Implicit visuospatial attention shapes numerosity adaptation and perception

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The perception of numerical quantities is susceptible to adaptation: after inspecting a numerous dot array for a few seconds a subsequent dot array is grossly underestimated. In a recent work we showed that the mere appearance of an additional numerically neutral stimulus significantly reduces the adaptation magnitude. Here we demonstrate that this reduction is likely due to a numerosity underestimation of the adaptor caused by a change of numerosity-related attentional resources deployed on the adapting stimulus. In Experiment 1 we replicated previous findings revealing a robust reduction of numerosity adaptation when an additional adaptor (even if neutral) was displayed. In Experiment 2 we used the method of magnitude estimation to demonstrate that numerosity is underestimated whenever a second task-irrelevant numerical stimulus appears on screen. Furthermore we demonstrated that the same experimental manipulations were not effective in modulating orientation adaptation magnitude as well as orientation estimation accuracy. Our results support the hypothesis of a tight relationship between numerosity perception and implicit visuospatial attention and corroborate the notion that numerosity adaptation depends on perceived rather than physical numerosity. However the lack of an effect of visuospatial attentional deployment for orientation perception suggests that attention might differently shape adaptation aftereffects for different features along the visual hierarchy.

Introduction

Despite the fact that the visual environment continuously changes, our visual system has an extraordinary ability to stabilize perception to provide a coherent visual experience. Among others, perceptual adaptation and visual attention play a primary role in this process.

Visual adaptation is defined as a temporary change in sensitivity caused by a prolonged exposure to an "intense" stimulation (Webster, 2015). After inspecting an adaptor stimulus for a few seconds, the subsequent presented stimulus (test) is misperceived. Adaptation usually generates a repulsive shift from the adapted feature, making the observer perceive it as opposite relative to the adaptor (Thompson & Burr, 2009). For instance, the prolonged view of a downward motion produces the transient perception of an opposite upward drift of an otherwise static stimulus (Anstis, Verstraten, & Mather, 1998). Basically, all visual features are susceptible to adaptation, highlighting the extraordinary ability of the visual system to dynamically shape its responses based on even very short-term experiences (for recent reviews on visual plasticity see Castaldi, Lunghi, & Morrone, 2020; Grasso, Gallina, & Bertini, 2020). Although adaptation had long been viewed as a by-product of neuronal fatigue, it is now thought rather to reflect an adaptive dynamic adjustment enabling an increased sensitivity to discriminate changes in the environmental features (Kohn, 2007; Webster, 2011). Specifically, adaptation would reduce the neuronal response to recent recurring stimuli in order to optimize resources for the processing of deviants. In this view, it would represent a very important mechanism guaranteeing a high discriminative power despite the varying environmental conditions (Benucci, Saleem, & Carandini, 2013).

Another core mechanism of visual perception is attention, that is the process through which our brain prioritizes relevant information at the expense of irrelevant information. For instance, it is known that visuospatial attention can robustly enhance the processing of stimuli appearing in an attended location through the enhancement of basic stimulus features like contrast sensitivity and spatial resolution (Carrasco, Penpeci-Talgar, C., & Eckstein, 2000; Carrasco, Ling, & Read, 2004). The process of shifting visuospatial attentional resources can be acted upon both voluntarily (i.e., endogenous attention) and involuntarily (i.e., exogenous attention). More specifically, visuospatial attention can be oriented endogenously in the direction of stimuli that are relevant for the task at hand but it can also be exogenously captured by the appearance of salient stimuli attracting attention regardless of observer's intentions (Corbetta & Shulman, 2002a; Kastner & Ungerleider, 2000). The two processes are thought to be implemented in overlapping but partially segregated brain circuits (Chica, Bartolomeo, P., & Lupiáñez, 2013).

Although visual adaptation and visual attention both have the adaptive scope to reduce the cost of cortical computation and to increase discriminability, they are based on opposite neural effects. Indeed, although adaptation is thought to reduce neural response to the adapted feature, attention is supposed to increase neural response to the attended feature/location (Pestilli, Viera, G., & Carrasco, 2007). What has not been fully clarified so far is how the two processes interact. Do the effects of attention amplify or diminish visual adaptation? Is there a unique way this interaction occurs, or does it depend on the characteristics of the adapted feature? Despite the consistent number of studies dedicated to answering these questions, no definitive answer has been achieved as yet, because the results are rather conflictual. Some studies reported amplified effects of attention on adaptation (e.g., Kreutzer, Fink, & Weidner, 2015; Rezec, Krekelberg, & Dobkins, 2004; Rhodes, Jeffery, Evangelista, Ewing, Peters, & Taylor, 2011) while others showed that attention had either no effect or even reduced adaptation (e.g., Chaudhuri, 1990; Morgan, 2012, 2013; Tonelli, Pooresmaeili, & Arrighi, 2020).

