Numerosity adaptation along the Y-Axis affects numerosity perception along the X-Axis: does numerosity adaptation activate MNLs?

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Abstract The current study characterized the spatial selectivity of numerosity adaptation. In Experiment 1, adaptors were arranged vertically with 8 dots at the top of the visual field and 400 dots at the bottom, and participants' perceived magnitude in the left field decreased compared to that in the right, as revealed in the numerosity comparing task after adaptation. In contrast, the perceived magnitude in the right field decreased compared to that in the left with inversed adaptors (400 dots at top, 8 at bottom). In Experiment 2, adaptors were presented horizontally, and they showed no significant effect on numerosity perception, which was tested vertically. This study demonstrated that numerosity adaptation along the vertical orientation could affect numerosity perception along the horizontal orientation, and the latter was affected by the former according to a rule of associating “top” with “right” and “bottom” with “left.” The spatial selectivity of numerosity adaptation showed distinguishing features that should function to abstract spatial relationships rather than create purely retinotopic mapping. We proposed that numerosity adaptation is based on spatial-numerical-associated codes. Vertical adaptors could activate both the vertical and horizontal Mental Number Lines (MNLs) and involve an interaction between these types of MNLs. According to behavioral data, horizontal adaptors showed no significant influence on perception along

the vertical orientation, which might be due to the higher threshold required to activate the vertical MNL.

Keywords Numerosity adaptation · Spatial selectivity · Mental number line · Spatial-numerical-associated codes

Introduction

Numerosity adaptation refers to adaptation to the numerical property of a stimulus, with an aftereffect that can be revealed by changes in perceived numerical magnitude in consequent numerosity judging tasks (Burr & Ross, 2008a; Liu, Zhang, & Zhao, 2012). In the study by Burr and Ross (2008a), 400 dots and 10 dots were presented in two circular areas in the horizontal direction. Subjects were asked to maintain fixation in the middle of the two circles to establish an adaptation. Then, the probe and test were presented instead of adaptors, and subjects compared the numerosity of these images. A significant increase was found in the perceived numerosity (Dehaene, 1992) of the probe. The point of subjective equality (PSE) of the probe was more than three times of the real number of dots, demonstrating a significant aftereffect of adaptation (Burr & Ross, 2008a).

In Burr's experiments, number was correlated with density (Durgin, 2008). More studies need to be conducted before we can describe the adaptation as a “numerosity adaptation.” Previous studies (Burr & Ross, 2008b; Burr, Turi, & Anobile, 2010) investigated the influencing factors of numerosity adaptation, confirming that it could occur independently of other, nonnumerical visual properties (e.g., contrast, orientation, or density). Our group has demonstrated that numerosity adaptation is based on numerosity perception (Liu, et al., 2012; Liu, Zhang, Zhao, Liu, & Li, 2013). In our 2012 study, we induced a perceptual grouping by controlling the

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color and distribution of dots: 9 dots with the same color were constructed into a bigger “chunk,” and 405 dots were divided into 45 chunks. In that test, both the perception and adaptation of the number of chunks decreased. Moreover, the adaptation effect remained constant as long as the observers’ perception of numerosity remained unchanged. Any change in the aftereffect would synchronize with that of the numerosity perception: dots with an equal perceived numerosity (45 chunks and 45 dots), rather than an equal density (45 chunks and 405 dots), had an equal effect on adaptation. We proposed that the adaptation should be based on the processing of numerosity. In our 2013 study, we found that distinct mechanisms exist in numerosity adaptation under different awareness conditions. With awareness, numerosity adaptation was binocular (Durgin, 2001), and grouping (chunking) influenced numerosity coding through altered numerical units (i.e., chunks, rather than dots, if stimuli were grouped). However, the adaptation was monocular (Durgin, 2001) and not affected by grouping without awareness. The idea that numerosity is a property computed from the perceived area and density (Allik & Tuulmets, 1991) is not applicable in explaining these results. Instead, we proposed that distinct mechanisms involving high-level cognitive processing, such as object representation, may be involved in conscious numerosity perception and adaptation. Based on this evidence, it is plausible to label the described adaptation as “numerosity adaptation,” and a correlation between the adaptation and representation of numerosity can be proposed.

The spatial selectivity feature, which is typically demonstrated by the retinotopic characteristic (Burr & Morrone, 2011; Zhang, Liu, Zhao, Zhang, & Wu, 2014), refers to the phenomenon in which some aftereffects only affect particular areas, typically the area where adaptors were presented before. Spatial selectivity often is observed in the aftereffect of visual properties associated with specific detector units, such as contrast. As the detecting neurons in the neuronal receptive field typically have limited and clearly circumscribed receptive fields, they respond solely to the local stimulus within a retinotopic area (Burr & Ross, 2008b). This selective feature is proposed to be a common characteristic of primary properties (Melcher, 2005; Afraz & Cavanagh, 2009; Avidan et al., 2002).

Numerosity adaptation is also suggested to be spatially selective or retinotopic (Burr & Ross, 2008b; Zhang et al., 2014), and research has cited neurons in the intraparietal sulcus (IPS) as the physiological substrate of its selectivity (Burr & Ross, 2008a; 2008b). However, the retinotopic feature of numerosity adaptation would make it difficult to use IPS as a candidate because IPS represents numerosity quite abstractly, independently of whether the objects are distributed in space or time and independently of modality (Butterworth, 2008). In fact, it is not easy to find compelling reason to accept the idea that numerosity is an elementary quality of perception, similar to color or other primary features (Morgan, Raphael, Tibber &

Dakin, 2014; Raphael & Morgan, 2015). Numerosity cognition is proposed to be accompanied by processes for a combination of surrogate features (Franconeri, Bemis, & Alvarez, 2009). A series of studies demonstrated that approximating numerosity is affected by some statistic of the image, such as contrast, size, or density signals (Raphael, Dillenburger & Morgan, 2013; Raphael & Morgan, 2015; Dakin, Tibber, Greenwood, Kingdom, & Morgan, 2011). Therefore, with regard to the selective feature of numerosity adaptation, we proposed that it is not a simple phenomenon.

