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Contrast dependency of saccadic compression and suppression

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Abstract

In the occurrence of a saccadic eye movement vision becomes suppressed. Supra-threshold visual stimuli that are briefly presented at that time become perceptually compressed towards the saccade target (saccadic compression) and shifted in saccade direction (saccadic shift). We show that the strength of saccadic compression, like the strength of saccadic suppression, varies with stimulus contrast. Low contrast stimuli lead to stronger compression than high contrast stimuli. The similarity of contrast dependence and time course suggests that saccadic compression is related to saccadic suppression. Because the saccadic shift did not depend on contrast we suggest that shift and compression are different effects.

1. Introduction

1.1. Saccadic mislocalization

A number of short-lived perceptual distortions are associated with the occurrence of saccades (Ross, Morrone, Goldberg, & Burr, 2001). One of them is a distortion of visual space. It was already described by von Helmholtz (1896) in the context of the cancellation theory and later studied in depth by Matin and Pearce (1965). They showed that objects which were briefly presented either immediately before, during or immediately after a saccade were perceived at illusory positions. These mislocalizations depend on the spatial position at which the test stimulus was flashed (see also Bischof & Kramer, 1968). Further studies (Bridgeman, Van der Heijden, & Velichkovsky, 1994; Matin, 1972) proposed a concept of an 'extraretinal position signal' (ERPS), which involves the afferent signal of the extra-

ocular muscles (Sherrington, 1918) as well as the efferent signal that drives the eye movement (Sperry, 1950; Von Holst & Mittelstaedt, 1950). Matin and coworkers suggested that the ERPS does not exactly correspond to the actual eye movement but is a more sluggish signal that has a different time course from the saccade. This concept was supported in further studies which suggested that the ERPS started about 100 ms before the saccade and lasted until 50 ms after the saccade (Dassonville, Schlag, & Schlag-Rey, 1992, 1995; Honda, 1989, 1991; Schlag & Schlag-Rey, 1995).

More recent investigations have suggested that the mislocalization errors can be generally divided into two types: The first is a shift along the saccade direction that effects all spatial positions similarly (Cai, Pouget, Schlag-Rey, & Schlag, 1997; Dassonville et al., 1995; Honda, 1989, 1991; Lappe, Awater, & Krekelberg, 2000; Miller, 1996). Objects presented before or during the early phase of the saccade are misperceived in the direction of the eye movement. Objects presented later during the saccade or shortly after the saccade are sometimes mislocalized against the direction of the eye movement. The shift can most clearly be observed when

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experiments are performed in complete darkness. In that case, the perceptual system can only use information that comes from the neuronal in- and outflow, i.e. the extraretinal position's signal. Therefore, it is believed that the shift reflects the time course of the sluggish ERPS. The shift starts about 100–200 ms before the onset of the saccade, peaks near saccade onset, reverse direction during the saccade and continues for up to 300 ms after the saccade.

1.2. Saccadic compression of visual space

The second mislocalization error is a compression of positions across the visual field towards the saccade target. In this case the magnitude and direction of the mislocalizations depend on the spatial position of the flashed object (Bischof & Kramer, 1968; Honda, 1995; MacKay, 1970; Matin & Pearce, 1965; Miller & Bockisch, 1997; O'Regan, 1984). Ross, Morrone, and Burr (1997) described that during rightward horizontal saccades, objects which were presented at a position left of the saccade target were perceived in the direction of the saccade whereas objects which were presented at a position right of the saccade target were mislocalized against the direction of the saccade. They called this pattern of mislocalization saccadic compression. This compression has since been confirmed by a number of studies (Honda, 1999; Lappe et al., 2000; Matsumiya & Uchikawa, 2001, 2003; Santoro, Burr, & Morrone, 2002; Sogo & Osaka, 2002). It occurs not only along saccade direction but also orthogonal to it (Kaiser & Lappe, 2004). Saccadic compression begins 100 ms before the eyes starts to move, peaks at saccade onset, and vanishes directly after the saccade. In comparison to the time course of the shift the time course of compression is thus more restricted in duration.

A compression of visual space cannot be explained by the substraction of a single reference signal of the saccade amplitude, such as the ERPS, because a substraction of the reference signal form the true eye position cannot simultaneously yield mislocalizations in different directions. The studies that have described compression were all performed in slightly illuminated rooms. Thus visual information is involved in the process of localization across saccadic eye movements, in addition to, or in replacement of, extraretinal signals. Lappe et al. (2000) found a dependence of perisaccadic mislocalization on the availability of visual spatial references directly after the saccade. They suggested that primarily postsaccadic visual information is used for the visual process of transsaccadic spatial localization of objects.

