



An investigation of the spatial selectivity of the duration after-effect



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ABSTRACT

Adaptation to the duration of a visual stimulus causes the perceived duration of a subsequently presented stimulus with a slightly different duration to be skewed away from the adapted duration. This pattern of repulsion following adaptation is similar to that observed for other visual properties, such as orientation, and is considered evidence for the involvement of duration-selective mechanisms in duration encoding. Here, we investigated whether the encoding of duration – by duration-selective mechanisms – occurs early on in the visual processing hierarchy. To this end, we investigated the spatial specificity of the duration after-effect in two experiments. We measured the duration after-effect at adapter-test distances ranging between 0 and 15° of visual angle and for within- and between-hemifield presentations. We replicated the duration after-effect: the test stimulus was perceived to have a longer duration following adaptation to a shorter duration, and a shorter duration following adaptation to a longer duration. Importantly, this duration after-effect occurred at all measured distances, with no evidence for a decrease in the magnitude of the after-effect at larger distances or across hemifields. This shows that adaptation to duration does not result from adaptation occurring early on in the visual processing hierarchy. Instead, it seems likely that duration information is a high-level stimulus property that is encoded later on in the visual processing hierarchy.

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1. Introduction

Human observers can readily encode duration information from events that vary in duration, and use that information to guide their behavior (Fraisse, 1984; Gibbon, 1977). Especially in the sub-second range, accurate duration encoding is instrumental for many complex behaviors such as precise motor control (i.e. in activities such as sport and dance), speech recognition and generation, and the processing of social cues (Ambadar, Cohn, & Reed, 2009; Buhusi & Meck, 2005; Diehl, Lotto, & Holt, 2004; Janata & Grafton, 2003; Mauk & Buonomano, 2004; Merchant & Georgopoulos, 2006; Schmidt, Ambadar, & Cohn, 2005). Recently, there has been a renewed interest in studying this temporal aspect of our behavior and the way in which our brain encodes this information. This has resulted in several different types of models on duration encoding that each propose different mechanisms for the encoding of duration (Gibbon, 1977; Ivry & Schlerf, 2008; Jones & Boltz, 1989; Karmarkar & Buonomano, 2007; Matell & Meck, 2004; Van Wassenhove, 2009).

A recent model suggests the involvement of duration-selective neurons in the processing of duration information (Becker & Rasmussen, 2007; Heron et al., 2012). Evidence for these models come from adaptation studies that demonstrate a duration after-effect following adaptation. For example, Heron et al. (2012) showed that adapting to the duration of a visual or auditory event causes the perceived duration of a subsequently presented event with a slightly different duration to be skewed away from the adapted duration. This pattern of repulsion following adaptation to duration occurred when both stimuli were of the same modality but not for different modalities, implicating modality specific processing of duration. Importantly, this duration after-effect only occurred when the adaptation duration was close to the tested duration, disappearing when the difference between the two stimuli exceeded ~1.5 octaves. As such, adaptation to duration resulted in a pattern of repulsion similar to that observed for other visual properties such as orientation, spatial frequency, and temporal frequency, which are known to be processed by groups of neurons that show feature selectivity (De Valois, 1977; De Valois, Albrecht, & Thorell, 1982; Smith, 1971).

Similar results have been reported by studies investigating the effect of trial history on duration judgments (Becker & Rasmussen, 2007; Walker, Irion, & Gordon, 1981). These studies also show that presentation of a particular duration causes the perception of

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subsequent shorter or longer durations to shift away from the duration that was presented earlier (Becker & Rasmussen, 2007; Walker et al., 1981). Finally, studies investigating duration discrimination training have shown that training benefits such as increased discrimination sensitivity do not transfer to other non-trained durations (Bartolo & Merchant, 2009; Buetti & Buonomano, 2014; Karmarkar & Buonomano, 2003; Wright, Buonomano, Mahncke, & Merzenich, 1997). All these studies are consistent with a channel-based model of duration processing in which duration is processed by groups of neurons that selectively respond to specific durations (Hayashi et al., 2015; Heron et al., 2012). Reading out the relative activation of groups of these neurons would allow for an explicit representation of duration that can be used for further processing. The observation that the duration after-effect does not transfer across modalities suggests that duration information is encoded separately for each modality, and combined later on during processing to form a more complete, multimodal representation of duration (Heron, Hotchkiss, Aaen-Stockdale, Roach, & Whitaker, 2013; Heron et al., 2012; Van Wassenhove, 2009).

