Distinct temporal mechanisms modulate numerosity perception

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Our ability to process numerical and temporal information is an evolutionary skill thought to originate from a common magnitude system. In line with a common magnitude system, we have previously shown that adaptation to duration alters numerosity perception. Here, we investigate two hypotheses on how duration influences numerosity perception. A channel-based hypothesis predicts that numerosity perception is influenced by adaptation of onset/offset duration channels which also encode numerosity or wire together with numerosity channels (duration/numerosity channels). Hence, the onset/offset duration of the adapter is driving the effect regardless of the total duration of adaptation. A strength-of-adaptation hypothesis predicts that the effect of duration on numerosity perception is driven by the adaptation of numerosity channels only, with the total duration of adaptation driving the effect regardless of the onset/offset duration of the adapter. We performed two experiments where we manipulated the onset/offset duration of the adapter, the adapter's total presentation time, and the total duration of the adaptation trial. The first experiment tested the effect of adaptation to duration on numerosity discrimination, whereas the second experiment tested the effect of adaptation to numerosity and duration on numerosity discrimination. We found that the effect of adaptation to duration on numerosity perception is primarily driven by adapting duration/numerosity channels, supporting the channel-based hypothesis. In contrast, the effect of adaptation to numerosity on numerosity perception appears to be driven by the total duration of the adaptation trial, supporting the strength-of-adaptation hypothesis. Thus, we show that adaptation of at least two temporal mechanisms influences numerosity perception.

Introduction

Imagine yourself being at a rather boring party and feeling quite hungry. Suddenly a few plates with appetizers appear, and you have to act fast, since more and more people approach them and the amount of food decreases rapidly. Within a few seconds, you are able to detect the plate with the most food on it, the smallest number of people around it, and the fastest access to it. Soon you manage to satiate your hunger, feeling proud of your efficient action.

This is only one example of the many situations illustrating how humans, among many other species, are able to process and integrate information about quantity and time in order to act efficiently in their environment (Dehaene, Dehaene-Lambertz, & Cohen, 1998; Grondin, 2010; Leon & Shadlen, 2003).

This is the core idea behind "a theory of magnitude" (ATOM), which proposes that numerosity (i.e., the

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number of items in a set), time, and space are magnitudes derived from a partly shared magnitude system and linked by a common metric (Bueti & Walsh, 2009; Walsh, 2003; see also Cantlon, Platt, & Brannon, 2009; Cappelletti, Freeman, & Cipolotti, 2011). According to ATOM, the interaction of these magnitudes is essential for learning about our environment and generating action.

How do these different magnitudes interact? From a theoretical perspective, Meck and Church (1983) proposed the "mode control" model, uniting number and time processing (Gibbon, Church, & Meck, 1984; Meck, Church, & Gibbon, 1985). This model proposes that number and time are represented by an internal clock that consists of "pacemaker"-type pulses which accumulate in a counter. Based on this model, number and duration discrimination rely on a single magnitude system which operates in either the counting or the timing mode (Fetterman, 1993). From an experimental perspective, a number of behavioral (Alards-Tomalin, Walker, Kravetz, & Leboe-McGowan, 2016; Cappelletti, Freeman, & Butterworth, 2011; Cappelletti et al., 2009; Chun, Lee, Lee, & Cho, 2018; Dormal, Seron, & Pesenti, 2006; Gilaie-Dotan, Rees, Butterworth, & Cappelletti, 2014; Javadi & Aichelburg, 2012; Lambrechts, Walsh, & Van Wassenhove, 2013; Martin, Wiener, & Van Wassenhove, 2017; Tokita & Ishiguchi, 2011; Tsouli, Dumoulin, te Pas, & van der Smagt, 2019) and neuroimaging (Bueti & Walsh, 2009; Cappelletti et al., 2014; Castelli, Glaser, & Butterworth, 2006; Hayashi et al., 2013; Javadi, Brunec, Walsh, Penny, & Spiers, 2014) studies provide support for a partly shared processing system for numerosity and time, whereas other studies suggest that numerosity and time are independent and are processed by distinct mechanisms (Agrillo, Piffer, & Adriano, 2013; Agrillo, Ranpura, & Butterworth, 2010).

One useful behavioral method for inferring about the neural underpinnings of a given perceptual property is sensory adaptation (Frisby, 1980). Specifically, after prolonged exposure to a specific stimulus, both the response of the neurons processing that stimulus and the perceptual experience of a subsequently presented (similar) stimulus change (Grill-Spector, Henson, & Martin, 2006; Kohn, 2007; Mollon, 1974; Thompson & Burr, 2009; Wade & Verstraten, 2005). A number of models have been proposed to account for the neural mechanisms underlying adaptation, including neuronal fatigue with less overall activation (fatigue model), fewer neurons responding (sharpening model), and less processing time (facilitation model; see review by Grill-Spector et al., 2006).

Numerosity, similarly to other visual properties such as color or contrast, is susceptible to adaptation (Anobile, Cicchini, & Burr, 2016; Burr, Anobile, & Arrighi, 2018; Burr & Ross, 2008). Even brief adaptation to a visual numerosity changes the perception of a subsequently viewed numerosity at the same location (Aagten-Murphy & Burr, 2016; Castaldi, Aagten-Murphy, Tosetti, Burr, & Morrone, 2016). Likewise, time is also susceptible to adaptation, with adaptation to a previous duration influencing the perception of a subsequently presented duration (Becker & Rasmussen, 2007; Heron et al., 2012; Heron, Hotchkiss, Aaen-Stockdale, Roach, & Whitaker, 2013; Johnston, Arnold, & Nishida, 2006; Li, Chen, Xiao, Liu, & Huang, 2017; Maarseveen, Hogendoorn, Verstraten, & Paffen, 2017; Magnussen & Johnsen, 1986; Shima, Murai, Hashimoto, & Yotsumoto, 2016).

We have recently replicated the finding that both numerosity and duration adapt, using very few trials and brief exposures (Aagten-Murphy & Burr, 2016; Tsouli et al., 2019). In addition, we explored the interaction between numerosity and time perception using a cross-adaptation paradigm. We hypothesized that if numerosity and time rely on a shared processing network, then adaptation to numerosity should affect temporal judgments and adaptation to duration should affect numerosity judgments. We found a unidirectional effect of adaptation to duration on numerosity discrimination, where adaptation to visual duration altered the perception of numerosity. However, adaptation to numerosity did not affect the perception of duration. Hence, we concluded that numerosity and time processing rely on partially overlapping neural networks.

Based on these findings, the first goal of the present study was to elucidate how duration affects numerosity perception. Specifically, we investigated two hypotheses, even though these hypotheses are not mutually exclusive. First, there is evidence supporting the existence of numerosity-selective "channels" or groups of neurons tuned to a preferred numerosity (Harvey & Dumoulin, 2017; Harvey, Fracasso, Petridou, & Dumoulin, 2015; Harvey, Klein, Petridou, & Dumoulin, 2013; Kutter, Bostroem, Elger, Mormann, & Nieder, 2018; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). Likewise, there is evidence suggesting that there are duration-selective channels tuned to a preferred duration that are dedicated to processing specific temporal features (Hayashi et al., 2015; Heron et al., 2012; Heron, Fulcher, Collins, Whitaker, & Roach, 2019; Ivry, 1996; Motala, Heron, McGraw, Roach, & Whitaker, 2018; Protopapa et al., 2019; Walker, Irion, & Gordon, 1981). The duration channels revealed using adaptation appear to encode the interval between the onset and offset duration of an event (Heron et al., 2012; Maarseveen, Paffen, Verstraten, & Hogendoorn, 2019), a finding which is further supported by neurophysiological studies in animals (Duysens,

Schaafsma, & Orban, 1996; Ehrlich, Casseday, & Covey, 1997; He, Hashikawa, Ojima, & Kinouchi, 1997).

Based on the foregoing, we hypothesized that the effect of duration on numerosity (Tsouli et al., 2019) could reflect the adaptation of onset/offset duration channels which influence numerosity perception. This could occur either because these duration channels are also tuned to numerosity or because channels tuned to either duration or numerosity wire together (duration/numerosity channels; Figure 1a). Both possibilities would be in accordance with the idea of a common processing network for numerosity and time (Bueti & Walsh, 2009; Cantlon et al., 2009; Cappelletti, Freeman, & Cipolotti, 2011; Gibbon et al., 1984; Meck & Church, 1983; Meck et al., 1985; Walsh, 2003).

The second hypothesis suggests that the effect of adaptation to duration is driven by the total strength of adaptation of numerosity-selective channels only. Specifically, a common notion in adaptation research suggests that a longer adaptation period results in stronger perceptual aftereffects (Kohn, 2007). This would mean that a long duration leads to stronger adaptation not as a result of adapting duration/numerosity channels but as a result of adapting numerosity channels for a long period. Since the strength-of-adaptation hypothesis would entail the adaptation of numerosity channels only, it is not conceptually related to the idea of a shared magnitude system as the ATOM postulates (Bueti & Walsh, 2009; Walsh, 2003).

Based on these hypotheses, we made the following predictions. If the effect of adapting to duration is caused by adaptation of duration/numerosity channels, the channels with preferred durations closest to that of the adapter would be most strongly adapted, and those with different duration preferences would be less strongly adapted. More specifically, the initial presentation of a duration with a short onset/offset (e.g., 67 ms) would elicit a high response from duration/numerosity channels tuned to a short duration. After repeated presentation of that short duration across adaptation trials, these channels would adapt and show a decreased response (Figure 1a). This would alter the perceived numerosity of a subsequently presented stimulus, similar to how adaption to a low numerosity would alter numerosity perception (i.e., overestimation of the subsequently presented numerosity; Burr & Ross, 2008). However, given the duration preference of these channels, a single presentation of a short onset/offset duration would produce the same adaptation effects as would a repeated presentation (three or nine times) of the same duration within the same adaptation trial (Figure 1b, dark-blue, green, and orange bars). Therefore, although a repeated presentation would lead to a longer total duration of the adapter stimulus, the adaptation effects would still be similar, due to the assumed existence of duration/numerosity channels tuned to a short onset/offset duration. In the case of adapting to duration/numerosity channels tuned to a long onset/offset duration (e.g., 600 ms; Figure 1b, light-blue bar), the predicted effect on numerosity perception would be similar to that produced by adaptation to a high numerosity (i.e., underestimation of the subsequently presented numerosity).

