the PSE (unilateral = -3% and bilateral = -6%). The lack of any significant PSE shift confirms the notion that using a neutral adaptor does not influence subsequent numerosity judgments and, therefore, interpretation of results from [Experiment 1](#) are unlikely to be explained by a perceptual interplay between the effects produced by the two adaptor stimuli.

Experiment 2

[Experiment 2](#) was designed to test whether reduced adaptation magnitude induced by the double adaptor presentation in [Experiment 1](#) reflected a specific numerosity-tuned visuo-spatial capture or a general reduction of attention dedicated to the high numerosity adaptor due to the mere presence of an additional stimulus. To examine this point, we designed a new experiment, which was identical to [Experiment 1](#) but, here, the neutral adaptor was replaced with a non-numerical stimulus (two bars).

Experimental paradigm

Most of the experimental design was identical to [Experiment 1](#) (see above for details). However, in this experiment, the neutral adaptor was replaced with two parallel and randomly oriented bars (one black and one white; [Figure 3](#)) designed to match the same luminance level of the neutral adaptor in [Experiment 1](#). More specifically, the area covered by the bars was the same covered by a 24 dots neutral adaptor stimulus. Again, for each numerosity and adaptation condition, 10 trials were collected both in the baseline and in the adaptation phase. Trials with reaction times exceeding three standard deviations from the individual mean

were discarded as assumed to reflect a condition of reduced focusing on task execution (mean excluded trials on baseline = 2% ; single adaptor condition = 1.8% ; and adaptor + bars condition = 0.9%).

Moreover, in order to test the absence of any relevant influence of bars stimuli on subsequent numerosity judgments, all participants were also tested on a control condition where the sole bars were used as “adaptor” stimuli either presented bilaterally or presented unilaterally.

Results

The proportion of trials in which the test stimulus was perceived more numerous was plotted as a function of test numerosities and fitted with a cumulative gaussian function to obtain an estimate of the PSE. [Figure 4A](#) shows the results by aggregating all participants data together. Like [Experiment 1](#), in the baseline condition (black curve), the PSE was around the physical value of the reference stimulus (24), whereas in the two adaptation conditions (red and blue curves) the curves shifted rightward, indicating an underestimation of the test stimulus.

As in [Experiment 1](#), in order to quantify the effects, the PSEs were measured for each participant separately and a one-way ANOVA with the within factor adaptation (baseline, adaptor, and adaptor + bars) was used to compare PSE values. Results revealed a main effect of adaptation ($F_{(2, 22)} = 43.417$; $p < 0.001$). The post hoc analysis (Newman-Keuls method) showed that both the adaptor and the adaptor + bars condition significantly differed from the baseline condition (baseline = 24.86 and adaptor = 34.21 , $p < 0.001$; adaptor + bars = 33.77 , $p < 0.001$), whereas the two adaptation conditions were not different ($p = 0.699$). Again, we expressed the adaptation magnitude as the percentage normalized shift from baseline for each of the two adaptation conditions. Percentage change obtained in the adaptor condition was compared to the percentage change in the adaptor + bars condition using a two-tailed dependent sample t -test. Results revealed no significant difference between the two conditions ($t_{(11)} = 0.631$, $p = 0.541$; [Figure 4B](#)).

An ANOVA was also conducted on the control condition of sole bars presentation (PSEs obtained in the single or double adaptor) in order to exclude any possible influence of bars on numerosity judgments. Results revealed no main effect of adaptation ($F_{(2, 22)} = 0.259$, $p = 0.686$) suggesting that bars did not produce any change in numerosity judgments. The two-tailed t -test comparing percentage change from baseline in the single and double bars conditions revealed no difference ($t_{(11)} = 0.291$, $p = 0.777$) suggesting that the effects produced by single or double bars presentation were

