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Adaptation reveals unbalanced interaction between numerosity and time

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ABSTRACT

Processing quantities such as the number of objects in a set, size, spatial arrangement and time is an essential means of structuring the external world and preparing for action. The theory of magnitude suggests that number and time, among other continuous magnitudes, are linked by a common cortical metric, and their specialization develops from a single magnitude system. In order to investigate potentially shared neural mechanisms underlying numerosity and time processing, we used visual adaptation, a method which can reveal the existence of a dedicated processing system. We reasoned that cross-adaptation between numerosity and duration would concur with the existence of a common processing mechanism, whereas the absence of cross-adaptation would provide evidence against it. We conducted four experiments using a rapid adaptation protocol where participants adapted to either visual numerosity or visual duration and subsequently performed a numerosity or duration discrimination task. We found that adapting to a low numerosity altered the estimation of the reference numerosity by an average of 5 dots, compared to adapting to a high numerosity. Similarly, adapting to a short duration altered the estimation of the reference duration by an average of 43 msec, compared to adapting to a long duration. In the cross-dimensional adaptation conditions, duration adaptation altered numerosity estimation by an average of 1 dot, whereas there was not sufficient evidence to either support or reject the effect of numerosity adaptation on duration judgments. These results highlight that there are partially overlapping neural mechanisms which are dedicated for processing both numerosity and time.

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1. Introduction

Our ability to distinguish between stimuli that differ in numerosity, the number of objects in a set, is an evolutionary pivotal trait identified in humans from early developmental stages (Barth, La Mont, Lipton, & Spelke, 2005; Schlegel et al., 2014; Xu & Spelke, 2000), and shared by many non-human species (Cantlon & Brannon, 2007; Ditz & Nieder, 2016; Jones et al., 2014; Miletto, Agrillo, Izard, & Bisazza, 2016). This apparent innate sense of number is implicated in the development of complex mathematical abilities (see meta-analyses by Schneider et al., 2016; Schwenk et al., 2017). However, it is currently debated whether numerosity is a primary sensory property processed by dedicated neural mechanisms, or whether it is part of a unified magnitude system which processes all kinds of quantity information (Kadosh, Lammertyn, & Izard, 2008; Leibovich, Katzin, Harel, & Henik, 2016). Similarly, the existence of a dedicated system for time perception remains elusive, with some studies demonstrating that temporal processing relies on specialized neural networks (see reviews by Ivry & Schlerf, 2008; Grondin, 2010), and others showing that time is strongly associated with numerosity as part of a generalized magnitude system (De Hevia, Izard, Coubart, Spelke, & Streri, 2014; Lourenco & Longo, 2010).

An influential theoretical framework accounting for the abovementioned findings is the “A Theory Of Magnitude” (ATOM) proposed by Walsh (2003; Buetti & Walsh, 2009). According to this theory, the specializations for number, time and space processing develop from a single magnitude system. Indeed, a number of studies support the existence of shared processing mechanisms between numerosity, time and space (Cai & Connell, 2015; Hubbard, Piazza, Pinel, & Dehaene, 2005; Schwiedrzik, Bernstein, & Melloni, 2016; Srinivasan & Carey, 2010).

Most of the evidence supporting ATOM come from neuroimaging studies which show that numerosity and duration processing rely on spatially overlapping cortical systems (Dormal, Dormal, Joassin, & Pesenti, 2012; Hayashi et al., 2015; Hayashi, Kanai, et al., 2013; Skagerlund, Karlsson, & Träff, 2016). However, the overlapping activations do not necessarily imply overlapping mechanisms. Moreover, these studies use distinct tasks for evaluating numerosity and duration discrimination, a method which does not allow robust conclusions on whether numerosity and duration truly interact. There are a few behavioral studies which employ a cross-dimensional paradigm and use non-symbolic numerosities but have yielded conflicting findings, showing either a unidirectional interference of numerosity on duration judgments (Alards-Tomalain, Walker, Kravetz, & Leboe-McGowan, 2016; Dormal, Seron, & Pesenti, 2006), or a unidirectional influence of duration on numerosity (Lambrechts, Walsh, & van Wassenhove, 2013; Martin, Wiener, & van Wassenhove, 2017). Conversely, Javadi and Aichelburg (2012) found a bidirectional interference, while Agrillo, Ranpura, & Butterworth, 2010 found no interference.

A powerful psychophysical tool which can further elucidate whether numerosity and time rely on similar neural networks as ATOM postulates, is perceptual adaptation. Adaptation has been described as the “psychophysicist's

microelectrode” (Frisby, 1979), since the visual aftereffects produced after adapting to a stimulus isolate the neural networks which respond selectively to the features of that stimulus, offering a behavioral window in the underlying cortical processes (Blake & He, 2005; Thompson & Burr, 2009). Both numerosity and duration perception adapt (Burr & Ross, 2008; Heron, Aaen-Stockdale, et al., 2012). Adapting to a low numerosity leads to an overestimation of the numerosity subsequently presented in the adapted location, whereas adapting to a high numerosity leads to an underestimation (Aagten-Murphy & Burr, 2016; Anobile, Cicchini, & Burr, 2014, 2016; Anobile, Turi, Cicchini, & Burr, 2015). Moreover, adaptation to numerosity can occur across sensory modalities and across presentation formats, supporting the existence of an abstract quantity system (Arrighi, Togoli, & Burr, 2014). Similarly, adaptation to a short and long auditory or visual duration induces expansion and contraction of subsequently heard or viewed durations respectively (Heron, Hotchkiss, Aaen-Stockdale, Roach, & Whitaker, 2013). However, and contrary to numerosity adaptation, the spatial selectivity of visual duration adaptation remains unclear (Heron, Roach, Hanson, McGraw & Whitaker, 2012; Johnston, Arnold, & Nishida, 2006; Li, Yuan, Chen, Liu, & Huang, 2015; Maarseveen, Hogendoorn, Verstraten, & Paffen, 2017).

