

# Visual Feature Processing in the Early Visual Cortex Affects Duration Perception

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Event timing engages a distributed neural network including cortical and subcortical structures. However, it remains unclear whether the early visual cortex contributes to event timing. Here we showed that the processes of nontemporal visual features such as orientation and spatial location, which are coded by the early visual cortex, contribute to the temporal representation of a visual stimulus. Participants were presented with 2 successive Gabor patches (a prime and a target) with different orientations or spatial locations. The subjective duration of the target was significantly reduced when it was preceded by the prime compared with when presented alone. More important, this duration-compression effect varied systematically as a function of orientation similarity or spatial proximity between the prime and the target and was influenced by how the prime and the target were perceptually grouped. Our results suggest that repetition suppression of neural activity in response to orientation may contribute to the observed duration distortion and that neurons in the early visual cortex with small receptive fields and orientation selectivity may be involved in visual temporal perception. Our findings help to understand the functional role of early visual cortex in event timing in humans.

**Keywords:** temporal perception, visual cortex, orientation, spatial proximity, perceptual grouping

When an event is presented briefly for several hundred milliseconds, it seems to last for a certain time. Such duration perception in the subsecond range is critical for timing events in daily life and has been the focus of studies of human timing mechanisms. As temporal information is an essential parameter in human perception, cognition, and movement, its underlying mechanisms have been studied extensively in psychology and cognitive neuroscience (Buhusi & Meck, 2005; Pöppel, 1997). Recent research has shown that a neural network including the cerebellum, basal ganglia, and frontal and parietal cortices is involved in event timing (Coull, Vidal, Nazarian, & Macar, 2004; Jahanshahi, Jones, Dirnberger, & Frith, 2006; Lewis & Miall, 2003). It has also been hypothesized that modality-specific clocks located in the respective sensory

cortices are involved in subjective temporal processing (Buetti, Lasaponara, Cercignani, & Macaluso, 2012; Ivry & Schlerf, 2008).

In agreement with this latter hypothesis, it has been shown that the apparent duration of a moving stimulus is overestimated and that the temporal dilation increases with the velocity (Kaneko & Murakami, 2009). The perceived durations of visual events are also modulated by local motion adaptation (Ayhan, Bruno, Nishida, & Johnston, 2009; Johnston, Arnold, & Nishida, 2006), and the effect is attuned to retinotopic spatial location and cannot be transferred between eyes (Bruno, Ayhan, & Johnston, 2010; but see Burr, Tozzi, & Morrone, 2007). In addition to the distortion effect caused by the temporal dynamics of events, nontemporal features, such as size and luminance, also modulate the subjective duration of a visual target (Matthews, Stewart, & Wearden, 2011; Xuan, Zhang, He, & Chen, 2007). The mechanism underlying these effects has been argued to be the efficiency of neural encoding, which supports duration representation (Eagleman & Pariyadath, 2009). Consistent with this hypothesis, stronger neural responses in the ventral visual areas are associated with longer subjective durations of visual stimuli (Noguchi & Kakigi, 2006). Although these findings suggest that the visual cortex may be involved in duration perception, there has been no direct evidence for the association between duration perception and features of visual stimuli that are specifically encoded by neurons in the early visual cortex.

Neurons in the early visual cortex are characterized by small receptive fields restricted to specific locations (Hirsch & Martinez, 2006; Kastner et al., 2001; Smith, Singh, Williams, & Greenlee, 2001) within which neural responses are selective to stimulus orientation (Boynton & Finney, 2003; Fang, Murray, Kersten, & He, 2005; Hubel & Wiesel, 1998; Nelson, 1991). Recent studies have reported that the duration of an oddball in a sequence of

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repeated stimuli is subjectively dilated, and the distortion effect increases with the orientation difference between the oddball and repeated stimuli (Pariyadath & Eagleman, 2012; Schindel, Rowlands, & Arnold, 2011). This finding indicates the contribution of orientation processing to duration perception but cannot rule out effects of cognitively engaging processes, such as prediction-error monitoring. In a sequence of stimuli following certain rules, the temporal regularity is automatically detected to predict the forthcoming stimuli (Bendixen, Roeber, & Schröger, 2007; Kimura, 2012). The occurrence of an oddball stimulus (Pariyadath & Eagleman, 2007, 2012; Schindel et al., 2011) thus causes a violation of the regularity prediction, which by itself may affect the perceived duration of the oddball. The prediction process may also modulate neural responses elicited by the oddball (Pariyadath & Eagleman, 2007, 2012). Thus it remains unclear where such modulation occurs in the visual processing pathway and how it interacts with duration computation. To examine the contributions of the early visual cortex to time perception, a task design should be largely independent of cognitively engaging processes and measure the effect of visual features specifically encoded by neurons in the early visual cortex. Because neurons in the early visual cortex code specific orientations of stimuli presented at specific locations, it may be inferred that these neurons contribute to temporal perception if the subjective duration of a stimulus in a sequence of repeated stimuli is affected by the orientation and spatial position of preceding stimuli.