A relevant question that is currently being investigated is that of the relative position of these duration-selective channels along the visual processing hierarchy (Hayashi et al., 2015; Heron et al., 2013; Li, Yuan, & Huang, 2015). It has been proposed that duration-selective neurons are present in early sensory areas for both auditory and visual information (Heron et al., 2012). Evidence for this claim comes from single cell recording studies in different mammals that have reported duration-selective neurons in both early auditory processing areas such as inferior colliculus and the auditory midbrain (Brand, Urban, & Grothe, 2000; Casseday, Ehrlich, & Covey, 1994; Ehrlich, Casseday, & Covey, 1997; He, Hashikawa, Ojima, & Kinouchi, 1997), as well as early visual areas such as area 17 & 18 (Duysens, Schaafsma, & Orban, 1996; Eriksson, Tompa, & Roland, 2008). One can argue that an early locus for duration processing can be beneficial given that the temporal integration window of neurons is known to increase along the visual processing hierarchy (Hasson, Yang, Vallines, Heeger, & Rubin, 2008). Therefore, encoding duration information at an early stage of visual processing would potentially allow for more precise encoding of the onset and offset of an event, resulting in more accurate duration encoding. Furthermore, several studies on duration perception have shown that adaptation to both temporal and non-temporal visual features can cause changes in the perceived duration of subsequent events, which are restricted to the location at which adaptation took place (Johnston, Arnold, & Nishida, 2006; Ortega, Guzman-Martinez, Grabowecy & Suzuki, 2012; Zhou, Yang, Mao, & Han, 2014). For example, it has been shown that adapting to the temporal frequency content of a stimulus can cause spatially localized shifts in the perceived duration of subsequent events. These spatially selective after-effects following adaptation have been attributed to modulation in neurons in LGN and V1 (Ayhan, Bruno, Nishida, & Johnston, 2009; Johnston et al., 2006; Ortega et al., 2012; but see Burr, Tozzi, & Morrone, 2007; Fornaciai, Arrighi, & Burr, 2016). These findings suggest a strong relation between low-level visual processing and the encoding of temporal information.

The above studies suggest that duration information is processed at early levels of processing. However, behavioral studies have shown that trial history effects and the duration after-effect do not show any selectivity to low-level visual features such as orientation (Li, Yuan, & Huang, 2015; Walker et al., 1981), arguing against a role of early visual cortex in channel based duration processing. Furthermore, many other different brain areas have been implicated in duration processing, providing alternative possible neural loci for the channel based encoding of duration (Hayashi et al., 2015; Ivry & Schlerf, 2008; Mauk & Buonomano, 2004). For example, single cell recordings in macaques have revealed

duration selectivity in striatal neurons (Mello, Soares, & Paton, 2015) as well as in the pre-supplementary motor area (pre-SMA) (Merchant, Pérez, Zarco, & Gámez, 2013). More recently, Hayashi et al. (2015) investigated single duration repetitions in humans using fMRI. They showed a decrease in BOLD response in the right-supramarginal gyrus (r-SMG) when the duration of a stimulus was similar to a previously presented stimulus, as compared to when both were dissimilar. This suppressed response to repetition was replicated for several different intervals and did not seem to be the result of a general similarity judgment, only occurring for duration judgments (Hayashi et al., 2015).

In sum, it is clear that the mechanisms involved in duration processing and their related structures in the human brain are yet to be established. The goal of this study was to further investigate the relative position of duration-selective mechanisms along the visual processing hierarchy by investigating the spatial selectivity of the duration after-effect. It is well known that the spatial scale over which sensory information is integrated increases along the visual processing hierarchy (Smith, Singh, Williams, & Greenlee, 2001). This is the result of differences in receptive field size of individual neurons in different cortical areas. For early visual areas such as V1, receptive fields have been found to be as small as 0.5°, with the estimate receptive field size steadily increasing along the visual processing hierarchy (Amano, Wandell, & Dumoulin, 2009; Dumoulin & Wandell, 2008; Harvey & Dumoulin, 2011; Smith et al., 2001). This characteristic has often been used to dissociate between processes occurring at different levels of the visual processing hierarchy. For example, in the domain of visual motion processing this has been used to dissociate between motion after-effects occurring in V1 and those occurring later in processing in areas MT (Kohn & Movshon, 2003). Applying this type of paradigm will allow us to make similar distinctions for the mechanisms involved in the encoding of duration information. If the encoding of duration – by duration-selective mechanisms – occurs early in the visual processing hierarchy, the duration after-effect should be restricted to within a few degrees of visual angle from the adapted location. Conversely, if duration information is encoded later on in the visual processing hierarchy, the duration after-effect should remain relatively constant across visual space.

Here, we present two experiments investigating the spatial selectivity of the duration after-effect by parametrically varying the distance between adaptation and test stimulus. We adopted the paradigm introduced by Heron et al. (2012, 2013) and adapted participants to visual stimuli of varying duration. Following adaptation, participants completed a cross-modal duration judgment task comparing an auditory reference to a visual test stimulus. To evaluate the effect of visual distance on the duration after-effect, test stimuli were placed at a range of distances from the adapted location. In a second experiment, we further explore the impact of visual and cortical distance on the duration after-effect by measuring the duration after-effect for both within- and between-hemifield presentations.

2. Experiment 1

2.1. Method

2.1.1. Participants

Nine participants completed the experiment (1 male, $M_{\text{age}} = 20.91$ $SD = 3.02$). All participants had normal or corrected-to-normal vision and were naïve as to the purpose of the experiment. Before the experiment all participants gave written informed consent. After completing the experiment, participants received a monetary reward or course credits. The experiment was conducted in line with the principles expressed in the Declaration of Helsinki and received approval by the Local Ethics Committee.

2.1.2. Materials and stimuli

All visual stimuli were presented on a linearized 22-inch CRT monitor (screen resolution at 1024×768 pixels, 100 Hz refresh rate) controlled by an Apple Mac Mini. Participants viewed the screen from a distance of 57 cm. Head movement was restrained using a chinrest.

