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The effect of retinal illuminance on visual motion priming

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ABSTRACT

The perceived direction of a directionally ambiguous stimulus is influenced by the moving direction of a preceding priming stimulus. Previous studies have shown that a brief priming stimulus induces positive motion priming, in which a subsequent directionally ambiguous stimulus is perceived to move in the same direction as the primer, while a longer priming stimulus induces negative priming, in which the following ambiguous stimulus is perceived to move in the opposite direction of the primer. The purpose of this study was to elucidate the underlying mechanism of motion priming by examining how retinal illuminance and velocity of the primer influences the perception of priming. Subjects judged the perceived direction of 180-deg phase-shifted (thus directionally ambiguous) sine-wave gratings displayed immediately after the offset of a primer stimulus. We found that perception of motion priming was greatly modulated by the retinal illuminance and velocity of the primer. Under low retinal illuminance, positive priming nearly disappeared even when the effective luminance contrast was equated between different conditions. Positive priming was prominent when the velocity of the primer was low, while only negative priming was observed when the velocity was high. These results suggest that the positive motion priming is induced by a higher-order mechanism that tracks prominent features of the visual stimulus, while a directionally selective motion mechanism induces negative motion priming.

1. Introduction

Perception of visual patterns is influenced by other visual inputs presented separately both in space and time. Since visual inputs are continuously provided, how the visual system integrates spatio-temporally separate information is one of fundamental questions in human vision. It has been reported that visual motion perception is influenced by temporally neighboring events. The perceived direction of a directionally ambiguous stimulus is greatly influenced by the moving direction of the preceding stimulus. Previous studies showed that a brief preceding stimulus induces "motion assimilation" or "positive motion priming", in which a following directionally ambiguous stimulus is perceived to move in the same direction as the preceding one (Anstis & Ramachandran, 1987; Campana, Pavan, & Casco, 2008; Jiang, Pantle, & Mark, 1998; Jiang, Luo, & Parasuraman, 2002; Kanai & Verstraten, 2005; Pantle, Gallogly, & Piehler, 2000; Pavan, Campana, Guerresch, Manassi, & Casco, 2009; Piehler & Pantle, 2001; Pinkus & Pantle, 1997; Ramachandran & Anstis, 1983; Raymond, O'Donnell, & Tipper, 1998).

Ramachandran and Anstis (1983) reported a phenomenon they named "visual inertia", in which the perception of a bi-stable long-range motion display is constrained by a pair of flashed priming dots (see also Anstis & Ramachandran, 1987). In their stimulus, four dots form an imaginary diamond in which the top and bottom dots are replaced by the right and left dots, which causes an impression of ambiguous motion. When two priming dots are flashed before the flash of the first dots, the perceived direction of motion is governed by the position of these priming dots. The perceived path from the first dot to the second dot is determined as if inertia is induced by the priming dots.

Pinkus and Pantle (1997) used a moving sine-wave grating and showed that visual inertia occurs with a periodic pattern. A successively presented directionally ambiguous test pattern made of a 180-deg shifted grating is perceived to move in the same direction as that of the priming grating when the presentation duration of the second frame of the primer is less than approximately 300 ms. They named this phenomenon "positive motion priming". Pantle et al. (2000) concluded that a primer of less than 100 ms induces positive motion priming. Kanai and Verstraten (2005) showed that a primer moving for 80 ms induces stronger positive priming than one moving for 160 ms. When the presentation duration of the primer is longer, a so-called "negative motion priming" (Pantle et al., 2000) or "rapid MAE" (Kanai & Verstraten, 2005) was observed, in which the perceived direction of directionally

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ambiguous test stimulus is reversed (see also Pavan et al., 2009). The main purpose of this study was to clarify how retinal illuminance influences the perception of visual motion priming, especially that of positive priming. However, as explained below, since positive and negative motion priming are observed antagonistically, speculation regarding the underlying mechanism of positive motion priming necessarily leads us to the consideration of negative priming.

Most previous studies of visual motion have been concerned with vision under photopic conditions, where the average luminance level is high enough to activate the cone system in the retina. Since luminance levels vary over a range as wide as 10^{11} in our daily lives (Hood & Finkelstein, 1986, chap. 5; Stockman & Sharpe, 2006), the visual system must also deal with motion information under mesopic and scotopic vision, where the rod system is active. An understanding of the characteristics of visual motion computation and perception under low retinal illuminance levels is therefore very important from both scientific and practical viewpoints (Hess, Sharpe, & Nordby, 1990).

Human visual motion perception changes as retinal illuminance decreases. Velocity perception (Gegenfurtner, Mayser, & Sharpe, 2000; Hammett, Champion, Thompson, & Morland, 2007; Vaziri-Paskham & Cavanagh, 2008), velocity discrimination thresholds (Takeuchi & De Valois, 2000), short-range motion perception (Dawson & Di Lollo, 1990), complex-motion perception (Billino, Bremmer, & Gegenfurtner, 2008), biological motion perception (Billino et al., 2008; Grossman & Blake, 1999), perception of static motion illusions (Hisakata & Murakami, 2008), perception of ISI-reversal (Sheliga, Chen, FitzGibbon, & Miles, 2006; Takeuchi & De Valois, 1997, 2009; Takeuchi, De Valois, & Motoyoshi, 2001), perception of two-stroke motion (Mather & Challinor, 2008), the coherent motion threshold (Billino et al., 2008; Lankheet, van Doorn, & van de Grind, 2002; van de Grind, Koenderink, & van Doorn, 2000), and moving texture segregation (Takeuchi, Yokosawa, & De Valois, 2004) have all been shown to vary with the retinal illuminance level.