Here, we investigate the presence of a common perceptual system underlying numerical and temporal processing using cross-dimensional visual adaptation. More specifically, we examined whether adapting to numerosity can alter duration perception and vice versa. We hypothesized that if numerosity and time perception rely on shared processing networks, then adaptation to visual numerosity should affect duration discrimination, and adaptation to visual duration should affect numerosity discrimination.

2. Materials and methods

2.1. Participants

Twenty participants completed the experiment (8 female, 12 male). All subjects had normal or corrected-to-normal visual acuity and were naïve to the purpose of the study. Three authors (AT, StP, MvdS) also did the experiment and their results corroborated the results of the naïve subjects but were excluded from the final analysis since they were aware of the hypotheses of the study. One additional participant was also excluded because of misunderstanding the experiment's instructions. Participants gave written informed consent and received a monetary reward or course credits. The experiment was conducted in accordance with the Declaration of Helsinki and was approved by the Ethics Committee of the Faculty of Social and Behavioural Sciences of Utrecht University.

2.2. Apparatus and stimuli

Participants sat at about 60 cm distance from a 60 × 34 cm, Asus liquid crystal display (LCD) monitor with 2560 × 1440 resolution and a refresh rate of 60 Hz. The display was

linearized using a photometer (Mavo Monitor USB, Gossen, Nürnberg, Germany). The stimuli (viewed binocularly) were circular patches containing an equal proportion of black and white dots displayed on a mean luminance background (60 cd/m²) at 80% Michelson contrast. Each dot had a diameter of .2° of visual angle and the circular patches had a diameter of 12°. In each trial, dots were scattered randomly within the circular patches and were not allowed to overlap.

In numerosity adaptation, the adapters were circular patches of 20 or 80 dots, while the reference was a patch of 40 dots (Fig. 1a). The numerosity of the test patch varied from trial to trial using the Minimum Expected Entropy staircase method (Saunders & Backus, 2006). In duration adaptation, the adapters were circular patches of 40 dots presented for either 67 msec or 600 msec, while the reference was a patch of 40 dots lasting for 333 msec. The test stimuli were bursts of white noise (70 dB) presented binaurally through Sennheiser HD201 headphones and their duration varied using the aforementioned staircase method (Maarseveen et al., 2017). The numerosity adapters (20 vs 80 dots) were chosen to produce strong and repulsive adaptation aftereffects on the reference numerosity of 40 dots. Likewise, the duration adapters (67 vs 600 msec) were chosen to produce strong and repulsive adaptation aftereffects on the reference duration of 333 msec. Thus, we ensured significant adaptation aftereffects on the unidimensional adaptation conditions, which were a prerequisite for the cross-dimensional adaptation conditions. Furthermore, the adapters used are in line with other studies on numerosity (Aagten-Murphy & Burr, 2016; Castaldi, Aagten-Murphy, Tosetti, Burr, & Morrone, 2016; Turi et al., 2015) and duration adaptation (Heron, Aaen-Stockdale, et al., 2012; Heron et al., 2013; Maarseveen et al., 2017). Moreover, our choice of a visual reference stimulus and an auditory test stimulus was based the suggestion that duration adaptation is not spatially selective (Li et al., 2015; Maarseveen et al., 2017), contrary to numerosity adaptation (Burr & Ross, 2008). Hence, adapting to a visual duration would produce perceptual aftereffects on the same side as the adapter and on the opposite side. In addition, using an auditory test stimulus instead of a visual one is in line with previous studies on duration adaptation (Heron, Aaen-Stockdale, et al., 2012; Maarseveen et al., 2017).

All stimuli were generated and presented using MATLAB 2016b (MathWorks, Inc.) and the Psychophysics Toolbox 3.0.13 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

In numerosity adaptation, subjects first performed the neutral adaptation condition (40 dots), and then adapted to a low (20) or high (80) numerosity (see Fig. 1b for a schematic illustration of a single trial). The center of the dot patches was at 8° eccentricity left of fixation for the first half of the trials and right of fixation for the other half (100 trials in total), with the “side”-block also being counterbalanced across participants. The reference patch (40) appeared at the adapted location and the test patch at the opposite side. We used a rapid adaptation paradigm similar to Aagten-Murphy and Burr (2016), where the adapter was presented for 333 msec with no top-up adaptation. After a 300 msec pause, the reference patch was presented for 333 msec, followed by another 300 msec pause and then the test patch appeared for 333 msec. Using the two-alternative forced-choice (2AFC) paradigm, participants were asked to respond as accurately as

possible (guessing if unsure) which of the two patches, the reference or the test, appeared to have more dots by pressing the appropriate key. After responding, the next trial started after 500 msec.

