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Slant perception, and its voluntary control, do not govern the slant aftereffect: Multiple slant signals adapt independently

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Abstract

Although it is known that high-level spatial attention affects adaptation for a variety of stimulus features (including binocular disparity), the influence of voluntary attentional control—and the associated awareness—on adaptation has remained unexplored. We developed an ambiguous surface slant adaptation stimulus with conflicting monocular and binocular slant signals that instigated two mutually exclusive surface percepts with opposite slants. Using intermittent stimulus removal, subjects were able to voluntarily select one of the two rivaling slant percepts for extended adaptation periods, enabling us to dissociate slant adaptation due to awareness from stimulus-induced slant adaptation. We found that slant aftereffects (SAE) for monocular and binocular test patterns had opposite signs when measured simultaneously. There was no significant influence of voluntarily controlled perceptual state during adaptation on SAEs of monocular or binocular signals. In addition, the magnitude of the binocular SAE did not correlate with the magnitude of perceived slant. Using adaptation to one slant cue, and testing with the other cue, we demonstrated that multiple slant signals adapt independently. We conclude that slant adaptation occurs before the level of slant awareness. Our findings place the site of stereoscopic slant adaptation after disparity and eye posture are interpreted for slant [as demonstrated by Berends et al. (Berends, E. M., Liu, B., & Schor, C. M. (2005). Stereo-slant adaptation is high level and does not involve disparity coding. *Journal of Vision 5* (1), 71–80), using that disparity scales with distance], but before other slant signals are integrated for the resulting awareness of the presented slant stimulus.

Keywords: Adaptation; Binocular vision; Slant perception; Bistability; Slant aftereffect

1. Introduction

Adaptation is the process through which nervous systems change their performance based upon recent input history. Aftereffects evoked by prolonged exposure to an adaptation stimulus are ubiquitous among sensory modalities and have traditionally been used to separate processing streams. Here, we asked whether an observer's perceptual state affects the generation of aftereffects. To investigate such top-down influence we used ambiguous perception and developed an adaptation stimulus that capitalizes on voluntarily controlled perceptual awareness.

In bistable ambiguous perception a single unchanging stimulus, such as the Necker cube, instigates two mutually exclusive perceptual interpretations, which compete for perceptual dominance. In the current study, we take advantage of the capability of observers to exert voluntary mental control to select one of the two competing alternative perceptual interpretations (review by Blake & Logothetis, 2002, for recent comparison studies, see Meng & Tong, 2004; van Ee, van Dam, & Brouwer, 2005). The role of voluntarily controlled perceptual awareness can be studied using bistable ambiguous perception because it dissociates the observer's perceptual state from the stimulus. The influence of voluntarily controlled perception on the generation of aftereffects has not yet been explored but it is not unlikely to exist, as influences of attention on aftereffects are well-documented for a variety of stimulus features, among which motion

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(Chaudhuri, 1990; Culham, Verstraten, Ashida, & Cavanagh, 2000; Rezec, Krekelberg, & Dobkins, 2004), orientation (Montaser-Kouhsari & Rajimehr, 2004) and disparity (Rose, Bradshaw, & Hibbard, 2003). Generally, diversion of attention from the adapting stimulus causes a smaller aftereffect and a selective increase in attention to a stimulus increases the strength of the aftereffect produced. For instance, attention to a stimulus has a multiplicative effect on the gain of tuning curves of orientation-selective neurons in V4 (McAdams & Maunsell, 1999; Reynolds & Chelazzi, 2004).

We focused on an aftereffect that has been widely examined: the slant aftereffect (SAE). Slant refers to the three-dimensional rotation of a surface. Prolonged exposure to a slanted surface causes subsequently viewed unslanted surfaces to be perceived as slanted in the opposite direction (Köhler & Emery, 1947; Wenderoth, 1970) and occurs for both monocular and binocular cues to slant (Balch, Milewski, & Yonas, 1977; Bergman & Gibson, 1959). Adaptation to slant is not dependent on the presence of both these cues; either cue can produce SAEs when adapted to in isolation (Bergman & Gibson, 1959; Ryan & Gillam, 1993). To study the role of high-level influence on the SAE, we developed an adaptation paradigm based upon an ambiguous slant stimulus, referred to as slant rivalry. In slant rivalry two distinct cues, monocular perspective and binocular disparity, specify conflicting slants which can be parametrically varied (van Ee, van Dam, & Erkelens, 2002). An observer experiencing slant rivalry alternately perceives a rectangular plane slanted in one direction (a perspective-dominated percept) and a competing interpretation of a trapezoidal plane slanted in the opposite direction (a disparity-dominated percept). The two percepts in slant rivalry alternate in a stochastic fashion similar to other bistable stimuli (van Ee, 2005). Slant rivalry has longer perceptual durations and higher susceptibility to voluntary control compared to other stimuli (van Ee et al., 2005), features which facilitate the examination of the influence of voluntarily controlled perception of surface slant on adaptation. Moreover, a recent SAE study, utilizing the fact that disparity-slant scales with distance (an approach pioneered by Domini, Adams, & Banks, 2001), demonstrated that the SAE correlated mainly with high-level slant processing, as opposed to low-level retinal disparities (Berends, Liu, & Schor, 2005). This implies that voluntarily controlled slant perception might play a significant role in the generation of SAEs.