Morrone, Ross, and Burr (1997) presented a model to simulate the compression during saccades. The model based on two assumptions: (1) a shift in the assumed external reference point for the center of the fovea and

(2) retinal eccentricities are liable to a horizontal compression. These very coarse signals were sufficient to model their results.

1.3. Saccadic suppression

Another perceptual effect during saccadic eye movements is a reduction of visual sensitivity called saccadic suppression. The immediate and most striking demonstration of saccadic suppression is the fact that we do not perceive the massive motion signals that are induced by the shift of the image on the retina when the eye is moved in a saccade. But there is also a second, possibly related, effect on the perception of brief stimuli presented during a saccade. Dodge (1900) described saccadic suppression as an increase of the luminance threshold for the perception of flashed stimuli when they were presented during a saccade. More recent studies showed that the luminance threshold to detect an object is increased by about 0.6 log units near the time of a saccade (Bridgeman, Hendry, & Stark, 1975; Latour, 1962; Volkmann, 1962; Volkmann, Schick, & Riggs, 1968). Dodge (1900) proposed that there is no need for a central change in visual functions because image motion during saccades is too fast to be seen. Later studies supported this view (Campbell & Wurtz, 1978; Castet & Masson, 2000; MacKay, 1970; Matin, Clymer, & Matin, 1972) whereas others put it into question (Burr, Morrone, & Ross, 1994; Burr & Ross, 1982; Diamond, Ross, & Morrone, 2000). Investigations of contrast sensitivity during fixation demonstrated that if moved at saccadic speeds, gratings with high spatial frequencies (small features) become invisible while gratings with low spatial frequencies (large features) remain visible (Burr & Ross, 1982). A further restriction of saccadic suppression was demonstrated by comparing equiluminant (modulated only in color) and non-equiluminant (modulated in luminance) stimuli and a spatial frequency analysis of the presented stimuli (Bridgeman & Macknik, 1995; Burr et al., 1994). Burr et al. (1994) found a reduction of sensitivity only for non-equiluminant stimuli implying that saccadic suppression affects predominantly the magnocellular pathway which is concerned with the analysis of spatial representation and motion. Indeed saccadic suppression is especially strong for motion stimuli (Burr, Johnstone, & Ross, 1982; Ilg & Hoffmann, 1993; Shiori & Cavanagh, 1989). Burr et al. (1994) suggested that saccadic suppression reduces the perception of low-spatial frequency visual motion induced by saccades. Saccadic suppression is not restricted to just the time of the eye movement. It starts before the eye moves, has its maximum at saccade onset and disappears directly after the saccade is finished (Diamond et al., 2000). This temporal characteristics is very similar to that of saccadic compression and shift as described above.

1.4. Neural origin of saccadic suppression and compression

It has been proposed that decreasing the gain of cortical or lateral geniculate nucleus (LGN) cells could yield the observed reduction in sensitivity during saccades (Ross et al., 2001). Electrophysiological investigation of the effects of saccades on the activity of geniculate neurons both in cats and monkeys revealed controversial results however, documenting both suppression and facilitation effects (Bartlett, Doty, Lee, & Sakakura, 1976; Fischer, Schmidt, Stuphorn, & Hoffmann, 1996; Lee & Malpeli, 1998; Noda, 1975; Ramcharan, Gnadt, & Sherman, 2001). Similar divergent results have been obtained in cortical areas V1, V2, and V4 (Battaglini, Galletti, Aicardi, Squatrito, & Maioli, 1986, 1996; Leopold & Logothetis, 1998; Wurtz, 1969).

Thiele, Henning, Kubischik, and Hoffmann (2002) and Bremmer, Kubischik, Hoffmann, and Krekelberg (2002) described neuronal correlates of saccadic suppression in parietal cortical areas (Bremmer et al., 2002; Thiele et al., 2002). Thiele et al. compared responses in areas MT and MST when a rhesus monkey performed saccades over a structured background and when the background was moved at saccadic speeds during fixation. Some cells (25%) responded during simulated but not during real saccades. A second cell population (35%) showed a reversion of their preferred tuning direction during the saccade. The authors suggested that these reversed motion signals cancel out the motion signals coming from the non-reversing population and therefore lead to a reduced awareness of retinal motion which leads to suppression. Bremmer et al. (2002) compared responses in parietal areas, MT, MST, LIP and VIP to stimuli flashed during a saccade and during fixation. The results showed a reduced neuronal response in the saccade condition in motion sensitive areas MT, MST and VIP. The time course of this reduced neuronal activity was similar to the time course of the saccadic suppression in humans (e.g. Diamond et al., 2000).