In duration adaptation, we used a modified version of the duration adaptation method by Heron, Aaen-Stockdale, et al. (2012), and applied the same, rapid adaptation protocol we used for numerosity adaptation (Fig. 1b). Subjects first performed the neutral adaptation condition (40-dot patch; 333 msec) and then adapted to a short (67 msec) or a long (600 msec) duration. The reference was a 40-dot patch (333 msec) presented in the adapted location, while the test was an auditory burst of white noise of varying duration. Participants were asked to respond using a 2AFC paradigm whether the reference or the test lasted longer by pressing the appropriate key.

The same procedure was followed in the cross-dimensional adaptation conditions, with subjects being adapted to a low or high numerosity and tested on duration discrimination and adapted to a short or long duration and tested on numerosity discrimination (Fig. 1b). The order of the magnitude of adaptation (low/high numerosity; short/long duration) was counterbalanced within and across participants. Moreover, in order to avoid carry-over effects, participants were adapted to numerosity/duration and tested on the numerosity discrimination task on one day and adapted to duration/numerosity and tested on the duration discrimination task the following day, with the order of the task (numerosity or duration discrimination) being, again, counterbalanced across participants.

2.3. Data analysis

All data analyses were conducted using MATLAB, SPSS (version 24.0, SPSS Inc., Chicago, IL, USA) and JASP (version 0.8.1.2, JASP Team, 2017; jasp-stats.org). After the experiment, we ordered the data by adding the values obtained per side block (left vs right presentation side), sorting them on test numerosity or test duration and subsequently creating 10 equally sized bins of 10 trials. We then fitted these data with cumulative Gaussian functions to yield estimates of the point of subjective equality (PSE) and slope for each condition and used the PSE and slope values for subsequent analyses on the effects of numerosity and duration adaptation.

Given that adaptation stimuli were presented at one side (e.g., left) for half trials and at the opposite side (e.g., right) for the other half, we wanted to ensure that this design would not yield significant differences in the average PSE and slope values. Indeed, there were no statistically significant differences in the obtained measurements when the adaptation stimuli were presented to the left compared to the right side in each adaptation condition-task, after using false discovery rate (FDR)-corrected significance thresholds. Likewise, there were no statistically significant main or interaction effects of the presentation side block (adaptation trials starting from the left or right side) and task order (performing the numerosity discrimination tasks at day 1 and the duration discrimination tasks at day 2, and vice versa) on average PSE values in each adaptation condition-task using FDR-corrected significance thresholds.