The stimulus display consisted of a white central fixation cross (64.1 cd/m^2 ; $0.40 \times 0.40^\circ$) presented on a gray background (8.28 cd/m^2). All visual stimuli were Gaussian blobs ($\sigma = 0.75^\circ$, 76% peak Michelson contrast) presented at 8° from the center of the screen. The auditory stimuli consisted of bursts of white noise (65.4 dB) presented through a Sennheiser HD201 on ear headset. In a pilot study, we found that the relation between the perceived duration of auditory and visual stimuli varied considerably between participants. To assure that the visual presentation was similar for each participant, we set the auditory reference duration to be perceived as equal to a 320 ms visual stimulus. Participants completed a cross-modal duration judgment task in which the auditory reference duration was varied using an Accelerated Stochastic Approximation (ASA) staircase procedure (Kesten, 1958). This resulted in an average auditory reference duration of 321.14 ms ($SD = 66.73$). All stimuli were generated and presented using MATLAB 2015b (MathWorks, Inc.) and the Psychophysics Toolbox 3.0.12 (Brainard, 1997; Pelli, 1997). All timings were verified using a dual channel oscilloscope.

2.1.3. Procedure

In separate blocks, participants adapted to 100 repetitions of a visual stimulus lasting either 160 ms or 640 ms. The adaptation stimulus was always presented directly above the fixation cross at a distance of 8° of visual angle. To avoid clear temporal patterns or adaptation to on-off temporal frequency the inter-stimulus interval (ISI) was varied randomly between 500 and 750 ms. During the adaption phase, the participants' task was to maintain central fixation while attending the repetitions of the adaption stimulus. Following the adaptation phase the text "duration judgment phase" appeared for 2 s to inform the participants that they had entered the test phase.

Each trial of the test phase started with 4 top-up repetitions of the adaptation stimulus followed by a cross modal duration judgment task. For this task participants were instructed to compare the duration of an auditory reference tone to that of a visual test stimulus presented randomly at one of five possible adapter-test distances (center to center distance: 0, 6, 8, 11, 15°). For each distance, the location of the test stimulus was varied randomly between left and right of the fixation cross. The duration of the test stimulus was varied using the Minimum Expected Entropy staircase method (Saunders & Backus, 2006). Participants reported their judgment by pressing either the left ('sound longer') or right ('visual longer') arrow key. After reporting their judgment the next test trial was initiated after a 500 ms delay. An overview of both phases can be found in Fig. 1.

After completing 40 trials participants were informed on their progress ("Block x of 10") and were allowed to take a short self-timed break. Participants completed 10 blocks and a total of 400 trials. This equates to 40 trials for each unique combination of conditions. All measurements were conducted over two 50-min sessions separated by a 15-min break.

2.2. Results & discussion

We calculated the point of subjective equality (PSE) based on the psychometric function estimated by the Minimum Expected Entropy staircase for each condition, for each participant. These data can be found in the Supplementary materials (Fig. S1). Next we calculated the average PSE for each of the 10 conditions

(Fig. 2). This data was then subjected to a 2×5 repeated-measures ANOVA with PSE as the dependent measure and Adaptation Duration and Distance as independent measures. All test were evaluated at $\alpha = 0.05$. Post-hoc comparisons were adjusted for multiple comparisons using the Holm-Bonferroni correction method (Holm, 1979). The error bars in all images reflect within-subject variability, calculated using per-subject normalization of the data (Cousineau, 2005; Morey, 2008).

The results reveal a main effect of Adaptation Duration ($F(1,8) = 46.49$, $p < 0.001$, $\eta^2 = 0.85$) with lower PSE estimates following adaptation to a 160 ms stimulus compared to adaptation to a 640 ms stimulus. In other words, adaptation to a longer duration resulted in a shorter perceived duration for the test stimuli compared to adaptation to a shorter duration. In addition, we found a main effect of Distance ($F(4,32) = 8.72$, $p < 0.001$, $\eta^2 = 0.52$), reflecting a general decrease in PSE for higher distances indicating an increase in perceived duration with increasing adapter-test distance. Subsequent paired sample t-tests for the main effect of Distance revealed that the PSE was significantly higher when the test stimulus was present at the same location as the adapter stimulus (0°) compared to an adapter-test distance of 15° ($t(8) = -4.99$, $p < 0.001$). No other comparisons reached statistical significance (all $p > 0.064$). We also analyzed the slope for the main effect of Distance by calculating the mean PSEs across the two Adaptation Durations for each participant followed by a linear regression. We then conducted a simple t-test and found that the slope was significantly lower than zero ($t(8) = 4.80$, $p < 0.001$).

Importantly, we found no evidence for a significant interaction between Adaptation Duration and Distance ($F(4,32) = 0.75$, $p = 0.567$, $\eta^2 = 0.09$) indicating that the effect of Adaptation duration did not significantly change across the different adapter-test distances. To underpin this finding, we conducted an additional Bayesian analysis using JASP (Love et al., 2015) to evaluate the likelihood that the magnitude of the duration after-effect was constant across all measured distances. First, we calculated the magnitude of the duration after-effect by subtracting the PSEs for the 640 ms Duration adaptation conditions from those of the 160 ms Duration Adaptation conditions (Fig. 3). The resulting score, which reflected the magnitude of the duration after-effect, was then further analyzed using a Bayesian repeated-measures ANOVA with Duration After-effect as a dependent variable and Distance as an independent measure. This analysis revealed that the data was almost five times more likely to reflect a null effect compared to the alternative hypothesis of a significant change in the duration after-effect across adapter-test distance ($BF_{01} = 4.74$).

We observed a clear duration after-effect, corroborating the findings by Heron and colleagues (Heron et al., 2012, 2013). More importantly, the effect of adaptation was present at each of the measured distances and did not decrease for larger adapter-test distances. This result indicates that the duration after-effect does not show the spatial selectivity that would be expected if the duration-selective mechanisms were located early on in the visual processing hierarchy. Instead, it seems more likely that the channel based encoding of duration occurs further upstream in the visual processing hierarchy, where receptive fields are not confined to relatively small areas of visual space.