In this regard, we used a paradigm that presented a pair of stimuli and measured the subjective duration of the second stimulus as a function of the difference in orientation and spatial distance between the two stimuli. By limiting the number of stimuli in a series, the automatic generation of sequence regularity can be largely avoided (Bendixen et al., 2007; Horváth, Czigler, Sussman, & Winkler, 2001; Winkler, Karmos, & Näätänen, 1996), and the influence of predictability on the observed duration effect can thereby be reduced. Using a similar setup, previous studies reported a distorted subjective duration in a pair of stimuli, leading to time-order errors when the interstimulus interval (ISI) is brief (Jamieson & Petrusic, 1975; Zhou, Qin, Mao, Han, & Pöppel, 2010). Duration perception of a stimulus is not only modulated by its immediate vicinity but also sensitive to a global temporal context (Jazayeri & Shadlen, 2010). Perceptual grouping, an important contextual factor, substantially alters the perceived length of intervals between and within perceptual groups (Thorpe, Trehub, Morrongiello, & Bull, 1988; Thorpe & Trehub, 1989). In the visual domain, perceptual grouping has been reported to occur in both spatial and temporal dimensions (Han, Humphreys, & Chen, 1999; Han, Song, Ding, Yund, & Woods, 2001; Otto, Ögmen, & Herzog, 2009; Spinozzi, De Lillo, Truppa, & Castorina, 2009) and to modulate neural responses in the early visual cortex (Han et al., 2001; Nelson, 1991; Sugita, 1999). When two stimuli are presented successively, their feature similarity or spatial proximity leads to suppressed neural responses to the second stimulus (Nelson, 1991). Furthermore, proximity dominates similarity in assembling parts into global structures (Han, 2004; Han et al., 1999; Han, Jiang, Mao, Humphreys, & Gu, 2005; Han, Jiang, Mao, Humphreys, & Qin, 2005; Spinozzi et al., 2009). On the basis of these findings, we further assessed whether perceptual grouping of two successive stimuli produces stronger effects on subjective

duration of the second stimulus when the grouping is dominated by spatial proximity compared with feature similarity.

## Experiment 1

Previous studies have repeatedly demonstrated duration compression, that is, repeated exposure to a visual stimulus leads to a shortened perceived duration of its presence (Matthews, 2011; Pariyadath & Eagleman, 2007, 2012). These behavioral results establish a relationship between subjective duration and neural responses (*repetition suppression*; Eagleman & Pariyadath, 2009). Most experiments in this regard used a train of stimuli (Eagleman & Pariyadath, 2009; Pariyadath & Eagleman, 2007, 2012; Rose & Summers, 1995; Schindel et al., 2011), where regularity extraction and stimulus predictability may also participate in temporal computation. Other studies used photographs (Matthews, 2011) or geometric figures (Noguchi & Kakigi, 2006), which may cause repetition suppression among multiple processes in different brain regions. Furthermore, in these experiments, the duration of the target was compared with the duration of a stimulus immediately preceding or following the target. Results obtained using such paradigms are difficult to interpret because durations of both stimuli are likely to be distorted by the sequential presentation with a brief ISI (Hellström & Rammsayer, 2004; Jamieson & Petrusic, 1975). For example, in the setup of paired stimuli (Matthews, 2011), it is unclear whether the first or the second stimulus undergoes duration distortion and whether the distortion of comparison stimulus is equal across conditions. To overcome this uncertainty, we developed a paradigm in which the duration of the target was estimated by a comparison stimulus in the opposite visual hemifield (Zhou et al., 2010). The ISI between the target and the comparison was longer than 1,000 ms. The mutual influences between successively presented stimuli diminish when the ISI increases (Jamieson & Petrusic, 1975; Hellström & Rammsayer, 2004), and an ISI longer than 1,000 ms can eliminate the compression effect in duration judgment (Zhou et al., 2010, Experiment 4). Therefore, presenting the comparison 1,000 ms before or after the target may keep the apparent duration of the comparison relatively consistent in different conditions, providing a measure in which differences between conditions are mainly attributed to distortions of target duration.

In Experiment 1, we used the paradigm applied in our previous work (Zhou et al., 2010) to estimate the apparent duration of the target by a spatially and temporally dissociated comparison stimulus. We examined whether a prime stimulus preceding the target compresses the perceived duration of the target independently of their orientation differences. It has been well established that repeated presentation of stimuli causes repetition suppression of neural responses (Grill-Spector, Henson, & Martin, 2006). In the case of oriented stimuli, such neural activity suppression acts as a function of the orientation difference between stimuli, being stronger for stimuli with more similar orientations (Nelson, 1991). Considering that the magnitude of neural activities in response to a stimulus serves as a predictor of the perceived duration (Matthews, 2011; Pariyadath & Eagleman, 2007, 2012), we manipulated the orientation differences between the prime and the target and predicted that their orientation similarity modulates the apparent duration of the target. Because the orientation selectivity is encoded by neurons in the early visual regions (Hubel & Wiesel,

1998; Nelson, 1991), our design allowed us to estimate the stages of neural processes engaged in the duration perception.

In Experiment 1A, we manipulated the orientation difference between the prime and the target by 45° or 90° to test our hypothesis. Experiment 1A also served as a basis to estimate the sample sizes for the following experiments. The interested effect size in Experiment 1A reached 0.75 in *t* tests (see the Results and Discussion section), which, according to Cohen's convention (Cohen, 1988, 1992), is between a medium and a large effect. We thus conducted a priori power analyses (Faul, Erdfelder, Lang, & Buchner, 2007) on repeated measures analyses of variance (ANOVAs) with expected effect size of 0.3 (medium to large; Cohen, 1988, 1992) for the following experiments. A sample size of 16 would result in sufficient power (>0.8) and was thus used in each of the successive experiments. Experiment 1B further investigated the relationship between the subjective duration and the orientation processing by systematically varying the orientation difference between the prime and the target. The orientation selectivity of neurons in the early visual cortex shows a "Mexican-hat" tuning curve (Ferster & Miller, 2000; Moore, Alitto, & Usrey, 2005). If the timing system uses signals from neurons selective for stimulus orientations to compute the duration information, it is likely that the duration effect also follows a Mexican-hat-like profile. Systematically manipulating orientation differences also enables us to investigate whether the orientation-based duration effect is a generic phenomenon or specific to certain orientations (e.g., horizontal or vertical orientations).

## Method

**Participants.** Sixteen healthy university students participated in Experiment 1A (eight women and eight men;  $M_{\text{age}} = 24.63$  years,  $SD_{\text{age}} = 3.34$  years) and another 16 (seven women and nine men;  $M_{\text{age}} = 22.94$  years,  $SD_{\text{age}} = 2.02$  years) in Experiment 1B. All participants were paid volunteers and had normal or corrected-to-normal vision. They were naive about the purpose of the study and gave written informed consent prior to their participation.