For one well-studied domain of bistable perception, namely binocular rivalry (where the two retinae are presented with unfusable stimuli), several studies have investigated the influence of perceptual suppression on aftereffects (Blake, Yu, Lokey, & Norman, 1998; O'Shea & Crassini, 1981; Wade & Wenderoth, 1978; Wiesenfelder & Blake, 1990; Wiesenfelder & Blake, 1992; Wolfe, 1983). For example, Wiesenfelder and Blake (1990) found that only complex motion adaptation is inhibited by suppression, whereas simpler translational motion adaptation remains unaffected, pointing to a locus of rivalry suppression between the successive motion processing stages. For slant rivalry in particular, as multiple cues are involved, an interesting question is where in the processing stream the bifurcation of information into the separate perceptual representations occurs. One possibility is that the perceptual alternation occurs at the cue-level, entailing that at the moment of an alternation one slant cue, say disparity, becomes dominant and the other slant cue, perspective, becomes cut off (low-level switch). Another possibility is that the perceptual alternation is a higher-level selection of a certain slant, irrespective of the constituting cues.

In our experiments, subjects were instructed to hold either one or the other slant percept under fixed stimulus conditions. We presented intermittent blank intervals (Orbach, Ehrlich, & Vainstein, 1963), which were recently developed into a psychophysical technique (Leopold, Wilke, Maier, & Logothetis, 2002; Maier, Wilke, Logothetis, & Leopold, 2003), to facilitate the dominance of one of the two alternative percepts for extended periods, and measured simultaneous SAEs for both monocular and binocular cues separately using different test stimuli. We used briefly flashed test stimuli in a staircase procedure to avoid the spurious motion cue confounds that occur when employing the often-used technique of manual rotation settings.

We found that the voluntary perceptual control during adaptation had no effect on the magnitude of the SAEs for both cues, and that adaptation to both cues occurred independently and simultaneously. As a further investigation into the independence of the SAE for both depth cues we determined the amount of cross-cue SAE in a second experiment and found only small amounts of cross-cue adaptation. In experiment 3, we investigated the influence of the often-used manual rotation test method of measuring SAEs for both monocular and binocular cues, showing that this method is flawed. Experiment 4 was conducted to clarify the role of perceived slant magnitude on the SAE, with results showing that perceived slant and SAE magnitude are not correlated, meaning that it is not perceived slant that governs the SAE.

2. Experiment 1

2.1. Methods

2.1.1. Apparatus

Subjects viewed stereoscopic images in a darkened room on a LaCie monitor that subtended $40° \times 30°$ at a viewing distance of 57 cm. The edges of the display were not visible during the experiment. The display was driven by a Macintosh G4 computer using custom OpenGL-based software. Monitor refresh was 100 Hz and every pixel subtended 1.5×1.5 min of arc. The stereograms were presented to the two eyes by means of the standard red-green anaglyph technique. Luminances of red and green stereogram half-images were adjusted to appear equally bright. Photometric measurements showed that miniscule amounts (0.3%) of the green and the red light leaked through the custom-made red and the green filter, respectively. To avoid informative aliasing of tilted lines and dots, full-screen antialiasing was applied. Gaze data were collected using an SMI Eyelink data acquisition system at 250 Hz. Four subjects, three of them naive as to the purpose of the experiment, participated.

2.1.2. Stimuli

2.1.2.1. Adaptation stimulus. The bistable adaptation stimulus was a grid consisting of 8 vertical and 6 horizontal lines, each with a width of 1.5 min of arc, arranged as shown in Fig. 1. The adaptation stimulus was 5.5° wide, and varied in height between 4.5° and 5.2° due to foreshortening. Perspective projection information specified the slant of the plane about a vertical axis to be either 55° or −55°. A horizontal size ratio between right and left eye was applied in order to present a disparity-defined slant of −55° or 55° (also about a vertical axis), amounting to a 110° slant conflict. This amount of conflict is well within the range for which slant rivalry occurs (van Ee et al., 2002). All adaptation stimuli were surrounded by a background of open squares subtending 12 min of arc each. These background squares were randomly arranged in a rectangular array with a density of 80% to avoid binocular mismatching (the wallpaper effect). The aperture in the background measured 14.6° × 9.8°. A dot (4.5 min of arc) was presented in the center of the display as a fixation point at all time during adaptation.

2.1.2.2. Test stimuli. To test for adaptation to binocular and monocular slant cues separately we used both binocular and monocular test stimuli. Test stimuli were presented against an empty background to avoid a frontoparallel reference.