3. Experiment 2

Given the distances used in Experiment 1, it seems likely that the neuronal mechanisms responsible for channel based duration processing of visual information have relatively large receptive fields, arguing against a role for low-level visual processing areas in duration perception. To further explore this notion, we investigated the hemifield specificity of the duration after-effect. Due to

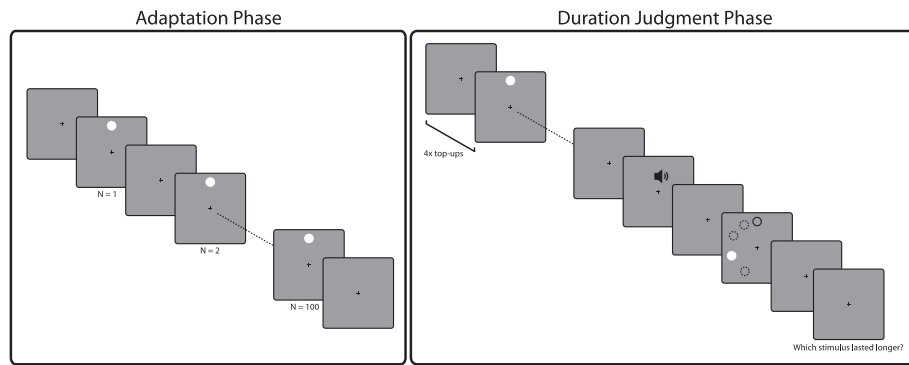


Fig. 1. Schematic representation of a single adaptation block. Each block started with an Adaptation Phase (left) in which participants were presented with a 100 repetitions of the adaptation stimulus (160, 640 ms) presented 8° above central fixation. In the following Duration Judgment Phase, participants were presented with 4 repetitions of the adaptation stimulus (top-up) followed by a cross-modal duration judgment task (right). In this task, they compared an auditory reference to a visual test stimulus presented at one of the 5 possible test locations. The dashed line annuli only serve to illustrate the alternative locations of the test stimulus and were not actually shown on the screen.

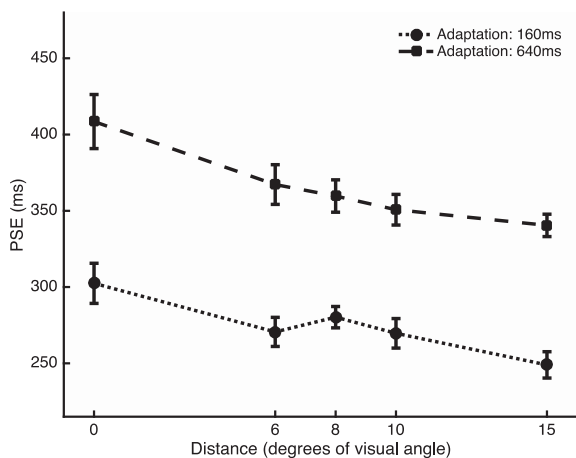


Fig. 2. Average PSEs for the 160 and 640 adaptation durations are plotted as a function of adapter-test distance. Higher PSEs reflect a shorter perceived duration of the test stimulus.

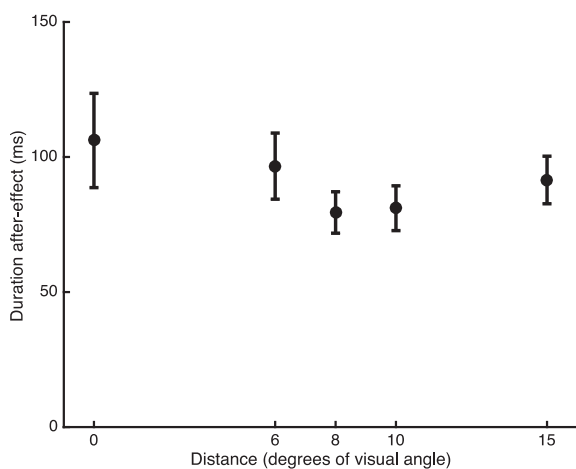


Fig. 3. Magnitude of the duration after-effect as a function of adapter-test distance. The magnitude of the adaptation after-effects is calculated by subtracting the PSEs for the 640 ms Duration adaptation conditions from those of the 160 ms Duration Adaptation conditions.

the anatomical separation between hemispheres, the degree of interhemispheric transfer of visual information is different at different levels of processing. As a result, there is no direct