**Stimuli and procedure.** Stimulus presentation and data collection were controlled by a PC running Matlab 7.1 and Psychophysics Toolbox extensions (Brainard, 1997). Stimuli were presented on a CRT monitor (ViewSonic Professional Series P97f+) with a refresh rate of 75 Hz and a gray background (7.7 cd/m<sup>2</sup>). Each trial began with the presentation of a fixation cross (0.3° × 0.3°, 44.6 cd/m<sup>2</sup>), which stayed on the screen throughout the trial. After a variable interval of between 800 and 1,000 ms, two randomly ordered stimulus periods separated by an interval of 1,200–1,600 ms were presented. In each period, a prime–target pair or a comparison stimulus was shown on the screen. The prime, the target, and the comparison were all Gabor patches with a fixed size (1.6° × 1.6° in Experiment 1A and 2.0° × 2.0° in Experiment 1B), spatial frequency (2.5 c/deg in Experiment 1A and 2.0 c/deg in Experiment 1B), standard deviation of the spatial Gaussian window (0.27° in Experiment 1A and 0.33° in Experiment 1B), and contrast (100% with a mean luminance of 7.7 cd/m<sup>2</sup>). Being presented randomly to the left or right of the fixation at the eccentricity of 5°, the prime and the target were displayed at the same position, while the comparison appeared at the mirror position in the opposite hemifield (see Figure 1A). The prime (107 ms) always preceded the target (307 ms) with an ISI of 187 ms. The

duration of the comparison varied among 120, 200, 267, 307, 347, 400, or 480 ms in Experiment 1A. In Experiment 1B, a modified QUEST adaptive procedure (Watson & Pelli, 1983) determined the duration of the comparison in each trial using information accumulated from preceding trials. At the end of each trial, participants were required to make a two-alternative forced-choice response to judge which, the target or the comparison, appeared longer by pressing the left or right button to indicate its position.

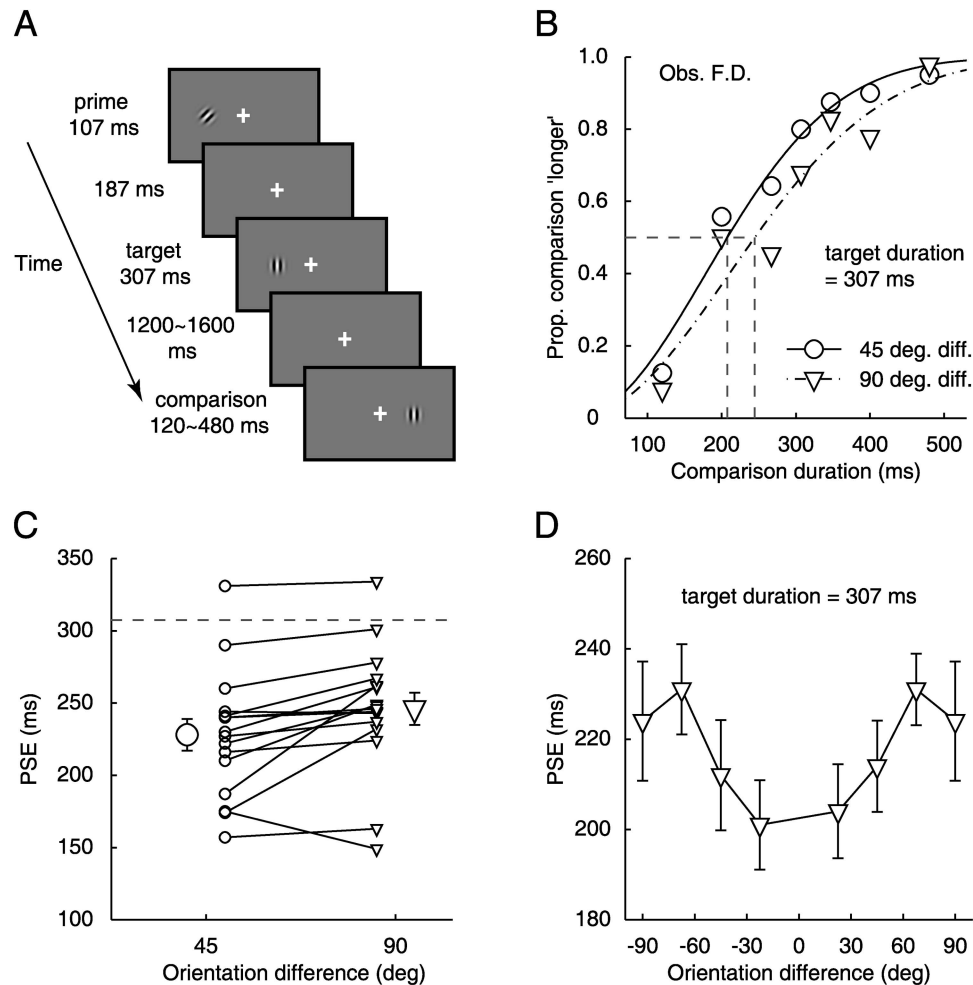
In Experiment 1A, the orientation of the prime differed from that of the target by 45° in half of the trials and by 90° in the other half. The direction of orientation difference was either clockwise or counterclockwise. The comparison was identical to the target, and its orientation was either horizontal or vertical. In Experiment 1B, a parametric assessment of the duration effect was designed in which the prime was tilted relative to the target by 22.5°, 45°, 67.5°, or 90°. Orientations of the target and the comparison were vertical.

Trials with different combinations of the prime, the target, and the comparison were randomly interspersed in one block. After one to two blocks of practice trials, participants performed 10 blocks of 56 trials in both experiments. Five participants in Experiment 1B repeated the task several times on different days, whereas the remaining participants in both experiments performed the task only once.