According to the strength-of-adaptation hypothesis, the initial presentation of a short duration stimulus would produce a high neural response on numerosity channels only (Figure 1c). After repeated presentation of that short duration across adaptation trials, the numerosity channels would adapt and show a decreased response. However, contrary to the duration/numerosity-channels hypothesis, the repeated presentation of that duration (three or nine times) within the same adaptation trial would lead to further adaptation of the numerosity channels due to the longer total duration produced. This would alter the perception of a subsequently presented numerosity stimulus. Thus, the strongest adaptation effect would be produced by the longest duration, regardless of the specific temporal elements this duration has (i.e., onset/offset duration; Figure 1d and 1e).

In summary, the first hypothesis entails the involvement of duration/numerosity channels, where the effect of adaptation is driven by the onset/offset duration of the adapter, whereas the second hypothesis entails the involvement of numerosity channels only, where the effect of adaptation is driven by the total duration of the adapter, even if the onset/offset duration of the adapter is short.

Based on our research goals we conducted two experiments; the first examined the effect of adaptation to duration on numerosity discrimination, and the second examined the combined effect of adaptation to numerosity *and* duration on numerosity discrimination. In both experiments, we manipulated the adapter's onset/offset duration, its presentation time, and the total duration of the adaptation trial. In order to test the duration/numerosity-channels hypothesis, the preferred duration was operationally defined as the onset/offset duration of the adapter (Heron et al., 2012; Maarseveen et al., 2019). We hypothesized that the duration conditions comprising a short (67 ms) versus a long (600 ms) onset/offset duration should yield relative over- and underestimation of the reference numerosity, respectively, similar to the effect produced by adapting to a low versus a high numerosity. Conversely, in order to test the hypothesis on the strength of adaptation of numerosity channels, the adapter's total presentation time or the total duration of the adaptation trial was hypothesized to produce the

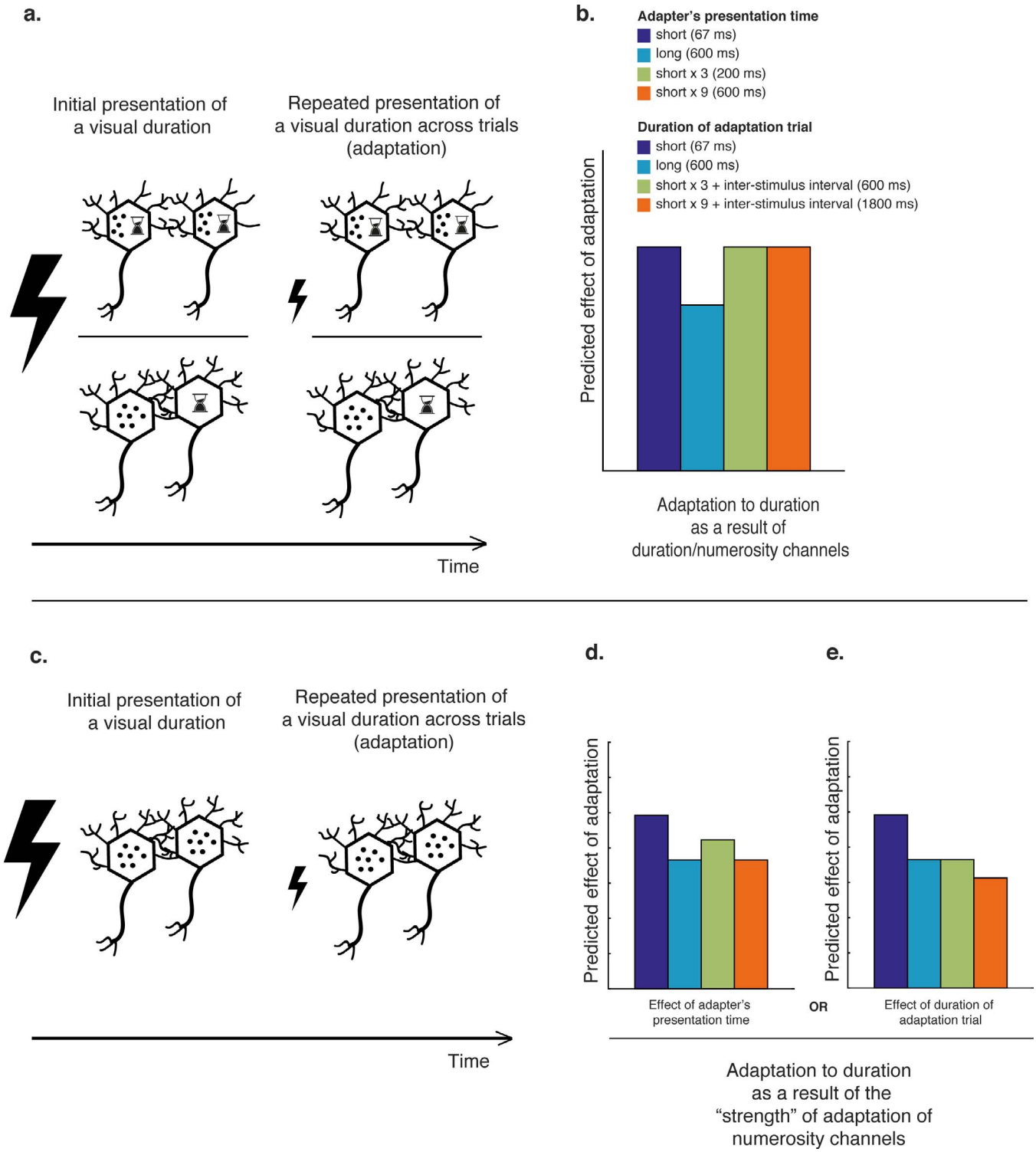

Figure 1. Hypothesized mechanisms of adaptation to duration on underlying neural responses and predicted outcomes. The initial presentation of a duration would first elicit a high neuronal response, but upon repeated presentation of that duration across trials, that response would be decreased due to adaptation. According to the duration/numerosity-channels hypothesis (a), adaptation alters the response of channels encoding both duration and numerosity (or neurons tuned to duration and neurons tuned to numerosity which wire together) which are tuned to the onset/offset interval of a duration event. Hence, the adaptation conditions where the adapter's onset/offset duration (i.e., 67 ms) is the same (b; dark-blue, green, and orange bars) will yield similar adaptation effects, regardless of other duration parameters (e.g., the duration of the adapter's total presentation time or the total duration of the adaptation trial). According to the strength-of-adaptation hypothesis (c), adaptation alters the response of numerosity channels only, with the longest duration (600 or 1,800 ms) driving the adaptation effect. Thus, the adaptation conditions with the longest total adapter presentation time (d; light-blue and orange bars) or the longest total duration of the adaptation trial (e; orange bars) will lead to stronger adaptation, even if these durations are composed of a short onset/offset duration (green and orange bars).

strongest adaptation effects, regardless of the onset/offset duration of the adapter.

We found that the effect of adaptation to duration on numerosity discrimination in our first experiment was mainly driven by adapting duration/numerosity channels. In contrast, the effect of adaptation to numerosity *and* duration on numerosity discrimination in our second experiment appeared driven by the total duration of the adaptation trial. Thus, we found that different temporal mechanisms modulate numerosity perception.

Methods

Participants

Thirty participants (20 women, $M_{age} = 23.35$ years, $SD_{age} = 2.62$; 10 men, $M_{age} = 23.40$ years, $SD_{age} = 3.86$) participated in Experiment 1. Twenty-four participants (18 women, $M_{age} = 22.23$ years, $SD_{age} = 2.46$; six men, $M_{age} = 24.0$ years, $SD_{age} = 2.37$) participated in Experiment 2. All participants had normal or corrected-to-normal visual acuity and were unaware of the purpose of the study. Participants gave written informed consent and received a monetary reward or course credits. The experiments were conducted in accordance with the Declaration of Helsinki and approved by the Ethics Committee of the Faculty of Social and Behavioural Sciences of Utrecht University.

Apparatus and stimuli

The apparatus and stimuli were identical to the ones described in our previous study (Tsouli et al., 2019). Briefly: Participants sat at a distance of about 60 cm from a 60 × 34 cm Asus LCD monitor with a resolution of 2,560 × 1,440 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/m^2) at 80% Michelson contrast. Each dot had a diameter of 0.2° 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. 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 counterbalanced across participants. All stimuli were generated and presented using MATLAB (Version 2016b; MathWorks, Inc., Natick, MA) and the Psychophysics Toolbox (Version 3.0.13; Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

Procedure

Both Experiment 1 (adaptation to duration) and Experiment 2 (adaptation to numerosity *and* duration) had four duration adaptation conditions (Figure 2). In Conditions 1 (67 ms) and 2 (600 ms), the adapter's onset/offset duration was equal to the adapter's total presentation time and the total duration of the adaptation trial. In Condition 3, the adapter's onset/offset duration was 67 ms, its total presentation time was 200 ms (three repetitions of 67 ms interleaved with a 133-ms interstimulus interval [ISI]), and the total duration of the adaptation trial was 600 ms. In Condition 4, the adapter's onset/offset duration was 67 ms, its total presentation time was 600 ms (nine repetitions of 67 ms interleaved with a 133-ms ISI), and the total duration of the adaptation trial was 1,800 ms.

In each trial, the adapter was shown first and lasted for one of the four duration adaptation conditions. After a 300-ms pause, the reference patch was presented for 333 ms at the same location as the adapter, followed by another 300-ms pause, and then the test patch appeared for 333 ms at the opposite side of fixation. Our choice of presenting the adapter and reference stimulus on one side and the test stimulus on the opposite side was based on findings suggesting that adaptation to numerosity is spatially specific (Aagten-Murphy & Burr, 2016; Arrighi, Togoli, & Burr, 2014; Burr & Ross, 2008).