Even if numerosity processing begins with the coding of primary features (Franconeri et al., 2009; Stoianov & Zorzi, 2011), the representation and processing of numerosity retain distinguishing features compared with those of other primary properties. For example, according to previous studies, coding and processing of numerosity are associated with spatial representation (Fischer, 2003a; 2003b; Fischer, Castel, Dodd, & Pratt, 2003; Hubbard, Piazza, Pinel, & Dehaene, 2005; Fias & Fischer, 2005). Because the numerosity adaptation aftereffect is suggested to be based on numerosity representation, and the latter is proposed to be associated with spatial representation, it is possible that the “spatial selectivity” has a new feature of numerosity adaptation: the spatial-numerical-associated codes may expand the affected area of numerosity adaptation. In other words, if observers have adapted to the numerosity of a particular visual area, their numerosity perception in extra areas (which did not present adaptors before) also may be affected by the adaptors. Conversely, if the selectivity of the numerosity adaptation aftereffect exhibits a feature that could be explained by an abstract spatial association rather than a pure retinotopic mapping, then it will be very helpful to demonstrate whether numerosity adaptation can be based on spatial-numerical-associated codes. Therefore, in the current study, our goal was to characterize the “spatial selectivity” involved in numerosity adaptation.

The spatial-numerical-associated codes can be described as a mental number line (MNL; Restle, 1970). In the horizontal direction, a smaller number is represented on the left of this line and a larger number on the right (Dehaene, 2002). It was proposed that people could automatically extract magnitude from a variety of stimuli, representing such information in a common left-to-right format, reflecting a mental magnitude line. For example, in the study by Holmes and Laurencio (2011), the spatial-numerical-associated codes were shown to be extended to emotional expression. In the study by Gabay, Leibovich, Henik, and Gronau (2013), the conceptual object size influenced the numerical value perception and both types of magnitudes exhibited similar mental representations. Moreover, previous studies have proposed the existence of an MNL in the vertical direction, in which smaller numbers are associated with lower locations and larger numbers are associated with upper locations (Schwarz & Keus, 2004; Ito & Hatta, 2004). The horizontal and the vertical MNLs may share

cognitive mechanisms. It has been suggested that an internal number map or a number field may replace the MNL to describe completely how we represent numerical magnitude (Schwarz & Keus, 2004). In this coding format, these two irrelevant dimensions, which have no overlap in space, are integrated. A particular numerical magnitude corresponds to a particular location on this internal number map (e.g., the lower left quadrant of the map is associated with smaller numbers and the upper right quadrant is associated with larger numbers).

The spatial-numerical-associated codes can be inferred from the Spatial Numerical Association of Responds Codes (SNARC) effect. In a classical demonstration of the SNARC effect (Dehaene, Bossini, & Giraux, 1993; Mapelli, Rusconi, & Umlita, 2003), participants are asked to perform a parity judgment task (odd vs. even) in a bimanual response setting. Smaller numbers are responded to faster with the left hand, and larger numbers are responded to faster with the right hand, although magnitude information is irrelevant to the task. MNLs provide an appropriate framework with which to explain the SNARC effect: numerical coding causes attention shift along the MNL and facilitates answering with a response code rather than another code for the same stimulus (Dehaene et al., 1993; Gevers, Lammertyn, Notebaert, Verguts, & Fias, 2006). Further evidence of SNARC has been provided by various studies showing multiple responses (Fischer, 2003a, b; Fischer, Warlop, Hill, & Fias, 2004; Fias, Lauwereyns, & Lammertyn, 2001), demonstrating that an automatically activated MNL is able to affect behavior even if numerical magnitude is irrelevant to the response to a task. Importantly, the horizontal and the vertical MNLs can interact. If response keys were assigned to be discriminant along both orientations and participants were asked to respond vertically in the parity judgment, there also was a SNARC effect in the horizontal direction (Gevers et al., 2006). The top-right/bottom-left advantage also was shown if the location of the stimulus was irrelevant to the task (Gevers et al., 2006; Cho & Proctor, 2003), suggesting a strong correlation between the horizontal and the vertical orientations. There may be an association between the left and the lower part of the space as well as the right and the upper part (Gevers et al., 2006; Cho & Proctor, 2003).

Consistent with these studies, Schwarz and Keus (2004) proposed that coding a particular numerical magnitude may automatically activate the representation of corresponding spatial locations in both the horizontal and the vertical directions. Additionally, it has been proposed that the activating threshold of the horizontal MNL is lower than that of the vertical MNL (Shen, Tian, & Ding, 2006; Gevers et al., 2006). In other words, if a cognitive process activates the vertical MNL, it may simultaneously activate the horizontal MNL. However, if a process activates the horizontal MNL, it is possible that the higher threshold prevents the activation of

the vertical MNL. With regard to the numerosity adaptation, which is proposed to be based on the numerosity representation associated with spatial codes, the adaptation may activate MNLs in both orientations. Then, the aftereffect should transfer to the orientation orthotomic to adaptors. If this hypothesis holds, the distinguishing feature of the spatial selectivity of numerosity adaptation will be revealed, i.e., the selectivity functions as an abstract association between MNLs rather than a pure retinotopic mapping, which is dominant in the spatial selectivity of primary features (Burr & Morrone, 2011).

In short, numerosity adaptation and perception may be based on numerosity representation (Liu et al., 2012; 2013), and the representation may be able to activate MNLs in both dimensions. Our hypothesis is based on these views. Specifically, we hypothesized that numerosity adaptation in the vertical direction may affect numerical perception in the horizontal direction. A change in numerosity perception in the horizontal direction may be observed if observers have been exposed to vertical adaptors compared with the control condition. A symmetrical effect of horizontal adaptors on vertical perception was not included in our hypothesis, because it is possible that the effect of vertical adaptors on numerosity perception along the vertical orientation may be absent given the possible higher activating threshold in the vertical orientation.