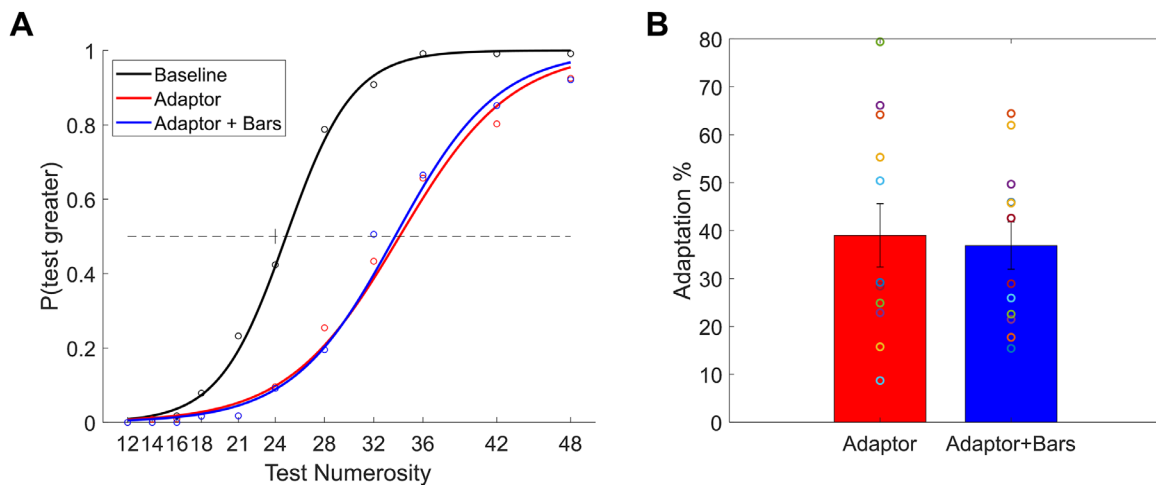


Figure 4. (A) Psychometric fitting of the aggregate data for the baseline (black line) and the two adaptation conditions (adaptor = red line; adaptor + bars = blue line). (B) Normalized percentage of PSE shift from baseline in the two adaptation conditions. Error bars indicate 1 SEM while circles represent single participants data.

comparable and very close to a zero PSE shift (single = 2.4% and double = 3.1%).

Experiment 3

In [Experiment 3](#), we investigated whether exogenously cued visuo-spatial attention could modulate numerosity discrimination judgments at baseline and during adaptation. The allocation of visuo-spatial attention was manipulated using briefly flashed rings surrounding one or both of the locations where stimuli appeared.

Experimental paradigm

In the adaptation phase, each trial began with a unilateral adaptor presented for 2000 ms, which was followed by the presentation of a brief red ring (70 ms) either surrounding the test (test cue condition), or the reference (reference cue condition), or both stimuli (bilateral cue condition). The rationale was to test the modulation of numerosity discrimination judgements produced by the abrupt presentation of unilateral cues (test and reference conditions) compared to a neutral condition where visuo-spatial resources were not unilaterally captured (bilateral cue condition). Participants were instructed to ignore the cueing rings while remaining focused on the numerosity discrimination task. The three different cueing conditions were randomized on a trial-by-trial basis. Afterward, test and reference stimuli appeared simultaneously (200 ms) and participants were asked to report which of the two was more numerous by pressing

the left or the right arrow of the keyboard. Baseline was always administered before the adaptation phase with trials that had the same structure as the adaptation phase, except for the lack of the adaptor stimulus ([Figure 5](#)). For each numerosity and each cueing condition, 10 trials were collected both in the baseline and in the adaptation phase. Trials with reaction times exceeding three standard deviations from the individual mean were discarded as assumed to reflect a condition of reduced focusing on task execution (mean excluded trials on baseline test cue condition = 2%; baseline bilateral cue condition = 1.1%; baseline reference cue condition = 1.4%; adaptation test cue condition = 1.3%; adaptation bilateral cue condition = 1.1%; and adaptation reference cue condition = 1.9%).

Results

The proportion of trials in which the test stimulus was perceived more numerous was plotted as a function of test numerosities and fitted with a cumulative gaussian function to obtain an estimate of the PSE. [Figure 6A](#) shows the results by aggregating all participants data together. All the adaptation conditions (solid curves) showed the expected PSE shift from the associated baseline conditions (dashed curves) indicating an underestimation of the test stimulus, which was roughly the same for each of the three cueing conditions.