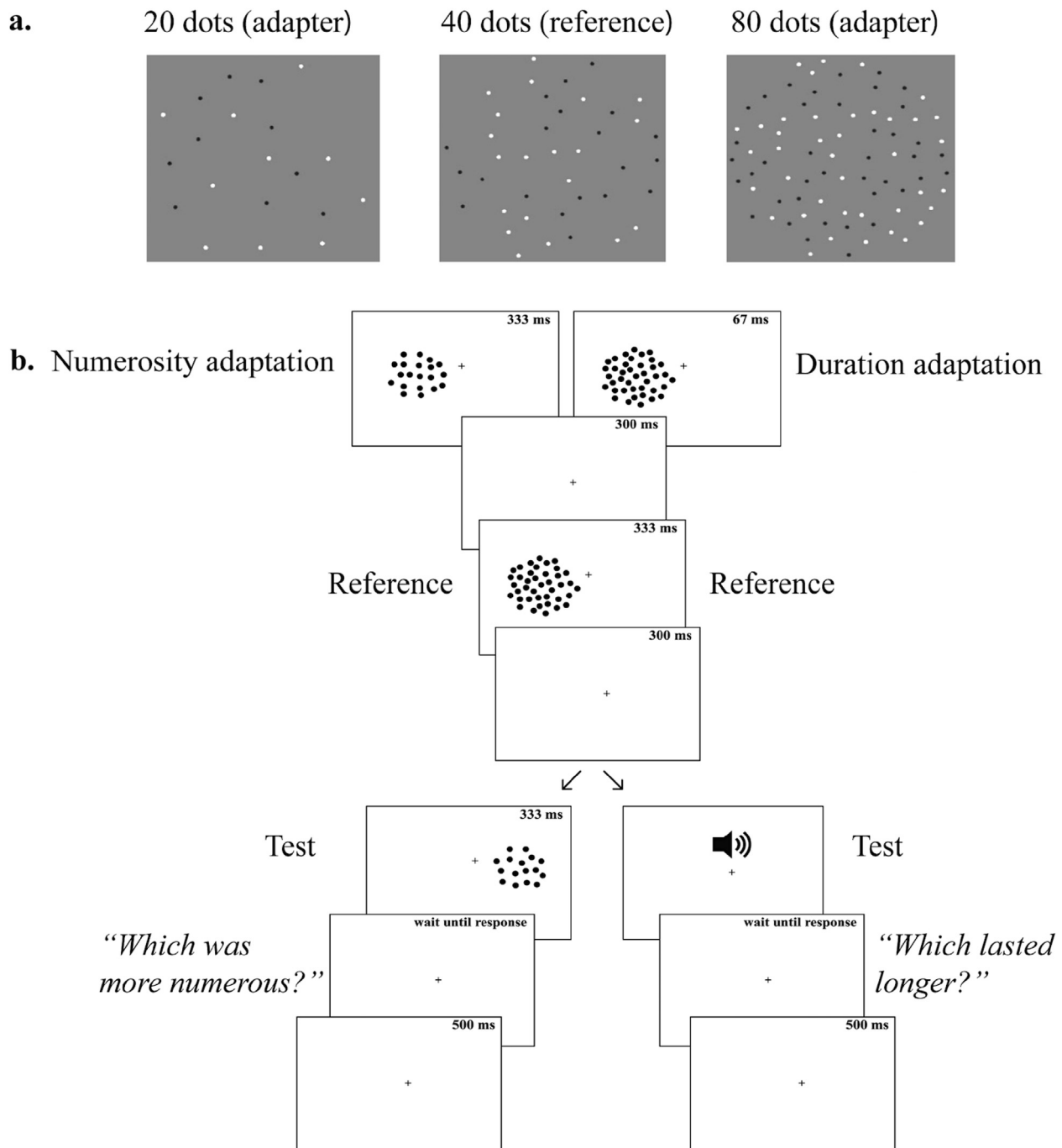


Fig. 1 – Illustration of the stimuli and procedures. (a) The adapters and reference used for numerosity and duration adaptation (note that the dots were not overlapping and their position within the circular patch was random in every trial). (b) Schematic illustration of a single trial in each adaptation-task condition. In numerosity adaptation, a low (20 dots) or high (80 dots) numerosity adapter would be presented either to the left or the right of the fixation cross. The reference numerosity (40 dots) was presented at the adapted location, and the test (varying in numerosity) was presented at the opposite side. The same design was followed in the duration adaptation-numerosity discrimination condition, with the only change being a 40-dots adapter lasting for 67 msec (short) or 600 msec (long). In duration adaptation, a short or long duration adapter of 40 dots would be presented either to the left or the right of the fixation cross. The reference was a 40-dot patch (333 msec) presented at the adapted location. The test (white noise of varying duration) was presented binaurally via headphones. In the numerosity adaptation-duration discrimination condition, the same design was followed, with the only change being a low or high numerosity adapter presented for 333 msec.

3. Results

Fig. 2 demonstrates the shift in the psychometric curves of a single subject depending on the magnitude of the adapter, after plotting the proportion of trials where the test was perceived as more numerous or longer in duration than the reference (40 dots; 333 msec).

There were no outliers and the average PSE values in each adaptation condition-task were normally distributed, as assessed by boxplot and the Shapiro–Wilk test ($p > .05$). A series of two-tailed, paired-samples t -tests were conducted to examine whether average PSE values in numerosity and duration discrimination tasks were significantly different after adapting to a low and high numerosity, and a short and long duration. The p values obtained were FDR-corrected for multiple comparisons where applicable, and the reported Cohen's d effect sizes were corrected for dependence between means (Morris & DeShon, 2002).

In numerosity adaptation (Fig. 3b), the mean PSE values in the numerosity discrimination task were significantly higher after adaptation to a low numerosity (20 dots; $M = 37.41$ dots, $SD = 3.25$) compared to a high numerosity (80 dots; $M = 32.66$

dots, $SD = 2.84$ dots), $t(19) = 4.57$, $p < .001$, Cohen's $d = 1.02$. These data were also examined by estimating a Bayes factor using Bayesian Information Criteria (Jarosz & Wiley, 2014, p. 6; Wagenmakers, 2007), comparing the fit of the data under the null hypothesis and the alternative hypothesis. An estimated Bayes factor (null/alternative) suggested that the data were 143.62 times more likely to occur under the model including an effect of numerosity adaptation on numerosity discrimination, rather than the model without it.

In duration adaptation (Fig. 3d), the mean PSE values in the duration discrimination task were significantly higher after adaptation to a short duration (67 msec; $M = 257.67$ msec, $SD = 76.84$ msec) compared to a long duration (600 msec; $M = 214.84$ msec, $SD = 64.08$ msec), $t(19) = 3.50$, $p < .01$, Cohen's $d = .80$. An estimated Bayes factor suggested that these data were 16.88 times more likely to occur under the model including an effect of duration adaptation on duration discrimination, rather than the model without it.

As shown in Fig. 4b, the mean PSE values in duration discrimination task were marginally higher after adaptation to a low numerosity ($M = 224.62$ msec, $SD = 52.64$ msec) compared to a high numerosity ($M = 211.89$ msec,