In the beginning of each experiment, participants were given the following instructions:

> You will see one cloud of dots appearing on one side of the screen, followed by another cloud of dots in the same location, and then another cloud of dots in the opposite location. Your task is to respond as fast and accurately as possible (guessing if unsure) which of the two clouds you saw last seemed to have more dots. On the keyboard placed in front of you, press the "f" key if you think it was the left cloud of dots that had more dots, or the "j" key if you think it was the right cloud that had more dots.

The paradigm used was a two-alternative forced-choice task. After the participant gave a response, the next trial started after 500 ms.

Experiment 1: Adaptation to duration

The visual stimuli used as duration adapters comprised 20, 40, or 80 dots, and the respective

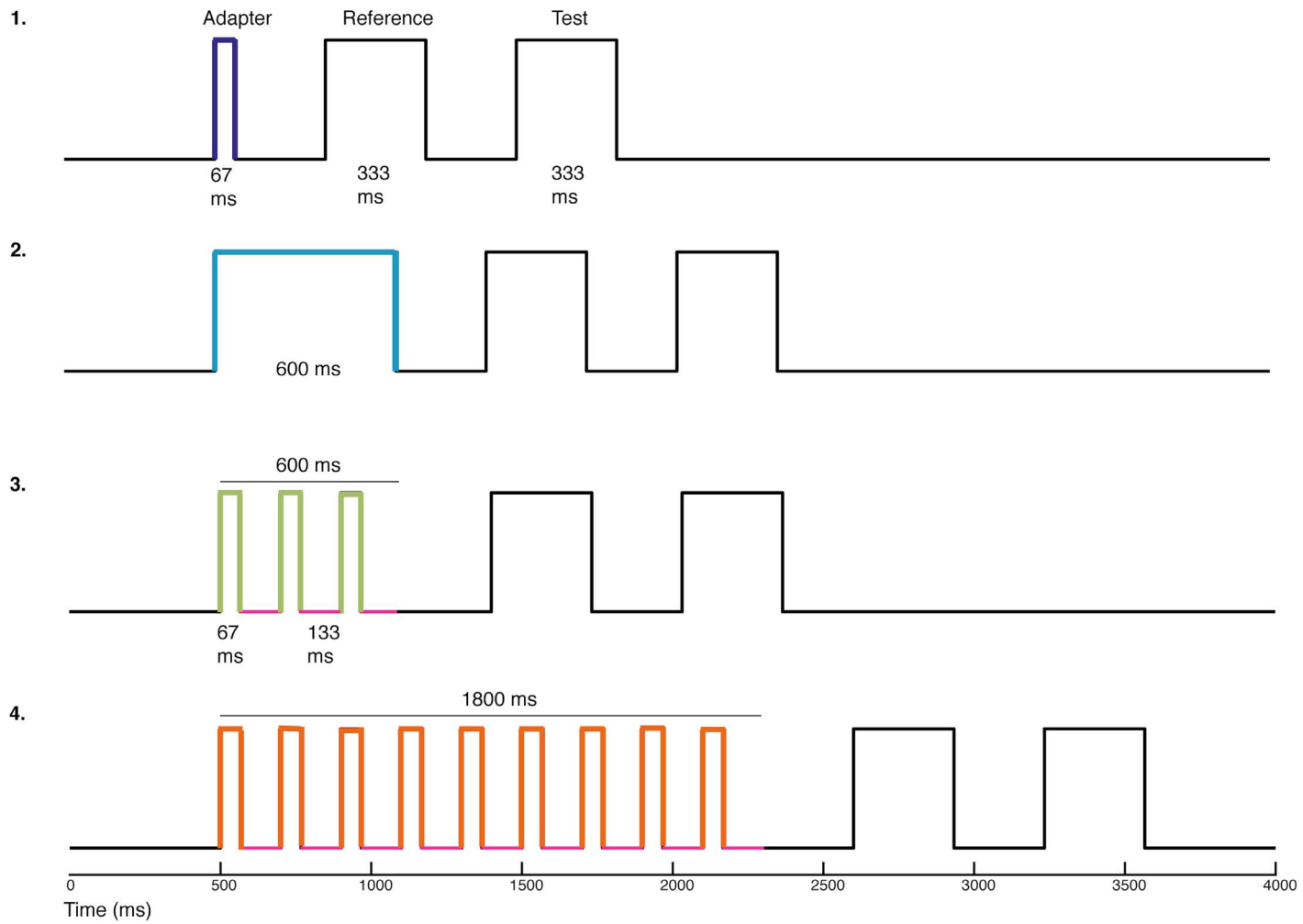

Figure 2. Schematic representation of the adaptation to duration conditions in Experiments 1 and 2. In Conditions 1 (67 ms) and 2 (600 ms), the adapter's onset/offset duration was equal to its total presentation time and the total duration of the adaptation trial. In Condition 3, the adapter's onset/offset duration was 67 ms, its total presentation time was 200 ms (three repetitions of 67 ms), and the total duration of the adaptation trial was 600 ms. In Condition 4, the adapter's onset/offset duration was 67 ms, its total presentation time was 600 ms (nine repetitions of 67 ms), and the total duration of the adaptation trial was 1,800 ms. This stimulus design evaluated the influence of the adapter's onset/offset duration (67 vs. 600 ms) compared to the total duration of the adaptation trial (67 vs. 600 vs. 1,800 ms).

reference patches also comprised 20, 40, or 80 dots (Figure 3a). The numerosity of the test patch varied from trial to trial using the minimum-expected-entropy staircase method (Saunders & Backus, 2006). Since the adapter and reference stimuli were matched in numerosity but not duration, no adaptation to numerosity was expected to occur, only adaptation to duration (Figure 3b). Regarding our choice of numerosity stimuli, the effect of adaptation to duration on numerosity discrimination that we found in our previous study (Tsouli et al., 2019) was induced using numerosity and reference stimuli of 40 dots. However, it could be possible that the observed adaptation phenomenon is affected by the specific visual stimulus used as a duration adapter. Therefore, we now investigated whether the effect of adaptation to duration on numerosity perception would be present with an intermediate numerosity of 40 dots as we did before, and also with a low (20 dots) and a high (80 dots) numerosity. The order of the duration conditions and the numerosity stimuli used as visual duration adapters was counterbalanced across participants.

Experiment 2: Adaptation to numerosity and duration

The visual stimuli used as numerosity adapters comprised 20, 40, or 80 dots, and the reference patch always comprised 40 dots (Figure 3c). Similar to Experiment 1, the numerosity of the test patch varied from trial to trial using the minimum-expected-entropy staircase method (Saunders & Backus, 2006).

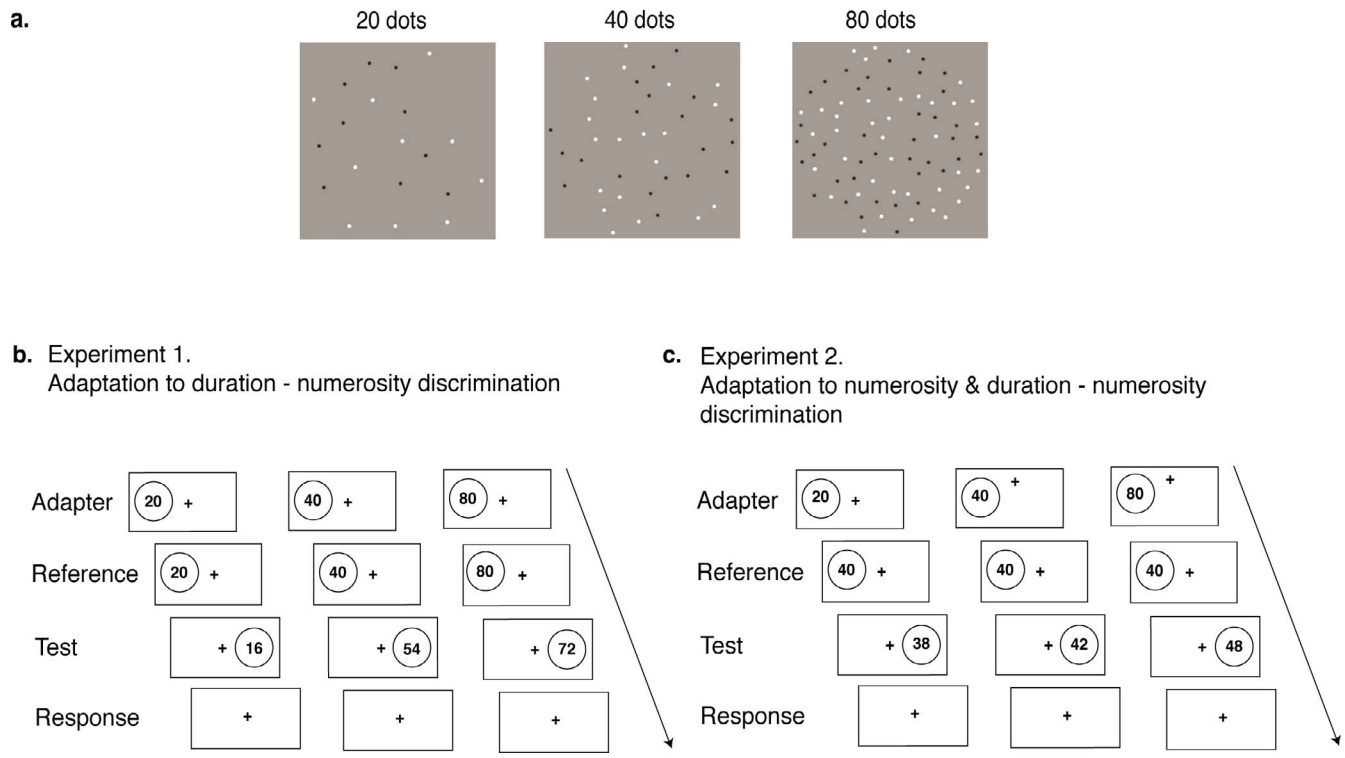

Figure 3. The stimuli used as duration and numerosity adapters (a), and a schematic representation of a single trial in Experiments 1 (b) and 2 (c). In Experiment 1, the stimuli used as duration adapters and reference stimuli comprised 20, 40, or 80 dots. Given that the adapter and reference stimuli were matched only in numerosity, not duration, no adaptation to numerosity was expected to take place, only adaptation to duration. The numerosity of the test stimuli varied based on a staircase method. In Experiment 2, the stimuli used as numerosity and duration adapters comprised 20, 40, or 80 dots and the reference stimulus was always 40 dots. Given that the adapter and reference stimuli were not matched in numerosity or duration, adaptation to numerosity *and* duration was expected to take place. Similar to Experiment 1, the numerosity of the test stimuli varied based on a staircase method. In Experiment 2, the condition where the adapter and reference stimuli had 40 dots was identical to Experiment 1 and was used for replicating the respective condition in Experiment 1. In both experiments, participants were instructed to respond, as fast and accurately as possible, which of the two clouds presented last appeared to contain more dots, by pressing (on a keyboard) the F key for the left cloud or the J key for the right cloud.