To better quantify the effects, the PSEs were measured for each participant separately and a 2×3 ANOVA with the within-subject factors adaptation (baseline and adaptation) and cue (test cue, reference cue, and bilateral cue) was used to compare PSEs shifts produced by adaptation and the three visuo-spatial

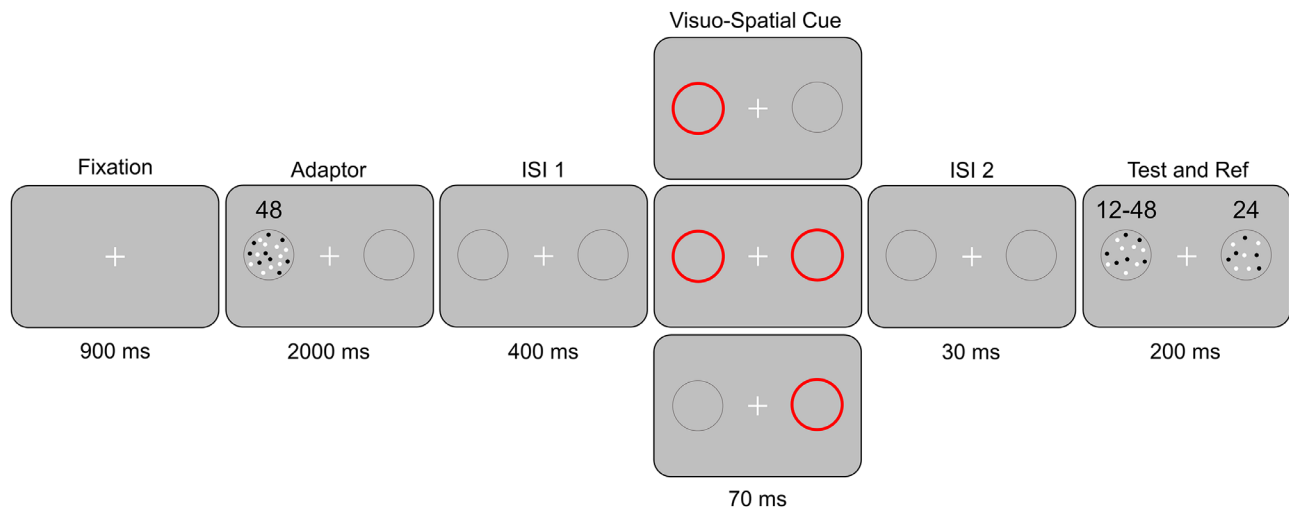


Figure 5. General trial's structure. Adaptor and ISI1 were not presented during the baseline phase, whereas the initial fixation was not presented during the adaptation phase.

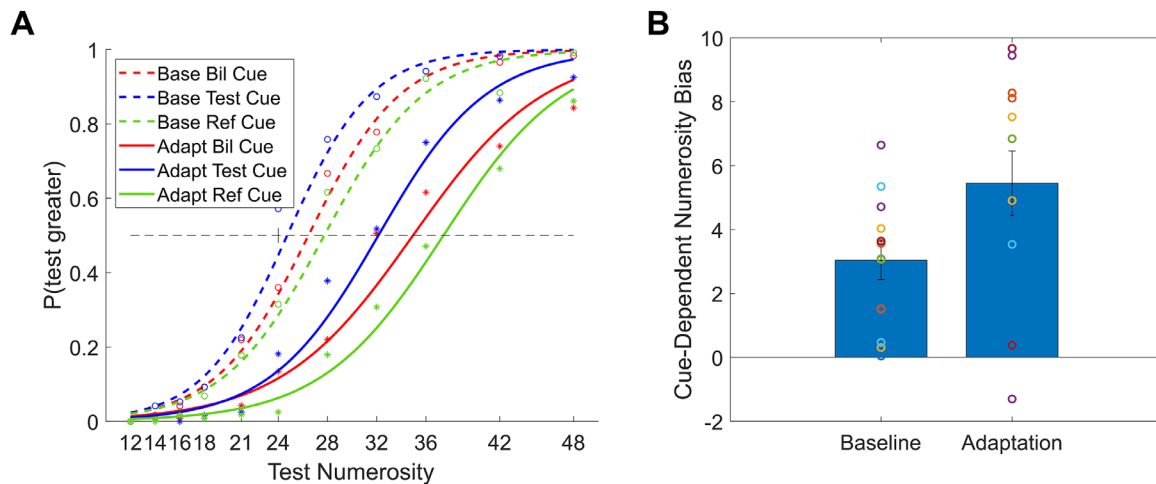


Figure 6. (A) Best fitting psychometric functions for the aggregate data in the baseline (dashed lines) or adaptation (solid lines) condition. Red lines refer to the bilateral cue condition, blue lines to the test cue condition, and green lines to the reference cue condition. (B) Cue dependent PSE shift (i.e. PSE in the reference cue condition minus PSE in the test cue condition) in the baseline and adaptation phase. Error bars indicate 1 SEM, whereas the circles represent single participants' data.