Therefore, we suggest a particular spatial selective property of numerosity adaptation: numerosity adaptation may not be restrained to the area where the adaptors were presented. Adaptation in the vertical direction may selectively affect perception in particular areas in the horizontal direction. If the hypotheses are verified, then numerosity adaptation should be based on an abstract representation that combines the numerical and the spatial information rather than only a retinotopic representation that is typical in early stages of neural visual processing.

Two experiments were conducted. Adaptors were represented in the vertical (Experiment 1) and the horizontal (Experiment 2) directions, and the statuses of numerosity perception were tested correspondingly in the horizontal (Experiment 1) and the vertical (Experiment 2) directions.

Experiment 1: effects of vertical numerosity adaptation on horizontal numerosity perception

Experiment 1 examined whether numerosity adaptation in the vertical direction would affect numerosity perception in the horizontal direction. We adopted a paradigm similar to the study by Burr and Ross (2008a) to study numerosity adaptation and perception. Participants were asked to compare the numerical magnitude of two stimuli (probe and test) after they had adapted to the adaptors.

Ethics statement

The data were analyzed anonymously. Subjects verbally provided their informed consent and confirmed it in writing by signing a form to receive compensation for participating. The study was approved by the ethics committee of Yunnan University for Nationalities and Zhejiang University.

Methods

Participants Sixteen right-handed volunteers (age range = 20–29 years, 8 males, 8 females) with normal or corrected-to-normal vision participated in Experiment 1. They were paid for their participation after the experiments.

Apparatus The experimental stimuli were produced using Walk Script 1.0 (ZJU Walkinfo Co., Ltd., Hangzhou, China). The stimuli were presented on a Philips 17" flat-screen monitor with a resolution of 1024×768 pixels and a refresh rate of 85 Hz in a dark room. All stimuli were displayed using E-prime 1.0. Head and chin rests were used in all experiments to ensure a consistent viewing distance of 70 cm.

Stimuli For the adaptors, square dots ($0.14^\circ \times 0.14^\circ$) were generated and randomly distributed within two fixed circles with diameters of 8.13° and centers at 6.52° above/below the center of the computer screen. Figure 1 shows the adaptors of various adapting conditions in Experiment 1. In Treatment 1 (left side), 8 dots were arranged in the upper circle and 400 dots in the lower. In Treatment 2 (right side), 400 dots were arranged in the upper circle and 8 dots in the lower. In the test stage, test and probe stimuli were represented in two circles with diameters of 8.13° in the horizontal direction centered at 6.92° from the left/right part of screen center. The field that presented the test/probe was not spatially overlapped with the field that presented the adaptors (see Fig. 2 for details).

Procedure We adopted a 2 (adapting area: fewer dots were presented on the upper/lower part) $\times 2$ (test area: tests were presented on the left/right) within-subject design. Specifically, the adapting area refers to the two circles in the vertical direction described above (Treatment 1, adapted to 8:400; Treatment 2, adapted to 400:8; Fig. 1); the test area refers to the two circles in the horizontal direction (Fig. 2). There were two test conditions according to whether the tests were represented on the left (Treatment 1) or right (Treatment 2). Moreover, there were two unadapting conditions in which participants conducted the testing procedure directly without any adaptation (pretests). We used these conditions as baselines for further analysis.

The testing stage used a point of subjective equality (PSE) to quantify numerosity perception; the numerosity adaptation aftereffects were measured by subtracting the PSEs before from those after adaptation. We used a 2AFC (temporal) task to produce a psychometric function (dependent variable: probability of test > probe) from which the PSE was extracted as a measure of any perceptual bias. Two sets of dots were successively shown in the two fixed circles in the horizontal direction, and each trial was presented to all participants with a forced-choice question: "Which circle contained more dots?" Participants pressed buttons ("f" controlled by the left hand meant that the left circle contained more dots, and "j" controlled by the right hand indicated the right circle) to respond. The constant stimulus (i.e., the probe) contained 33 dots. The quantities of the comparing stimuli (i.e., the tests) were chosen using an equidistance logarithmic scale (Dehaene, Izard, Spelke, & Pica, 2008) with the probe assigned to the center of these serial comparisons in a range from 18 to 60. Specifically, the tests contained 18, 22, 27, 33, 40, 49, and 60 dots. Eight equivalent stimuli were provided for the probe (each containing 33 randomly spread dots), and four equivalent stimuli were provided for each test. A total of 32 paired stimuli were generated if we matched the probe to each test; one-

Fig. 1 Adaptors used in Experiment 1. The adaptors of adaptation Condition 1 are shown on the left side, and the adaptors of adaptation Condition 2 are shown on the right. Square dots ($0.14^\circ \times 0.14^\circ$) were

generated and randomly distributed within two fixed circles above/below the center of the screen. Half of the dots are white, and half are black; 400 dots are arranged in one circle and 8 dots in the other

Fig. 2 Schematic of the paradigm in Experiment 1 (adaption Condition 1, test Condition 1). Each trial began with a fixation for 200 ms, and then participants entered a top-up adapting stage that lasted for 5,000 ms (30 s for the first trial). A fixation was shown for 400 ms after the adaption stage ended, and then, the test stage began with a test stimulus displayed on the left side of screen for 200 ms, followed by a probe stimulus

displayed directly on the right for 200 ms. The two stimuli were separated by a blank screen lasting 400 ms. Participants were asked to fix their gaze on the fixation point during the trial and to report whether the probe appeared more or less numerous than the test and to guess if they were unsure

quarter of them (8 pairs) were randomly chosen for the experiment, and 56 comparison judgments were made.