interhemispheric integration in early visual areas, with the amount of interhemispheric integration increasing along the visual processing hierarchy. This anatomical property has functional consequences for the processing of information presented in different hemifields. For lower-visual areas (V1-4) responses are strongly restricted to stimulation in the contralateral visual field, extending no more than 3–4° into the ipsilateral field (Amano et al., 2009; Gattass, Gross, & Sandell, 1981; Gattass, Sousa, & Gross, 1988; Winawer, Horiguchi, Sayres, Amano, & Wandell, 2010). For other areas receptive fields show much larger responses to stimulation in the ipsilateral visual field (Amano et al., 2009). However, the response to ipsilateral stimulation is often found to be weaker due to large amount of feedforward input stemming from lower-level visual neurons that only respond to stimulation in the contralateral field (Ffytche, Howseman, Edwards, Sandeman, & Zeki, 2000; Huk, Dougherty, & Heeger, 2002). One example of the functional consequences of cortical separation is the fact that adaptation to numerosity – believed to originate in parietal areas of the brain (Harvey, Klein, Petridou, & Dumoulin, 2013) – has been shown to transfer across visual space, but not visual hemifield (Burr & Ross, 2008; Choo & Franconeri, 2010). While parietal areas have relatively large receptive fields – as well as areas that do not show any form of retinotopic mapping – crossing into the opposite hemifield reduces the magnitude of the numerosity after-effect. Beyond cortical distances there are other difference between intra- and inter-hemispheric processing. One example of this is the observation that subjects can track twice as many items when they are presented in separate hemifields, compared to when they are presented in the same hemifield. This finding points towards the existence of separate attentional networks for each hemisphere (Alvarez & Cavanagh, 2005; Cavanagh & Alvarez, 2005). As such, hemifield specificity of the duration after-effect could be considered another case of spatial specificity. Alternatively, it could reflect a form of lateralization related to separate attentional processing.

Because the adaptation stimuli in Experiment 1 were always presented on the vertical midline, we could not evaluate the possibility of hemifield specific processing. To address this we conducted a second experiment in which the duration after-effect was evaluated at two different adapter-test distances with the largest distance falling either within- or between-hemifields. If adaptation to duration occurs only within the adapted hemifield, we would expect the duration after-effect to disappear for test stimuli presented in the opposite hemifield. We also addressed a possible issue in experiment one, where we did not control for any eye-movements and changes in gaze position. Given the large number of adaptation repetitions and the salience of test stimuli presented

away from the adapted location, it is possible that participants did not strictly maintain central fixation throughout the experiment. Fixating on adaptation, top-up, or test stimuli while they are being presented would inflate the maximum distance at which the after-effect could be observed. More problematically, fixating both adaptation and test stimuli would lead to a duration after-effect that appears to ‘transfer’ across spatial distance, while simply reflecting adaptation measured at a distance of ~ 0 degrees of visual angle. To control for this issue, we measured gaze-position throughout the experiment.

3.1. Method

3.1.1. Participants

Sixteen participants completed the experiment (4 male, $M_{\text{age}} = 25.00$, $SD = 4.57$). All participants had normal or corrected-to-normal vision and were naïve to the purpose of the experiment. Before the experiment, all participants gave written informed consent. After completing the experiment, participants received a monetary reward or course credits. The experiment was conducted in line with the principles expressed in the Declaration of Helsinki and received approval by the Local Ethical Committee. For half of the participants ($N = 8$) we measured gaze position throughout the experiment.

3.1.2. Materials and stimuli

For the non-eyetracking runs of the experiment, materials were the same as in Experiment 1 & 2. For the runs including eyetracking, a different setup was used to accommodate the use of our eye-tracker. Stimuli were presented on the same monitor but were controlled by a Dell OptiPlex 7040 workstation running Windows 10 and Matlab 2015b. Display luminance for all stimuli was matched for both setups, with all deviations < 0.05 cd/m^2 . Average luminance values are reported for this experiment. All timings were evaluated using a dual channel oscilloscope. Gaze position was measured using an EYE TRIBE tracker sampling at 30 Hz, controlled using the PyGaze software package and eye tribe toolbox for Matlab (Dalmajer, 2014; Dalmajer, Mathôt, & Van der Stigchel, 2014). Finally, we used a chin- and headrest, to increase head stability.

All stimuli were equal to those used in Experiment 1 (Gaussian blob: $\sigma = 0.75^\circ$, 76% peak Michelson contrast) and were accompanied by a central fixation dot (64.2 cd/m^2 ; $0.50 \times 0.50^\circ$) presented on a gray background (8.29 cd/m^2). Once more, an ASA staircase procedure was used to set the duration of the auditory stimulus ($M = 291.29$ ms, $SD = 57.87$ ms). All other presentation conditions and timings were identical to experiment 1.

3.1.3. Procedure

The procedure was similar to that of the first experiment. Participants adapted to a 100 repetitions of a visual stimulus lasting 160 ms or 640 ms. All stimuli were presented 8° from the center of the screen at 4 different possible angles (45 , 135 , 225 , and 315 degrees; see Fig. 4). The location of the adaptation stimuli was counterbalanced across these 4 locations, with a single location being used for each participant. For each participants test stimuli were always presented at one of three possible locations: At the adapted location, in the horizontally adjacent quadrant, or in the vertically adjacent quadrant. This resulted in two adapter-test distances (center-to-center distance: 0 , 11.31°), with the non-zero distance being presented either within- or between-hemifield (Fig. 4).

For the eyetracking group, the procedure was expanded to include gaze measurements. At the start of each experiment we tested the fidelity of the gaze signal by running two test 9-point calibrations. In case the eyetracking signal was too poor to complete calibration, another unrelated experiment was conducted

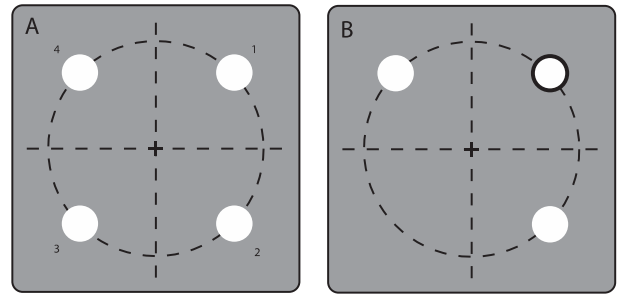


Fig. 4. Schematic representation of the stimulus display in Experiment 3 (dotted lines for illustrative purposes only). A) For each participant adaptation stimuli were presented at one of the 4 positions. Test stimuli were presented at either the same location, or in the adjacent horizontal and vertical quadrants. This led to three possible presentation conditions: same locations (0°), within-hemifield (11.31°) or between-hemifield (11.31°). B) An example display for a single participant, the outlined circle indicates the adapted location and the white circles show possible test locations.