cueing conditions. As expected, results revealed a significant main effect of adaptation ($F_{(1, 11)} = 44.013$, $p < 0.001$) explained by higher PSEs values in the adaptation condition (mean PSE at baseline = 26.32 and mean PSE at adaptation = 36.16) suggesting that a significant adaptation to numerosity was present in each of the three cueing conditions. In addition, a significant main effect of cue was evident ($F_{(2, 22)} = 19.953$, $p < 0.001$). Post hoc analysis conducted on the main effect of cue (Newman-Keuls method) revealed that both test cue and reference cue significantly differed from the neutral bilateral cue condition (test cue = 28.51 and bilateral cue = 30.95, $p = 0.001$; reference cue = 32.75, $p < 0.001$) suggesting that cue-dependent visuo-spatial

attentional capture was capable of significantly affecting numerosity discrimination judgments both during baseline trials and during adaptation trials (see Figure 4A). Finally, the interaction between the factors adaptation and cue did not turn out to be significant ($F_{(2, 22)} = 2.577$, $p = 0.122$) suggesting that the three cueing conditions did not produce different magnitudes of adaptation. In other words, the shifts in PSE (i.e. difference in PSE obtained during adaptation trials minus PSE during baseline trials) measured separately for each cueing condition were not statistically different. Despite the lack of a significant interaction between adaptation and cue, we further explored potential differences in the amount of cue-dependent PSE shifts

between baseline and adaptation. To this aim, we measured the individual absolute cue-dependent PSE shift (i.e. PSE in the reference cue condition minus PSE in the test cue condition) obtained during baseline trials and during adaptation trials and a two-tailed dependent sample *t*-test was used to compare the two conditions. Results revealed a significantly greater cue-dependent PSE shift in the adaptation phase ($t_{(11)} = 3.615$, $p = 0.004$) suggesting that manipulating the allocation of visuo-spatial attentional resources had a stronger effect during adaptation trials (see [Figure 6B](#)).

General discussion

The present study aimed at testing the role played by visuo-spatial attention in shaping numerosity adaptation. We developed three separate experiments using different methodologies to shed light on the involvement of involuntary visuo-spatial attentional shifts during a typical task of numerosity adaptation.

Effects of splitting attentional resources during adaptation

In [Experiment 1](#), we provided evidence that adding a contralateral neutral adaptor (i.e. an adaptor having the same numerosity of the reference; [Aagten-Murphy & Burr, 2016](#); [Burr & Ross, 2008](#)) significantly reduced the magnitude of adaptation as compared to the condition where a single unilateral adaptor was used. This result suggests that part of the phenomenon of adaptation could be dependent on mechanisms that are not strictly perceptual and could, rather, reflect the influence of visuo-spatial attention. Indeed, it is known that presenting a visual stimulus in a specific spatial location can temporally bias subsequent visuo-perceptual performances around that region of space (e.g. [Handy, Jha, & Mangun, 1999](#); [Klein, 2000](#); [Mertes et al., 2016](#); [Müller & Kleinschmidt, 2007](#); [Simons, 2000](#); [Theeuwes & Chen, 2005](#)). Interestingly, the effect can be either attractive or repulsive. For instance, an event occurring in a peripheral location produces an initial visuo-spatial attentional capture, which is then followed by a significant reduction of attention as indexed by increased reaction times and decreased accuracy scores to detect or discriminate stimuli appearing within the same spatial location ([Handy et al., 1999](#); [Klein, 2000](#)). Although we acknowledge that the paradigm used here was not adequately designed to allow for a complete comparison with previous evidence describing such fine-grained attentional shifts, we speculate that a similar phenomenon could be potentially present even in classical adaptation studies and could explain results