The procedure of treatment with adaptation is described in Fig. 2 (we will use the adaption Treatment 1 and test Treatment 1 as an example). Participants initiated the first trial by pressing the space bar. In the adaption stage, a fixation point was presented in the center of the screen for 200 ms, and then adaptors were presented in the vertical direction. The adaptors were presented for 30 s the first time and for 5,000 ms in each subsequent trial (readaptation). In the testing stage, a fixation point was shown in the center for 400 ms, followed by a presentation of the left circle with test stimuli in it for 200 ms. Then, the right circle with a probe stimulus was shown for 200 ms. A blank frame with a fixation cross isolated the test and the probe for 400 ms. The next trial began after a participant's response or after 1,000 ms without a response. In test Treatment 2, the positions of the test and probe were reversed: the test was first presented on the right, followed by the probe on the left.

In the beginning of Experiment 1, brief practice trials with feedback were added to improve the participants' familiarity with the formal experiment. Then, the participants completed two pretests before their adaptation tasks to create adaptation aftereffect baselines (measured as a control in this study). After these tasks, they began the adaptation tasks with four treatments. The procedure of the adaption and test Treatment 1 was as described above. In the adaption Treatment 2, the adaptors were presented in reverse (Fig. 1), and the sequence was similar to Fig. 2. Again, in test Treatment 2, the test was first presented in the right circle, followed by the probe in the left circle. The sequences of the treatments were counterbalanced between participants. Participants were given sufficient rest between treatments to avoid fatigue.

Results

Cumulative normal functions were fitted to the psychometric functions of each participant using the *psignifit* toolbox version 2.5.41 for Matlab (<http://www.bootstrap-software.com/psignifit/>) to implement the maximum-likelihood method described by Wichmann and Hill (2001) and thereby quantitatively measure the magnitude of the adaptation aftereffect. The 50 % points of the fitted functions were obtained (Fig. 3). The values of the test stimuli (x-axis) corresponding to the 50 % points were calculated from the fitted curves. These values were PSEs representing the number of test dots that appeared to equal the number of probe dots for participants (Fig. 4). Therefore, the change in numerosity perception in the tests can be demonstrated by the difference in the average values for PSEs under different conditions (Table 1). The magnitude of the numerosity adaptation aftereffect can be indicated by the PSEs under adaptation conditions minus the PSEs in the control conditions (baselines).

There was a significant difference between the two baselines ($p = 0.027 < 0.05$), showing that participants were more likely to consider the dots on the left as less numerous compared with those on the right (i.e., the tests were more likely to be underestimated if they were presented on the left compared to the right). With adaptors 8:400, if the tests were presented on the left field, there was a significant difference between treatment and its baseline ($p = 0.003 < 0.05$), and the number of the tests (presented on the left) was underestimated compared with the baseline. If the tests were on the right, there was a marginally significant difference between treatment and baseline ($p = 0.051$), in which participants tended to overestimate the tests compared to the baseline. With adaptors 400:8, there was no significant difference between treatments and baselines ($p = 0.687$; $p = 0.407 > 0.05$).

Fig. 3 Samples of psychometric functions under different conditions in Experiment 1. The proportion of trials is plotted in which the tests seem more numerous as a function of the number of test dots. The vertical dashed lines indicate the PSEs (i.e., the point of subjective equality) of the match. The probe number is indicated by the arrow. A composition of participants' typical behavior curves is shown in Fig. 3 to indicate the

average results of PSEs. In the pretests, filled circles, dark blue curve = test Condition 1; open circles, green curve = test Condition 2. In the adaptation Condition 1, filled triangles, purple curve = test Condition 1; open triangles, brown curve = test Condition 2. In the adaptation Condition 2, filled rectangles, red curve = test Condition 1; open rectangles, light blue curve = test Condition 2

The aftereffect of numerosity adaptation was calculated by the subtraction of PSEs between treatments against their

baselines (Liu et al., 2012; 2013). A 2×2 repeated analysis of variance (ANOVA) was conducted with adaption area (8

Fig. 4 Aggregate of single-subject data under different conditions in Experiment 1. Black circles and blue rectangles represent males and females, respectively. Green lines denote the mean value of PSEs, and

red lines denote the upper and lower boundary of 95 % confidence intervals of the data in each condition. Left or right represents the position of tests

Table 1 Mean and SD for PSEs in the adaption and test conditions in Experiment 1

Condition	Pretest		Adapting to 8:400		Adapting to 400:8	
	Left	Right	Left	Right	Left	Right
PSE	35.26	32.33	37.68	30.11	34.91	33.34
SD	3.45	3.17	4.27	3.83	3.19	4.61

Note. PSE stands for the point of subjective equality of participants, representing the number of test dots that appeared to equal the number of probe dots (33). SD represents the standard deviation of PSE. Adapting to 8:400/400:8 = adaptation Condition 1/2. Right/Left refers to the position where the test was presented (i.e., right/left = test Condition 1/2). In the pretest, there was no adaption stage but there were two test conditions

dots were on the top or bottom field) and test area (tests were on the left or right field) as the independent variables and the adaptation aftereffect as the dependent variable. This model yielded no significant main effect of adapting area ($p = 0.699 > 0.05$) or test area ($p = 0.168 > 0.05$). Importantly, there was a significant interaction between the two factors (Fig. 4), $F(1, 15) = 11.80$, $p = 0.004 < 0.05$, $\eta_p^2 = 0.44$. A significant difference in adaptation aftereffects was found between the two test areas (left or right) in adaption Treatment 1, $F(1, 15) = 8.58$, $p = 0.01$, $\eta_p^2 = 0.37$. In other words, if participants were adapted to the adaptors with 8 dots at the top and 400 dots at the bottom (8:400), their numerosity perception in the left visual area significantly decreased compared to that in the right. A significant difference was also found between the two test areas in adaption Treatment 2: $F(1, 15) = 8.04$, $p = 0.013 < 0.05$, $\eta_p^2 = 0.35$, suggesting that participants' numerosity perception in the right field decreased compared to that in the left with adaptors 400:8 (Fig. 5).