2.1.2.3. Binocular test stimulus. The binocular test stimulus was a horizontal line of 12 small dots whose positions were randomly jittered, which was slanted by applying a disparity gradient. This stimulus contains a minimum of non-disparity cues, to avoid contamination with monocular visual input during test presentations. The stimulus subtended 4.3° in width and 0.7° in height, and its constituent dots measured 1.5 min of arc.

2.1.2.4. Monocular test stimulus. Monocular test stimuli were presented to either the left or the right eye. They consisted of a grid of the same structure as that shown during adaptation, scaled in width in order to subtend approximately the same visual angle.

2.1.3. Procedure

2.1.3.1. Adaptation. Using the periodic stimulus removal paradigm (Orbach et al., 1963) developed by (Leopold et al., 2002; Maier et al., 2003), subjects were able to hold either one of the two possible percepts for extended periods of time. During the adaptation phase of each trial, the stimulus alternated in a regular 0.5 s off 1.5 s on fashion. A dot in the background on either the right or the left side of the

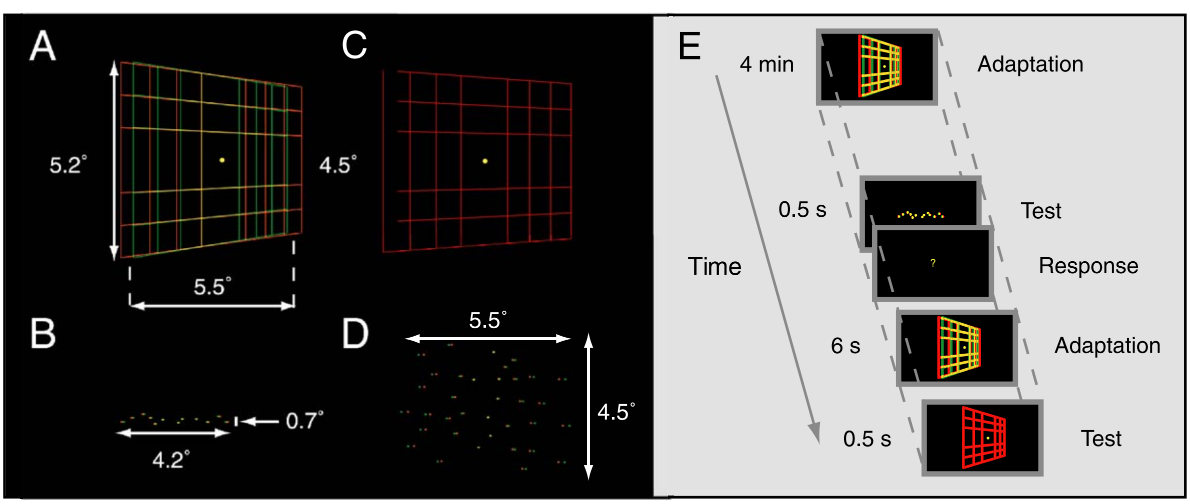

Fig. 1. Renderings of the anaglyphic stimuli used. (A) The slant rivalry adaptation stimulus used in experiment 1, containing both binocular and monocular slant signals. In this stereogram, both perspective and binocular disparity specify surface slant about the vertical axis. With red-over-left viewing, two relatively stable percepts can be distinguished. In the first percept, the grid recedes in depth with its right side further away (it is perceived as a slanted rectangle). In the other percept, the left side of the grid is further away (it is perceived as a trapezoid with the near-edge shorter than the far-edge). When the red filter is over the right eye, perspective and disparity specify similar slants and the observer perceives a single stable slanted grid with its left side closer. Demonstrations of slant rivalry can be found on http://www.phys.uu.nl/~vanee/. (B) The binocular test stimulus; an elongated patch of randomly jittered sparse and small dots with minimal texture cues to slant. (C) The monocular test stimulus consisting of only perspective cues to slant when viewed with one eye. The dimensions were variable, as the slant of the test stimulus was changed during the experiment. This was also the monocular adaptation stimulus used in experiment 2, with dimensions equal to those of the bistable adaptation stimulus in A. (D) The binocular adaptation stimulus used in experiment 2, consisting of 60 randomly and sparsely placed small dots with a minimum of monocular slant signals. (E) The experimental procedure. The first adaptation duration was 4 min, subsequent top-up adaptation durations lasted 6 s. These times are net viewing periods, discounting the periods when the stimulus was not presented as a result of periodic stimulus removal during adaptation. Subjects were instructed to fixate the center fixation dot.

slant stimulus indicated which side the subject was instructed to hold in front. Subjects reported their percepts continuously during the bistable adaptation phase. Percepts were reported as left or right side towards the observer. This avoided the need for subjects to know the different cues involved and discriminate between them. The durations of the percepts were used to calculate the dominance time fractions. We used a top-up adaptation paradigm (Graham & Rogers, 1982) in which the total duration of on times was 4 min in the first trial, and 6 s in each subsequent trial. For two subjects, gaze data were collected during adaptation in order to investigate if eye movements were used to aid voluntary control of percept dominance. This was done in separate sessions.