obtained in our first experiment. More specifically, the exposure to the single adaptor stimulus may have produced a temporary reduction of attentional resources allocated to the position where the test stimulus would subsequently appear, and this would induce a bias toward judging the reference stimulus as being more numerous than test. Here, we mainly refer to subtle covert attentional modulations given that participants were instructed to maintain central fixation throughout the entire experiment. However, we acknowledge that the lack of an online ocular monitoring does not allow us to completely rule out the possibility that also overt shifts intervened in some trials and that this behavior could have shaped the present results. Nevertheless, this phenomenon would be minimized whenever another numerical adaptor stimulus (although neutral) is presented in the location where the reference stimulus would appear. In other words, the presence of a bilateral percept during the adaptation phase might reduce the possibility of an unbalanced visuo-spatial attentional allocation affecting the discrimination task and this, in turn, would mitigate the contribution of nonperceptual processes. One alternative interpretation would consider the present result in the light of a reduced strength of the non-neutral adaptor because of an averaging procedure of the quantities presented in the two visual hemifield during the adaptation period. However, we believe that this explanation would unlikely account for the present result as the “interaction” between two numerical quantities was found to be maximal whenever the spatial separation is close to 0 degrees, whereas it becomes null when the spatial separation exceeds 10 to 15 degrees of visual angle ([Zimmermann, 2018](#)). Given that in all our experiments the center-to-center separation was 20 degrees of visual angle we consider safe enough to discard this alternative interpretation while considering visuospatial attentional shifts the main cause of the phenomenon reported here. However, it is important to point out that we do not believe that visuospatial attentional shift could entirely explain the whole magnitude of numerosity adaptation but, rather, it suggests that numerosity adaptation is a multifaceted phenomenon, which depends on a mixture of both perceptual and attentional processes. From a quantitative point of view, how much is the proportion of numerosity adaptation dependent on attentional processes? Our data suggest that the weight of spatial attention in numerosity adaptation might be approximately one-third of the whole magnitude, which usually induces changes in the perceived numerosity of the adapted stimulus between 30% and 40%. In this view, two-thirds of the numerosity adaptation magnitude could be dependent on an adapted neural response to numerical features while the remaining part would be mainly related to adaptor-mediated shifts of attentional resources allocation.

Evidence for numerosity-contingent attentional capture

It is known that salient stimuli can temporarily deviate visuo-spatial attention even when participants are explicitly asked to ignore them and/or to pay attention to another location. This phenomenon is thought to be mainly related to an involuntary response to low-level stimulus features, such as luminance transients, which would imply a prominent role played by bottom-up processes (Yantis & Jonides, 1984; Yantis & Jonides, 1990). However, some evidence revealed a more active role of top-down control in mediating visuo-spatial attentional shifts by showing that a cue stimulus presented prior to the target is capable of attracting attention only if it contains overlapping properties with the target stimulus (Anderson & Folk, 2010; Folk, Leber, & Egeth, 2002; Folk, Remington, & Wright, 1994; Theeuwes, Olivers, & Belopolsky, 2010). Following this evidence, in *Experiment 2*, we aimed to further understand if the attentional-related component of numerosity adaptation exhibited in *Experiment 1* was generally linked to the mere presence of an additional stimulus or, rather, reflected a numerosity-contingent visuo-spatial attention shift. To this aim, we used the same paradigm employed in *Experiment 1* while replacing the neutral adaptor with a two bars stimulus, which had the same aggregate area of the neutral adaptor. Interestingly, the presentation of a non-numerical adaptor on the reference location did not significantly change the magnitude of adaptation aftereffect relative to the condition in which a single lateralized adaptor was displayed. In other words, presenting a single numerical adaptor or presenting a numerical adaptor together with a non-numerical stimulus (i.e. bars) in a diametrical opposite position, produced comparable results in terms of adaptation magnitude. This evidence suggests that the reduced adaptation magnitude reported in *Experiment 1* was mainly numerosity-contingent. This result might be accounted for in, at least, two different ways. A first possibility is that numerosity, independently from the task that participants are performing, has a relative higher saliency compared with bars length perception and thus dragging more attention. This is in line with recent studies showing that numerosity is spontaneously perceived and has higher saliency compared to other non-numerical features (Anobile, et al., 2019; Cicchini, Anobile, & Burr, 2016; Cicchini, Anobile, & Burr, 2019; Ferrigno, Jara-Ettinger, Piantadosi, & Cantlon, 2017). A second possibility is that, given participants were engaged in a numerosity task, the numerical adaptor was more effective in dragging attentional resources because it was relatively more task-relevant compared to the bars adaptor (Anderson & Folk, 2010; Folk et al., 2002; Folk, Remington, & Johnston, 1992; Theeuwes et al., 2010). Whichever of these