Because the effects showed a composition influence of the 400-dot and 8-dot adaptors, a control treatment was designed to exclude the possibility that only the 400-dot adaptor affected the horizontal numerosity perception. If the 8-dot adaptor affected the horizontal perception by increasing the magnitude of a particular area (top-right, bottom-left), then the increasing effects should disappear if we replace the 8-dot adaptor with a 33-dot adaptor because 33 dots were equal to the dots in the probe, and the number was in the center of serial tests. Therefore, 33-dot adaptor was expected to have no significant effect on the magnitude perception of the 33-dot probe. Therefore, we repeated the experiment within the same participants, maintaining all parameters except replacing the 8-dot adaptor with a 33-dot adaptor. Table 2 shows the results.

There was a significant difference between the two baselines ($p = 0.043 < 0.05$), showing a built-in bias of MNL. With adaptors 33:400, there was a similar significant difference between test areas ($p = 0.000$, the tests presented on the left were significantly underestimated compared to the right). However, with adaptors 400:33, there was no significant

Fig. 5 Results of ANOVA in Experiment 1. There was a significant interaction between adapting conditions (two shapes on the left of Fig. 5 = adapting to 8:400; the other two shapes on the right of Fig. 5 = adapting to 400:8) and test conditions (circles = the tests were presented on the left; rectangles = the tests were presented on the right). In the pretests, the tests were underestimated if they were presented on the left and were overestimated if they were presented on the right (Table 1). In adaption Condition 1, the tests were further underestimated compared to the baseline if they were presented on the left and were further overestimated if they were presented on the right. In adapting Condition 2, however, the tests were less underestimated compared to the baseline if they were presented on the left and were less overestimated if they were presented on the right. Error bars denote 1 SEM

difference between test areas ($p = 0.075 > 0.05$). In other words, the effect of MNL was absent with adaptors 400:33. Moreover, with adaptors 400:33, if the tests were presented on the right, there was a significant difference between treatment and its baseline ($p = 0.024 < 0.05$), in which the tendency to ‘overestimate stimuli presented on the right’ was significantly weakened (the tests were less overestimated). In other words, vertical adaptors 400:33 still had effect on horizontal numerosity perception.

A 2×2 repeated ANOVA was conducted with adaption area (33 dots were on the top or bottom field) and test area (tests were on the left or right field) as the independent variables and the adaptation aftereffect (subtraction) as the dependent variable. This model yielded no significant main effect of adapting area ($p > 0.05$) or test area ($p > 0.05$). There was a significant interaction between the two factors, $F(1, 15) = 4.899$, $p = 0.043 < 0.05$. However, no statistical significance

Table 2 Mean and SD for PSEs in different adapting and test conditions in Experiment 1 (control condition)

Condition	Pretest		Adapting to 33:400		Adapting to 400:33	
	Left	Right	Left	Right	Left	Right
PSE	35.58	31.47	37.14	32.22	36.31	34.14
SD	6.37	3.38	5.17	3.40	5.15	3.17

was found if the simple effect was analyzed with regard to the interaction between the two factors. Adaptors 400/33 showed a similar but less robust effect compared to that of 400/8.

A 3×3 repeated ANOVA was conducted with adaption area (Factor A: adaptation area, fewer dots were on the top or bottom field), test area (Factor B: test area, tests were on the left or right field), and adaptors (Factor C: adaptors' mode, 400/8 mode or 400/33 mode) as the independent variables. The adaptation aftereffect was again chosen as the dependent variable (data in Tables 1 and 2 were both used). This model yielded a significant interaction between A and B ($p = 0.021 < 0.05$), a significant interaction between B and C ($p = 0.024 < 0.05$), and a significant overall interaction of A, B, and C ($p = 0.02 < 0.05$). According to the results, the composition of adaptors affected the horizontal numerosity perception: even if the 400-dot-adaptor was unchanged, the 8-dot adaptor and 33-dot adaptor had different effects on the relative numerosity-comparing tasks in our study, which was indicated by the interaction between B and C.

Importantly, a slight decrease in adaptors' influence could be assumed if we replaced the 8-dot adaptor with the 33-dot adaptor. With the adaptors 400/33, the interaction between A (adaptation area) and B (test area) was close to the marginal significance ($p = 0.043$), showing a decrease compared to that with 400/8 ($p = 0.004$). Moreover, no statistical significance was found if the simple effect was analyzed with regard to the interaction between A and B with the adaptors 400/33. In other words, a similar effect was revealed on horizontal perception with adaptors 400/33, and a decrease in the effect of adaptors 400/33 also was suggested compared to that of 400/8.

These results indicate that the 8-dot adaptor should have its own effect on horizontal numerosity perception, and the effect was attributed to increasing the perceived magnitude in particular visual fields, according to the top-right and bottom-left correlations.

In conclusion, Experiment 1 demonstrated that the adaptors presented in the vertical direction significantly affected the numerosity perception of participants in the horizontal direction.

Experiment 2: effects of horizontal numerosity adaptation on vertical numerosity perception

Experiment 1 examined whether the numerosity adaptation in the vertical direction would affect numerosity perception in the horizontal direction and found that numerosity perception in the horizontal direction could be significantly affected if participants were adapted to particular adaptors (i.e., 8:400) arranged in the vertical direction. In Experiment 2, we adopted a similar method to investigate whether numerosity adaption in the horizontal direction would affect numerosity perception in the vertical direction. The apparatus, design and procedure were similar to those in Experiment 1.

Methods

Participants The same 16 participants as those in Experiment 1 were asked again to complete Experiment 2.