In a recent work, we introduced a very simple experimental manipulation during the adaptation period, to reveal the impact of exogenously driven visuospatial attentional shifts (Grasso, Anobile, & Arrighi, 2021). By leveraging on a numerosity task, we measured the magnitude of visual non-symbolic numerosity adaptation (i.e., set of dots) in a "standard" condition in which a single lateralized adaptor was presented before the testing stimulus

as well as in a "split-attention" condition where a second neutral adaptor (i.e., containing the same number of elements as the subsequently presented stimulus) was also displayed in the opposite spatial position. The results showed a robust reduction of numerosity adaptation effect in the split-attention (i.e., double adaptor) compared to the standard (i.e., single adaptor) condition. Moreover, the study showed a signature of feature-based attentional selectivity. When the second adaptor, irrelevant to the task, was not numerical (i.e., two bars instead of a set of dots), the magnitude of adaptation remained unchanged compared to the single adaptor condition. In brief, this study showed that the susceptibility to visual numerosity adaptation was modulated by a feature-specific attentional deployment over space during the adaptation period.

In the current work we developed two new experiments to better understand which factors are involved in the manipulation of the adaptation magnitude previously reported. At first, we investigated whether attention-related manipulation of adaptation is selective for numerosity perception or also generalize to other perceptual features thought to occur at different stages of the visual processing hierarchy, such as orientation (Castaldi, Aagten-Murphy, Tosetti, Burr, & Morrone, 2016; Dragoi, Sharma, & Sur, 2000; Piazza, Pinel, Le Bihan, & Dehaene, 2007). Then, we aimed at identifying which factors induce the reduction of the numerosity adaptation when additional stimuli are presented at the same time with the adaptor. In particular, we tested the hypothesis that the reduction of adaptation is due to the allocation of less attentional resources to the adaptor, making it appear less numerous (and thus less effective) than what physically is. To this aim, we developed a simple numerosity estimation task where participants were required to estimate the numerosity of a stimulus (a cloud of dots) presented either alone (single condition) or together with another, task-irrelevant, stimulus (double condition). The prediction is straightforward: if the double condition modulates attentional deployment, we should expect a change in perceived numerosity with respect to the single condition, a result that would also be in line with recent reports about attention-mediated distortions of numerosity estimation (Pomè, Thompson, Burr, & Halberda, 2020). If this is the case, the previously reported reduction of adaptation during the presentation of another numerical stimulus would be accounted for in terms of a reduction of the perceived numerosity of the adaptor that, in turn, would attenuate the difference in perceived numerosity between the adaptor and the test stimulus and, thus, the magnitude of the adaptation aftereffect.

General methods

Participants

In the main task of Experiment 1, a total of twelve participants were recruited (mean age: 27.3 years, *SD*: 4.03 years; one male, two authors) whereas eight participants were recruited for the control condition of the same experiment (mean age: 31.8 years, *SD*: 3.2 years; three males, three authors). In Experiment 2 a total of ten participants were recruited (mean age: 29.2 years, *SD*: 2.4 years; four males, two authors).

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

Experiments were performed in a dimly lit, low-noise environment with participants sitting 57 cm away from the monitor. Stimuli used for all the numerosity tasks consisted of clouds of non-overlapping random dots (half black and half white to balance luminance; diameter: 0.23°) whereas stimuli used in all the orientation tasks consisted of Gabor patches composed of two-dimensional sinusoidal luminance grating with a spatial frequency of 1.3 cycles/deg. Stimuli were always inserted in a 7° diameter circle with its center spaced 10° left or right from a central fixation point. Stimuli were generated and presented with PsychToolbox 3 routines (Kleiner Brainard, D. H., Pelli, D. G., Broussard, C., Wolf, T., & Niehorster, 2007) in Matlab 2020b (The Mathworks, Inc., http://mathworks.com).

Experiment 1

Experiment 1 comprised two different perceptual adaptation tasks in which participants had to compare either the numerosity (Numerosity Adaptation Task) or the orientation (Orientation Adaptation Task) of two lateralized stimuli after being exposed to an adaptation period. 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 stimulus kept constant across the two experiments for each participant. Participants were not explicitly informed about the side of presentation of the adaptor.

Numerosity adaptation task

A typical 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 Single Adaptor condition, the adaptor stimulus was a lateralized cloud of 48 dots while in the Double Adaptor condition, the adaptor stimulus (i.e., 48 dots) was always presented together with a neutral adaptor, that is, a stimulus having the same numerosity of the subsequently presented reference (i.e., 24 dots). The two adaptation conditions were randomized on a trial-by-trial basis and were followed by an ISI (500 ms) which preceded the simultaneous presentation (200 ms) of the test (i.e., a stimulus randomly varying between 14, 20, 24, 29, 34, 40 and 48 dots) and reference. 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 not being preceded by any adaptation phase (Figure 1 left panel). For each test numerosity and adaptation condition, 10 trials were collected both in the baseline and in the adaptation phase.

Furthermore, in order to test previous reports of an adaptor having the same numerosity of the reference not influencing subsequent numerosity judgements (Aagten-Murphy & Burr, 2016; Burr & Ross, 2008; Grasso et al., 2021) we also ran a control condition on a group of eight participants using 14, 17, 20, 24, 29, 34, and 40 dots for the test stimulus and 24 dots for the reference stimulus. The control condition was identical to the main experiment but in this case only neutral adaptors were used (i.e., 24 dots) although still being presented both unilaterally (same location of either test or reference) and bilaterally.