2.1.3.2. Test. The experimental procedure is shown in Fig. 1. On each trial, the test stimulus was shown for 0.5 s, after which time a question mark appeared in the center of the screen. Subjects responded by pressing a key to indicate whether the left or right side of the test stimulus was slanted towards them, and a new trial commenced. Slant perceived as frontoparallel was measured using 4 randomly interleaved one-up–one-down staircases, two for monocular aftereffects (one for each eye) and two for binocular aftereffects. Starting points for the staircases were random between −12.5° and 12.5°, and the initial stepsize was 5°. Staircases were terminated after 18 reversals and the last 12 reversal values, of stepsize 0.3° slant were averaged to yield the point of subjective equality (PSE), or aftereffect. We conducted PSE measurements prior to adaptation, in order to subtract the resultant values from the SAEs after adaptation. These null-values increased the variability of our data when compared to the averaging of data from symmetric conditions. Therefore, all conditions were tested twice; left–right symmetrical stimulus configurations were tested in separate sessions and their absolute values averaged to rule out any effect of bias on the results. These pairs of measurements were conducted on the same day, with at least 30 min of rest separating the sessions.

2.2. Results

Before considering the SAE results, we first review the success of intermittent stimulus presentation as a means of percept stabilization, and we consider SAE biases.

Fig. 2A shows the fractions of the total adaptation period subjects reported seeing the two different percepts. These fractions illustrate the amount of control subjects exerted over the slant rivalry alternations implying that subjects were successful in holding a percept, thus ensuring steady adaptation. Shown in Fig. 2B, the gaze data plotted as the density of fixation positions, demonstrate that no specific eye movement patterns or excentric gaze positions were used to aid voluntary control. In accordance with prior results (van Dam & van Ee, 2005), the control over perception was the result of central mechanisms.

Fig. 3 shows raw data for two subjects, selected to illustrate different bias patterns. Bars represent an average of two separate interleaved staircases for one cue. Each pair of bars represents the data from a single session, one for ‘hold disparity (D)’ and one for ‘hold perspective (P)’ control exertion instructions. The graphs in the left column show SAEs for adaptation slants P = 55° and D = −55°, while the right column graphs show P = −55° and D = 55° adaptation data, as indicated in the legend above the graphs. Our tests were used to null the SAE; therefore the SAE ought to be in the same direction as the adapting slant. We define biases as the average of data collected after adaptation to positive slants and data collected after adaptation to negative slants. Subject JB shows a large consistent bias in favor of right-towards slants for both disparity- and perspective-based SAEs. Subject LD shows a bias close to zero. Biases were also examined using pre-adaptation measurements, and these confirmed the biases found using the adaptation data, which we used in our analysis. To examine the effects

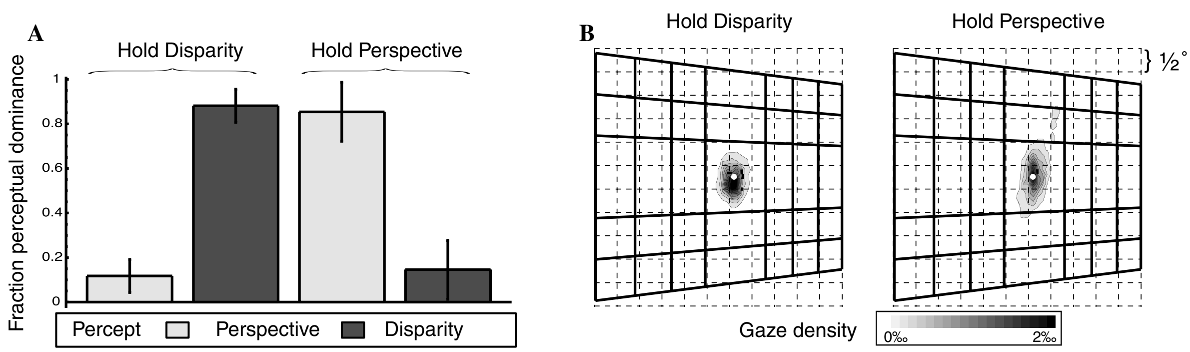

Fig. 2. (A) The fractions of perceptual dominance during the first adaptation period of a session, defined as the total amount of time spent in a percept divided by the total net viewing duration of the first adaptation period, when subjects were instructed to hold either percept. These dominance fractions illustrate the amount of voluntary control over perceptual state in slant rivalry when intermittent stimulus presentation is used. Bars represent mean dominance fractions across four subjects, error bars indicate standard deviations. (B) Contour plots of one subject’s gaze position data for ‘hold disparity’ and ‘hold perspective’ instructions. Gaze density is plotted as a fraction of the total amount of gaze samples during an entire session. Angular precision of the gaze data is 0.5°. The different instructions do not cause a shift in fixation position or gaze behavior.