**Data analysis.** Behavioral data were initially analyzed in each condition to estimate the point of subjective equality (PSE) at which the observer perceives equal durations of the comparison and the target. In Experiment 1A, the percentages of judging the comparison to be of longer duration than the target were fitted with a Weibull function (Zhou et al., 2010). PSEs were then calculated from the sigmoid function at the point of 50% performance. In Experiment 1B, the PSE of each condition was estimated with a modified QUEST adaptive procedure with a 50% performance criterion for a 40-trial run (Watson & Pelli, 1983). The results of multiple QUEST runs were averaged to get a final estimate of the PSE in each condition for each participant. Statistical analysis was focused on estimated PSEs using repeated-measures ANOVAs and *t* tests. The Greenhouse–Geisser procedure was used to correct the degree of freedom whenever the sphericity assumption was violated for within-subject comparisons. The calculated probability *p* value was adjusted using Bonferroni correction for multiple comparisons.

## Results and Discussion

Experiment 1A demonstrated that the percentage of the comparison stimulus (vs. the target stimulus) being of a longer subjective duration increased with the comparison duration, showing a monotonous trend that can be fitted by a Weibull function (see Figure 1B for an example). It is interesting that the psychometric curve for a 45° orientation difference between the prime and the target shifted to the left of the curve for a 90° difference, suggesting that the duration of the target tended to be judged shorter in the 45° relative to 90° conditions. To statistically confirm these effects, we entered the estimated PSEs of targets in a series of *t* tests. Consistent with our previous findings (Zhou et al., 2010), the target was judged to be briefer than its physical duration (307 ms) when a visible prime preceded it—in the 45° condition,  $t(15) = -7.19$ ,  $p < .001$ , Cohen's  $d = -1.8$ ; in the 90° condition,



**Figure 1.** A. Schematic illustration of the general experimental procedure. B. Performances of a typical observer (F.D.) and the fitted psychometric functions in Experiment 1A. Dashed lines indicate the durations of comparison stimuli at a performance of 0.5 (i.e., points of subjective equality, or PSEs). C. Mean and individual PSEs in Experiment 1A. The dashed line indicates the physical duration of the target (i.e., 307 ms). Error bars show 1 standard error of the mean. D. Mean PSEs in Experiment 1B. The negative degrees indicate a counterclockwise tilt of the prime relative to the target, whereas the positive degrees indicate a clockwise tilt. Error bars show 1 standard error of the mean. For the purpose of visualization, the data for 90° was reflected to have a symmetrical illustration at -90°. Prop. = proportion; deg. diff. = degree difference.

$t(15) = -5.46, p < .001$ , Cohen's  $d = -1.37$  (see Figure 1C)—indicating a significant duration-compression effect. The orientation difference between the prime and the target significantly modulated the perceived duration of the target; that is, the more similar in orientation the prime and the target were (45° vs. 90°), the briefer the target was perceived to be (228 vs. 246 ms),  $t(15) = -3.03, p = .025$ , Cohen's  $d = -0.75$ . This result suggests that the duration-compression effect was sensitive to the orientation similarity between consecutive stimuli with a brief ISI.

In the visual field, the sensitivity to vertical and horizontal orientations is much higher than that to oblique ones (Westheimer, 2003). It is possible that the stronger duration compression in the 45° (oblique) condition than in the 90° (vertical and horizontal) condition was a consequence of different sensitivities between orientations rather than different orientation similarities between

the prime and the target. In Experiment 1B, we varied the orientation of the prime systematically to investigate whether an obliquely oriented prime could modulate the apparent duration of the target on the basis of the orientation similarity between stimuli. As shown in Figure 1D, there was an inverted Mexican-hat profile of PSEs. The subjective duration of the target decreased, whereas the compression effect increased as a function of the orientation similarity between the prime and the target. Before applying the significance test of this trend, we first checked whether the compression effect depended on the direction of orientation difference using an ANOVA with direction (clockwise and counterclockwise) and orientation difference (22.5°, 45°, and 67.5°; data from the 90° condition were not included because the 90° condition did not distinguish between clockwise and counterclockwise directions) as within-subject variables. There was a significant main



effect of orientation difference,  $F(2, 30) = 14.97, p < .001, \eta_p^2 = .50$ . We thus pooled data from clockwise and counterclockwise directions and ran another ANOVA with the factor of orientation difference ( $22.5^\circ, 45^\circ, 67.5^\circ$ , and  $90^\circ$ ). Again, mean PSEs differed significantly among  $22.5^\circ, 45^\circ, 67.5^\circ$ , and  $90^\circ$  conditions,  $F(3, 45) = 5.91, p = .002, \eta_p^2 = .28$ , with a trend of linear increase,  $F(1, 15) = 8.89, p = .009, \eta_p^2 = .37$ . Post hoc  $t$  tests further indicated that PSEs in the  $67.5^\circ$  condition were significantly larger than those in  $22.5^\circ$  and  $45^\circ$  conditions: For  $67.5^\circ$  vs.  $22.5^\circ$ ,  $t(15) = 5.29, p < .001$ , Cohen's  $d = 1.32$ ; for  $67.5^\circ$  vs.  $45^\circ$ ,  $t(15) = 3.03, p = .05$ , Cohen's  $d = 0.76$ . Thus, the orientation-based duration effect also occurs in oblique orientations, and the primary factor determining the size of compression is the orientation difference between stimuli.

Taken together, the results of Experiment 1 indicate that participants tended to underestimate the duration of a visual stimulus when it was preceded by another stimulus with a similar orientation. The effect showed a tuning profile in accord with the orientation-tuning property of neurons in the early visual cortex (Ferster & Miller, 2000; Moore et al., 2005). This suggests that neurons in the early visual cortex contribute to the temporal processing of stimuli. However, because neurons in both primary and extrastriate areas are characterized by orientation selectivity (Boynton & Finney, 2003; Fang et al., 2005; Hubel & Wiesel, 1998), it remains unclear at which cortical stages the first wave of neural signals enter the cascade of duration computation. This was examined in Experiment 2.