Orientation adaptation task

A typical 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 Single Adaptor condition, the adaptor stimulus was a lateralized 20° oriented Gabor while in the Double Adaptor condition, the adaptor stimulus (i.e., 20° oriented Gabor) was always presented together with a neutral adaptor, that is a stimulus having the same orientation of the subsequently presented reference. The two adaptation conditions were randomized on a trial-by-trial basis and were followed by an ISI (500 ms) which preceded the simultaneous presentation of test and reference (200 ms). The test stimulus was a Gabor that could be randomly oriented between −3.04°,
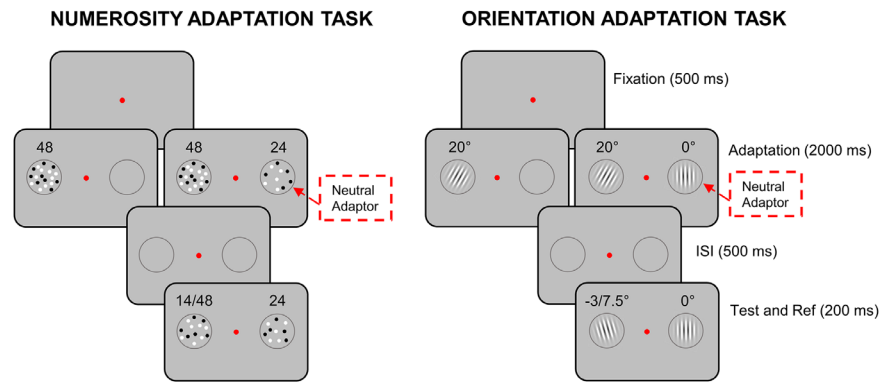
Figure 1. Experimental paradigms. During adaptation, each trial began with a fixation period (500 ms) followed by the appearance of a single or a double adaptor (2000 ms). In the Double Adaptor condition one of the two adaptors was always neutral (i.e., had the same numerosity/orientation of the subsequent reference stimulus) while the other significantly differed from the reference for being consistently more numerous or tilted. The adaptation period was followed by an interstimulus interval (500 ms), which preceded the appearance of test and reference stimuli (200 ms). In the numerosity adaptation task, participants were asked to respond which of the two stimuli was more numerous while in the orientation adaptation task they were asked to report which of the two was more clockwise oriented using the left and right arrow of the keyboard. Baseline consisted in discrimination trials between the test and reference with the presentation of these stimuli not being preceded by any adaptation phase.

−1.19°, 0°, 1.42°, 3.11°, 5.11°, and 7.5°, whereas the reference was a vertically oriented Gabor with a random jitter varying between −2°, −1°, 0°, 1°, and 2°. The jitter of the reference was introduced to prevent participants from judging the orientation of the test stimulus based on absolute vertical or memory mediated judgements. Participants were asked to report which of the two stimuli was more clockwise oriented by pressing the left or the right arrow of the keyboard. For each orientation of the test and each condition, 10 trials were collected both in the baseline and in the adaptation phase.

Analysis procedure

Before any analyses, to make the tested values (i.e., numerosities and orientations) comparable across tasks, each tested stimulus value was normalized as follows:

$$\text{Norm value} = \frac{Xi - Xmin}{Xmax - Xmin},$$

where X_i is the Ith value, X_{min} and X_{max} are, respectively, the lower and the higher values in the tested range of each task. This procedure made the tested values comparable across tasks and always spanning from a minimum of 0 to a maximum of 1 with 0.29 being the value corresponding to the reference stimulus.

The proportion of trials in which the test stimulus was perceived as more numerous (Numerosity Adaptation Task) or more clockwise oriented (Orientation Adaptation Task) than the reference was plotted as a function of normalized tested values and

fitted with a cumulative gaussian function. The 50% point of the function estimates the point of subjective equality (PSE).

PSEs were analyzed using a 2 × 3 repeated-measures analysis of variance (ANOVA) with the within-subjects factors Task (Numerosity and Orientation) and Condition (Baseline, Single Adaptor and Double Adaptor). An additional repeated-measure ANOVA with the within-subjects factor Condition (Baseline, Single Test, Double, Single Ref) was administered to compare results obtained in the control experiment.

To compensate for violations of sphericity, Greenhouse-Geisser corrections were applied whenever appropriate and corrected *p*-values (but uncorrected degrees of freedom) are reported. For post-hoc comparisons the Bonferroni correction was applied.