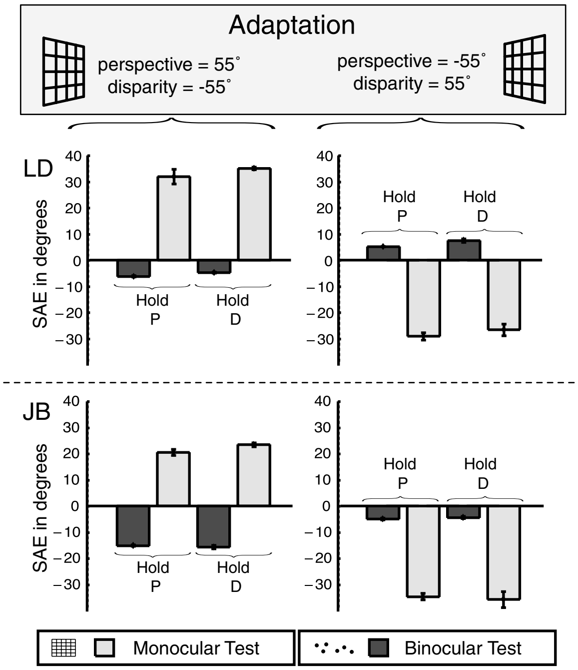

Fig. 3. Raw data from frontoparallel settings of test stimuli for two subjects after adaptation to a slant rivalry stimulus. These two subjects are explicitly shown here to illustrate the occurrence of biases in the frontoparallel slant settings. The left graph for each subject shows data after adaptation to positive perspective-defined slant and negative disparity-defined slant, the right graphs show the data after adaptation to opposite slants. Each pair of bars represents data obtained from a single session devoted to one control exertion instruction. Abbreviations P and D stand for the perceptual "hold" conditions of perspective and disparity, respectively. Error bars indicate standard deviations across two staircase measurements, and units on the ordinate are degrees of slant. Biases are calculated as the average of each bar and its opposite adaptation counterpart. Subject JB shows a right towards bias of 10° in both cues, whereas subject LD shows no appreciable bias (1°). The biases were highly stable across sessions for all subjects. To examine the effects of perceived slant on SAEs we removed the biases in subsequent plots.

of perceptual control exertion instruction, biases were subtracted from the data, and unbiased data were collapsed, i.e., data collected after adaptation to slant values P = 55° and D = −55° were combined with the negative values of the data collected after adaptation to slant values P = −55° and D = 55°. The resultant values are shown in Fig. 4A, which illustrates for each subject the total SAE for both perceptual control instructions measured with both the binocular and monocular test stimulus. Fig. 4B shows these data averaged across subjects. The aftereffects tested with the monocular test stimulus are much larger than those tested with the binocular test stimulus, amounting to more than 50% of the adapting slant, whereas for the binocular test stimulus this is ca. 10%. It is evident from the SAEs in Fig. 4A and B that adaptation to a bistable stimulus produces oppositely oriented SAEs for the two different test stimuli. The difference in aftereffects can be as large as 40°. It is of interest to note here, that in pilot experiments we included test stimuli in which both monocular perspective and binocular disparity cues were congruent. The SAEs recorded using these test stimuli were highly variable and inconsistent within subjects. When debriefed, subjects reported the experience of a percept of bistable slant when actually viewing a congruent-slant test stimulus. During the test periods in these experiments, the subjects could base their judgment of slant on either cue, responding for one SAE in one trial and for the other SAE in another. Clearly, this response behavior produces divergent staircases and inconsistent results.

Differences in SAE as a result of the instructions are shown in Fig. 4C and D. For monocular tests, the 'hold disparity' instruction SAE was subtracted from the 'hold perspective' instruction SAE, whereas for binocular tests the 'hold perspective' instruction SAE was subtracted from the 'hold disparity' instruction SAE. Thus, positive values indicate that attentional state facilitates the development of SAEs for a particular cue. For our monocular test, the effect of perceptual control exertion on the SAE is inconsistent over subjects and the SAEs for the two instructions do not differ significantly (post hoc Tukey, $F(1,3) = 1.39$, $p = 0.12$). Although our binocular test shows positive values for all subjects, these values are not significant ($F(1,3) = 2.60$, $p = 0.25$). In sum, whether the subjects perceived either the perspective-dominated or disparity-dominated slant during adaptation to a 110° slant conflict stimulus does not influence the SAEs recorded using both monocular and binocular test stimuli.

3. Experiment 2

The results of experiment 1 show that SAEs for both perspective and disparity cues are generated independently of the dominantly perceived slant in slant rivalry. Previous research (Balch et al., 1977; Poom & Borjesson, 1999), however, showed large cross-cue slant aftereffects that have been taken to point to a considerable role of perceived slant in the generation of SAEs. For instance, in one experiment (Balch et al., 1977) used a monocularly viewed test stimulus composed of a rotatable square grid pattern to measure SAEs after either binocular or monocular adaptation to a single line drawn on white paper slanted about a horizontal axis. The single line was used to minimize the amount of monocular information to slant in the adaptation stimulus. They found an aftereffect of 2.7° after binocular adaptation, whereas after monocular adaptation the aftereffect was 0.4°, showing a considerable SAE that crosses over from binocular adaptation to monocular test stimulus. We conducted a second experiment to examine slant adaptation cross-over between cues.