## Experiment 2

Neurons in the early visual cortex selectively respond to stimuli presented in their receptive fields (Hirsch & Martinez, 2006; Kastner et al., 2001; Smith et al., 2001) within which neural responses are attuned to stimulus orientations (Hubel & Wiesel, 1998; Nelson, 1991). It is important to note that the sizes of receptive fields are not homogenous along the visual pathway. For neurons responding to stimuli at the eccentricity of  $\sim 5^\circ$ , the sizes of the receptive fields have been estimated to be less than  $2^\circ$  in the primary visual cortex V1, between  $2^\circ$  and  $4^\circ$  in the extrastriate cortex V2, and larger than  $4^\circ$  in the area V4 (Kastner et al., 2001; Smith et al., 2001). For an orientation-selective neuron in the early visual cortex, repetition suppression of responses occurs only when stimuli with similar orientations are presented successively in its receptive field (Nelson, 1991). If the duration compression reported in Experiment 1 was due to neural suppression in the early visual cortex, this effect may occur only when the prime and the target are presented in the same receptive field of a responding neuron. Thus, Experiment 2 assessed the spatial extent of duration compression to estimate the associated cortex in which neurons are involved in duration perception. If neurons in multiple cortical areas contribute to the timing process, the duration compression should vary as a function of the spatial separation of the prime and the target.

## Method

**Participants.** Sixteen university students (seven women and nine men;  $M_{\text{age}} = 24.19$  years,  $SD_{\text{age}} = 3.39$  years) participated in Experiment 2. They had normal or corrected-to-normal vision and

were naive about the purpose of the experiment. They gave written informed consent prior to the experiment and were paid for their cooperation after the experiment.

**Stimuli and procedure.** The stimulus presentation and the task were similar to those in Experiment 1B with the following exceptions. The orientation difference between the prime and the target was either  $22.5^\circ$  or  $67.5^\circ$ , whereas the spatial distance between them was varied among  $0^\circ, 1^\circ, 2^\circ$ , and  $4^\circ$ . The target was always on the horizontal meridian, and the prime was in the upper quadrant in half of the trials and in the lower quadrant in the remaining trials. Both the prime and the target appeared at an eccentricity of  $5^\circ$  in the same hemifield. Nine participants repeated the task three to four times on different days, and the remaining participants were tested only once.

## Results and Discussion

Similar to the results of Experiment 1, there were temporal compressions when the prime preceded the target. As predicted by the hypothesis that neurons in multiple cortical areas contribute to the duration representation, the compression effect varied as a function of the spatial distance between the prime and the target (see Figure 2): The closer the two stimuli, the larger the compression effect. Because primes were presented in upper and lower quadrants in different trials, we checked whether the stimulus quadrant affected the perceived duration using an ANOVA with factors of quadrant (upper and lower), orientation difference ( $22.5^\circ$  and  $67.5^\circ$ ), and spatial distance ( $1^\circ, 2^\circ$ , and  $4^\circ$ ;  $0^\circ$  was not included because it did not index the quadrant). Although the main effect of the quadrant was not significant,  $F(1, 15) = 0.15, p = .708, \eta_p^2 = .01$ , it interacted with spatial distance,  $F(2, 30) = 3.75, p = .035, \eta_p^2 = .20$ , showing a difference between upper and lower quadrants. We thus incorporated the quadrant information in the variable of spatial distance ( $-4^\circ, -2^\circ, -1^\circ, 0^\circ, 1^\circ, 2^\circ$ , and  $4^\circ$ ; negative signs indicate upper quadrants) and conducted an

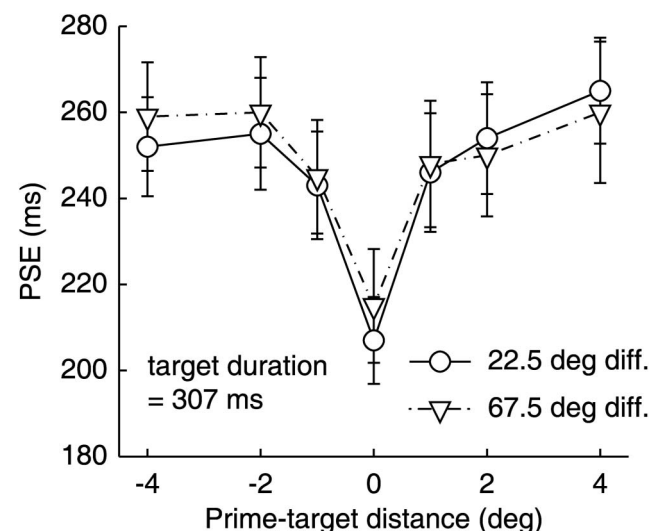


Figure 2. Mean points of subjective equality (PSEs) in Experiment 2. The negative prime-target distances indicate that the prime was in the upper quadrant, whereas the positive distances indicate the lower quadrant. Error bars show 1 standard error of the mean. deg diff. = degree difference.

ANOVA with another variable of orientation. The compression effect varied significantly among spatial distances,  $F(2.3, 34.0) = 11.96$ ,  $p < .001$ ,  $\eta_p^2 = .44$ , but not between orientation differences,  $F(1, 15) = 0.42$ ,  $p = .527$ ,  $\eta_p^2 = .03$ . Post hoc  $t$  tests revealed larger duration compressions when the prime and the target overlapped ( $0^\circ$ ) than spatially separated from each other,  $0^\circ$  versus  $-4^\circ$ ,  $t(15) = 4.48$ ,  $p = .009$ , Cohen's  $d = 1.12$ ;  $0^\circ$  versus  $-2^\circ$ ,  $t(15) = 6.74$ ,  $p < .001$ , Cohen's  $d = 1.69$ ;  $0^\circ$  versus  $-1^\circ$ ,  $t(15) = 4.77$ ,  $p = .005$ , Cohen's  $d = 1.19$ ;  $0^\circ$  versus  $1^\circ$ ,  $t(15) = 5.88$ ,  $p = .001$ , Cohen's  $d = 1.47$ ;  $0^\circ$  versus  $2^\circ$ ,  $t(15) = 5.31$ ,  $p = .002$ , Cohen's  $d = 1.33$ ;  $0^\circ$  versus  $4^\circ$ ,  $t(15) = 4.44$ ,  $p = .01$ , Cohen's  $d = 1.11$ . There were also significant differences between  $-2^\circ$  and  $-1^\circ$  conditions,  $t(15) = 5.81$ ,  $p = .001$ , Cohen's  $d = 1.45$ .