In this study we measured the strength of visual motion priming under different retinal illuminance levels. Pinkus and Pantle (1997) proposed a model of positive motion priming. Their model consists of an Adelson and Bergen (1985) type motion-energy stage followed by a second, low-pass filter stage, which extends the motion-energy signal from the first stage in time. By this extension of an imbalanced motion-energy from the priming stimulus, the perceived direction of successively presented ambiguous stimuli can be restricted to that of the priming moving stimulus (see Fig. 2 of Pinkus & Pantle, 1997). In this model the amount of the decay of the low-pass filter is crucial. A longer decay period extends the effect of the preceding stimulus that induces positive priming. Though the physiological basis of the proposed filtering operation at the second-stage is unclear, this model is intuitively appealing since the assimilation-type effects of other visual attributes, such as color and space, is also explained by the low-pass characteristics of the visual system. For example, color assimilation is explained by low-pass characteristics of color-sensitive channels (e.g., De Valois & De Valois, 1988). A larger receptive field of motion-detecting mechanisms is shown to be responsible for the spatial motion assimilation induced by surround moving patterns (Murakami & Shimojo, 1996).

It is well known that the temporal response of the visual system becomes slower as retinal illuminance decreases (Burr & Morrone, 1993; Hess, 1990; Hess, Waugh, & Nordby, 1996; Kelly, 1971; Snowden, Hess, & Waugh, 1995; Swanson, Ueno, Smith, & Pokorny, 1987). For example, Swanson et al. (1987), using psychophysical measures, estimated the shape of the temporal impulse response function and showed that the peak of the function becomes increasingly delayed as the average luminance falls. Thus, the overall temporal characteristic becomes low-pass under low retinal illuminance.

If the assumed second-stage low-pass filtering operation by Pinkus and Pantle (1997) is responsible for positive motion priming, the strength of the positive priming effect should increase as retinal illuminance decreases. Though we do not know whether the hypothesized second-stage low-pass filter is governed by retinal illuminance, it is parsimonious to predict that the entire temporal characteristic becomes low-pass under low retinal illuminance. Even without assuming the second-stage low-pass filtering operation, there are neurophysiological data supporting our prediction. The effect of lowering retinal illuminance is known to temporally enlarge the integration area of receptive fields of neurons at the primary cortex (Peterson, Ohzawa, & Freeman, 2001; Ramoa, Freeman, & Macy, 1985). If more temporal information is integrated under low retinal illuminance, this could lead to a prediction similar to that made from the model by Pinkus and Pantle (1997).

We performed two experiments. In experiment 1, contrary to our prediction, we found that positive priming is almost disappeared under low retinal illuminance. From the second experiment, we found that the perception of motion priming highly depends on the retinal illuminance and the velocity of the priming stimulus.

2. Experiment 1

In experiment 1, we measured the strength of visual motion priming under different retinal illuminance levels. It has been reported that positive motion priming is prominent when the preceding stimulus is as short as 100 ms (Kanai & Verstraten, 2005; Pantle et al., 2000; Pinkus & Pantle, 1997). Our hypothesis is that the frequency of perceiving positive motion priming increases with longer durations of preceding stimulus presentation due to the low-pass characteristic of temporal vision under low retinal illuminance.

As described above, Pantle et al. (2000) observed both positive and negative priming depending on the presentation duration of the priming moving stimulus. Positive motion priming switched to negative motion priming when the priming moving stimulus was presented for around 200–300 ms, where the motion of the ambiguous test stimulus was perceived in the direction opposite to that of the priming stimulus. The duration of the priming stimulus that elicits negative motion priming is much shorter than the case of the motion aftereffect (MAE), where tens of seconds of adaptation to the preceding stimulus is needed to induce the illusory motion impression on the stationary test stimulus. Kanai and Verstraten (2005) referred to the negative motion priming induced by a very short primer as rapid MAE (rMAE). If the perceived frequency of positive motion priming increases under low retinal illuminance, the frequency of reports of negative priming should be reduced since these two effects have been observed in an antagonistic manner.

2.1. Apparatus

Stimuli were generated on a PC with a VSG 2/5 (Cambridge Research Systems) graphics system and displayed on a 21-in. RGB monitor (SONY GDM F520). The monitor frame rate was 100 Hz, with spatial resolution of 1024 × 768 pixels and 15-bit gray-level resolution. The monitor output was linearized (gamma corrected) under software control. For all experiments using luminance-varying stimuli, the space-averaged chromaticity (CIE 1931) of the display was $x = 0.31$, $y = 0.33$. Subjects observed the display through a 2-mm artificial pupil, with head position maintained by a chin rest