Subjects adapted either to slant defined by perspective under monocular viewing, or to binocularly defined slant in a random dot pattern containing a minimum of texture cues. To investigate whether the different cues reinforce each other's adaptation when adapted to in concert, we also included an adaptation condition in which subjects adapted to a stimulus which contained both cues specifying the same slant, a congruent slant adaptation condition.

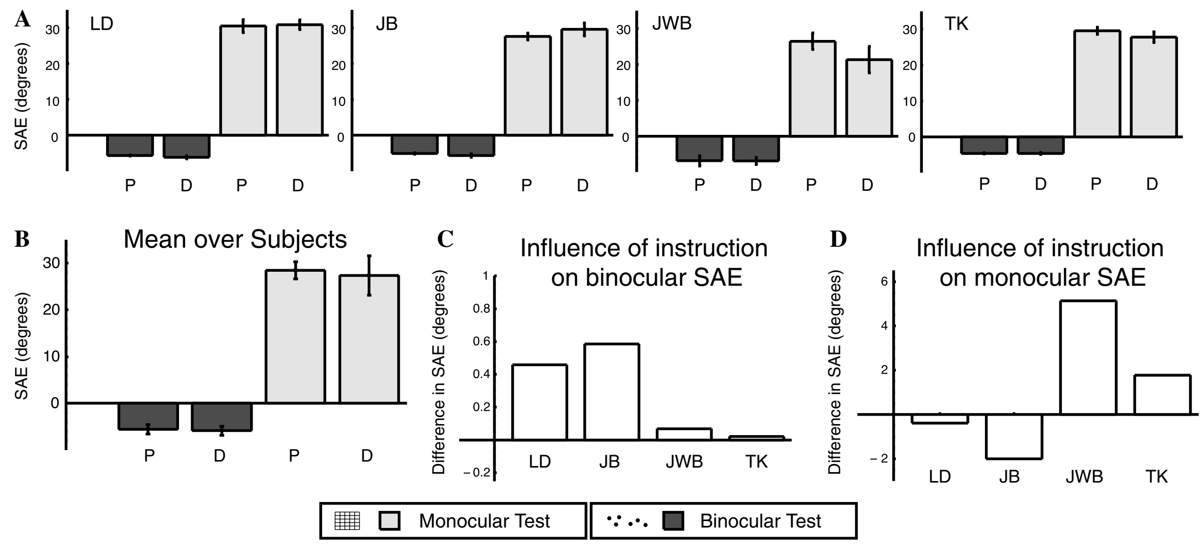

Fig. 4. Results of experiment 1. (A) Slant aftereffects for binocular test stimuli (dark gray) and monocular test stimuli (light gray) after adaptation to conflicting slants of ±55°. The perceptual conditions are denoted by P and D for 'hold perspective (monocular)' and 'hold disparity (binocular)', respectively. Bars represent means of collapsed data across four staircases with biases removed. Error bars denote standard deviations. (B) Data of A, averaged across subjects. (C) Increase in binocularly tested SAE induced by selective attention to the disparity-dominated percept, for all four subjects. Values are the differences between SAEs in the 'hold disparity' and 'hold perspective' instructions. (D) Increase in monocularly tested SAE induced by selective attention to the perspective-dominated percept. Values are the differences between SAEs in the 'hold perspective' and 'hold disparity' instructions. (C and D) In all, these differences that are smaller than the error bars in (A), demonstrate that perceptual instruction conditions alter the magnitude of neither binocularly nor monocularly tested SAEs.

3.1. Methods

Apparatus, test stimuli, subjects, stimulus/background dimensions and procedure were identical to those used in experiment 1. Only the adaptation stimuli differed. All adaptation stimuli are shown in Fig. 1. In random dot patterns, texture information indicates the plane has zero slant. This information may hamper adaptation to slant. To minimize the texture cue during adaptation we used a plane of sparse, small random dots (Adams, Banks, & van Ee, 2001). This binocular adaptation stimulus consisted of a random dot pattern of 60 dots, with a height of 5.2° and width of 5.5°, equal to the size of the adaptation stimuli in the other experiments. Dots subtended 1.5 min of arc. A horizontal size ratio between right and left eye was applied in order to present a disparity-defined slant of 55° or −55°. The monocular adaptation stimulus was composed of the same grid as was used for the adaptation to a bistable slant of experiment 1. It was monocularly presented to the dominant eye. The congruent adaptation stimulus was the same grid as was used in experiment 1, yet with identical disparity-defined and perspective-defined slant.