Since the adapter and reference stimuli were not matched in numerosity or duration, we expected adaptation to numerosity *and* duration to occur. The numerosity adapters were displayed for one of the four duration conditions described earlier. Participants adapted to a low (20 dots) or high (80 dots) numerosity, which was expected to result in over- or underestimation of the reference numerosity, respectively (Aagten-Murphy & Burr, 2016; Tsouli et al., 2019). The condition where both the adapter and the reference numerosity were 40 dots was identical to Experiment 1 and served as a control condition used for replicating the findings of Experiment 1. Participants were given the same instructions as in Experiment 1, and the paradigm used was again a two-alternative forced-choice task. The order of the duration conditions and the numerosity stimuli used as numerosity and duration adapters was counterbalanced across participants.

Data analysis

All data analyses were conducted using MATLAB, SPSS (Version 24.0; SPSS Inc., Chicago, IL), and JASP (Version 0.8.1.2; JASP Team, 2019).

After each experiment, we first collapsed the data across presentation side blocks (left vs. right). This yielded 100 data points per condition. We subsequently sorted these data points on the numerosity of the test stimulus. For these sorted data, we then created 10 equally sized bins (i.e., containing the data of 10 trials each). 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 (Tsouli et al., 2019).

In addition, we transformed the PSE values into values corresponding to the just-noticeable difference (JND) and performed the same statistical analyses. In

order to obtain the JND values for each participant, we first calculated a standardized slope for each numerosity condition using the following formula:

$$\textit{standardized slope} = \sqrt{\frac{\Sigma(slope^2)}{n(=4\ \textit{duration conditions})}}. \quad (1)$$

Our choice of calculating a standardized slope for each participant using Equation 1 was supported by the fact that there were no statistically significant differences in the slope values obtained from the four duration conditions within each numerosity condition, as assessed by a series of Wilcoxon signed-rank tests (due to violation of the normality assumption; false discovery rate [FDR]–corrected significance thresholds) in either Experiment 1 or 2 (see also Results).

The JND values in Experiment 1 were then calculated using the formula

$$\text{JND}: (PSE - \textit{reference numerosity}) / \textit{standardized slope}, \quad (2)$$

where the reference numerosity was 20, 40, or 80 dots, corresponding to the respective numerosity condition, and the standardized slope was that of the respective numerosity condition for each participant). The same formulas were used in Experiment 2, with the only difference being the reference numerosity used in Equation 2, which was always 40 dots.

Given that adaptation stimuli were presented at one side (e.g., left) for half of the trials and at the opposite side (e.g., right) for the other half, we wanted to examine whether this design would yield significant differences in our measurements. We calculated the average JND, PSE, and slope values for the left versus right presentation side across duration conditions for each numerosity-stimulus condition. We then performed nonparametric statistical tests, since a number of the measurements obtained were not normally distributed as assessed by box plots and the Shapiro–Wilk test. In Experiment 1, the JND values obtained when the adapter and reference stimulus were presented on the left side were significantly lower compared to when the adapter and reference stimulus were presented on the right side, in every numerosity-stimulus condition (adapter and reference stimulus = 20 dots: $\text{Mdn}_{\text{left}} = -0.49$, $\text{Mdn}_{\text{right}} = -0.15$, $Z = -2.81$, $p = 0.008$; adapter and reference stimulus = 40 dots: $\text{Mdn}_{\text{left}} = -1.02$, $\text{Mdn}_{\text{right}} = -0.46$, $Z = -2.91$, $p = 0.008$; adapter and reference stimulus = 80 dots: $\text{Mdn}_{\text{left}} = -1.11$, $\text{Mdn}_{\text{right}} = -0.46$, $Z = -2.27$, $p = 0.02$; FDR-corrected significance thresholds). The same was true for the PSE values (adapter and reference stimulus = 20 dots: $\text{Mdn}_{\text{left}} = 17.71$ dots, $\text{Mdn}_{\text{right}} = 19.41$ dots, $Z = -2.97$, $p = 0.009$; adapter and reference stimulus = 40 dots: $\text{Mdn}_{\text{left}} = 33.56$ dots, $\text{Mdn}_{\text{right}} = 36.91$ dots, $Z = -2.23$, $p = 0.03$; adapter and reference stimulus = 80 dots: $\text{Mdn}_{\text{left}} = 66.08$ dots, $\text{Mdn}_{\text{right}} = 73.60$ dots, $Z = -2.46$, $p = 0.02$; FDR-corrected). Nevertheless, no significant differences were found in the slope values, and no significant differences were found in the JND, PSE, or slope values in Experiment 2 using FDR-corrected significance thresholds. Moreover, there was no statistically significant effect of the presentation side block (adaptation trials starting from the left or right side) on the JND, PSE, or slope values in either experiment. Therefore, we decided to collapse all data across blocks and presentation sides.

Results

Adaptation of duration/numerosity channels affects numerosity discrimination after adaptation to duration (Experiment 1)

First, we examined which JND, PSE, and slope values differed using frequentist analyses. The JND and PSE values obtained from the numerosity-discrimination task were normally distributed in almost all duration adaptation conditions. The two exceptions were the JND values obtained after adapting to duration Condition 1, using 80 dots as a visual duration adapter and reference stimulus, as assessed by box plot and the Shapiro–Wilk test ($p = 0.002$); and the PSE values obtained after adapting to duration Condition 1, also when using 80 dots as a visual duration adapter and reference stimulus ($p = 0.031$). The slope values obtained were not normally distributed in almost all conditions. Therefore, we used nonparametric statistical tests (Friedman for assessing main effects, and Wilcoxon signed-rank tests as post hoc tests) for all comparisons. We corrected the significance thresholds of post hoc tests using FDR correction where applicable (see also Supplementary File S1 for the individual participants' data).

As seen in Figure 4a and 4b, there were no statistically significant differences in the JND, PSE, or slope values after adaptation to duration using 20 dots as a visual duration adapter and reference stimulus—both JND and PSE: $\chi^2(3) = 4.52$, $p = 0.21$; slope: $\chi^2(3) = 0.92$, $p = 0.82$. There were statistically significant differences in the JND and PSE values using 40 dots—both JND and PSE: $\chi^2(3) = 15.52$, $p = 0.001$. No statistically significant differences were found in the

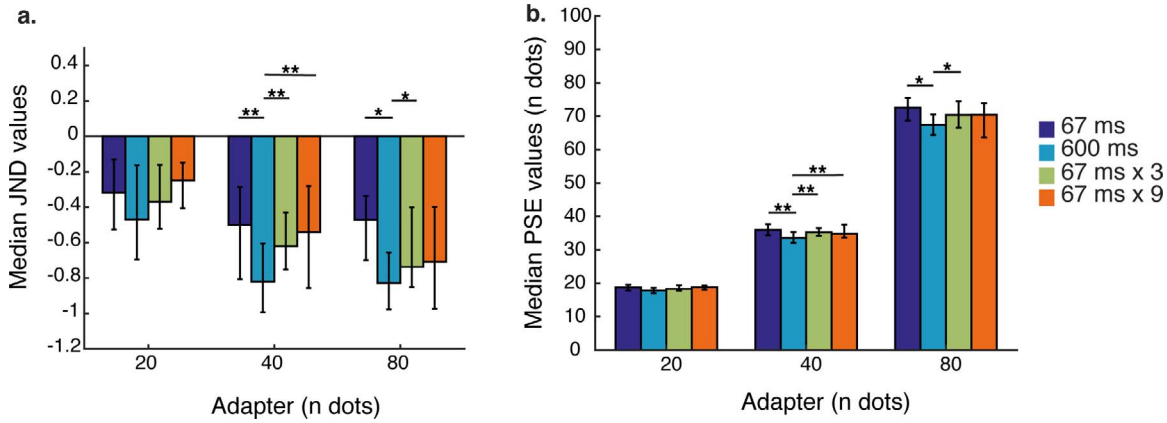

Figure 4. Median just-noticeable difference (a) and point of subjective equality (b) for Experiment 1 (adaptation to duration). The x-axis displays the numerosity of the visual duration adapters (20, 40, and 80 dots) and reference stimuli (20, 40, and 80 dots, respectively). The y-axis displays the median just noticeable difference or point of subjective equality obtained from the numerosity-discrimination task. The colored bars correspond to the four adaptation conditions (see also Figure 2). The dark-blue bars correspond to Condition 1 (adapter's onset/offset duration: 67 ms = total duration of the adaptation trial). The bright-blue bars correspond to Condition 2 (adapter's onset/offset duration: 600 ms = total duration of the adaptation trial). The green bars correspond to Condition 3 (adapter's onset/offset duration = 67 ms, total adapter presentation time = 200 ms [three repetitions of 67 ms], and total duration of the adaptation trial = 600 ms). The orange bars correspond to Condition 4 (adapter's onset/offset duration = 67 ms, total adapter presentation time = 600 ms [nine repetitions of 67 ms], and total duration of the adaptation trial = 1,800 ms). Error bars correspond to the bootstrapped 95% confidence interval of the median of each duration condition. As illustrated, the conditions where the adapter's onset/offset duration was the same (67 ms) did not differ significantly from each other across numerosity stimuli.

slope values, $\chi^2(3) = 2.60$, $p = 0.46$. The same was true using 80 dots—both JND and PSE: $\chi^2(3) = 13.96$, $p = 0.003$ (see Tables 1 and 2 for post hoc comparisons). No statistically significant differences were found in the slope values, $\chi^2(3) = 2.32$, $p = 0.51$.