Results

Figure 2A shows psychometric functions from a representative participant's data. In the baseline conditions (black dotted curves) the PSEs were slightly shifted with respect to the normalized physical value of the reference stimulus (i.e., 0.29), a small bias likely caused by the fact that test and reference locations never swapped across trials. As expected, under the two adaptation conditions (red and blue lines) the curves shifted more rightward, indicating that the test stimulus was perceived as less numerous in the Numerosity Adaptation Task and less clockwise oriented in the Orientation Adaptation Task. If the Single and Double Adaptor conditions had the same effect, the red (Single Adaptor) and blue (Double Adaptor) curves should be
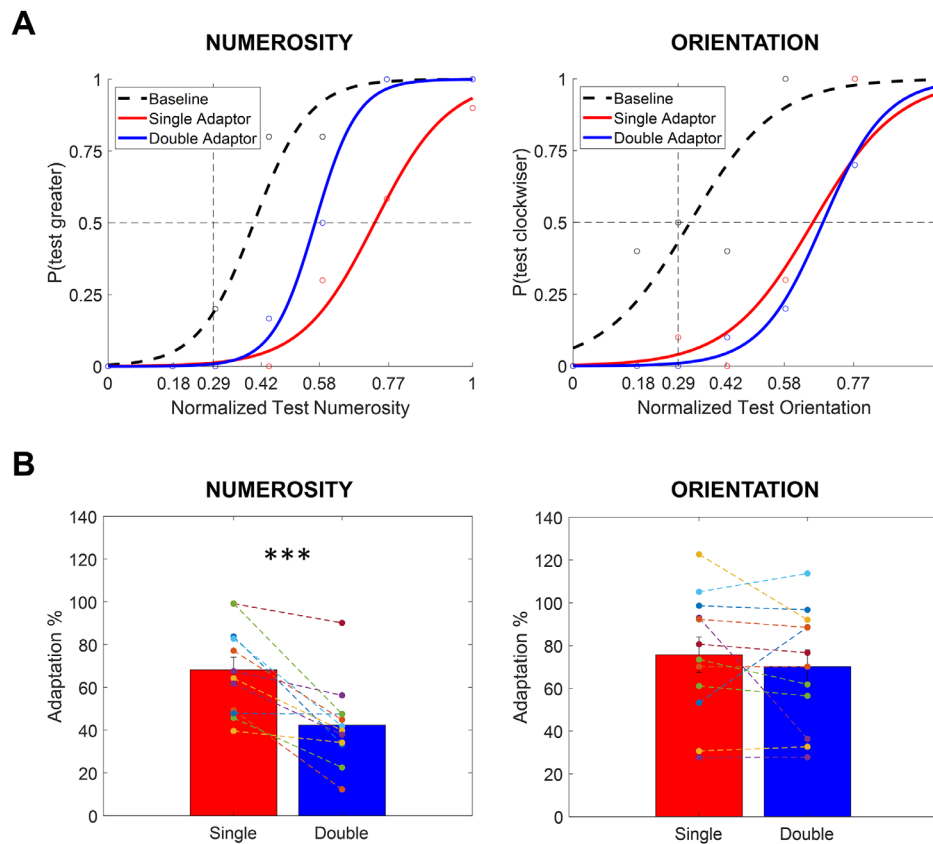
Figure 2. (A) Psychometric fitting of a representative participant's data for the baseline (black dotted line) and the two adaptation conditions (single adaptor: red line; double adaptor: blue line) on each task. (B) Bar plots depicting normalized percentage of PSE shift from baseline in the two adaptation conditions and symbols indicating the two-tailed *t*-test statistical comparison (***$p < 0.001$). Error bars indicate 1 SEM whereas filled circles represent single participants' data.

overlapped, whilst a more consistent rightward shift of the curve, corresponding to the Single Adaptor condition compared to the Double Adaptor curve, would indicate that the adaptation effect was stronger when only one adaptor was presented. On inspection, while for the Numerosity Adaptation Task the difference between the Double and the Single Adaptor appears evident, such difference seems to vanish for the Orientation Adaptation Task. In order to quantify the differences between the two tasks (i.e., Numerosity and Orientation Adaptation Tasks) in terms of PSEs shift from the baseline induced by the two different adaptation conditions (i.e., Single Adaptor, Double Adaptor) a repeated measures ANOVA on PSEs was conducted.

Results from the 2 × 3 ANOVA (*Task*: Numerosity and Orientation; *Condition*: Baseline, Single Adaptor and Double Adaptor) revealed a lack of the main effect of the Task ($F_{(1, 11)} = 0.092$; $p = 0.767$; $\eta_p^2 = 0.008$) and, as expected, a significant main effect of the Condition ($F_{(2, 22)} = 166.277$; $p < 0.001$; $\eta_p^2 = 0.937$) suggesting that, on average, the two adaptation conditions (i.e., Single and Double Adaptor) induced significant PSE shifts from baseline on both tasks (Baseline: 0.38,

Single: 0.66, Double: 0.59; all *ps* < 0.001). Crucially, a significant Task × Condition interaction emerged ($F_{(2, 22)} = 4.231$; $p = 0.028$; $\eta_p^2 = 0.278$) suggesting that the two adaptation conditions (i.e., Single and Double Adaptor) had a different effect across the two tested features (i.e., Numerosity and Orientation). To better clarify the interaction, we therefore decomposed the 2 × 3 ANOVA into two one-way ANOVAs independently performed on each task.