3.2. Results

Aftereffects measured with the monocular test stimulus are shown in Fig. 5A, SAEs measured binocularly are shown in Fig. 5B. Adaptation to one cue generates an aftereffect that is largest when measured using that cue, although SAEs measured with a test stimulus containing the other cue are significant (perspective, $p < 0.001$, disparity, $p < 0.05$). This means that there is cross-cue adaptation to slant. This cross-cue SAE can be expressed as a fraction of the SAE attained after adaptation to the stimulus used to test the SAE (monocular adaptation, monocular test or binocular adaptation, binocular test; Fig. 5C). Mean SAE cross-over across subjects is 17% for disparity, and 22% for perspective. These cross-cue SAEs might best be explained by assuming that adaptation occurs at a high, cue independent level.

However, SAEs after adaptation to one cue (when tested with a test stimulus containing that cue) are not significantly different from both SAEs obtained after adaptation to both congruently defined slants and SAEs obtained in experiment 1, for either binocular or monocular test stimuli. This means that for both cues there is no additive effect for adaptation to congruently defined slant (the other cue is adapted to the same slant) as compared to either adaptation to an incongruent slant stimulus or single-cue adaptation. Further comparison of these data with the incongruent slant SAEs from experiment 1 revealed that there is no significant diminutive effect of the other cue being directed oppositely during adaptation. In addition, no sign of weighted average combination of SAEs is present in the data. It is interesting to observe that adaptation to binocularly defined slant causes larger binocularly measured aftereffects than adaptation to congruent slant.

Cross-cue SAEs for the two cues used in our experiment is evident only in those cases when the other cue is being adapted in isolation. In cases where the cue being tested has been adapted, there is no evidence for cross-cue SAEs. Adaptation at a high cue-independent level, which accounts

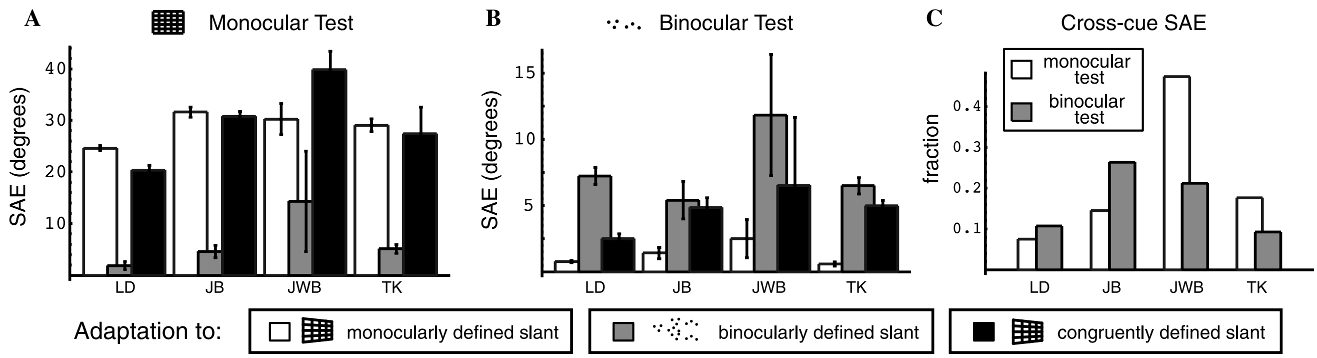

Fig. 5. Results of experiment 2 in which we examined the cross-cue SAE. (A and B) Slant aftereffects with adaptation to the cue being tested, with adaptation to the other cue, or both cues defining congruent slant. White bars indicate aftereffects after monocular adaptation, light gray bars represent aftereffects after binocular adaptation, black bars stand for SAEs after congruent adaptation, which elucidate that there is no additive effect of the different cues' simultaneous adaptation. All adaptation slants were ±55°. Error bars denote standard deviations. (C) Amount of cross-cue SAE (tested with the non-adapted cue) plotted as the fraction of the maximum SAE, i.e., when the adaptation stimulus contained only the cue being tested, calculated from the data shown in (A and B). White and gray bars represent cross-cue SAE fractions for monocular and binocular test, respectively.

for ca. 20% of the SAE found in within-cue adaptation and test, is present only when the cue used as a test has not been used in prior stimulation.

4. Experiment 3

From experiments 1 and 2, we conclude that slant cues adapt independently, although we also found that cross-cue slant adaptation, about 20% of the in-cue slant adaptation, is present. The previously found (Balch et al., 1977; Poom & Borjesson, 1999) considerable cross-cue SAEs that have generally been attributed to the perception of slant are in need of reconciliation with our data. Here, we demonstrate that the cross-cue SAEs depend on the use of a specific testing procedure used by these researchers. They employed manual rotation of the test plane by the subject or experimenter. The introduction of motion cues that are information sources to surface slant may influence the SAE measurements so that in fact, other cues to slant than those that have been adapted are being tested. This may lead to smaller SAEs, but more importantly the use of this procedure may be responsible for the alleged large dependency of SAEs on perceived slant. To quantify the role of the testing procedure we modified our test stimuli so that they could be rotated in depth about a vertical axis by the subject by means of a computer mouse.