In summary, we found that adaptation to a 600-ms adapter resulted in significantly different JND and PSE values when compared to adaptation to multiples of 67 ms, and when the adapter consisted of 40 or 80 but not 20 dots. In all cases, the duration conditions composed of multiples of 67 ms yielded similar—or at least not significantly different—JND and PSE values.

Adaptation of duration/numerosity channels yields *similar* effects on numerosity discrimination

Next we assessed which JND values were similar using Bayesian analyses. Our channel-based hypothesis predicts similar adaptation for identical onset/offset durations—that is, for the 67-ms adapter presentations. Whereas frequentist analyses focus on establishing whether two conditions are significantly different, Bayesian analyses can establish the probability that two conditions are similar.

	Conditions					
	67 vs. 600 ms	67 vs. 67 × 3 ms	67 vs. 67 × 9 ms	600 vs. 67 × 3 ms	600 vs. 67 × 9 ms	67 × 3 vs. 67 × 9 ms
JND values						
Z	−3.30	−1.43	−1.68	−2.81	−2.81	−0.48
p	**0.01**	0.18	0.14	**0.01**	**0.01**	0.63
r	0.43			0.36	0.36	
PSE values						
Z	−3.24	−1.33	−1.27	−2.77	−2.71	−0.48
p	**0.01**	0.25	0.25	**0.01**	**0.01**	0.63
r	0.42			0.36	0.35	

Table 1. Post hoc comparisons using Wilcoxon signed-rank tests for an adapter and reference stimulus of 40 dots. Statistically significant *p* values (corrected for false discovery rate) are in bold. *Notes*: JND = just-noticeable difference; PSE = point of subjective equality.

	Conditions					
	67 vs. 600 ms	67 vs. 67 × 3 ms	67 vs. 67 × 9 ms	600 vs. 67 × 3 ms	600 vs. 67 × 9 ms	67 × 3 vs. 67 × 9 ms
JND values						
Z	−2.79	−0.36	−1.24	−2.89	−1.12	−1.74
p	**0.02**	0.72	0.31	**0.02**	0.31	0.16
r	0.36			0.37		
PSE values						
Z	−2.62	−0.20	−0.69	−2.81	−1.29	−1.47
p	**0.03**	0.85	0.59	**0.03**	0.30	0.28
r	0.34			0.36		

Table 2. Post hoc comparisons using Wilcoxon signed-rank tests for an adapter and reference stimulus of 80 dots. Statistically significant *p* values (corrected for false discovery rate) are in bold. *Notes*: JND = just-noticeable difference; PSE = point of subjective equality.

The JND values obtained were examined by estimating a Bayes factor (BF) using Bayesian information criteria (Jarosz & Wiley, 2014; Wagenmakers, 2007), which compare the fit of the data under the alternative and the null hypothesis. We first performed a series of Bayesian paired-samples *t* tests comparing Conditions 1, 3, and 4, where the adapter's onset/offset duration was 67 ms (Figure 5, red lines).

For Conditions 1 versus 3, 1 versus 4, and 3 versus 4, the BF_{10} was 0.20, 0.21, and 0.26, respectively, with an adapter and reference of 20 dots; and for 40 and 80 dots the BF_{10} was, respectively, 0.64, 0.39, 0.20 and 0.20, 0.56, and 0.56. This suggests that these data were less likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it. In other words, the aforementioned Bayes factors provide support for the notion that the JND values in Conditions 1, 3, and 4 are similar in all three conditions, which is in line with the duration/numerosity-channels hypothesis.

We then performed a series of Bayesian paired-samples *t* tests comparing Condition 2 (adapter's onset/offset duration: 600 ms = total duration of the adaptation trial: 600 ms) with Conditions 1, 3, and 4 (Figure 5, green lines). For Conditions 2 versus 1 and 2 versus 3, respectively, the BF_{10} was 0.80 and 0.71 for 20 dots. This suggests that these data were *less* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than

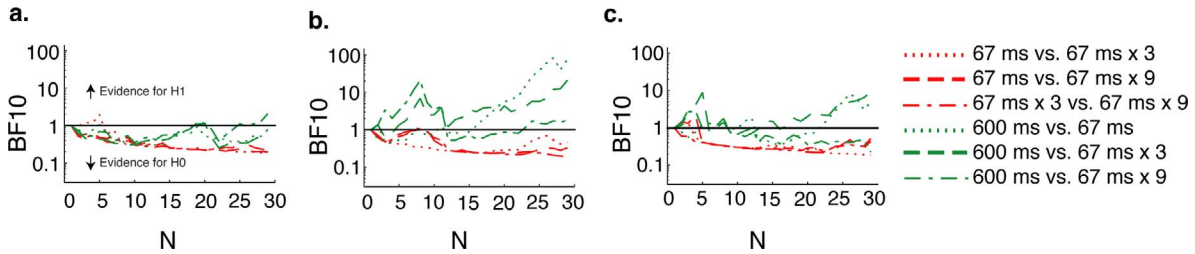

Figure 5. Sequential-analysis plots for the Bayesian paired-samples comparisons in Experiment 1. The plots display the flow of evidence for H_1 (just-noticeable differences in numerosity discrimination differ after adaptation to different duration conditions) versus H_0 (no difference in just-noticeable differences) as the data accumulate. The x-axis corresponds to the number of participants and the y-axis corresponds to the Bayes-factor values (ratios). The red lines correspond to the comparisons of Conditions 1, 3, and 4 with each other, where the adapter's onset/offset duration was 67 ms. The green lines correspond to the comparisons of Condition 2 (adapter's onset/offset duration: 600 ms = total duration of the adaptation trial) with Conditions 1, 3, and 4. (a) Using 20 dots as a visual duration adapter and reference stimulus, the evidence for H_1 (y-axis) decreases with the number of data points (x-axis) when Conditions 1, 3, and 4 are compared with each other. Comparing Condition 2 with Conditions 1 and 3, the evidence for H_1 decreases with the number of data points, whereas the evidence for H_1 increases in the comparison with Condition 4. (b) Using 40 dots as a visual duration adapter and reference stimulus, the evidence for H_1 decreases with the number of data points when Conditions 1, 3, and 4 are compared with each other. The opposite is true when Condition 2 is compared with Conditions 1, 3, and 4, where the evidence for H_1 increases. (c) Using 80 dots as a visual duration adapter and reference stimulus, the evidence for H_1 decreases with the number of data points when Conditions 1, 3, and 4 are compared with each other. The opposite is true when Condition 2 is compared with Conditions 1 and 3, where the evidence for H_1 increases, while it decreases in the comparison to Condition 4. These data suggest that the conditions which had the same onset/offset duration (67 ms) produced similar adaptation effects.

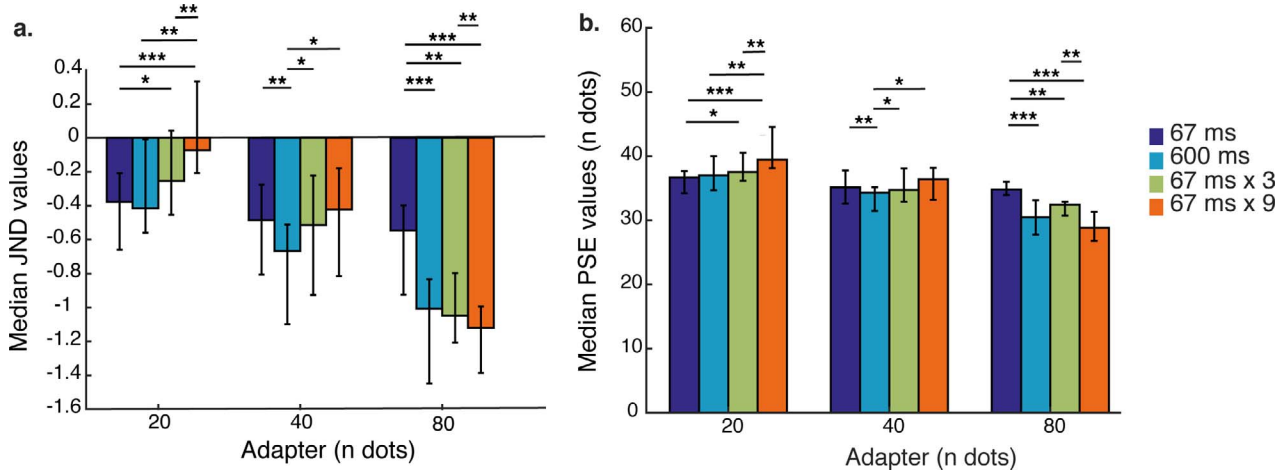

Figure 6. Median just-noticeable difference (a) and point of subjective equality (b) for Experiment 2 (adaptation to numerosity *and* duration). The x-axis displays the numerosity of the adapters (20, 40, or 80 dots). The y-axis displays the median just-noticeable difference or point of subjective equality obtained from the numerosity-discrimination task (the reference stimulus was always 40 dots). The colored bars correspond to the four duration adaptation conditions. The dark-blue bars correspond to Condition 1 (adapter's onset/offset duration: 67 ms = total duration of the adaptation trial). The bright-blue bars correspond to Condition 2 (adapter's onset/offset duration: 600 ms = total duration of the adaptation trial). The green bars correspond to Condition 3 (adapter's onset/offset duration = 67 ms, total adapter presentation time = 200 ms [three repetitions of 67 ms], and total duration of the adaptation trial = 600 ms). The orange bars correspond to Condition 4 (adapter's onset/offset duration = 67 ms, total adapter presentation time = 600 ms [nine repetitions of 67 ms], and total duration of the adaptation trial = 1,800 ms). Error bars correspond to the bootstrapped 95% confidence interval of the median of each duration condition. As illustrated, with adaptation to numerosity (20 and 80 dots), the condition where the total duration of the adaptation trial was the longest (1,800 ms) produced the strongest adaptation effects. In contrast, with adaptation to duration only (adapter and reference stimulus = 40 dots), the conditions where the adapter's onset/offset duration was the same (67 ms) did not differ significantly from each other (similar to Experiment 1).

the model without it. For 40 and 80 dots the BF_{10} was, respectively, 126.08 and 15.50, and 8.25 and 15.33, suggesting that these data were *more* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it.