As for suppression, the neural substrate of mislocalization is also debated. Some neurons in the lateral intraparietal area (LIP) area and a number of other areas anticipate the retinal consequences of an impending saccade by predictably responding to visual stimuli that will fall in their receptive field (RF) after the saccade is completed (Duhamel, Colby, & Goldberg, 1992; Goldberg, 1996; Nakamura & Colby, 2002; Walker, Fitzgibbon, & Goldberg, 1995). Such a presaccadic shift of the receptive fields could be used to maintain visual stability and may be related to perceptual mislocalizations before saccades. Kubischik and Bremmer (1999) have analyzed the response of neurons from LIP (and adjacent area VIP) to perisaccadically flashed stimuli.

Their results suggest that changes to the receptive fields in LIP may lead to perisaccadic compression effects in the population response.

Krekelberg, Kubischik, Hoffmann, and Bremmer (2003) investigated neuronal responses during saccades in areas MT and MST and suggest a different origin for perisaccadic distortion of perceptual space. They calculated the neuronal response to flashed stimuli in a defined time window after stimulus onset. From these responses they estimated the conditional probability for each neuron to encode, with a particular firing rate, the presentation of a flashed bar at a particular positions. They created a Bayesian lookup table linking firing rates to stimulated positions called a codebook. By using this codebook the retinal position could be faithfully retrieved from the population activity in MT and MST. However, analysis of responses of the same neurons just prior to a saccade led to large mislocalization errors in the encoding. Krekelberg et al. suggest that perisaccadically the neuronal response do not represent a reliable signal for visual space. In this view, the mislocalization arises because response rates during a saccade are different from response rates during fixation. If saccadic suppression would be responsible for the response rate difference it could be linked to compression.

1.5. Specific objectives of the study

It has been shown that saccadic compression and saccadic suppression possess similar time courses during saccadic eye movements (Diamond et al., 2000). Saccadic suppression can be understood as a reduction of visual sensitivity during saccades. It depends mainly on contrast and spatial frequency. Therefore saccadic suppression may change also the perceived contrast of stimuli presented at the time of the saccade. At the neuronal level, saccadic suppression correlates with a suppression of responses to flashed stimuli in MT/MST (Bremmer et al., 2002). On the other hand, changing firing rates in MT/MST correlate with mislocalizations (Krekelberg et al., 2003). Taken together these findings suggest that if saccadic compression is related to suppression it should also depend on contrast. To test this we measured saccadic compression and suppression as a function of contrast in a psychophysical experiment.

2. Methods

2.1. Observers

Three subjects (two male, one female, 24–39 years old) participated in the experiment. All subjects had normal vision and were experienced in psychophysical investigations. One subject was co-author, the other

two subjects were naive with respect to the purpose of the experiment.

2.2. Stimuli

Visual stimuli were generated on a 19 in. Monitor (Samtron 95P plus) with a visible screen-area of 36.6 cm×27.5 cm, subtending 51.6°×38.7° from a viewing distance of 40 cm. Images had a resolution of 800×600 pixel and were presented with a frame rate of 85 Hz. Stimuli consisted of light bars presented on a grey background (13 $cd m^{-2}$). The luminances of the bars were: 14.3 $cd m^{-2}$, 15.3 $cd m^{-2}$, 17.4 $cd m^{-2}$, 21.6 $cd m^{-2}$ and 61.3 $cd m^{-2}$ resulting in contrasts of 0.05, 0.08, 0.14, 0.25 and 0.65. Experiments were performed in a room with luminance below 0.1 $cd m^{-2}$. A black horizontal line (ruler) with vertical tick marks was present on the screen image throughout the experiment. One of the tick marks of the ruler fell on the fixation point, another on the saccade target (see Fig. 1).

2.3. Procedure

Each trial started with a fixation point (0.3°×0.3°) that appeared 10° left of the screen center. After a ran-
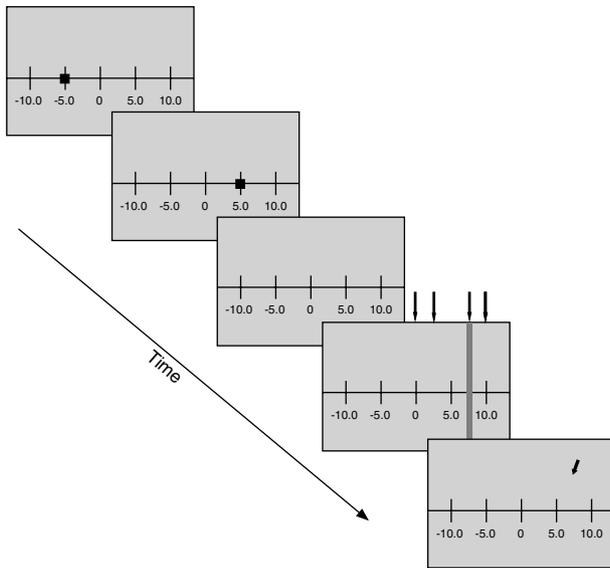