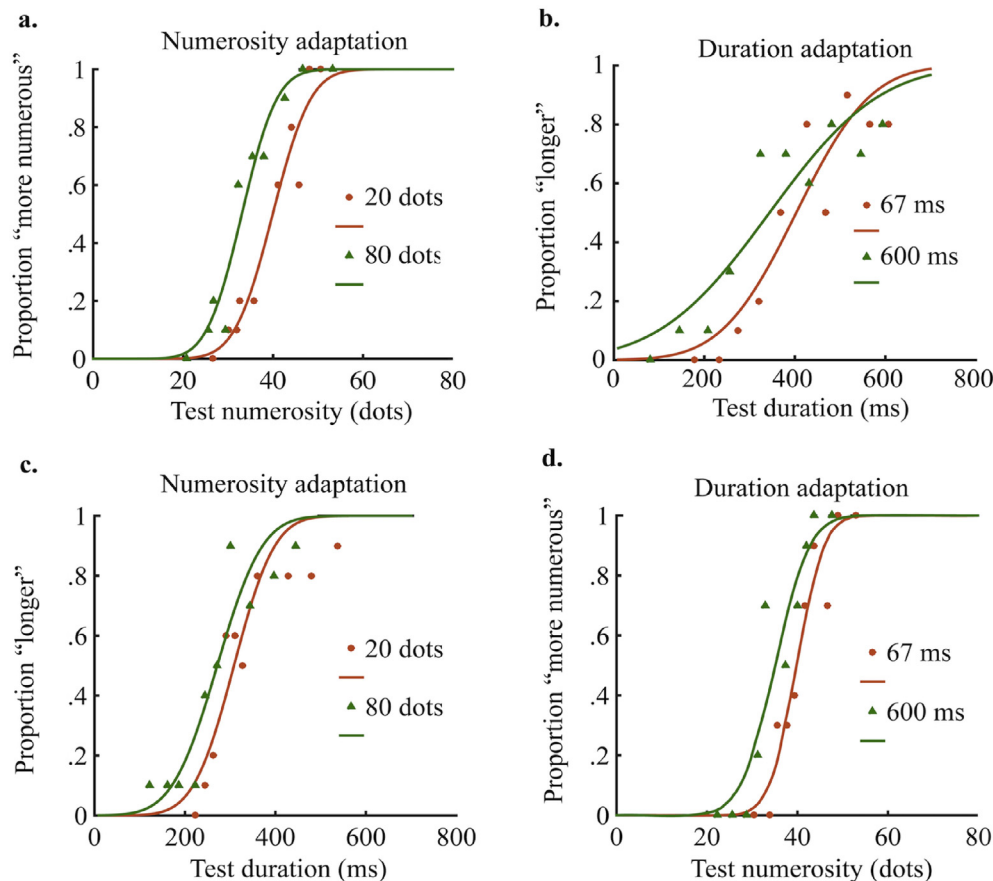


Fig. 2 – Psychometric curves of a single subject. Adaptation to a low numerosity resulted in an overestimation of the reference numerosity, and adaptation to a high numerosity resulted in an underestimation of the reference numerosity (a). Similarly, adaptation to a short and long duration resulted in an overestimation and underestimation of the reference duration respectively (b). In the cross-dimensional adaptation conditions, adaptation to a low and high numerosity resulted in an overestimation and underestimation of the reference duration respectively (c), whereas adaptation to a short and long duration resulted in an overestimation and underestimation of the reference numerosity respectively (d).

Unidimensional adaptation conditions

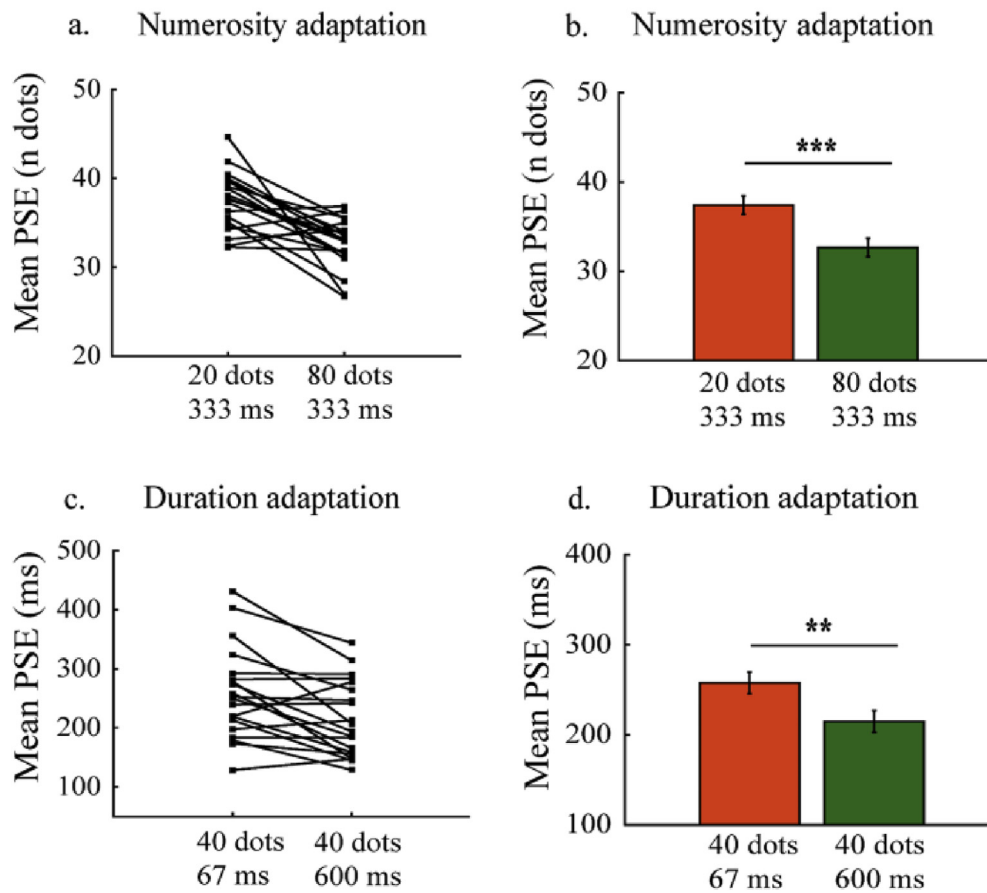


Fig. 3. – PSE values in the unidimensional adaptation conditions per participant (left) and on a group level (right). On a group level, numerosity discrimination was significantly affected by numerosity adaptation (b), and duration discrimination was significantly affected by duration adaptation (d). Error bars represent 95% Confidence Intervals, adjusted for a within-subjects design (Loftus & Masson, 1994).