For Condition 2 versus 4, the BF_{10} was 2.18 and 1.89, respectively, for 20 and 40 dots, suggesting that these data were slightly *more* likely to occur under the model including an effect, rather than the model without it. For 80 dots, the BF_{10} was 0.25, suggesting that these data were *less* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it. In general, Condition 2 differed from the other conditions, providing support for the duration/numerosity-channels hypothesis.

Based on the frequentist and Bayesian analyses we performed, these data suggest that the effect of adaptation to duration on numerosity discrimination was mainly driven by the onset/offset duration of the adapter, since Conditions 1, 3, and 4 (adapter's onset/offset duration = 67 ms) appeared similar to each other, while they were generally different from Condition 2 (adapter's onset/offset duration = 600 ms).

Total duration of adaptation affects numerosity discrimination after adaptation to numerosity (Experiment 2)

Similar to Experiment 1, we first examined which JND, PSE, and slope values differed using frequentist analyses. The JND and PSE values in almost all conditions were normally distributed. The two exceptions were the JND values obtained after adapting to a numerosity of 80 dots in Condition 4, as assessed by box plot and the Shapiro–Wilk test ($p = 0.003$), and the PSE values obtained using 80 dots as a visual duration adapter and reference stimulus in Condition 1 ($p = 0.013$). The slope values obtained were not normally distributed in the majority of conditions. Therefore, we used nonparametric statistical tests (Friedman and Wilcoxon signed-rank tests) for all comparisons. We corrected the significance thresholds using FDR correction where applicable (see Supplementary Materials for the individual participants' data).

As seen in Figure 6a and 6b, there were statistically significant differences in the JND and PSE values in the four duration adaptation conditions after adaptation to numerosities of 20 dots, $\chi^2(3) = 22.95$, $p < 0.001$), 40 dots, $\chi^2(3) = 9.0$, $p = 0.03$, and 80 dots, $\chi^2(3) = 27.95$, $p < 0.001$ (see Tables 3–5 for post hoc comparisons). No

	Conditions					
	67 vs. 600 ms	67 vs. 67 × 3 ms	67 vs. 67 × 9 ms	600 vs. 67 × 3 ms	600 vs. 67 × 9 ms	67 × 3 vs. 67 × 9 ms
JND values						
Z	−1.63	−2.20	−3.77	−0.914	−3.11	−3.31
p	0.12	**0.04**	**0.001**	0.36	**0.004**	**0.003**
r		0.32	0.54		0.45	0.48
PSE values						
Z	−1.46	−2.20	−4.03	−0.97	−3.29	−3.46
p	0.17	**0.04**	**<0.001**	0.33	**0.002**	**0.002**
r		0.32	0.58		0.47	0.50

Table 3. Post hoc comparisons using Wilcoxon signed-rank tests for an adapter of 20 dots. Statistically significant *p* values (corrected for false discovery rate) are in bold. *Notes*: JND = just-noticeable difference; PSE = point of subjective equality.

statistically significant differences were found in the slope values after adapting to either 20, 40, or 80 dots—20: $\chi^2(3) = 3.45$, $p = 0.33$; 40: $\chi^2(3) = 4.25$, $p = 0.24$; 80: $\chi^2(3) = 7.25$, $p = 0.06$.

In summary, we found that the strongest numerosity adaptation effects were produced under the duration condition which had the longest duration of the adaptation trial, even if the adapter's onset/offset duration was 67 ms. In contrast, in the case of adaptation to duration only (adapter and reference stimulus = 40 dots), the duration conditions composed of multiples of 67 ms yielded similar JND and PSE values (comparable to Experiment 1).

Adaptation of duration/numerosity channels yields *different* effects on numerosity discrimination

Similar to Experiment 1, the JND values obtained were examined by estimating a Bayes factor using Bayesian information criteria (Figure 7, red lines).

For Conditions 1 versus 3, 1 versus 4, and 3 versus 4, the BF_{10} was, respectively, 3.94, 679.98, and 113.75 for an adapter and reference of 20 dots; and for 80 dots its was 30.14, 4,278, and 18.50. This suggests that these data were *more* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it. Thus, the aforementioned Bayes factors provide support for the notion that the JND values in Conditions 1, 3, and 4 are different.

Using an adapter of 40 dots, the BF_{10} for Conditions 1 versus 3, 1 versus 4, and 3 versus 4 was 0.35, 0.31, and 0.22, respectively, suggesting that these data were *less* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it.

We then performed a series of Bayesian paired-samples *t* tests comparing Condition 2 with Conditions 1, 3, and 4 (Figure 7, green lines).

For Condition 2 versus 1, the BF_{10} was 0.74 for 20 dots, suggesting that these data were *less* likely to occur under the model including an effect of adaptation to numerosity on numerosity discrimination, rather than the model without it. In contrast, for 40 and 80 dots the BF_{10} was 19.0 and 1,538, respectively, suggesting that these data were *more* likely to occur under the model

	Conditions					
	67 vs. 600 ms	67 vs. 67 × 3 ms	67 vs. 67 × 9 ms	600 vs. 67 × 3 ms	600 vs. 67 × 9 ms	67 × 3 vs. 67 × 9 ms
JND values						
Z	−3.26	−0.51	−0.49	−2.51	−2.43	−0.29
p	**0.01**	0.75	0.75	**0.03**	**0.03**	0.78
r	0.47			0.36	0.35	
PSE values						
Z	−3.14	−0.43	−0.29	−2.49	−2.49	−0.11
p	**0.01**	0.91	0.91	**0.03**	**0.03**	0.91
r	0.45			0.36	0.36	

Table 4. Post hoc comparisons using Wilcoxon signed-rank tests for an adapter of 40 dots. Statistically significant *p* values (corrected for false discovery rate) are in bold. *Notes*: JND = just-noticeable difference; PSE = point of subjective equality.

	Conditions					
	67 vs. 600 ms	67 vs. 67 × 3 ms	67 vs. 67 × 9 ms	600 vs. 67 × 3 ms	600 vs. 67 × 9 ms	67 × 3 vs. 67 × 9 ms
JND values						
Z	−3.60	−3.09	−4.00	−1.40	−1.49	−3.00
p	**0.001**	**0.004**	**<0.001**	0.16	0.16	**0.005**
r	0.52	0.46	0.58			0.43
PSE values						
Z	−3.60	−2.97	−3.97	−1.63	−1.54	−3.20
p	**0.001**	**0.005**	**<0.001**	0.12	0.12	**0.003**
r	0.52	0.43	0.57			0.46

Table 5. Post hoc comparisons using Wilcoxon signed-rank tests for an adapter of 80 dots. Statistically significant *p* values (corrected for false discovery rate) are in bold. *Notes*: JND = just-noticeable difference; PSE = point of subjective equality.

including an effect of adaptation to numerosity on numerosity discrimination.

For Condition 2 versus 3, the BF_{10} was 0.27 and 0.56, respectively, for 20 and 80 dots, suggesting that these data were *less* likely to occur under the model including an effect of adaptation to numerosity on numerosity discrimination, rather than the model without it. In contrast, for 40 dots the BF_{10} was 4.76, suggesting that these data were *more* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it.

For Condition 2 versus 4, the BF_{10} was 40.53, 3.22, and 1.48, respectively, for 20, 40, and 80 dots, suggesting that these data were *more* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it.

Based on the frequentist and Bayesian analyses we performed, these data suggest that in this experiment, the effect of adaptation to *numerosity* was mainly driven by the total duration of the adaptation trial. In contrast, the effect of adaptation to *duration* on numerosity discrimination (both adapter and reference stimulus = 40 dots; the same condition as in Experiment 1) was, again, mainly driven by the onset/offset duration of the adapter.

Validation of the numerosity aftereffect

We also examined whether adaptation to a low versus a high numerosity would lead to over- or underestimation, respectively, of the reference numerosity, in accordance with previous studies on adapta-

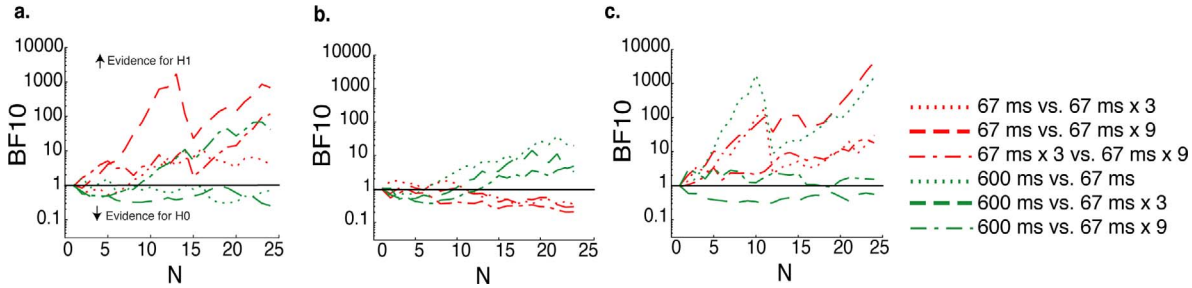

Figure 7. Sequential-analysis plots for the Bayesian paired-samples comparisons in Experiment 2. (a) Using 20 dots as a numerosity adapter, the evidence for H_1 (just-noticeable differences in numerosity discrimination differ after adaptation to numerosity and duration; y-axis) compared to H_0 (no difference in just-noticeable differences) increases with the number of data points (x-axis) when Conditions 1, 3, and 4 are compared with each other (red lines). When Condition 2 is compared with Conditions 1 and 3, the evidence for H_1 decreases with the number of data points, while the opposite is true when it is compared to Condition 4 (green lines). (b) Using 40 dots as a visual duration adapter and reference stimulus, the evidence for H_1 decreases with the number of data points when Conditions 1, 3, and 4 are compared with each other. The opposite is true when Condition 2 is compared with Conditions 1, 3, and 4, where the evidence for H_1 increases. Using 80 dots as a numerosity adapter, the evidence for H_1 increases with the number of data points when Conditions 1, 3, and 4 are compared with each other and when Condition 2 is compared with Condition 1. The trend is less definitive when Condition 2 is compared with Conditions 3 and 4. These data suggest that the conditions which had the same onset/offset duration produced different adaptation effects with adaptation to numerosity (adapter = 20 or 80 dots, reference stimulus = 40 dots) but not with adaptation to duration only (adapter and reference stimulus = 40 dots).

