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# 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.

## 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; Bueti & 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, Grabowecky & 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.