hypotheses is correct, we reported here the first evidence suggesting that numerosity adaptation partly depends on visuo-spatial attentional mechanisms specifically tuned to numerical quantities. These results are in line with a previous experiment showing a very weak effect of a non-numerical attentional manipulation on numerosity adaptation magnitude when numerical stimuli fall outside the subitizing range (Burr, Anobile, & Turi, 2011). Differently to the current work, the authors manipulated the attentive resources through a double non-numerical task (color-orientation conjunction task), which was performed during the presentation of the stimuli that was to be compared. Results showed a similar adaptation effect between the single task conditions (where the distracting task was not performed) and the dual-task condition. Despite the methodological differences, these results are in line with results from *Experiment 2* of the present work revealing the lack of a change in adaptation magnitude when a non-numerical stimulus is used to modulate visuo-spatial attentional resources allocation. An interesting aspect of the study of Burr and collaborators is that the same attentional manipulation had a very strong effect for very low numbers (i.e. subitizing). In that case, numerosity adaptation was present only in the dual task condition. Very low numerosities (usually up to four) are known to be processed by the subitizing system, a mechanism that makes the performance errorless and very fast compared with higher numerosities (Kaufman & Lord, 1949). The literature on the subitizing phenomenon reveals that it reflects a highly demanding attentional mechanism strongly suffering attentional deprivation across different sensory modalities and different dual-tasks paradigms (Anobile et al., 2020; Anobile et al., 2012; Burr, Turi, & Anobile, 2010; Olivers & Watson, 2008; Pomè et al., 2019; Vetter, Butterworth, & Bahrami, 2008). The attentive nature of such mechanisms likely explains why even a non-numerical attentive manipulation led to a strong effect in the adaptation magnitude for numerosity within the subitizing range.

Effects of visuospatial attentional cueing on numerosity adaptation

Finally, in *Experiment 3*, we tested the possibility of directly shaping the magnitude of adaptation by forcing participants to shift their visuo-spatial attentional resources either in the direction of the test stimulus or in the direction of the reference. This manipulation was produced with the use of briefly flashed red rings appearing after the adaptor stimulus and anticipating the discrimination task. Results revealed that both cueing test and reference position produced a significant shift of PSEs in both baseline and adaptation trials.

In other words, under uncertainty conditions (i.e. PSE that is the point where participants were most uncertain of which of the 2 clouds of dots was more numerous), participants tended to judge more numerous the previously cued position, a behavior that produced a significant PSE shift with respect to the neutral cueing condition where both the test and reference positions were flashed. Interestingly, despite the fact that the magnitude of the adaptation effect was not statistically different across the three attentional conditions, when considering the absolute cue-dependent PSE shift (i.e. PSE in the reference cue condition minus PSE in the test cue condition) results revealed that visuo-spatial cues had a higher impact during adaptation trials relatively to baseline trials. This evidence suggests that under a regime of adaptation, the visual system is much more susceptible to external influences driving attentional shifts.

General conclusions

To conclude, in the present study, we thoroughly investigated the relationship between numerosity adaptation and visuo-spatial attention. We provided the first evidence that the adaptation magnitude partly depends on attentional processes that are tuned to the numerical characteristics of the stimuli used. Furthermore, we showed that visuo-spatial attention allocation can significantly shape numerosity discrimination judgments both at baseline and during adaptation. Taken together, our results revealed that visuo-spatial attentional mechanisms may play an important role on the perception of numerosity.

Data availability statement

Raw data from this study are available in the Zenodo repository at the present link: <https://zenodo.org/record/4383158#.X-EkAdhKhPZ>.

Keywords: adaptation, visuo-spatial attention, numerosity perception

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