tion to numerosity (see review by Anobile et al., 2016). We calculated the average JND, PSE, and slope values across duration conditions for each numerosity adaptation condition. There were statistically significant differences in both the JND and PSE after adaptation to numerosity, $\chi^2(2) = 24.33$, $p < 0.001$. Post hoc analysis with Wilcoxon signed-rank tests revealed that adaptation to a low numerosity (20 dots) led to significant overestimation of the reference numerosity ($Mdn_{JND} = -0.23$, $Mdn_{PSE} = 37.36$ dots) compared to the condition without numerosity adaptation (adapter and reference stimulus = 40 dots; $Mdn_{JND} = -0.50$, $Mdn_{PSE} = 35.46$ dots; both JND and PSE: $Z = -3.43$, $p = 0.001$, $r = 0.50$). In contrast, adaptation to a high numerosity (80 dots) led to significant underestimation of the reference numerosity compared to the condition without numerosity adaptation ($Mdn_{JND} = -0.93$, $Mdn_{PSE} = 31.59$ dots): The JND and PSE values were significantly lower compared to the condition without numerosity adaptation (JND: $Z = -3.06$, $p = 0.002$, $r = 0.44$; PSE: $Z = -3.69$, $p < 0.001$, $r = 0.53$). Moreover, adaptation to a low numerosity led to significant overestimation of the reference numerosity compared to adaptation to a high numerosity (JND: $Z = -4.26$, $p < 0.001$, $r = 0.61$; PSE: $Z = -4.11$, $p < 0.001$, $r = 0.59$).

In regard to the slope values, there were statistically significant differences after adaptation to numerosity, $\chi^2(2) = 7.58$, $p = 0.023$. Post hoc analysis with Wilcoxon signed-rank tests revealed that adaptation to a low numerosity (20 dots) led to significantly higher slope values (Mdn = 8.68 dots) compared to the condition without numerosity adaptation (Mdn = 7.96 dots), $Z = -2.46$, $p = 0.04$, $r = 0.36$. No other significant differences were found.

These findings show that adapting to a low versus a high numerosity leads to overestimation versus underestimation of the reference numerosity, respectively, compared to the condition without numerosity adaptation.

Control experiment on the role of a time-order effect

In both experiments, there was a general underestimation in the numerosity-discrimination task which could be explained by a negative time-order effect (TOE). Specifically, when two stimuli are being discriminated, the stimulus presented last is judged as being of a greater magnitude, corresponding to a negative TOE.

In order to elucidate this further, we performed a control experiment with five individuals (four of whom were the authors). Specifically, we used an adapter and reference stimulus of 40 dots (the same condition as in Experiments 1 and 2) and two durations (67 vs. 600 ms). We introduced four adaptation conditions (Figure 8, left to right; see also Supplementary File S1 for the individual participants' data). In Condition 1, there was no visual adapter stimulus. The reference stimulus appeared on the left of the fixation cross and after an ISI, the test appeared on the opposite side (the sides switched after 50% of the trials were complete). Condition 2 was the same as in Experiments 1 and 2 (adapter and reference = 40 dots). In Condition 3, the test stimulus appeared first (opposite side of the adapter), and after an ISI the reference stimulus appeared on the side of the adapter. In Condition 4, the reference and test stimulus appeared simultaneously (again, at opposite sides of the fixation cross), after the adapter was presented.

Based on the data shown in Figure 8, in the case of no visual adaptation there is again a general underestimation of the reference stimulus (67 ms: $Mdn_{JND} = -0.58$, $Mdn_{PSE} = 37.92$ dots; 600 ms: $Mdn_{JND} = -0.35$, $Mdn_{PSE} = 37.72$ dots), similar to Condition 2 (67 ms: $Mdn_{JND} = -0.66$, $Mdn_{PSE} = 36.88$ dots; 600 ms: $Mdn_{JND} = -1.01$, $Mdn_{PSE} = 35.88$ dots) and as found in Experiments 1 and 2. This could point to a general response bias, which could indeed derive from a TOE, with the test stimulus presented last being consistently judged as more numerous. In regard to Condition 3 (reference stimulus presented last; 67 ms: $Mdn_{JND} = 0.48$, $Mdn_{PSE} = 43.59$ dots; 600 ms: $Mdn_{JND} = -0.04$, $Mdn_{PSE} = 39.82$ dots) and Condition 4 (reference and test stimulus presented simultaneously; 67 ms: $Mdn_{JND} = -0.003$, $Mdn_{PSE} = 39.98$ dots; 600 ms: $Mdn_{JND} = -0.49$, $Mdn_{PSE} = 37.55$ dots), there is a trend for JND and PSE values to be higher when adapting to a short duration, which is not the case in Conditions 1 and 2. This difference could confirm that the general underestimation we found in our reported experiments is an outcome of a TOE.

However, if the explanation for our findings about the effect of adaptation to duration on numerosity perception is that it is merely an outcome of a TOE, then adapting to a long duration (600 ms; Conditions 3 and 4) would not lead to underestimation of the reference stimulus, and the two duration conditions would yield similar JND and PSE values. So overall, the order of the stimulus presentation appears to matter, but it does not explain why adapting to a short versus a long onset/offset duration leads to differences in the JND and PSE values, or the differential effect of duration we found in Experiments 1 and 2.

Discussion

We have previously shown that adaptation to duration alters numerosity perception (Tsouli et al.,

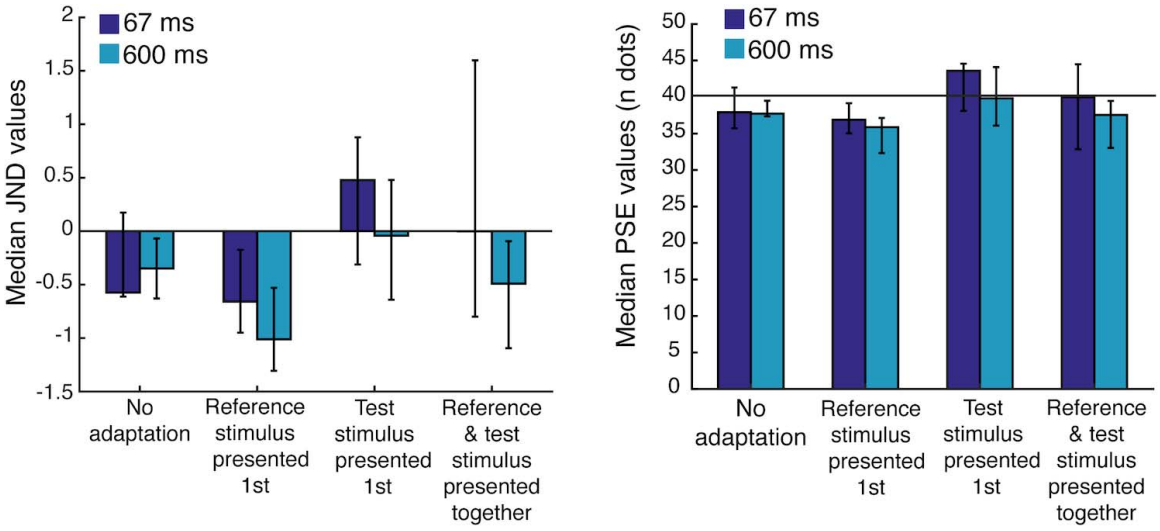

Figure 8. Median just-noticeable difference and point of subjective equality across participants ($N = 5$) for the control experiment. Error bars correspond to the bootstrapped 95% confidence interval of the median of each condition. Irrespective of presentation-order condition, adaptation to a long onset/offset duration (600 ms; light-blue bars) resulted in lower just-noticeable differences and points of subjective equality (i.e., underestimation of reference numerosity) compared to adaptation to a short onset/offset duration (67 ms; dark-blue bars).

2019). Here we examined *how* it influences numerosity perception. In addition, we examined whether the nature of that effect would be similar when adapting to duration only and when adapting to numerosity as well. In both experiments, we hypothesized that if the influence of duration on numerosity perception is driven by the adaptation of duration/numerosity channels tuned to specific durations/numerosities, then the conditions where the adapter's onset/offset duration was the same (67 ms) would produce similar adaptation effects. On the other hand, if the effect of duration on numerosity perception is driven by the strength of adaptation of numerosity-selective channels only (i.e., the longer the adaptation period, the stronger the perceptual aftereffects), then the conditions where the adapter's total presentation time or the total duration of the adaptation trial was longest (i.e., 600 or 1,800 ms) would produce the strongest adaptation effects. However, the hypotheses are not mutually exclusive.

Using both frequentist and Bayesian analyses, we found that the JND and PSE values on the duration adaptation conditions where the adapter's onset/offset duration was the same (multiple presentations of 67 ms) were generally similar and differed from the duration adaptation condition where the adapter's onset/offset duration was different (600 ms). These results support the channel-based hypothesis—that is, the effect of adaptation to duration on numerosity discrimination is driven by duration channels encoding the onset/offset duration of an event, and not the adapter's total presentation duration or the total duration of the adaptation trial. These onset/offset duration channels could also encode numerosity or wire together with numerosity channels (duration/numerosity channels). Specifically, adaptation to a long onset/offset duration (i.e., 600 ms) induced the same adaptation effect as would adaptation to a high numerosity (e.g., 80 dots). This finding was further replicated in Experiment 2. By contrast, when we induced adaptation to numerosity *and* to duration, our overall finding was that the condition with the longest total duration of the adaptation trial (i.e., 1,800 ms) produced the strongest perceptual aftereffects, even if the onset/offset duration of the adapter was short (i.e., 67 ms). Hence, the strength-of-adaptation hypothesis appears to capture the effect of duration when adapting to numerosity *and* duration.