Fig. 1. Schematic drawing of the experimental setup. The fixation point (black square at 10° left from screen center) vanished after a randomized time between 0.5 and 1.5 and the saccade target appeared for 50 ms (black square at 10° to the right of the screen center). After a random time between 50 and 300 ms after target onset a bar was presented for one frame (12 ms). The four arrows in the drawing indicate the possible bar locations at −0.4°, 5.9°, 14.9°, 20.4° from the screen center. Five hundred milliseconds after the bar presentation a mouse pointer appeared at a randomly position on the screen. Subjects used this pointer to report the apparent position of the bar. They were instructed to position the pointer at a predefined region if they failed to perceive the bar.

domized time between 0.5 and 1.5 s later the fixation point disappeared and the saccade target was shown for 50 ms 10° to the right of the screen center. Subjects were instructed to proceed with a 20° rightward saccade towards the target position as soon as the target appeared. After a random time between 50 and 300 ms after target onset a bar was presented for one frame (12 ms) at one of four possible positions (−0.4°, 5.9°, 14.9° and 20.4°). Five hundred milliseconds later a mouse pointer became visible which the subject used to report the perceived position of the bar. In the case subjects failed to perceive the bar because of saccadic suppression they were instructed to position the mouse pointer at a predefined region on the right border of the screen. Later, these responses were used to determine the total number of omitted bars in the time window of every experimental session.

Each experimental session contained 150 trials, with bar positions and two to four contrast conditions in randomized order. Presentation time for the flashed bar was within the range of −150 to 150 ms from the start of the saccade.

2.4. Eye movements and data analysis

Eye position was measured with an EyeLink-System (SensoMotoric Instruments GmbH) at a sample rate of 250 Hz. Data analysis was programmed in Mathematica 4.1 (Wolfram Research) running under OS X on an Apple Computer. The start of the saccade was determined by a velocity criterion. First, the maximal eye velocity within the time window was determined and a threshold was set to 35° s^{-1}. The actual saccade onset was then determined within three successive recording samples. It was defined as the time of the first recording sample in which the actual velocity exceeded the threshold and stayed above it for at least two following samples. Only trials in which the latency was between 50 and 250 ms and the amplitude was near the saccade target (<2°) were used for further analysis. To visualize the time course of the mislocalization of the bar positions a sliding mean with a gaussian filter of 20 ms was calculated through the individual data points in a time window from 150 ms before and 150 ms after saccade onset.

To quantify the perceptual mislocalization across subjects and conditions in more detail, we used the compression index introduced by Lappe et al. (2000). This index measures the apparent separation of the bars. The standard deviation (SD) across the four perceived locations is calculated as a function of time and then normalized to the standard deviation of the four real bar positions. This index is one if no compression exists and zero if compression is maximal (all four positions would be seen in one point).

For the suppression index, sliding bins of 20 ms were used to show the detection ratio as a function of time (in

a window from 100 before and 100 ms after saccade onset). Within each bin the number of trials in which the subject detected the bar was divided by the total number of trials in that bin. For the total suppression in a given contrast condition the total number of perceived flashes was divided by the total number of presented flashes, independent of the presented time.

3. Results

3.1. Saccadic compression

Fig. 2 shows the apparent positions of the flashed bars for the five different contrast values for each of the three subjects. In each panel, the apparent positions of the four bars are plotted as a function of time relative to saccade onset. The horizontal black line at 10° to the right of the screen center indicates the position of the saccade target. The grey rectangle represents the mean duration of the saccade (64 ms). The four real bar positions ($-0.4°$, $5.9°$, $14.9°$ and $20.4°$) are indicated by short lines on the left of every panel. The curves show sliding-means for the apparent positions.

The mislocalizations of the presented bars clearly show a compression of perceived bar positions towards the saccade target. In all contrast conditions, the compression starts before the eye starts to move, reaches a maximum at saccade onset and disappears during the time of a saccade. These results are in accordance with several studies of saccadic compression that revealed the same pattern of mislocalization and the same time course (Lappe et al., 2000; Matsumiya & Uchikawa, 2001; Morrone et al., 1997; Ross et al., 2001).