Our finding that spatially close stimuli produced a larger compression suggests that neural responses in the visual areas earlier than V4 contribute to the duration process. There was also temporal compression even when the spatial distance was as large as  $4^\circ$ , indicating that higher visual cortices characterized by large receptive fields and cortical regions processing memory and cognitive functions may also contribute to the perceived duration. This reflects the previous findings of positive time-order errors (Allan & Gibbon, 1994; Hellström, 1985), where the second relative to the first of paired stimuli is underestimated. In addition, the effects in the upper and lower quadrants appeared to be different, possibly reflecting the neurophysiological and functional specialization of the upper and lower visual fields (Previc, 1990). The orientation-based effect, however, failed to reach significance in Experiment 2. Unlike those in Experiment 1B, the prime and the target in Experiment 2 were different in both orientation and spatial location, which might attenuate the orientation-based effect. However, different participants took part in Experiments 1B and 2. Therefore, the absence of an orientation effect in Experiment 2 might also result from the sampling difference. Experiment 3 tested these possibilities by assessing the duration suppression in different prime-target contexts in a same sample of observers.

### Experiment 3

Different contexts of perceptual organization were adapted in Experiments 1B and 2. The relationship between the prime and the target was defined by their orientation similarity in Experiment 1B and by both spatial proximity and orientation similarity in Experiment 2. Because some grouping mechanisms (e.g., proximity) may dominate others (e.g., similarity) in perceptual organization (Han, 2004; Han, Jiang, Mao, Humphreys, & Gu, 2005; Han, Jiang, Mao, Humphreys, & Qin, 2005; Spinozzi et al., 2009), this change in contexts gave rise to different principles dominating the grouping process in Experiment 1B (orientation similarity) and Experiment 2 (spatial proximity). Given that activities in the early visual cortex are modulated by perceptual grouping (Han et al., 2001; Han, Jiang, Mao, Humphreys, & Gu, 2005; Han, Jiang, Mao, Humphreys, & Qin, 2005; Nelson, 1991; Sugita, 1999), such a contextual profile possibly reduced the effectiveness of orientation similarity on modulating the neural responses in Experiment 2. If the variation of neural responses in the early visual cortex rather than the inhomogeneity of observer samples led to the perceived durations in Experiments 1B and 2, we predicted that the context of perceptual organization modulates the perceived duration in a

way primarily determined by the dominant grouping mechanisms in a within-subject design.

### Method

**Participants.** Sixteen naive volunteers (11 women and five men;  $M_{\text{age}} = 21.69$  years,  $SD_{\text{age}} = 3.55$  years) with normal or corrected-to-normal vision were recruited. They gave written informed consent prior to the test and were paid for their participation.

**Stimuli and procedure.** There were two task sessions for each participant (see Figure 3A). In the ORIEN session with two blocks of 40 trials, the setting was similar to that in Experiment 1B, except that the orientation of the prime was either  $22.5^\circ$  or  $67.5^\circ$  different from that of the target. In the SPACE session with six blocks of 40 trials, the configuration was identical to that in Experiment 2, except that the prime was presented either at the

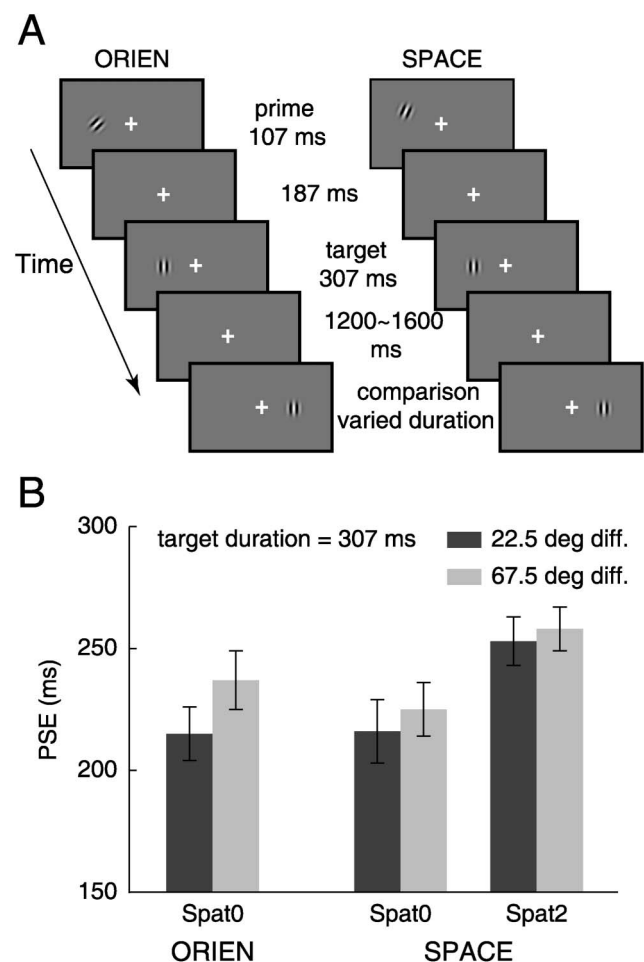


Figure 3. A. Schematic illustration of the experimental procedure in Experiment 3. ORIEN refers to the session in which the prime and the target were presented at the same location (Spat0); SPACE refers to the session in which the prime was presented either at the same location (Spat0) or at a location  $2^\circ$  away (Spat2) from the target. B. Mean points of subjective equality (PSEs) in Experiment 3. Error bars show 1 standard error of the mean. deg diff. = degree difference.

target position (Spat0) or at a position in the upper or lower quadrant 2° away from the target (Spat2). Participants repeated both sessions in a reversed order.