SD = 49.13 msec), but this difference failed to reach statistical significance, $t(19) = 1.91$, $p > .05 = .071$, Cohen's $d = .43$. An estimated Bayes factor suggested that these data were only 1.06 times more likely to occur under a model including an effect of numerosity adaptation on duration discrimination rather than a model without it.

As shown in Fig. 4d, the mean PSE values in numerosity discrimination task were significantly higher after adaptation to a short duration ($M = 36.59$ dots, $SD = 1.67$ dots) compared to a long duration ($M = 35.29$ dots, $SD = 1.72$ dots), $t(19) = 2.84$, $p < .05 = .013$, Cohen's $d = .64$. An estimated Bayes factor suggested that these data were 5.24 times more likely to occur under the model including an effect of duration adaptation on numerosity discrimination, rather than the model without it.

In order to examine whether adaptation yielded changes not only in task accuracy as measured by the PSE values, but also precision, we analyzed the slope values obtained in each experimental condition. The assumption of normality was violated in the slope values. Thus, a series of Wilcoxon signed-rank tests were conducted to examine whether the slopes of

the psychometric curves of the numerosity and duration discrimination tasks were significantly different after adapting to a low and high numerosity, and a short and long duration. No comparison reached statistical significance after using FDR-corrected significance thresholds.

4. Discussion

The purpose of this study was to investigate whether numerosity and duration processing rely on a single magnitude system as postulated by the ATOM theory. To achieve this, we used cross-dimensional visual adaptation to numerosity and duration and a rapid adaptation paradigm. Our rationale was based on the idea that the aftereffects produced by visual adaptation are selective to the adapting stimulus, revealing dedicated coding strategies for that stimulus (see review by Webster, 2012). Hence, we hypothesized that if numerosity and time are processed by similar neural networks, then the visual aftereffects following numerosity and

Cross-dimensional adaptation conditions

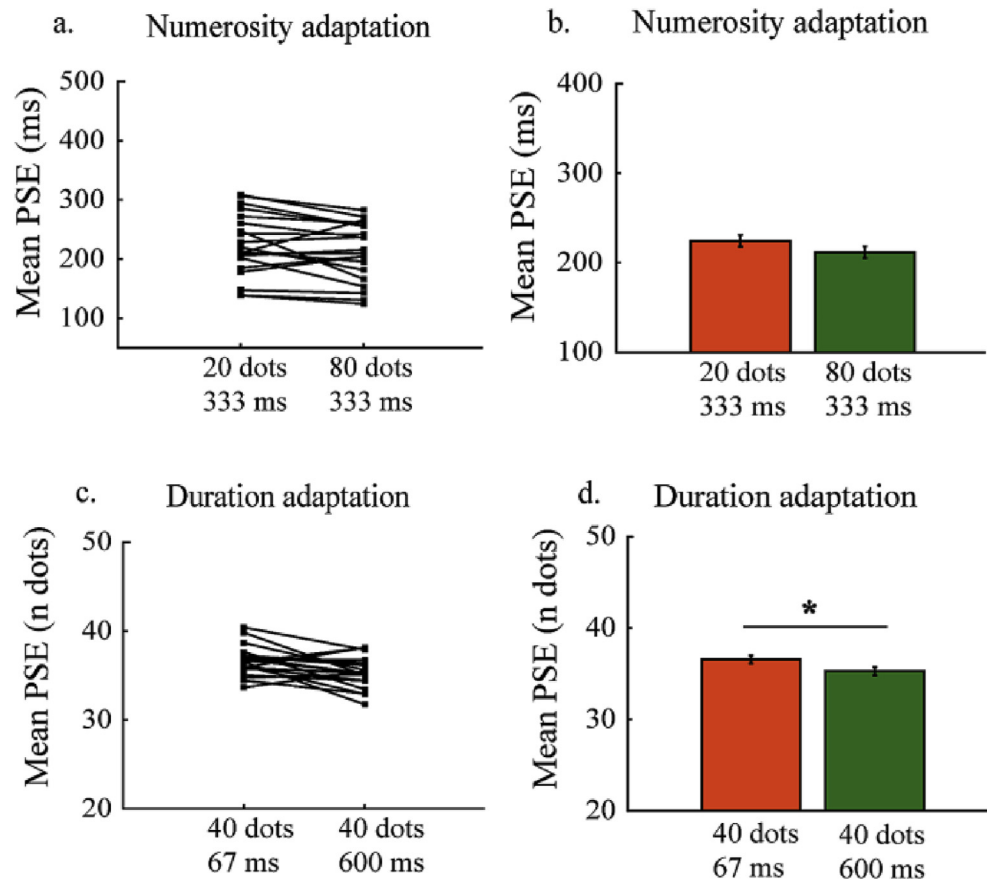


Fig. 4. – PSE values in the cross-dimensional adaptation conditions per participant (left) and on a group level (right). On a group level, duration discrimination was not significantly affected by numerosity adaptation (b), while numerosity discrimination was significantly affected by duration adaptation (d). Error bars represent 95% Confidence Intervals, adjusted for a within-subjects design (Loftus & Masson, 1994).

duration adaptation should affect duration and numerosity discrimination respectively. Our results partially confirm this hypothesis, since we found an unbalanced interaction between numerosity and duration perception.

More specifically, and in the unidimensional conditions, we found that visual adaptation to a low numerosity (20 dots) compared to a high numerosity (80 dots) altered the estimation of the reference numerosity (40 dots) by an average of 5 dots, in agreement with previous studies (Aagten-Murphy & Burr, 2016; Burr & Ross, 2008). Similarly, adapting to a short visual duration (67 msec) compared to a long duration (600 msec) altered the estimation of the reference duration (333 msec) by an average of 43 msec, confirming the work by Heron, Aaen-Stockdale, et al. (2012).