For the Numerosity Adaptation Task, a significant main effect of Condition was evident ($F_{(2, 22)} = 115.081$; $p < 0.001$; $\eta_p^2 = 0.913$). The post-hoc analysis revealed that PSEs in the Single (0.66) and in the Double Adaptor (0.56) conditions significantly differed from PSE at Baseline (0.40; all *ps* < 0.001). Importantly, Single and the Double Adaptor conditions also yielded a statistically significant difference in PSEs values ($p < 0.001$). To better quantify the magnitude of adaptation across conditions, we devised an index as the difference between PSE at baseline and PSE post-adaptation normalized by the PSE at baseline (i.e., [(PSE$_{\text{adaptation}}$ − PSE$_{\text{baseline}}$)/PSE$_{\text{baseline}}$)] × 100). The percentage of PSE shift obtained in the Double Adaptor condition was roughly one third smaller than that obtained in
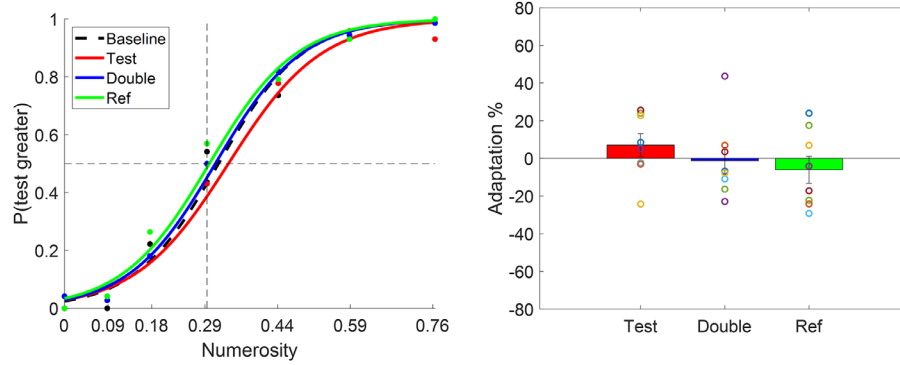
Figure 3. Left panel depicts psychometric fitting of aggregate data for the Baseline condition (black dotted line) and the three control conditions of neutral adaptor presented on test location (test condition; red line), reference location (ref condition; green line) and both (double condition; blue line). Right panel depicts bar plots of normalized percentage of PSE shifts from baseline in the three conditions. Error bars indicate 1 SEM, whereas circles represent single participants' data.

the Single Adaptor condition (Single: 68%, Double: 42%; Figure 2B).

For the Orientation Adaptation Task, a significant main effect of Condition was found ($F_{(2, 22)} = 60.302$; $p < 0.001$; $\eta_p^2 = 0.846$). Again, post-hoc analysis revealed that both the PSEs obtained in the Single (0.65) and in the Double Adaptor (0.63) conditions differed significantly from PSE at Baseline (0.37; all *ps* < 0.001). However, unlike the Numerosity Adaptation Task, they did not differ from each other ($p = 1$) and the percentage of adaptation was virtually the same (Single: 76%, Double: 70%; Figure 2B) suggesting that presenting one or two adaptors did not change adaption magnitude (Figure 2).

The results from Experiment 1 revealed that presenting one or two adaptor stimuli during the adaption phase produced the expected rightward shift of the psychometric curves, which indicates a perceptual distortion of the test stimulus being perceived less numerous (Numerosity Adaptation Task) or less clockwise oriented (Orientation Adaptation Task) than its physical value. However, although in the Orientation Adaptation Task the presence of a second (neutral) adaptor did not reduce adaptation, this was the case for the Numerosity Adaptation Task. This result could be interpreted in terms of reduced attentional resources deployed in the direction of the non-neutral adaptor whenever a second numerical adaptor (although neutral) is presented. However, an alternative interpretation is that even the presentation of a neutral stimulus produced an underestimation bias driving the reported adaptation reduction. In order to discard this alternative hypothesis, we ran a control experiment with the same experimental procedures as Experiment 1 but implementing the presentation of sole neutral adaptors appearing either unilaterally (i.e., in the location of subsequent test or reference stimulus) or bilaterally. Results from the ANOVA revealed a lack of

the main effect of Condition ($F_{(3, 21)} = 1.055$; $p = 0.389$; $\eta_p^2 = 0.131$) suggesting that none of the three neutral adaptation conditions produced relevant PSE shifts with respect to baseline. A two-tailed dependent sample *t*-test was also conducted to check for the possibility that a statistical difference could emerge when selecting the two conditions that differed most (i.e., neutral adaptor on test location vs neutral adaptor on reference location). The analysis revealed that the two conditions were not statistically different ($t_{(7)} = 1.219$, $p = 0.262$), thus confirming the notion that the neutral adaptor does not influence subsequent numerosity judgements (Figure 3).

Experiment 2

Experiment 2 was designed to deepen the understanding of the results achieved in the previous experiment. More specifically, we tested the hypothesis that the reduced numerosity adaptation magnitude in the Double Adaptor condition might be yielded by a reduced attentional deployment in the direction of the non-neutral adaptor which, in turn, would lead to an underestimation in its physical numerosity and thus to a reduction of the adaptation power. Indeed this would be in line with previous evidence showing that, on the one hand, the deployment of visuospatial attention in the direction of a numerical stimulus produces more accurate enumeration judgements than when attention is diverted elsewhere (Pomè et al., 2020) and, on the other hand, that adaptation to numbers operates on perceived, rather than physical, numerosity (Fornaciai, Cicchini, & Burr, 2016). Thus, if the aforesaid hypothesis is correct, we should expect numerosity estimates for a lateralized cloud of dots to be influenced by the presence of another numerical
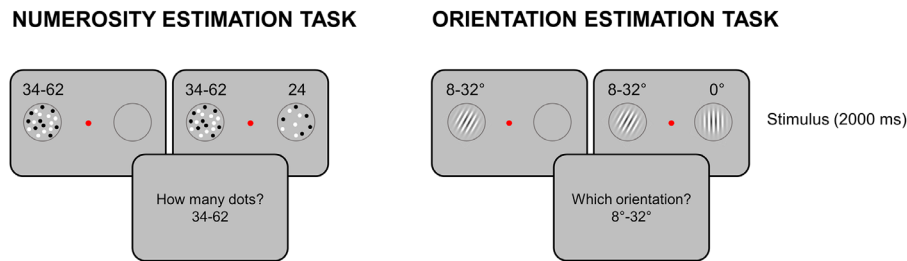
Figure 4. Experimental paradigm. Participants were presented with one or two stimuli (2000 ms) and were asked to estimate the numerosity (numerosity estimation task) or the orientation (orientation estimation task) of the varying stimulus while ignoring the fixed one.