## Results and Discussion

We manipulated the dominant grouping principle with orientation similarity dominating in the ORIEN session and spatial proximity dominating in the SPACE session. An initial ANOVA with orientation difference (22.5° and 67.5°) and space context (Spat0 in ORIEN session, Spat0 in SPACE session, and Spat2 in SPACE session) as within-subject variables revealed significant effects of orientation difference,  $F(1, 15) = 20.09$ ,  $p < .001$ ,  $\eta_p^2 = .57$ , and space context,  $F(2, 30) = 28.71$ ,  $p < .001$ ,  $\eta_p^2 = .66$ , as well as their interaction,  $F(2, 30) = 4.37$ ,  $p = .022$ ,  $\eta_p^2 = .23$ . To examine whether the orientation-based effect differed between Spat0 in the ORIEN session and Spat0 in the SPACE session, which were physically identical but contextually different, we conducted another ANOVA with factors of orientation difference and context (Spat0 in ORIEN session and Spat0 in SPACE session). This revealed a significant effect of orientation difference,  $F(1, 15) = 15.67$ ,  $p = .001$ ,  $\eta_p^2 = .51$ , and a significant interaction between orientation difference and context,  $F(1, 15) = 8.17$ ,  $p = .012$ ,  $\eta_p^2 = .35$ . Post hoc  $t$  tests for both contexts showed a significant orientation-based duration compression in the Spat0 of ORIEN session ( $PSE_{67.5^\circ}$  vs.  $PSE_{22.5^\circ}$ : 237 ms vs. 215 ms),  $t(15) = 4.67$ ,  $p < .001$ , Cohen's  $d = 1.17$ , but not in the Spat0 of the SPACE session ( $PSE_{67.5^\circ}$  vs.  $PSE_{22.5^\circ}$ : 225 ms vs. 216 ms),  $t(15) = 2.10$ ,  $p = .05$ , Cohen's  $d = 0.53$ , although a trend of compression in the latter session can be observed. These results indicate that the task context modulates temporal perception.

There remains the possibility that the contextual effect is the result of spatial attention rather than the perceptual organization processes, because there was a tendency to shift the focus of attention from the prime to the target in the SPACE session but not in the ORIEN session because of the spatial dissociation between the prime and the target in the former but not in the latter (see Figure 3A). If this were the case, one would observe an overall change of duration compression in the Spat0 conditions between sessions regardless of the orientation difference. However, we found a significant contextual effect in 67.5° trials,  $t(15) = 2.62$ ,  $p = .038$ , Cohen's  $d = 0.66$ , but not in 22.5° trials,  $t(15) = 0.27$ ,  $p > .99$ , Cohen's  $d = 0.07$  (cf. the Spat0 conditions in Figure 3B). This indicates that the spatial attention did not play a key role in determining the duration pattern. The duration compression was probably dominated by spatial proximity, and the orientation effect was weakened when both the orientation and the spatial location differed between the prime and the target.

## General Discussion

In the current study, we investigated whether the processes of a nontemporal visual feature mediated by the early visual cortex contribute to the temporal representation of a visual stimulus. We found evidence that orientation similarity (Experiment 1) and spatial proximity (Experiment 2) between the prime and the target significantly influenced the perceived duration of the target. Specifically, increasing the orientation similarity or decreasing the spatial distance significantly reduced the perceived duration of the

target. We also found that the compression effect depended on task contexts because the orientation-based duration compression was significantly attenuated when spatial proximity dominated orientation similarity in grouping the prime and the target (Experiment 3). This contextual effect, independent of the physical properties of the stimulus and retinal processes, cannot be fully explained by a spatial attention shift and highlights the effect of perceptual organization on the subjective perception of time.

Our findings provide new evidence for the involvement of the early cortical areas in the computation of apparent duration of a visual stimulus. The duration compression was not only attuned to orientation differences between the prime and the target but also sensitive to the spatial distance between them. In some cases, a spatial separation as small as 1° dramatically changed the perceived duration of the target (Experiment 2). This finding suggests that area V1, in which neurons are orientation selective in receptive fields smaller than 1° (Kastner et al., 2001; Nelson, 1991; Smith et al., 2001), may play a role in time perception. To our knowledge, this is the first evidence that timing processes engage neurons that code nontemporal features that characterize the receptive field property of cells in the early visual cortex. Previous studies also found duration distortions when stimuli with certain visual features repeat (Matthews, 2011; Noguchi & Kakigi, 2006; Pariyadath & Eagleman, 2007, 2012). However, these studies did not distinguish between contributions of basic-feature encoding and high-level processes, which are cognitively engaging and have a neural locus beyond V1. For example, in an oddball paradigm with a train of visual stimuli (Pariyadath & Eagleman, 2007, 2012; Schindel et al., 2011), the sequence regularity is automatically extracted to predict the forthcoming stimuli (Horváth et al., 2001), and the duration effect may largely depend on the discrepancy between expected and actual inputs rather than on low-level neural responses (Schindel et al., 2011). Such predictive coding requires a series of multiple stimuli from which the sequence regularity is drawn (Bendixen et al., 2007; Horváth et al., 2001; Winkler et al., 1996) and is negligible when only one stimulus precedes the target (Pariyadath & Eagleman, 2012). By limiting the stimulus sequence to a prime–target pair, we were able to control the prediction effect caused by sequence regularities to a certain degree in the current study. It is worthy to note that targets were still predictable when the task used only pairs of primes and targets. However, targets occurred with equal probability following the presentation of different primes and there seemed to be no a priori reason for an observer to favor one condition over the others. Thus the prediction based on task contexts would have similar effects in different conditions and was unlikely to explain the results in the current study. We also used Gabor patches, which optimally activate orientation-selective neurons with small receptive fields to explore the contribution of the early visual cortex to subjective time, which is difficult to examine in studies using complex natural images and geometric figures (Matthews, 2011; Noguchi & Kakigi, 2006). Some previous work also found spatially attuned temporal distortion and localized the neural substrate at an early stage (V1) of the visual pathway (Ayhan et al., 2009; Bruno et al., 2010). However, these studies adapted stimuli to temporal frequencies, and changes in temporal dynamics of neurons are probably responsible for the time illusion (Ayhan et al., 2009; Johnston et al., 2006). Considering that orientation tuning is invariant to the temporal dynamics of neural responses (Moore et al., 2005), the effects observed in