instead. Three people were excluded via this procedure. After this initial check, we started the experiment. At the start of each block, participants were (re)calibrated to assure good calibration. Additionally, at the start of each trial an automated drift check was conducted, continuing after participants had successfully fixated within 2° of the center of the fixation dot for 250 ms. If participants failed the automated drift check, the eye tracker was recalibrated. Gaze position was monitored throughout both the adaptation and test phase. Additionally, presentation of the test stimulus was gaze contingent, with failed fixation (deviation $> 2^\circ$) leading to a disappearance of the test stimulus and re-run of the same trial. In total, participants completed 6 blocks each containing 50 trials (300 trials total). This equated to 50 trials for each unique combination of conditions. All measurements were conducted across two 50-min sessions separated by a 15-min break.

3.2. Results & discussion

3.2.1. Eyetracking data

The eyetracking signal was stable throughout most of the experiment with only a small percentage of missed samples during stimulus presentation: adaptation presentations (3.94%), top-up presentations (5.42%), and test stimulus presentation (0%). We analyzed the successfully measured samples by calculating the percentage of fixations that fell within 2 degrees of visual angle from the central fixation dot. We found that participants fixated the fixation dot 97.03% (SD: 1.10%) of the time during the presentation of adaptation stimuli, 96.25% (SD: 1.66%) of the time during top-up presentation, 99.79% (SD: 0.28) of the time during the presentation of the test stimulus. Additionally, we looked at the percentage of trials that was canceled due to the loss of fixation during the presentation of the test stimulus. On average this occurred on 1.70% (SD: 2.54) of the trials. Together these data show that participants were able to follow instruction and maintain fixation throughout the experiment.

3.2.2. Behavioral data

We calculated the point of subjective equality (PSE) based on the psychometric function estimated by the Minimum Expected Entropy staircase for each condition, for each participant (Fig. S2). Average PSEs for each of the 9 conditions can be found in Fig. 5. This data was then subjected to a 3×3 ANOVA with PSE as the dependent measure and Adaptation Duration (160, 640 ms) and Locations (0° , 11.31° Within, 11.31° Between) as within-subject factors.

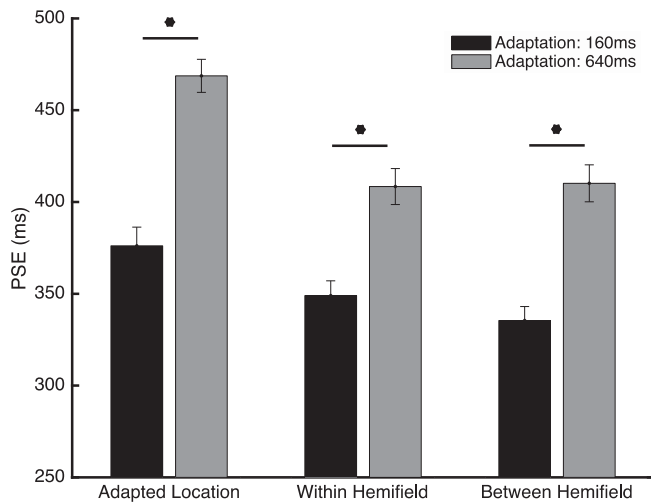


Fig. 5. Average PSEs for the 160 and 640 ms adaptation durations plotted for each of the three test locations.

We again found a main effect for Adaptation Duration ($F(1,15) = 48.93$, $p < 0.001$, $\eta^2 = 0.77$), replicating the duration after-effect reported in experiment 1. We also observed a main effect for Location ($F(2,30) = 22.85$, $p < 0.001$, $\eta^2 = 0.604$). Paired sample t -test for the main effect of Location reveal a significantly shorter perceived duration for the 0° distance presentations compared to both non-zero distance presentations (both $p < 0.001$). No significant difference was observed between the between- and within-hemifield presentations was observed ($t(15) = 0.64$, $p < 0.53$). Importantly, we found no evidence for an interaction between Adaptation Duration and Location ($F(2,75) = 2.34$, $p < 0.114$, $\eta^2 = 0.0135$). A Bayesian repeated measure ANOVA with Magnitude of the Duration After-effect as a dependent variable and Distance as an independent measure revealed no clear evidence for either the null hypotheses or alternative hypothesis ($BF_{01} = 1.23$), indicating uncertainty about whether the duration after-effect varied across the different adapter-test locations. Visual inspection of the magnitude of the duration after-effect for each of the three Location conditions shows that the after-effect is numerically highest for presentation at the adapted location and lowest at the within-hemifield location. As such it is unlikely that this uncertainty reflects evidence for a smaller after-effect for between-hemifield presentations.

In Experiment 2, we replicated the results from Experiment 1, demonstrating a clear duration after-effect at all measured locations. We also replicated the general increase in perceived duration for increasing adapter-test distances observed in Experiment 1. More relevant to answering our question, we found no evidence for a decrease in the magnitude of the duration after-effect at a distance of 11.31° for both within- and between-hemifield presentations. Additionally, we demonstrate that our findings cannot be explained by a failure to fixate during presentation of the adaptation or test stimuli.