In the cross-dimensional adaptation conditions, our study shows that visual adaption to a short compared to a long duration altered numerosity discrimination judgments by an average of 1 dot. On the other hand, adapting to a low compared to a high numerosity did not significantly alter duration discrimination. Moreover, and based on the sequential analyses of the Bayes factors obtained (Schönbrodt, Wagenmakers, Zehetleitner, & Perugini, 2017;

see [Supplementary materials](#)), there was not sufficient evidence to either support or reject the effect of numerosity adaptation on duration judgments. Since there was no definitive trend found, and to address a potential concern, increasing our sample size would not necessarily change this inconclusive finding.

A general theory on how adaptation operates on a neural level is that the adapting stimuli will cause the excitation of a large assembly (or network) of neurons which have the same type of specificity (Barlow & Foldiak, 1989). Based on this, the repeated presentation of a visual numerosity or duration could lead to the joint excitation of many neurons which are all tuned to numerosity and duration discrimination, thus leading to a common pattern of perceptual aftereffects (i.e., under- or overestimation). In other words, if adaptation to duration alters sensitivity to numerosity, then it can be inferred that both dimensions are detected by a common network (Webster, 2012).

The effects of adaptation can also be understood in terms of a Bayesian estimation framework. More specifically, Stocker and Simoncelli (2006) proposed that adaptation increases the signal-to-noise ratio resulting in changes in the

likelihood function. Therefore, a Bayesian estimator model can account for the perceptual aftereffects and changes in the discrimination threshold induced by adaptation (Stocker & Simoncelli, 2006). In respect to our findings, the unidirectional influence of time on numerosity perception is corroborated by the work of Lambrechts et al. (2013) and Martin et al. (2017) who used a Bayesian approach. According to these studies, a plausible explanation for the unidirectional influence of time on numerosity perception would be the conceptualization of the ATOM theory in terms of a Bayesian framework and by inferring the existence of multiple priors (Martin et al., 2017). Martin et al. (2017) suggested that when sensory information needed for numerosity processing accumulate over a varying duration (short or long), then the varying degrees of uncertainty associated with temporal processing can add noise to the sensory accumulation of numerosity information, altering thus, the perception of numerosities (p.11–12).

Hence, we argue that although unbalanced, there is indeed an interaction of numerosity and time processing in the brain in accordance with the ATOM theory (Bueti & Walsh, 2009; Dormal et al., 2012; Hayashi et al., 2013; Skagerlund et al., 2016; Walsh, 2003). This is further exemplified by the same pattern of overestimating and underestimating the reference numerosity or duration after exposure to a low and high magnitude respectively (see Figs. 2 and 3). Hence, we argue that there are dedicated neural mechanisms for processing both numerosity and duration, with both numerosity and time perception undergoing adaptation-based recalibration (Anobile et al., 2016; Heron et al., 2013).

In order to further explain the unbalanced interaction we found between numerosity and duration processing, a possible explanation could reside on the size of the receptive fields (RFs) of neurons tuned to numerosity and duration processing. More specifically, there is robust evidence showing that numerosity adaptation is spatially selective (Aagten-Murphy & Burr, 2016; Burr & Ross, 2008) which could be attributed to the relatively circumscribed RFs of neurons tuned to numerosity (Anobile et al., 2016). On the other hand, the spatial selectivity of the duration after-effects remains unclear (Heron, Roach, et al., 2012; Li et al., 2015; Maarseveen et al., 2017), which might imply that the size of the RFs of neurons tuned to duration is larger and much less defined compared to the RFs of neurons tuned to numerosity. Hence, it is reasonable to assume that if duration and numerosity rely on similar cortical networks, then the larger RFs of neurons tuned to duration are more likely to affect the response of the smaller RFs of neurons tuned to numerosity. To further examine this possibility, we increased the size of the dot stimuli used as numerosity adapters and retested 12 participants from our original sample on duration discrimination (see Supplementary materials). We found no significant effect of numerosity adaptation on duration discrimination, which could imply that the RFs of neurons tuned to duration processing are less sensitive to changes in numerosity and object size. Nevertheless, it should be mentioned that the method of adaptation cannot separate the aftereffects induced on individual neurons from aftereffects induced on a neural network level, rendering the aforementioned account on the size of the RFs of neurons only speculative.

Perceptual adaptation is thought to induce changes in sensitivity which appear early in the visual system and can spread to later stages, with complex aftereffects such as the ones examined in our study reflecting changes inherited from earlier levels (Webster, 2012). Based on this, another explanation for the unbalanced interaction we found in the cross-dimensional adaptation conditions could be that numerosity and duration adaptation occurs at different processing stages leading to a differential influence of one over the other. More specifically, a recent functional magnetic resonance imaging (fMRI) study found that activation in the IPS but not V1, classified numerosity well, both before and after adaptation to a high (80 dots) numerosity (Castaldi et al., 2016). Similarly, there is robust evidence for the existence of numerosity selective neurons in the parietal cortex in humans (Harvey & Dumoulin, 2017; Harvey, Klein, Petridou, & Dumoulin, 2013; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004) and non-human primates (Nieder & Miller, 2004; Nieder, 2012). On the other hand, duration adaptation could involve lower areas of the visual cortex, with Heron et al. (2013) finding that duration adaptation precedes multisensory integration. The authors argued that there are duration selective networks in early areas of the visual and auditory system. Several neurophysiological studies have suggested that neurons in early visual and auditory systems of non-human animals are selective for temporal-frequency or tuned to duration (Brand, Urban, & Grothe, 2000; Duysens, Schaafsma, & Orban, 1996; Eriksson, Tompa, & Roland, 2008; Ghose & Maunsell, 2002; Hawken, Shapley, & Grosof, 1996; Mendelson & Cynader, 1985; Perez-Gonzalez, Malmierca, Moore, Hernandez, & Covey, 2006).