When comparing the different contrast conditions it is evident that the amount of compression depends on the contrast between the bar and the background. Compression is strongest for the bars with the lowest contrasts (0.05, top three panels) and weakest for the bars with the highest contrast (0.65, low three panels). Fig. 3A shows the compression index, i.e., the relative separation across the four bar positions as a function of
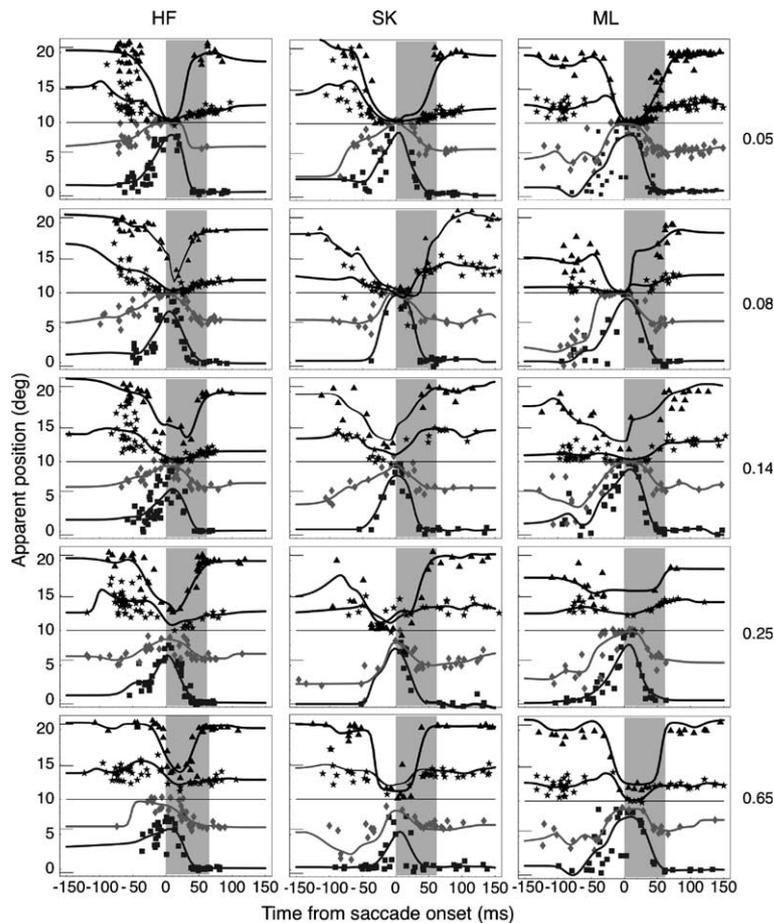

Fig. 2. Mislocalization of perisaccadic flashes in five contrast conditions. Results for the subjects are shown in three vertical panels. Each dot represents a single perceived positions of a flashed bar; the appropriate lines show the time-solved mean perceived positions of the bar. True bar positions are shown by short lines on the left of each subpanel. The horizontal line represents the position of the saccade target. The labels on the right for the horizontal sub-panel row indicating the contrast level. Saccade duration of horizontal 20° saccades were approximately 64 ms (vertical grey bar).
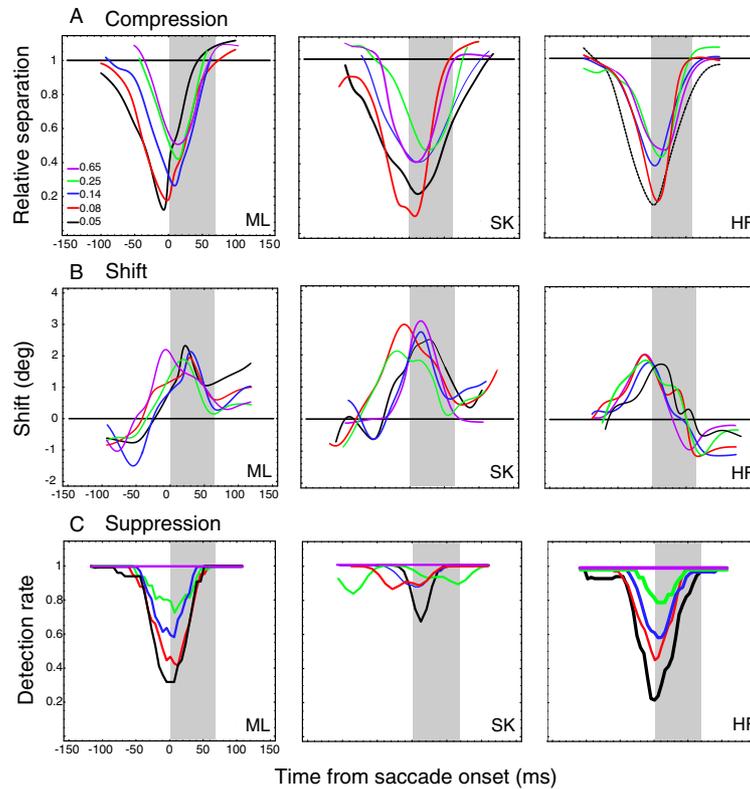
Fig. 3. (A) Relative separation as index for compression strength. This index measures the apparent separation of the bars. The standard deviation (SD) across the four perceived locations is calculated as a function of time and then normalized to the standard deviation of the four real bar positions (colored lines). An index of one indicates that no compression exists and an index of zero indicates that compression is maximal. (B) Shift relative to saccade onset. The colored lines represents the shift over all for bar positions at each of the five contrast levels. The mean of the true bar positions was 10°. It is indicated by the horizontal black line in the figure. The horizontal grey bar indicates the duration of the saccade. In contrast to suppression and compression no contrast dependency is visible. (C) Detection rate as index for saccadic suppression. Suppression is strongest (lowest detection rates) at saccade onset and increases further with decreasing contrast (colored lines).