4. General discussion

The goal of this study was to investigate the relative position of duration-selective mechanism along the visual processing hierarchy. More specifically, we aimed to evaluate the possibility that the duration after-effect originates from duration-selective mechanisms that are located in early visual areas, as has previously been suggested (Heron et al., 2012). To address this issue we investigated the spatial selectivity of the duration after-effect by parametrically varying the distance between adapter and test stimuli in two experiments. In both experiments we observed a duration

after-effect, replicating the pattern of repulsion following duration adaptation demonstrated in earlier studies (Heron et al., 2012, 2013; Li, Yuan, & Huang, 2015). Furthermore, the duration after-effect occurred at all measured distances, with no evidence for a decrease in the magnitude of the after-effect at larger distances. In Experiment 2 we investigated the possibility of hemifield specificity for the duration after-effect. We observed similar results for both within- and between-hemifield adaptation to duration, with no evidence for any hemifield specificity. Finally, we demonstrate that the effects observed in our study are not the result of fixating adaptation/test stimuli during the experiment.

In these experiments we observed a duration after-effect that transfers over distances up to 15° , as well as transfers to locations in the hemifield opposite to the adapted location. From these findings we conclude that it is unlikely that the duration after-effect originates from adaptation in early visual areas as has originally been proposed. This conclusion is further supported by recent work reporting transfer across hemifields following adaptation to duration (Li, Yuan, Chen, Liu, & Huang, 2015). In their experiment, the duration after-effect was assessed for two locations located in opposite hemifields, confounding distance and hemifield. The findings reported here corroborate their finding as well as providing an independent, parametric measurement of the duration after-effect across visual space as well as between hemifields.

To provide a more descriptive discussion about the transfer across different adapter-test distances and its relation to retinotopically mapped visual areas we can compare our data to population receptive field size estimates from human fMRI data. It is important to note that receptive field size in these studies is expressed as the sigma of the Gaussian describing the receptive field. Calculating the full-width-half-max for these Gaussians increases its size by a factor of ~ 2.35 . For early visual areas such as V1-3, estimated population receptive field size at an eccentricity of 8° ranges from 2° to 4° (Amano et al., 2009; Harvey & Dumoulin, 2011; Zuiderbaan, Harvey, & Dumoulin, 2012). As such it is very unlikely that adaptation in these areas underlie the duration after-effect reported here. For later visual areas such as V4, lateral occipital cortex (LO), and middle temporal visual areas (MT/MST), these estimates are much larger (6 – 14°) (Amano et al., 2009; Harvey & Dumoulin, 2011; Winawer et al., 2010). This relatively large size (FWHM: ~ 14.1 – 32.9°) makes it more difficult to exclude these areas based on the distances measured here. When looking at visual field maps and their responsiveness across hemifields, a similar but complementary image emerges. For early visual areas (V1-4) response are strongly restricted to information in the contralateral visual field, extending no more than 3 – 4° into the ipsilateral field (Amano et al., 2009; Winawer et al., 2010). This corroborates our earlier statement about V1-3 and includes V4 as an unlikely candidate based on our between hemifield data. For later visual areas receptive fields extend into the ipsilateral visual field to a large extent (Amano et al., 2009). However, response to ipsilateral stimulation for areas such as V5 is often weaker compared to responses to contralateral stimulation due to the abundance of feed-forward input from lower-level neurons that only respond to stimulation in the contralateral field (Ffytche et al., 2000; Huk et al., 2002). This property has been used to dissociate related areas such as MT and MST (Ffytche et al., 2000; Huk et al., 2002). Based on these findings one might predict some decrease in the duration after-effect for between hemifield presentations for areas such as MT. Our current results did not show any significant decrease in the magnitude of the duration after-effect. However, one could argue that a numerical decrease is apparent for the non-zero conditions in our second experiment. As such, we should be careful in making strong claims about the involvement of areas that have large receptive fields, such as MT, based on the data and adapter-test distances used in our experiments. To further dissociate the

involvement of higher visual areas with large receptive fields (MT, LO, TO) in the encoding of duration, it would be more appropriate to use other experimental methods that focus on specificity based on visual features that are relevant to these ‘middle/higher-level’ areas (i.e. motion direction selectivity for V5). For now, we conclude that areas V1–V4 are unlikely to play a role in duration selective processing as measured by the duration after-effect reported here. Instead the data suggests that duration selective processing occurs at later stages of the visual processing hierarchy in visual areas with relatively large receptive fields, or in areas that do not show any spatial sensitivity.

Several studies support the idea of an involvement of higher-level visual areas in the encoding of duration. For example, recent work using single cell recordings and fMRI have reported duration-selective responses in different cortical areas. These areas included the r-SMG (Hayashi et al., 2015), medial premotor cortex (Merchant et al., 2013), and the striatum (Mello et al., 2015). As of now it is unclear what the exact role of these different areas is in the encoding of duration information. Several authors have suggested the possibility that duration is first encoded in a modality specific manner before being combined into a single duration code used for further processing (Heron et al., 2012; Heron et al., 2013; Van Wassenhove, 2009). As such, the duration selectivity in different brain areas might reflect further processing of duration information and the application of that information for other processes such as the temporal aspects of motor preparation and cognitive control (Coull, Davranche, Nazarian, & Vidal, 2013; Van Wassenhove, 2009).