stimulus appearing in a diametrical opposite location. More specifically, we test the hypothesis that the enumeration judgements of a cloud of dots could be biased towards lower values whenever another cloud of dots is concurrently presented elsewhere on screen. However, given the lack of reduction in the Double Adaptor condition for the Orientation Discrimination Task, it should also be the case that the presentation of a second stimulus does not affect perceived tilt in an orientation estimation task.

Numerosity estimation task

In an intermingled paradigm, participants were presented with either a single lateralized cloud of dots or two clouds of dots bilaterally presented with respect to a central fixation point. The numerosity of one of the two clouds was fixed at 24 dots while the other cloud randomly varied between 34, 38, 43, 48, 53, 58 and 62 dots. Each cloud of dots was newly generated from trial to trial and remained on screen for 2000 ms (to mirror the duration of the adaptors in the Experiment 1; Figure 4). Participants were asked to provide an estimate of the numerosity of the varying cloud while ignoring the possible appearance of a second cloud of dots. Before the experiment began, participants were familiarized with the less (i.e., 34 dots) and the more (i.e., 62 dots) numerous stimuli by showing examples of such stimuli. For this reason, these two anchoring values were then discarded from the statistical analysis. A total of 10 trials for each numerosity and each condition was collected. In half of the participants the varying stimulus was presented in the left visual field while in the other half it was in the right visual field.

Orientation estimation task

Participants were presented, in an intermingled paradigm, with either a single lateralized Gabor or with two bilaterally presented gabors. One of the two Gabors was always oriented vertically while the other

one randomly varied between 8, 12, 16, 20, 24, 28 and 32 degrees. During each trial, stimuli remained on screen for 2000 ms (Figure 4). Participants were asked to provide an estimate for the orientation of the varying Gabor while ignoring the possible appearance of the fixed oriented one. Before the experiment began, participants were familiarized with the less (i.e., 8°) and the more (i.e., 32°) oriented Gabors by showing examples of such stimuli. For this reason, the two anchoring values were then discarded from the statistical analysis. A total of 10 trials for each orientation and each condition was collected. In half of the participants the varying stimulus was presented in the left visual field while in the other half it was in the right visual field.

Results

A 2 × 5 repeated measures ANOVA with the within factors condition (single and double) and numerosity (38, 43, 48, 53 and 58) was performed for the numerosity estimation task.

Results revealed a significant main effect of Condition ($F_{(1, 9)} = 14.860$; $p = 0.004$; $\eta_p^2 = 0.623$) explained by lower average estimation values in the double condition than those reported in the single condition (double: 47, single: 48.5; Figure 5). As expected, a main effect of Numerosity was also evident ($F_{(4, 36)} = 138.741$; $p < 0.001$; $\eta_p^2 = 0.939$) that was explained by increased numerosity judgements as physical numerosity increased, showing that participants were focused on task execution. No significant interaction Condition x Numerosity was evident ($F_{(4, 36)} = 0.715$; $p = 0.587$; $\eta_p^2 = 0.073$).

A similar 2 × 5 ANOVA with the within factors condition (single and double) and orientation (12, 16, 20, 24 and 28) was performed for the orientation estimation task. In this case no significant main effect of Condition was evident ($F_{(1, 9)} = 0.071$; $p = 0.796$; $\eta_p^2 = 0.008$; Figure 5) suggesting that the estimation of the orientation of a Gabor is not biased by the presence of a concurrent task-irrelevant Gabor. The main effect of Orientation was significant ($F_{(4, 36)} = 78.171$; $p < 0.001$;
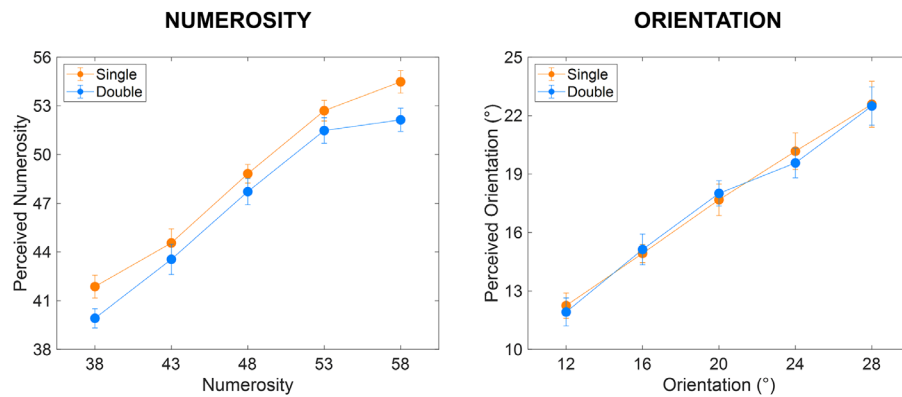
Figure 5. Mean estimate values for the numerosity (left panel) and orientation (right panel) estimation tasks. Error bars indicate 1 SEM.