time. The relative separation indicates a decrease of the perceived distances between the four bar positions. The relative separation starts to drop well before saccade onset, reaches a minimum at saccade onset and returns to the starting level at the end of the saccade. Compression for the bars with low contrasts (black and red curves) is characterized by a strong decrease in relative separation. It is weaker for high contrast bars (blue, green and purple curves). Fig. 4 shows the minimum values of the relative separation as a function of contrast. The data points were fitted with regression lines (HF: $r^2 = 0.95$; SK: $r^2 = 0.57$, ML: $r^2 = 0.9$). Differences in the strength of the compression for the different contrast values were significant (Non-parametric Friedmann-test, $p < 0.017$).

3.2. Shift

Next to compression, localization errors during saccades also typically show an overall shift of all perceived positions in the direction of the saccade. This shift occurs both in darkness and with visual references. When visual references are present the shift is seen in addition to the compression.
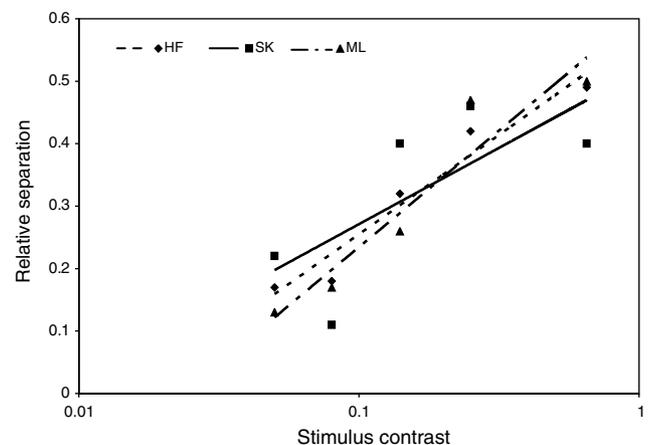

Fig. 4. Relative separation versus stimulus contrast. The different symbols (HF ◆, ML ▲, SK ●) show the minimum values for the specific contrast. Data were fitted by linear regression lines (HF (---), SK (—), ML (—·—)).

Whereas compression depends on retinal factors such as visual references or stimulus-background properties, the shift is usually explained by an inter-action with

extraretinal eye position signals (EEPS). If the shift is driven exclusively by extraretinal signals, changing the stimulus contrast should not have an effect. If, however, the mechanism of the shift is the same as that of the compression, changing contrast should affect the size of the shift. Following Lappe et al. (2000), we determined the magnitude of the shift by calculating the mean positions across the four bar positions as a function of time and then normalized to the mean of the four real bar positions (10°). In Fig. 3B the shift is plotted as a function of time relative to saccade onset. A sliding mean with a gaussian filter of 20 ms was calculated through the data points in a time window from 100 ms before and 100 ms after saccade onset (colored lines). The shift starts up to 100 ms before the saccade, reaches a maximum near the beginning of the saccade and levels off at the saccade's end. Clearly, the magnitude of the shift is similar for all contrast values which is also shown in Fig. 5.