In both of our experiments, we observed that the perceived duration of events increased as the distance from the adapted location increased. One possible explanation for these results is the adaptation to low-level visual stimulus properties (such as luminance, contrast, or spatial frequency) that occur for the 0° distance presentations. Previous studies have shown that adaptation to low-level visual features can cause compression in perceived duration and that these effects are spatially localized to about 2–4 degrees of visual angle (Zhou et al., 2014). As such, adaptation to low-level visual features could explain the increase in perceived duration for the stimuli presented at the non-zero distances. However, this would predict a steep decline between the 0° and all non-zero adapter-test distances, but not the general increase across distance observed in Experiment 1. Alternatively, the decrease observed in Experiment 1 could be due to the fact that adapter-test distance was confounded with vertical position. We controlled for this issue in Experiment 2 by counterbalancing the adaptation location but observed a similar pattern of decreasing perceived duration with adapter-test distance. Another possibility is that the general increase in perceived duration at increasing adapter-test distance could be the result of inhibition of return at the location of the adaptation stimulus. Inhibition of return (IOR) occurs when attention is drawn to a location in visual space that has been recently attended (i.e. in the previous 300–3000 ms; Klein, 2000; Samuel & Kat, 2003). IOR has been shown to have a spatial gradient, being strongest at the attended location and decreasing in magnitude with visual distance (Bennett & Pratt, 2001). Earlier studies on duration perception have shown that attended stimuli are perceived as having a longer duration compared to unattended stimuli or stimuli that receive less attention (Block, Hancock, & Zakay, 2010; Tse, Intriligator, Rivest, & Cavanagh, 2004; Ulrich, Nitschke, & Rammesayer, 2006). In our study, participants were presented with four top-up stimuli at the adapted location followed by the cross-modal duration judgment task, with the visual test stimulus being presented between 1000 and 2000 ms after the last top-up. As such, IOR at the location of the adaptation stimulus could explain the graded increase in perceived duration over visual space.

In the current study, we did not find any evidence for a decrease in the duration after-effect with increased adapter-test distance. While this indicates a strong role for later visual areas, it does not fully exclude a role for earlier areas. Many adaptation after-effects for more complex stimulus properties (i.e. motion, numerosity, faces) with processing loci in higher-level areas have been shown to also include a low-level adaptation component (Afraz & Cavanagh, 2008; Kovács, Zimmer, Harza, Antal, & Vidnyánszky, 2005; Kovács, Zimmer, Harza, & Vidnyánszky, 2007). One classic example is the contribution of adaptation in V1 in motion after-effects adaptation (Kohn & Movshon, 2003). The fact that we do not find any evidence for such a lower-level contribution in the duration after-effect might reflect a lack of sensitivity in the method deployed in this experiment. Incorporating neuroscientific methods such as fMRI might provide a more appropriate way to address this question. Despite this nuance about a lower-level contribution, it is safe to conclude that the main locus for duration encoding lies outside earlier visual areas.

The results reported here are in strong contrast with the result of studies investigating the effect of adaptation to other temporal and non-temporal stimulus features on perceived duration (Johnston et al., 2006; Ortega et al., 2012; Zhou et al., 2014). In general, these studies report strong spatial selectivity indicating an origin in early visual areas (e.g. LGN, V1). This suggests that the after-effects reported by these studies and the duration after-effect result from distinct mechanisms located at different stages of visual processing. This however raises the question of why distinct mechanisms exist. One answer to this question is to assume a hierarchical structure to the processing of duration (Heron et al., 2013; Van Wassenhove, 2009). Models proposing such a structure focus on the idea that temporal information is intrinsically present in any sensory signal (Buonomano, 2000; Buonomano & Maass, 2009; Karmarkar & Buonomano, 2007; Van Wassenhove, 2009). These patterns of different states of the network can then be extracted to form a more explicit duration code (e.g. via channel based encoding) so that it can be integrated across the senses. The resulting multimodal representation can then be stored and interact with other information to inform subsequent behavior. Assuming that the different after-effects reflect different hierarchical steps in duration processing could explain the observed differences in spatial selectivity of these after-effects. We would suggest that adaptation to temporal frequency and non-temporal factors occurs earlier in duration processing by causing modulations in the states of the network. The duration selective mechanisms then act upon these (modulated) states to explicitly encode duration. In other words, the different after-effects might not reflect the existence of distinct mechanisms that independently encode duration, but distinct steps in the hierarchical processing of duration.

The observed lack of spatial selectivity for the duration after-effect raises several questions about the selection and simultaneous processing of multiple events with different durations. During natural situations many different events can occur at once leading to an overlap in the durations of different events. However, if duration information from multiple sources cannot be dissociated based on their spatial location, it is unclear how the duration processing mechanisms deal with the presentation of multiple durations. One possibility is that attentional selection plays a role in the processing of multiple durations. A study by Cheng, Yang, Han, Ding, and Fan (2014) showed that human observers are able to process up to four multiple durations at once. Furthermore, duration tracking performance dropped steadily when attention had to be spread over a larger amount of different duration stimuli. This suggests that the processing of duration information from multiple sources relies on attentional selection to bind duration information to specific objects or spatial locations.

To summarize, we found a clear duration after-effect at all measured adapter-test distances. There was no evidence for a decrease in the magnitude of the duration after-effect at larger visual distances or across hemifields. We conclude that the duration after-effect does not result from adaptation occurring early on in the visual processing hierarchy. Instead, it seems likely that duration information is a high-level stimulus property that is encoded later on in the visual processing hierarchy.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.visres.2016.11.003>.

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