Stimuli The adaptors are shown in Fig. 6. Similar dots were generated and randomly distributed within two fixed circles centered at 6.92° from the center of the computer screen on the left/right. In adaption Treatment 1 (adapting to 8:400; Fig. 6, left side), 8 dots were arranged in the left circle and 400 dots in the right. In adaption Treatment 2 (adapting to 400:8, right side), 400 dots were arranged in the left circle and 8 dots in the right. In the tested stage, the test and probe were presented in two circles in the vertical direction, centered at 6.52° above/below the center. There also were two test conditions

Fig. 6 Adaptors used in Experiment 2. The adaptors of adaptation Condition 1 were shown on the left side, and the adaptors of adaptation Condition 2 were shown on the right. Similar dots were distributed within

two fixed circles on the left/right part of screen, respectively. For the adaptors, 400 dots were arranged in one circle and 8 dots were arranged in the other

according to the position where the test was presented (in test Treatment 1, the test was at the top; in test Treatment 2, the test was at the bottom).

Procedure The entire procedure was similar to that used in Experiment 1. Participants pressed “y” if the upper circle seemed to have more dots and “b” to indicate the bottom circle. These two keys were both controlled by one of the participants’ preferred hands, rather than two hands, to avoid the extra vertical-horizontal interaction caused by task assignment.

Results

As in Experiment 1, psychometric values under different conditions were fitted by cumulative normal distribution functions for each participant. PSEs were calculated as shown in Table 3.

There was a significant difference between the two baselines ($p < 0.01$). No significant difference was found when we compared the treatments with their baselines.

A 2×2 ANOVA was conducted similarly to Experiment 1. There was no significant main effect of adaption area ($p = 0.243 > 0.05$), test area ($p = 0.583 > 0.05$), or interaction between the two factors ($p = 0.106 > 0.05$; Fig. 7).

In conclusion, in Experiment 2, numerosity adaptation in the horizontal direction did not significantly affect numerosity perception in the vertical direction, asymmetrical to the effect of vertical adaptors, which affected horizontal perception. We will analyze this asymmetry in detail in the Discussion.

Discussion

Spatial selectivity of numerosity adaptation

It is generally believed that adaptation induced by visual properties is spatially selective (i.e., the aftereffects of adaptation are constantly limited to the area of the presented adaptors),

Table 3 Mean and SD for PSEs in different adaption and test conditions in Experiment 2

Condition	Pretest		Adapting to 8:400		Adapting to 400:8	
	Top	Bottom	Top	Bottom	Top	Bottom
PSE	33.36	38.45	34.90	37.66	32.66	37.78
SD	3.14	4.41	2.64	8.61	2.48	7.06

Note. Adapting to 8:400/400:8 = adaption Condition 1/2. Top/Bottom refers to the position where the test was presented (i.e., top/bottom = tested Condition 1/2)

Fig. 7 Results of ANOVA in Experiment 2. There was no significant interaction between adapting conditions (two shapes on the left of Fig. 7 = adapting to 8:400; the other two shapes on the right of Fig. 7 = adapting to 400:8) and test conditions (circles=the tests were presented at top; rectangles = the tests were presented at bottom). Error bars denote 1 SEM

because the receptive field of the neural population coding primary properties has a specific, limited range that can only respond to numerosity properties in particular areas of the visual field. Numerosity adaptation also may be spatially selective (Burr & Ross, 2008a; 2008b; Roitman, Brannon, & Platt, 2007; Burr, & Morrone, 2011).

However, numerosity adaptation may be an aftereffect based on numerosity representation and perception (Burr & Ross, 2008a; 2008b; Liu et al., 2012; 2013; Ross & Burr, 2010). A series of studies has demonstrated that representations of numerical and spatial properties are closely associated (Dehaene, 1992; Dehaene et al., 1993), and therefore, coding a particular numerical magnitude can automatically activate the spatial representation in the horizontal or vertical direction or in both directions (Gevers et al., 2006; Cho, & Proctor, 2003). Therefore, the horizontal and the vertical orientations, which are independent in visual perspective, might be associated via spatial-numerical-associated codes and interaction may appear between numerical processes along these orientations. Experiment 1 verified these hypotheses. Numerosity adaptation in the vertical direction affected numerosity perception in the horizontal direction. When observers were adapted to the adaptors that contained fewer dots in the upper part and more in the lower (8:400), the perceived numerical magnitude in the left visual field decreased relatively to the right. In contrast, participants’ numerosity perception in the right field decreased compared to that in the left with vertical adaptors 400:8. These changes in perception were revealed relative to their baselines and exhibited effects caused by adaptors.

The aftereffects in Experiment 1 are similar (but smaller) to those when observers were adapted to the horizontal adaptors, as revealed by previous studies (Burr & Ross, 2008a; Liu

et al., 2012). Specifically, “perceived numerical magnitude in the left visual field decreasing relatively to the right” is a typical aftereffect if we are adapted to adaptors with more dots in the left and fewer dots in the right (such as adaptors 400:8 in Experiment 2). Similarly, the decrease in perceived magnitude on the right against left adheres to inversed adaptors (8:400 in Experiment 2). In other words, the numerosity perception in the horizontal direction has similar changing modes when observers are adapted to 8:400 adaptors in the vertical direction or 400:8 adaptors in the horizontal direction. This pattern still holds for vertical 400:8 and horizontal 8:400 adaptors. Therefore, we propose that the upper location may be associated with the right and the lower to the left in numerosity adaptation, similar to findings in previous studies of numerosity perception (Gevers et al., 2006; Cho, & Proctor, 2003).

In short, the spatial selectivity of numerosity adaptation should involve additional areas compared with those for other primary visual properties. Importantly, the selective mechanism likely involves an abstract association between spatial locations (see details in the next section) rather than a pure retinotopic mapping, which is dominant in primary features.