3.3. Saccadic suppression

To examine the question of whether saccadic compression and saccadic suppression are related, the time course and the strength of saccadic suppression for the five stimulus contrasts were compared. Detection rates for the flashed bars at different contrasts are shown in Fig. 3C. The figure shows that the time course for saccadic suppression is similar to the time course for saccadic mislocalization indicated by the colored lines. Subjects ability to detect a bar started to drop just before the eye movement started, reached a minimum at or directly after saccade onset and vanished directly after the saccade was finished. The results were similar to findings of Diamond et al. (2000).
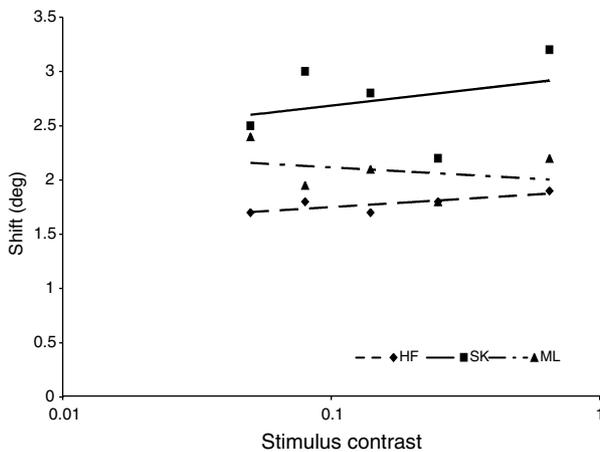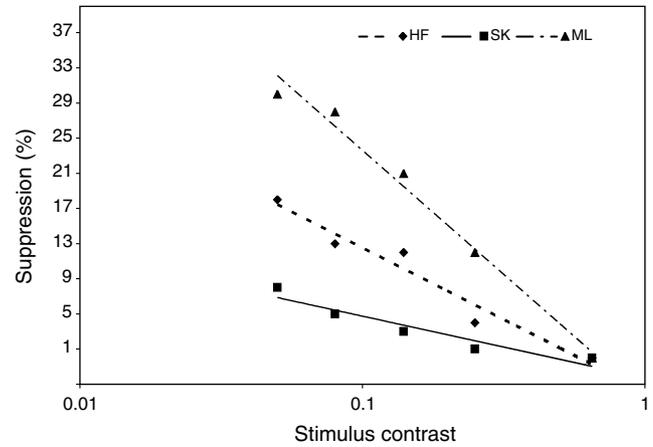

Fig. 6. Amount of saccadic suppression as a function of contrast. The percentage of unperceived bars for the each contrast level is indicated by the different symbols (HF ◆, ML ▲, SK ●). The lines through the data are linear regressions (HF (---), SK (—), ML (—·—)). The strength of suppression is contrast dependent but shows differences for the three subjects.

Fig. 6 shows the overall amount of saccadic suppression as a function of contrast for the three subjects. The percentage of unperceived bars for the single contrasts was calculated across the whole presentation time for the bars. The data were fitted with linear regression lines. As expected, saccadic suppression depends on contrast. The strength of suppression revealed individual differences, however (SK: $r^2 = 0.9$, ML: $r^2 = 0.99$, HF: $r^2 = 0.95$). Nevertheless, in all subjects differences in the strength of saccadic suppression for the different contrast levels were significant (Non-parametric Friedmann-test, $p < 0.029$).

Fig. 5. Saccadic shift versus stimulus contrast. The different symbols (HF ◆, ML ▲, SK ●) show the peak values for the specific contrast. Data were fitted by linear regression lines (HF (---), SK (—), ML (—·—)).
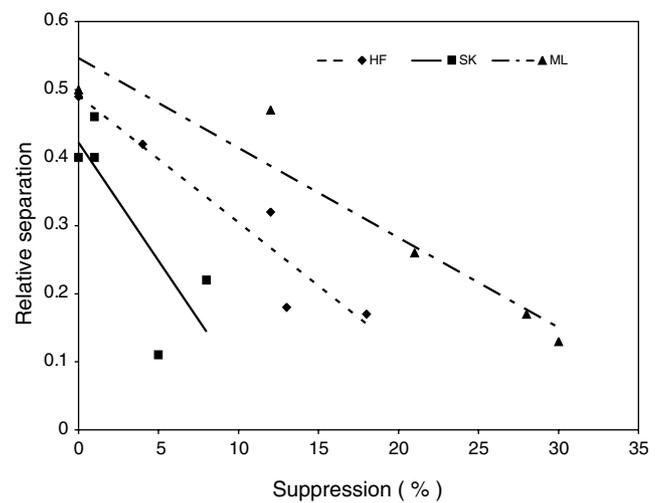

Fig. 7. Relative separation versus saccadic suppression. For compression, the minimum value at saccade onset and for suppression, the total amount of suppression (in percent) for each particular contrast are plotted (HF ◆, ML ▲, SK ●). The different slopes for the three subjects arises from differences in the strength of saccadic suppression (HF (---), SK (—), ML (—·—)).