$\eta_p^2 = 0.897$) and was explained by increased orientation judgements as physical orientation increased, suggesting once again that participants were correctly focused on task execution. Finally, no significant condition × orientation was made evident ($F_{(4, 36)} = 0.429$; $p = 0.786$; $\eta_p^2 = 0.045$).

To sum up, Experiment 2 revealed that numerosity estimation of a patch of dots is influenced by the concurrent appearance of another, though task irrelevant, patch of dots presented in a diametrical opposite location. This was not true for orientation judgements which were not affected by the appearance of a task-irrelevant stimulus.

Discussion

In the current work we investigated the interaction between two core processes of visual perception: adaptation and spatial attention. We capitalized on the automatic capture produced by the mere appearance of a task irrelevant (but feature relevant) stimulus, to study how visuospatial attention affects perceptual adaptation magnitude. A previous experiment from our group demonstrated that such subtle attentional manipulation is capable of reducing numerosity adaption, revealing a tight relationship between feature-contingent deployment of spatial attention and numerosity perception (Grasso et al., 2021). In the present study we aimed at testing whether the effects of the same manipulation generalize to a non-numerical visual feature (orientation) while also exploring the mechanisms subserving the reduced numerosity adaptation magnitude reported in the previous work.

In Experiment 1, we confirmed that adaptation to numerosity is reduced when, during the adaptation period, attentional resources are implicitly deployed toward two spatial locations with respect to one. The

reduction magnitude was around 38%, confirming that roughly one third of numerosity adaptation is likely to be explained by the allocation of attentional resources during adaptation. Importantly, likewise in our previous work, we ruled out the possibility that this reduction could be related to uncontrolled effects produced by the presence of the second adaptor stimulus by showing that the sole neutral adaptor did not produce any perceptual distortion on subsequent numerosity judgements. It is thus plausible that the reduction is entirely attributable to the change of attentional deployment on the adapting stimulus produced by the double adaptor condition. However, it remained to be clarified why splitting visuospatial resources reduced numerosity adaptation. Experiment 2 was designed to answer this question. We hypothesized that the reduction could be due to a reduced adapting power of the adapting stimulus caused by a lowered deployment of attentional resources dedicated to its location whenever a second (although neutral and task irrelevant) numerical stimulus appears. Indeed, it is known that visuospatial attention is associated with enhanced perceptual processing of attended stimuli (for a recent review see Carrasco, 2018) and, in the field of numerosity perception, it has been shown that numerical estimation judgements becomes less accurate when attention is diverted elsewhere (Pomè et al., 2020). Furthermore, given that adaptation to numerosity seems to mainly operate on perceived, rather than physical, numerosity (Fornaciai et al., 2016) it is plausible to assume that splitting attentional resources could lead to a distorted perception of the real adaptor, likely producing an underestimation of its perceived numerosity. Experiment 2 lent support to this interpretation. Indeed, we showed that the concurrent presentation of two numerical stimuli biased numerosity estimation judgements towards lower values. When asked to enumerate a lateralized patch of dots presented together with another patch of dots appearing in a diametrical opposite location, participants provided,

on average, lower estimation values with respect to the condition where the same patch of dots was presented alone. Given that participants were explicitly asked to remain focused on the stimulus to be estimated, it is likely that, again, involuntary split of visuospatial attentional resources caused the here reported effect.

Interestingly, all the above-described effects only hold true for numerosity related estimates, as we also showed that the same experimental manipulations did not produce any perceptual change when the task required judgement of the orientation of a Gabor. First, Experiment 1 showed that the concurrent presentation of a neutral adaptor during the adaptation period did not reduce orientation adaptation magnitude, an indication suggesting that the effect of implicit visuospatial attention on visual adaptation cannot be broadly generalized to all visual features. Second, in Experiment 2, we showed that orientation estimation judgements did not differ between the condition in which the Gabor was presented alone and the condition where it was accompanied with the appearance of another Gabor. Although we acknowledge that paradigms employed in Experiment 1 and Experiment 2 differed substantially in terms of task requirements (i.e., discrimination vs estimation) and that this difference could make direct comparisons of results hazardous, we speculate that the two tasks could provide alternative views of the same phenomenon. In Experiment 1, we brought an indirect measure of the change in perceptual processing of the real adaptor stimulus through a modulation of its adapting power caused by the presence of the neutral adaptor. In Experiment 2, we directly measured such change asking participants to provide an estimate of the numerosity of a long-lasting (two seconds) cloud of dots presented in isolation or together with another task-irrelevant (but feature relevant) cloud. The two tasks provided complementary reports of how implicit attentional deployment over space modifies numerosity judgements while leaving virtually unaffected the perception of orientation. To note, we admit that the present work used an unusual paradigm to modulate the allocation of attentional resources over space and that the lack of an independent measure of attention is a limitation of the study. However, on the one hand, we consider safe enough to assume that the presence of the neutral adaptor itself did produce a change in how attention was deployed over space as previous literature showed that the presentation of a visual stimulus is sufficient to attract attention when the stimulus at hand has a high contextual salience (i.e., shares the same features of the task-relevant stimulus) as in the case of the present study (e.g., Anderson, Laurent, & Yantis, 2011; Corbetta & Shulman, 2002b). On the other hand, we believe that the present paradigm has the merit to provide a rather pure way to modulate implicit attentional deployment over space as this is outreached

without changing task requirements or demands. This said, we consider important for future studies to directly explore the role played by attention during adaptation using more classical attentional paradigms also enabling to quantify the amount of attentional deployment over space and to correlate this measure with the adaptation magnitude.