Numerosity adaptation may activate the representation of MNLs

As an explanation for the current results, we proposed that numerosity adaptation activated the representation of MNLs. Below, we provide evidence to exclude two other possible explanations: 1) that the results were due to the spatial approach of adaption and test areas between the horizontal and vertical directions, which may cause the diffusion of the numerosity adaptation aftereffect, and 2) that built-in perceptual bias caused the results, as the numerosity-comparing tasks included in treatments and baselines can also activate MNLs.

First, the results of Experiment 1 could not be due to the spatial approach of the circular areas or diffusion of effects. In Experiment 1, the distances between the circles presented in the adaption stage and the circles in the test stage are equal (i.e., the adaption and test areas are symmetrically arranged). Therefore, the diffusion of the numerosity adaptation aftereffect (if any exists) should affect numerosity perception in the left and right fields to the same degree. However, Experiment 1 showed that the adaptors have distinct influences on different test areas, namely, a significant interaction between the adapting and test areas. In fact, the horizontal and vertical MNLs have their own positive directions. Numerosity adaptation is due to adaptors arranged in a particular direction. If it influences perception in its orthometric direction, then the influence should also have its own positive direction. Particularly, adapting the numerical association of fewer-upper/more-lower in the vertical direction (8:400) should make the perceived numerical magnitude decrease in the left field and

increase in the right. Effects should reverse (perceived number increases in the left field and decreases in the right) synchronizing with inversed adaptors (400:8). This prediction was compatible with the results of Experiment 1.

Second, the idea that MNL activated in numerosity comparisons accounted for the current results is not convincing. In numerosity-comparing tasks, the built-in MNL could be automatically activated by the magnitude of stimuli, and observers are more likely to believe that stimuli are more numerous if they are presented in the right of the visual field relative to the left (Holmes & Lourenco, 2011). This reasoning explains the perceptual bias that appeared in baselines, but it cannot explain the interaction between treatments. In Experiment 1, there was a significant bias in which the perceived magnitude of the tests in the left field was smaller than that in the right ($p < 0.05$), suggesting that the effect of MNL exists in numerosity-judging tasks. However, because the aftereffect of numerosity adaptation was calculated by the subtraction of PSEs between treatments against their baselines (Liu et al., 2012; 2013), any further change in perception should reveal the extra effect of the adaptors. According to the results, if observers were adapted to the less-upper/more-lower (8:400) adaptors in the vertical direction, their perceived numerical magnitude in the left visual field showed a further decrease relative to the right. In contrast, if observers were adapted to the more-upper/less-lower (400:8) adaptors, their numerosity perception in the right field decreased compared to that in the left relative to the baselines. In other words, the built-in tendency of perceiving that a stimulus presented in the right field as more numerous was reversed with horizontal adaptors 400:8. We propose that when observers are adapted to the adaptors in the vertical direction, the built-in perceptual bias caused by MNLs was enhanced (adapted to 8:400) or weakened (adapted to 400:8).

A plausible explanation of the interaction in Experiment 1 is that numerosity adaptation in the vertical direction and numerosity perception in the horizontal direction share certain processing stages. Therefore, the numerical processing of these directions interacts. We propose that numerosity adaptation activated spatial-numerical-associated codes, which connect the vertical and horizontal orientations. The vertical MNL may activate the horizontal MNL (Gevers et al., 2006). If observers are exposed to the vertical adaptors, they may adapt to a dual activation of MNLs in the vertical and horizontal directions so that the numerosity adaptation aftereffect transfers from the vertical to the horizontal direction.

Burr and Ross (2008a) cited IPS as evidence for implementing numerosity adaptation. According to Butterworth (2008), it would be difficult to consider IPS as a candidate because it represents numerosity abstractly, whereas the numerosity adaptation described in previous studies is retinotopic, showing a typical feature of visual processing in earlier stages (Butterworth, 2008). However, the current study

showed that numerosity adaptation can be based on an abstract representation, such as MNLs, which combine the numerical and the spatial representation. Based on the activation of MNLs, the aftereffect of numerosity adaptation in the vertical direction can be revealed in a particular area beyond where the adaptors were presented according to an abstract association, namely, the association of the top with the right and the bottom with the left. In recent studies, numerosity adaptation was shown to be a cross-modal and cross-format adaptation (Burr, 2013), and it was shown to be a process that unfolded across several levels of visual processing (Liu et al., 2013). This evidence supports the view that numerosity adaptation occurred in IPS.

Interaction between horizontal and vertical directions may be asymmetrical

In our experiments, both the horizontal and vertical pretests showed an effect of MNL representation (the tests seemed to have more dots if they were presented on the right in Experiment 1 and if they were presented at top in Experiment 2). However, although the vertical adaptors showed a significant effect on the horizontal perception in Experiment 1, no reliable influence of horizontal adaptors was shown on the vertical perception in Experiment 2. Given the potential behavioral tendency revealed by a marginal p value of interaction ($p = 0.106$), we suggest that numerosity adaptation in the horizontal direction could potentially affect numerosity perception in the vertical direction, similar to the effect of vertical adaptors affecting horizontal perception. To verify this hypothesis, further study with alternative methods might find new evidence of the interaction in Experiment 2, such as an fMRI study, in which the adaptation effect could be suggested by a decrease in the blood oxygen level-dependent (BOLD) activation before any effect could be revealed in the behavior study. Below, we discuss the asymmetrical interaction between the horizontal and vertical directions.