our and previous studies were possibly mediated by different neural substrates. Therefore, our findings indicate that neurons in V1 that are thought to encode nontemporal features of stimuli may, nevertheless, contribute to subjective timing.

Although we did not directly measure the neural responses evoked by the target, the current data suggest that the repetition suppression of neural activities probably underlies the compression of perceived duration in a similar framework outlined by other studies (Eagleman & Pariyadath, 2009; Matthews, 2011; Noguchi & Kakigi, 2006; Pariyadath & Eagleman, 2012). Spatially adjacent stimuli with similar orientations activate common neuron populations in the visual pathway (Fang et al., 2005; Ferster & Miller, 2000; Nelson, 1991), and rapid neural adaptation occurs when visual stimuli are presented successively with a brief ISI (Glasser, Tsui, Pack, & Tadin, 2011; Müller, Metha, Krauskopf, & Lennie, 1999; Nelson, 1991). As a result, a prime that is similar to a target in orientation and spatial position causes strong adaptation in the neural responses to the target, and the decreased neural responses to the target may lead to reduced subjective duration of the target. Thus, it is likely that the response magnitude of visual neurons provides a signal of the duration of a stimulus. This hypothesis is further supported by a contextual modulation of subjective duration in which the perceptual organization plays a crucial role. Previous studies have established that perceptual grouping modulates neural responses in the early visual cortex (Han et al., 2001; Han, Jiang, Mao, Humphreys, & Gu, 2005; Han, Jiang, Mao, Humphreys, & Qin, 2005; Nelson, 1991; Sugita, 1999). Depending on its relative strength (Han, 2004; Han, Jiang, Mao, Humphreys, & Gu, 2005; Han, Jiang, Mao, Humphreys, & Qin, 2005; Spinozzi et al., 2009), the effect of grouping by orientation similarity decreases when a concurrent grouping by spatial proximity exists in the context. Correspondingly, the orientation-based duration compression was attenuated (Experiment 3), suggesting that the subjective time is contingent on the perceptual organization of a prime and a target and is associated with neural responses that are modulated by grouping processes.

The behavioral results reported in our study do not indicate where the final registration of temporal information is accomplished (Buhusi & Meck, 2005; Ivry & Schlerf, 2008). Responses in the early visual cortex may directly compute subjective time, and the perceived duration depends on the quality (e.g., signal-to-noise ratio) of local signals. It is scarcely less likely that clock ticks occur in specified neural structures, such as basal ganglia and supplementary motor areas, which receive inputs from the early visual cortex, and the subjective time is determined by the number of signals communicated between cortical regions. These can be tested in future research.

Recent findings propose a Bayesian explanation of time perception (Jazayeri & Shadlen, 2010), stating that the perceived interval is biased toward the mean of sample intervals in a given context. However, Bayesian mechanisms seem to play a minor, if any, role in shaping the contextual effect in the current study. In Experiment 3, adding spatially dissociated primes led to a higher proportion of long-perceived durations in the SPACE session compared with the ORIEN session. In the context of a Bayesian process (Jazayeri & Shadlen, 2010), this change in subjective duration distribution would shift the PSEs of the Spat0 conditions in the SPACE session toward longer values (vs. those in the ORIEN session). However, the PSEs did not vary with session for the 22.5° condition and

actually decreased from the ORIEN session to the SPACE session for the 67.5° condition (see Figure 3B). This is apparently inconsistent with the prediction of the Bayesian mechanisms. Thus, our results are better explained by a change in dominant grouping mechanisms in which the grouping process based on orientation similarity is attenuated and thus leads to a reduced compression effect associated with orientation difference. Nevertheless, the Bayesian mechanisms may interact with the perceptual grouping processes at certain levels. Such interaction, however, is probably a consequence rather than a cause of the subjective time contingent on perceptual organization.

Our findings have several important implications to studies of multiple level neural and cognitive processes. First, the paradigm developed in our work provides a simple and efficient way to examine the neural properties of the early visual areas, including V1 and V2. This method does not require complex neurophysiological recordings and traditional adaptation procedures. The tuning profiles of neurons estimated by this subjective-time method are comparable to those in previous studies (Ferster & Miller, 2000), indicating that it can be used as a tool to examine the neural responses related to perception and cognition. Second, temporal information is critical for high-level cognitive processes involved in decision making, prediction, and motor control (Buhusi & Meck, 2005). Our findings of the engagement of early visual processing in event timing raise an interesting issue, that is, whether and how early perceptual processes in the visual cortex produce effects on high-level cognitive process involved in decision making and prediction. Thus our study calls attention to the contribution of sensory and perceptual processing to high-level cognitive processes. Finally, event timing and orientation similarity seem to be very different domains in terms of processes and functional significance for daily life and previous research usually investigated them separately. Our findings provide an example of the interaction between two apparently different domains in human mental processes, which may be taken into consideration in future research on mechanisms involved in different task domains.

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