Taken together, results from Experiment 1 and Experiment 2 reveal that implicit visuospatial processes could be tightly bound to the processing of numerosity while being mostly independent of the processing of orientation. An alternative interpretation would consider the present results arising from an a priori difference in the capability of the two type of stimuli to attract attentional resources with numerical stimuli owing higher attracting properties as compared to Gabors. Although we cannot categorically discard this possibility, we believe this to be unlikely for at least two reasons. First, the way the two paradigms (numerosity and orientation tasks) had been built allowed us to minimize between tasks differences as dot arrays and Gabors were both presented with high contrast, same eccentricity, same covered screen area and both entailed of black/white features (dots and bands). Second, there is no concrete reason to believe that Gabor stimuli could own low attentional capture properties since these type of stimuli have been widely used in the attentional literature (e.g., Berggren & Eimer, 2018; Laurent Hall, Anderson, & Yantis, 2015; Ling & Carrasco, 2006). In addition, we believe unlikely that the present results could be explained by changes in response and/or decisional bias as previous studies alerted (Morgan, 2012; Morgan, 2013). This is because, on the one hand, the majority of participants (ten out of twelve in Experiment 1) were unaware of the purpose of the study and, on the other hand, despite the high task similarity, the reduced adaptation magnitude was confined to the numerosity adaptation task suggesting that the paradigm itself cannot account for the here reported results. We thus believe that the results presented here could be rather explained by a significant difference in the way implicit spatial attentional modulates the perception of numerosity and orientation. This conclusion is also in line with neuroimaging evidence showing a close match between neural structures coding numerosity and those involved in spatial attention. Both processing of and adaptation to numerosity are reported to be subserved by the intraparietal sulcus (Castaldi et al., 2016; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Piazza et al., 2007) a core region deeply involved in the maintenance of attention at peripheral locations during sustained tasks (Corbetta & Shulman, 2002a; Kelley, , Serences, Giesbrecht, & Yantis , 2008). The neural overlap is much weaker for both processing of and adaptation to orientation which was found to mainly elicit the activation of striate and early ventral extrastriate cortices (Boynton & Finney, 2003; Dragoi

et al., 2000; Yacoub, Harel, & Uğurbil, 2008). In this view, it could be argued that orientation adaptation acts at a cortical level that is much less influenced by higher order cognitive processes like visuospatial attention, although we acknowledge that this interpretation is partially in contrast with results from previous works showing an attention-dependent increase of orientation adaptation (e.g., Spivey & Spirn, 2000). However, unlike previous studies where visuospatial attention was mostly endogenously deployed, we here relied on the sole exogenous implicit attentional capture produced by the appearance of the stimuli, a manipulation that may not have been sufficient to induce a strong attentional shift capable of interacting with neural mechanisms subtending orientation perception and adaptation. In other words, the presence of a "competing" feature-relevant stimulus during adaptation could have led to an attentional-related interference with the processing of numerical stimuli reducing the adapting power in Experiment 1 and lowering estimation judgements in Experiment 2. In agreement with a channel model of numerosity adaptation (Anobile, Arrighi, Castaldi, & Burr, 2021), it could be argued that a low-numerous adaptor would produce a reversed attentional-dependent modulation of the adapting power as a direct consequence of the adaptor stimulus being perceived less numerous when presented together with the neutral adaptor. However, this hypothesis relies on the assumption that the attentional-dependent underestimation of a numerical stimulus should be constant across different numerosities which seems not to be the case as revealed by dual task experiments showing stronger underestimations for relatively higher numerosities (Burr, Turi, & Anobile, 2010; Vetter Butterworth, & Bahrami, 2008). In this view, the lack of a reversed attentional modulation of the adapting power when a low-numerous adaptor is used could be explained by the existence of a gradient-like interaction between attention and numerosity perception.

Taken together, our results seem to reveal that subtle implicit visuospatial attentional shifts have an influence on perceptual adaptation only when this operates on the perceived rather than the physical characteristics of stimuli (Fornaciai et al., 2016). This divergence could be related to the intrinsic differences in perceptual mechanisms necessary for the processing of the numerosity and orientation to arise as non-symbolic numbers perception requires a binding procedure of multiple elements scattered in space while orientation perception mainly rely on the activity of sharply tuned detectors. To conclude, in the present study we provided firm evidence that both numerosity adaptation and numerosity estimation are influenced by the implicit allocation of visuospatial attentional resources, suggesting that neural substrates subserving numerical processing are highly intertwined with those pertaining

to implicit visuospatial mechanisms. This would not be the case for a lower-level attribute like orientation, in which visuospatial attention modulation was virtually absent.

Keywords: numerosity perception, orientation perception, visual adaptation, implicit visual attention

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