Theoretical implications

Based on these findings, a number of theoretical inferences arise. First of all, we have successfully replicated the finding that adaptation to duration affects numerosity perception in both of our experiments (Tsouli et al., 2019). This could to some extent support the theories which suggest that temporal and numerical representations share computation mechanisms and possibly neural resources (Bueti & Walsh, 2009; Cantlon et al., 2009; Cappelletti, Freeman, & Cipolotti, 2011; Walsh, 2003).

The novel finding of our study is that the effect of adaptation to duration on numerosity perception appears to be driven by the adaptation of duration channels tuned to the onset/offset duration of the

adapter. This channel-based hypothesis is in line with numerosity-tuned neural populations (Harvey & Dumoulin, 2017; Harvey et al., 2015; Harvey et al., 2013; Nieder, Freedman, & Miller, 2002; Nieder & Miller, 2004; Viswanathan & Nieder, 2013; Wagener, Loconsole, Ditz, & Nieder, 2018) and duration-tuned neural populations (Aubie, Sayegh, & Faure, 2012; Becker & Rasmussen, 2007; Duysens et al., 1996; Hawken, Shapley, & Grosof, 1996; Heron et al., 2012; Leon & Shadlen, 2003; Maarseveen et al., 2019; Mita, Mushiake, Shima, Matsuzaka, & Tanji, 2009), with our results implying either that onset/offset duration channels also encode numerosity or that there is neuronal communication between duration-selective and numerosity-selective channels (duration/numerosity channels).

Our second experiment reveals a very different pattern of the numerosity–time interaction. We found that the duration condition with the longest total duration of the adaptation trial (1,800 ms) produced the strongest perceptual aftereffects, even if the adapter's onset/offset duration was very short (67 ms). Based on this, we speculate that in the context of adaptation to numerosity, the influence of time can be explained by the strength of adaptation of numerosity-selective channels only, without the involvement of duration/numerosity channels. Thus, longer adaptation periods result in stronger perceptual aftereffects similar to adaptation effects for other visual features (Dragoi, Sharma, & Sur, 2000; Magnussen & Johnsen, 1986).

The role of the total duration of the adaptation trial we found in our study is seemingly at odds with the study of Aagten-Murphy and Burr (2016), who found that the numerosity aftereffect is driven by the number of trials or events, not by the duration of the numerosity adapter. However, we argue that indeed, the strongest perceptual aftereffects could result from the number of adaptation events or the frequency of visual events. More specifically, the duration condition with the longest total duration of the adaptation trial (1,800 ms) was composed of nine repetitions of 67 ms, which was the largest number of repetitions among all duration conditions and also had the highest frequency of events. Hence, we suggest that what could be considered an adaptation event is not only the number of trials but the number of repetitions of the adapter stimulus within a single adaptation trial, and also the frequency of events, regardless of the onset/offset duration of the adapter. Our finding that the strongest perceptual aftereffects are obtained with a repeated presentation of the adapter within the same trial, even with a very short adapter onset/offset duration, could serve as a methodological parameter for future numerosity adaptation experiments.

All in all, we speculate that the two demonstrated adaptation phenomena (one based on adapted duration/numerosity channels, the other on adapted numerosity channels only) might be governed by partially distinct neuronal populations. Such a speculation is in accordance with a number of neuroimaging studies revealing a number of different brain regions involved in time perception (Ferrandez et al., 2003; Harrington, Haaland, & Knight, 1998; Hayashi, Kantele, Walsh, Carlson, & Kanai, 2014; Pouthas et al., 2005), which do not always overlap with the brain regions involved in numerosity perception (Dormal, Andres, & Pesenti, 2008; Harvey & Dumoulin, 2017; Harvey et al., 2013). From examining neuroimaging studies that use an adaptation paradigm, the supramarginal gyrus appears to be involved in adaptation to duration (Hayashi et al., 2015), whereas the intraparietal sulcus appears to be involved in adaptation to numerosity (Castaldi et al., 2016). Therefore, we suggest that further functional neuroimaging studies could perhaps confirm our hypothesis that there are at least partially dissociable activations when examining the effect of *adaptation to duration* on numerosity perception, compared to the effect of the *duration of adaptation* on numerosity perception.

Multiple temporal mechanisms further imply that there are multiple duration mechanisms rather than a single, supramodal timing mechanism (Bruno & Cicchini, 2016; Ivry, 1996; Motala et al., 2018). Such an interpretation could mean that there are less specialized duration mechanisms interacting with different magnitudes, such as numerosity and space, as the ATOM theory suggests (Bueti & Walsh, 2009; Walsh, 2003), and other, more specialized duration mechanisms dedicated for duration processing only. This distinction could also explain the contradicting findings from (behavioral) studies examining the interaction of time and numerosity (Chun et al., 2018; Javadi & Aichelburg, 2012; Javadi et al., 2014; Lambrechts et al., 2013; Martin et al., 2017; Tsouli et al., 2019).

In regard to the predictions of ATOM (Bueti & Walsh, 2009; Walsh, 2003), we also hypothesized that if numerosity and time are indeed part of a common magnitude system, then low versus high numerosities could be perceptually associated with short versus long durations. Hence, in the context of adaptation to numerosity, adapting to, for example, a low numerosity using a short duration should produce greater overestimation of the reference numerosity. We did not find support for this postulation in our second experiment, at least when examining the combination of low numerical and temporal magnitudes. More specifically, adapting to a low numerosity (20 dots) using a short duration (67 ms; Condition 1) did not result in greater overestimation of the reference numerosity compared to the conditions with a longer duration. However, we do not know the exact perceptual correspondence of numerical and temporal magnitudes (e.g., whether 67

ms is perceptually associated with 20 dots) which could account for this discrepancy.

Further considerations

When we used a high numerosity (80 dots), it appeared that the conditions with the longest total adapter presentation time (600 ms; i.e., Conditions 2 and 4) did not differ significantly from each other in either experiment. Hence, the total adapter presentation time (600 ms) appeared to drive the effect of adaptation to duration, as well as adaptation to numerosity *and* duration, with a high-numerosity stimulus. This could imply different mechanisms for the interaction of time and numerosity, which could be modulated by not only duration channels tuned to specific durations but also numerosity channels tuned to specific numerosities. In addition, given that the size of the dot stimuli was kept constant across numerosities, it is possible that density-processing mechanisms which are more pronounced with a high-numerosity stimulus could have played a role (Dakin, Tibber, Greenwood, Kingdom, & Morgan, 2011; Durgin, 2008). Nevertheless, the conditions where the adapter's onset/offset duration was the same (67 ms) did not differ from each other in the first experiment, whereas they did in the second. This is in agreement with the hypothesis on the adaptation of duration/numerosity channels.

When we examine the overall effect of adaptation, the JND and PSE values we report show a general underestimation. We believe that this can be explained in terms of a time-order effect (TOE), according to which comparison judgments can be affected by the spatial or temporal separation between the compared stimuli (Fechner, 1860/1966; Needham, 1934). More specifically, in the presence of a negative TOE, when two stimuli are being discriminated, the stimulus presented last is judged as being of a greater magnitude. Recently, it has been shown that nonsymbolic numerosity comparisons are affected by a negative TOE (van den Berg, Lindskog, Poom, & Winman, 2017). Indeed, in our study the test stimulus was always presented last, which could mean that it was more frequently judged as more numerous, leading to underestimation of the reference stimulus. In order to examine the potential role of a TOE and its association with numerosity perception in our experiments, we performed a control experiment. Overall, we found that a negative TOE could at least partially explain the underestimation. Importantly, regardless of the underestimation, the results produced by the adaptation conditions still supported the differential effects of adaptation to a short versus a long duration.

Another finding of our first experiment, on adaptation to duration, was the lower JND and PSE values obtained when the adapter and reference stimulus were presented on the left compared to the right side of the screen, across duration and numerosity conditions. This difference could be interpreted as an extension of the spatial-numerical association of response codes, in which shorter reaction times are recorded when low numbers are presented to the left and high numbers are presented to the right (Cohen Kadosh, Lammertyn, & Izard, 2008; Dehaene, Bossini, & Giraux, 1993). This effect is thought to derive from an introspective association of numbers with spatial locations and the so-called mental number line, where low numbers are associated with the left side and high numbers with the right side (Dehaene et al., 1993). While the effect is well documented in examination of symbolic numerosities (e.g., Arabic numerals), recent evidence shows that the perception of nonsymbolic numerosities (e.g., arrays of dots) can also be affected by spatial manipulations (Fornaciai, Togoli, & Arrighi, 2018; Liu, Zhang, Li, Zhao, & Tang, 2015; Nemeh, Humberstone, Yates, & Reeve, 2018; Schwiedrzik, Bernstein, & Melloni, 2016). Hence, the underestimation of numerosities presented on the left side that we found in our first experiment could be an outcome of the aforementioned mental number line, with participants perceiving numerosities presented on the left as generally lower. Nevertheless, we are cautious in endorsing this finding, since we found no such difference in our second experiment nor in our previous research on numerosity and duration adaptation (Tsouli et al., 2019).

Conclusions

We found that adaptation to duration affects numerosity perception by adapting onset/offset-duration channels which also encode numerosity or wire together with numerosity-selective channels. This finding is in agreement with the channel-based hypothesis on the interaction of duration and numerosity. When examining the role of duration on adaptation to numerosity, we found that the numerosity aftereffects were driven by the total duration of the adaptation trial, not by the onset/offset duration of the adapter. This finding appears to support the strength-of-adaptation hypothesis, where only numerosity channels are adapted. We propose that different temporal mechanisms are involved in adaptation to duration compared to adaptation to numerosity.

Keywords: numerosity, duration, adaptation, channel, time

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