The asymmetrical activating pattern of MNLs in the horizontal and vertical directions was not specifically shown in the current study. Related studies also suggested that the threshold of automatically activating coding of the horizontal MNL is lower than that of the vertical MNL. In the study by Shen et al. (2006), when participants were performing parity judgments based on the active processing of numerosity, a SNARC effect appeared alone in both the horizontal and vertical orientations. However, when participants were performing tasks that might be based on shallow processing of numerosity (e.g., passively looking at numbers), the attention shift caused by MNL was only found along the horizontal orientation. Additionally, in the study by Gevers et al. (2006), participants were asked to respond by pressing keys that were arranged to be discriminant both in the horizontal and vertical directions. Four keys were arranged on the lower-left, lower-right, upper-left, and

upper-right positions. When participants were asked to respond along the vertical direction (to press the upper keys for odd numbers, the lower keys for even numbers, and then the opposite), a SNARC effect also appeared in the horizontal direction (reaction time for smaller numbers was shorter if the keys were on the left and longer if the keys were on the right, and the situation was inversed for large numbers). However, if participants were asked to respond along the horizontal direction, no SNARC effect was found along the vertical orientation. These studies suggested that the activating threshold of the vertical SNARC, which is based on the vertical MNL, is higher than that in the horizontal direction.

The asymmetry of the activation threshold between horizontal and vertical MNLs might be due to the inequality of the frequencies we correlate between numerosity and space positions in our daily lives. Generally, we relate numerosity to position in the horizontal direction more frequently compared with the vertical position. Therefore, an MNL would usually be built in a left-to-right format. Effects of MNLs activated in numerosity comparisons should be strong enough to appear in both the horizontal and vertical orientations, whereas the effect of MNL caused by the orthometric adaptors (e.g., vertical adaptation to horizontal perception) might be weak. Although the effect of vertical adaptors could activate the horizontal MNL, the effect from horizontal adaptors might not reach the threshold required to activate the vertical MNL. This factor may be the reason why effects of MNL appeared in both directions in numerosity-comparison tasks (baselines), whereas a further effect on perception caused by the orthometric adaptors was only revealed in the horizontal direction.

Notably, when participants adapted to vertical adaptors, the perception along the horizontal orientation changed, as was revealed in Experiment 1. The perception along the vertical orientation also changed greatly (e.g., 30 dots could be perceived as 100 dots after adaptation; Burr & Ross, 2008a; Liu et al., 2013). Although we proposed that vertical adaptors could simultaneously activate the vertical and horizontal MNLs, we should note that the dramatic change in vertical perception may be more attributable to the retinotopic adaptation of local visual neurons rather than the effect of the change in the vertical MNL. It was proposed that the retinotopic influence accounts for no less than 50 % in typical visual after-effects (Melcher, 2005; Afraz & Cavanagh, 2009; Zhang et al., 2014). It is natural that influence based on primary physiological substrates (visual neurons) is dominant in visual adaptation effects. With regard to numerosity processing, an intriguing fact is that an abstract representation of MNLs could underlie and reveal their influence in adaptation and perception processing. Mechanisms of primary visual neurons' activation could not provide intuitive explanations for the results revealed in the current study. Rather, the results demonstrate the idea that numerosity cognition unfolds across

several levels of processing, including both primary and abstract levels.

Interaction of MNLs between the vertical and the horizontal dimensions may occur in the coding stage

In both previous studies and the current study, an interaction was revealed in numerosity processing between the vertical and horizontal dimensions (Schwarz & Keus, 2004; Gevers et al., 2006). To characterize this interaction, additional details should be determined. For example, the stage at which this interaction occurs should be identified. We analyzed whether the spatial-numerical-associated codes in both directions were activated in parallel if a particular magnitude was coding or if the codes switched in distinct directions according to specific tasks during the responding stage. If the interaction occurs during the coding stage, the spatial representation in both directions should be automatically and simultaneously activated when a particular magnitude of dots is coded by the cognition system. In contrast, if this interaction occurs during the response stage, then the two MNLs should be independent in the coding stage and the interaction will only exist in response to specific properties of the responding assignment to particular tasks.

According to the internal number map proposed by Schwarz and Keus (2004), the horizontal and vertical MNLs should interact during the coding stage. However, in the study by Gevers et al. (2006), the interaction of the numerosity coding between the two directions depended on the arrangement of the responding keys and the possibility that this interaction occurs in the response stage could not be ruled out.

The idea that the horizontal and the vertical MNLs were activated simultaneously in the magnitude coding stage was clarified by the current study. In Experiment 1, numerosity adaptation in the vertical direction influenced numerosity perception in the horizontal direction. These results demonstrate that the interaction of numerosity processing between the two directions is complete by the adaption stage and before the response stage, because adaption occurs before the response stage. If observers were adapted to less-upper/more-lower adaptors, the perceived numerical magnitude in the left field decreased significantly. Reversed change synchronized with the inversed adaptors. Because the aftereffect of vertical adaptors 8:400 is similar to that of directly adapting to less-right/more-left adaptors in the horizontal direction (such as 400:8), these results suggest that vertical adaptors simultaneously activated the horizontal and the vertical MNLs. Numerosity adaptations may occur based on a dual activation of MNLs, and numerosity perception in the horizontal direction is affected later.

Notably, in the previous studies and the current study, the thresholds of activating MNLs in the two directions are shown to be unequal. This finding may additionally underline a

different aspect of the two dimensions in numerosity cognition, which is inconsistent with the idea that the horizontal and the vertical MNLs are a single representation with a task-dependent spatial orientation (Gevers et al., 2006).

Conclusions

Numerosity adaptation in the vertical direction significantly affects numerosity perception in the horizontal direction. Specifically, when observers are adapted to less-upper/more-lower adaptors, the perceived numerical magnitude in the left field significantly decreases relative to the right, and when observers are adapted to more-upper/less-lower adaptors, the perception in the right field decreases relative to the left compared with their baselines. The vertical numerical adaptation can affect the horizontal perception via an abstract association of spatial locations (i.e., to associate top with right and bottom with left). However, the horizontal adaptation did not affect the vertical perception, perhaps because of the higher activation threshold of the spatial-numerical-associated codes along the vertical orientation.

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