Finally, Fig. 7 displays relative separation against saccadic suppression. Data were fitted by linear regression lines. The result shows a clear correlation between saccadic suppression and saccadic compression (SK: $r^2 = 0.66$, ML: $r^2 = 0.92$, HF: $r^2 = 0.9$). Despite individual differences in the strength of saccadic suppression two general effects can be observed. First, saccadic omission, i.e. a lack of perception of the flash, increases when the stimulus is presented near its threshold, i.e. when the stimulus has a low contrast. Second, stimuli with low contrast are more mislocalized than stimuli with high contrast. We will discuss possible reasons for the contrast dependency of suppression and compression and the possible relationship between the two.

4. Discussion

We investigated the influence of contrast on perisaccadic mislocalization. Low contrast stimuli were often suppressed during saccades (saccadic suppression), but when they were perceived subjects reported their location shifted towards the saccade target (saccadic compression). We reproduced earlier findings that saccadic suppression possesses a typical time course reaching its maximum around saccade onset (Diamond et al., 2000) and showed that this time course is similar to the time time course of saccadic compression. We found that in addition to saccadic suppression compression is also contrast dependent and that stimulus contrast affects both perceptual effects in a similar manner. We suggest that both effects share parts of their origin. Saccadic shift on the other hand is not contrast dependent suggesting that shift and compression are caused by different mechanisms.

4.1. Dependence of compression on contrast in other studies

The dependence on contrast might help to explain differences in the strength of compression in other studies. For instance, Morrone et al. (1997) flashed a vertical green bar at different positions on an equiluminant red background. Subjects made horizontal 20° saccades in a darkened room and reported the perceived location of the flashed bar. Morrone et al. found a saccadic shift towards the saccade target of about half the size of the saccade. For bars behind the saccade target mislocalization errors were against the saccade direction (saccadic compression). In a second condition the bar was luminance-modulated relative to the background. The compression in the luminance condition was similar to the color condition, but the peak amplitudes of the mislocalization was somewhat stronger in the equiluminant condition than in the luminance condition.

Lappe et al. (2000) and Awater and Lappe (2004) conducted experiments in darkness except for postsaccadic visual reference provided by a ruler on the screen. Thus, contrast was very high in this study. The peak compression was about 25% i.e. less than the compression found by Morrone et al. (1997). In accordance with our conclusion the results from Lappe et al. indicate that compression occurs also under high contrast conditions but is smaller than under low contrast or equiluminant conditions.

In a study by Honda (1999) three experimental conditions were used (light, dark, frame) in which subjects performed horizontal 8° saccades. The contrast in the light condition was 0.41 and the compression observable in the data figures was about 4° (of the peak-to-peak amplitude in the mislocalization curve) or in other words, half size of the saccade's amplitude. This is similar to the compression that we found for the intermediate and high contrast condition.

Kaiser and Lappe (2004) used an experimental setup with a contrast of 0.54 (green dots on a red background). In one condition subjects made 20° horizontal saccades. From the description of their data we estimated the compression index for horizontal mislocalization at 0.6 which is comparable to our results at the same contrast level.

4.2. Saccadic shift

Unlike the strength of compression, the magnitude of the shift did not vary with stimulus contrast (Fig. 5). The lack of contrast dependency suggests that the shift reflects an extraretinal eye position signal rather than retinal information about stimulus properties. This is further evidence that saccadic compression and saccadic shift are two different effects. It adds to the findings of Morrone et al. (1997) that compression occurs during real saccades but not when saccades were simulated by a mirror movement and to Lappe et al. (2000) that shift and compression were differently affected by the presence of visual references: with visual references shift and compression was obtained whereas in darkness only the shift was seen. Theoretically, the saccadic shift could depend on stimulus properties. For instance, if the visual latency increases, the visual signal will reach the brain later, i.e. when the extraretinal position signal has acquired a new value. A small effect was shown by Boucher, Groh, and Hughes (2001) in the case of stimulus luminance.

4.3. Possible origin of compression and relation to suppression

Krekelberg et al. (2003) suggested that spatial coding in the neural activity in MT and MST is changed during a saccade such that visual space becomes compressed.

Responses to flashed stimuli in MT and MST are suppressed during a saccade leading to a lower average firing rate (Bremmer et al., 2002). Taking these findings together one may hypothesize that suppression causes a change in response strength that leads to the effects reported by Krekelberg et al. Our results show that contrast influences the strength of suppression and compression in an similar manner. We therefore suggest that neural responses that are reduced by saccadic suppression may be even lower when the stimulus contrast is reduced resulting in stronger compression for lower contrasts. Lower responses to low contrast stimuli in MT neurons were shown earlier by Martinez-Trujillo and Treue (2002). In this view, compression is a result of visual processes induced by modifications of neural firing rates through suppression and associated contrast reduction.

Acknowledgments

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