Hence, if duration adaptation involves lower areas of the visual cortex compared to the more parietal areas involved in numerosity adaptation, this could indicate that there is a processing hierarchy where temporal information processing precedes numerical processing. Based on this speculated processing hierarchy, time could encompass numerosity at a low perceptual level, and the information derived from both dimensions could be then integrated in the parietal cortex to generate guided action, as ATOM postulates. Nevertheless, the proposed processing hierarchy is rather unlikely since recent studies do implicate the lower areas of the visual cortex in numerosity processing (Fornaciai, Brannon, Woldorff, & Park, 2017; Park, DeWind, Woldorff, & Brannon, 2016). Therefore, and in order to elucidate how the adaptation aftereffects are produced within and across dimensions (i.e., numerosity and duration), future research could help identifying how neurons adapt at each stage and how adaptation-induced plasticity in early processing stages propagates throughout the processing hierarchy (Clifford et al., 2007).

Long and Beaton (1981) were one of the first to demonstrate an effect of numerosity on duration perception. More recent studies have also reported a strong interference of numerosity on duration processing (Alards-Tomalain et al., 2016; Dormal et al., 2006; Hayashi, Valli & Carlson, 2013), a finding which is not in agreement with the weak effect of numerosity adaptation on duration discrimination we found in our study. However, all the aforementioned studies used very low numerosities (up to 10 dots) which could account for the observed discrepancy by inferring distinct mechanisms for processing low compared to high numerosities. For instance,

perceiving low numerosities appears to be less affected by low-level stimulus characteristics, whereas perceiving high numerosities relies more heavily on density and size information (Dakin, Tibber, Greenwood, Kingdom, & Morgan, 2011; Gebuis & Reynvoet, 2012; Zimmermann & Fink, 2016). Moreover, numerosities within the subitizing range (up to 4 items) appear to rely more heavily on attentional resources compared to numerosities in the estimation range, a finding which further supports the existence of distinct processing mechanisms (Anobile, Turi, Cicchini, & Burr, 2012; Burr, Anobile, & Turi, 2011; Burr, Turi, & Anobile, 2010). Further research manipulating the range of numerosities and durations used could provide a greater insight on whether there are distinct mechanisms for processing low compared to high numerosities, and sub-compared to supra-second durations.

It is also worth mentioning that we did not find any statistically significant differences in the average PSE and slope values when the adaptation stimuli were presented to the left versus right side in each adaptation condition-task. This could be an outcome of successful counterbalancing of the presentation side (left vs right) and the order of the presentation side (adaptation trials starting from the left or right side). Nevertheless, the aforementioned lack of differences could be considered as being at odds with the ‘mental number line’ and the spatial-numerical association of response codes (SNARC) effect. These concepts describe an introspective left-to-right arrangement of ascending numbers. Based on this, shorter reaction times are recorded when low numbers are presented to the left, and high numbers are presented to the right (Dehaene, Bossini, & Giraux, 1993; Kadosh et al., 2008). However, no study to our knowledge has found evidence for the SNARC effect when using high numerosities (>30 dots), which could also account for the lack of differences in our study given the range of numerosities we used.

In the case of numerosity adaptation, some studies suggest that the adaptation effects examined are in response to density and not numerosity mechanisms (Durgin, 2008; Sun, Kingdom, & Baker, 2017; Tibber, Greenwood, & Dakin, 2012). Our rationale for choosing the specific numerosities used as adapters (20 vs 80 dots) and the rest of our stimulus characteristics (i.e., dot size, eccentricity), was based on the methodology used by a number of similar studies (Burr & Ross, 2008; Castaldi et al., 2016; Fornaciai, Cicchini, & Burr, 2016; Turi et al., 2015), and the model proposed by Anobile et al. (2016) which describes the eccentricity and density parameters implicated in inferring adaptation to numerosity and not texture. Thus, we are fairly confident that our experimental design was indeed appropriate for examining visual adaptation to numerosity and not texture-like mechanisms.

Another potential concern is that the rapid adaptation paradigm we used (100 trials with no top-up adaptation trials) may have hindered the full potential of numerosity and duration adaptation on duration and numerosity discrimination respectively. We do not believe this is the case because in the unidimensional adaptation conditions, this rapid adaptation paradigm was effective in inducing robust perceptual distortions in the expected direction. Therefore, it seems unlikely that this adaptation protocol could pose a serious methodological limitation in the cross-dimensional conditions.

5. Conclusions

Our study shows that both numerosity and time perception adapt under brief exposures and have a moderate ability to cross-adapt. We found a unidirectional influence of duration adaptation on numerosity judgments, with numerosity adaptation not affecting duration judgments significantly. We argue that numerosity and time processing rely on partially overlapping neural networks.

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Supplementary data

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