4.1. Methods

Apparatus and stimulus/background dimensions were identical to those used in experiments 1 and 2. Adaptation stimuli were the grids, as used in experiment 1 and 2. Binocular and monocular test stimuli were a binocular row of dots and a monocularly viewed grid, respectively. For this experiment we added a congruent combination test stimulus, which was the grid containing both cues specifying the same slant.

We mimicked the manual adjustment procedure from the literature. Two subjects participated in the experiment. Both had participated in experiments 1 and 2. Subjects rotated the test stimuli in a to-and-fro rotating fashion by use of a computer mouse. They were instructed to set the test stimulus in a frontoparallel orientation. There was no constraint on the duration of the test setting. Each type of test stimulus was tested a total of 12 times, six for each adapting direction. Subjects were instructed to fixate the center fixation dot. During the adaptation phase of each trial, we did not use the periodic stimulus removal paradigm (Leopold et al., 2002) used in experiments 1 and 2 to aid perceptual stabilization, as this had no effect on the magnitude of SAEs. The net duration of the first adaptation period was identical to that in experiments 1 and 2, however, as subjects were exposed to the test stimulus for a longer amount of time, which could lead to dissipation of the SAE, top-up adaptation duration was extended to 30 s.

4.2. Results

Fig. 6 shows the data contrasted to data from experiment 1 for two subjects. The different signs for SAEs measured using disparity and perspective test stimuli found in experiments 1 and 2 are evident in the manual rotation test data also, confirming the separate adaptation for both cues. Disparity results are significantly different from perspective measurements at the 1% level (post hoc Tukey test). The SAEs collected using the congruent combination test stimulus, that contains both cues to slant, are comparable to the monocular perspective SAEs. Earlier research (Poom & Borjesson, 1999), employing physical stimuli, used binocularly viewed monocular test stimuli as binocular test stimuli. Thus, these stimuli are not purely binocular stimuli, as they contain both cues, as do our combination test stimuli. The use of physical stimuli in this manner has lead researchers to the conclusion that there is large adaptation

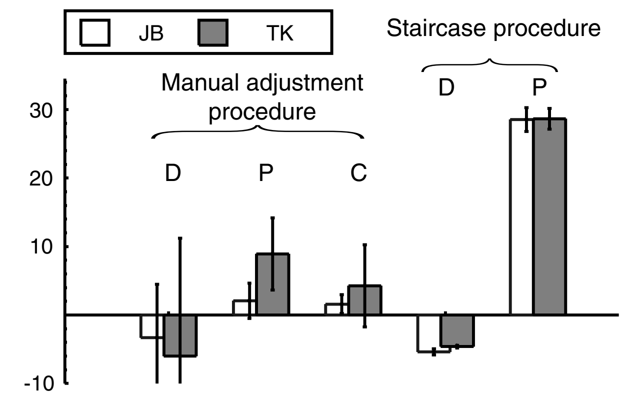

Fig. 6. Results of experiment 3, showing the SAEs after adaptation to a bistable stimulus for two subjects (differently colored bars) for the manual adjustment procedure, compared to the staircase data from experiment 1. All adaptation slants were ±55°. Results are displayed at the same scale as the results of experiment 1 in Fig. 4A. D and P stand for disparity and perspective defined test stimuli, respectively, and C stands for combination test stimuli in which both cues were present and defined a congruent slant. Error bars denote standard deviations. SAE cue segregation is far more evident when the superfluous, unadapted motion cues that are present in the manual rotation procedure are absent. More importantly, the manual rotation test procedure also causes the combination test data to be biased towards the monocular SAE. Also, intersubject variability decreases for the staircase procedure.

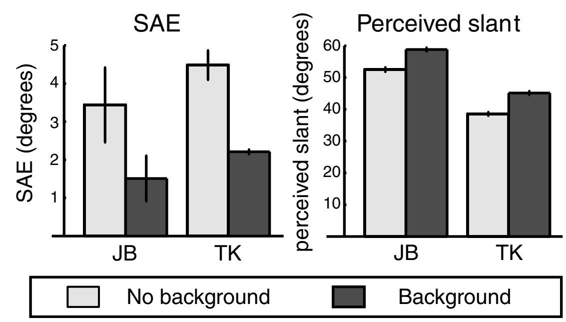

Fig. 7. Results of experiment 4, in which we investigated the role of the reference surround on perceived slant magnitude and SAE magnitude. Presented adaptation and estimation slants were ±55°. Error bars denote ±1 SEM. The left and right graphs depict SAEs and perceived slant, respectively. For both slant estimation and SAE there is a significant effect of the surround, however, these effects are reversed for the magnitude of perceived slant and the SAE. Although subjects perceive a greater slant when the stimulus is surrounded by a reference surface, adaptation results in SAEs of smaller magnitude. Evidently, binocular SAEs are not governed by the perceived slant during adaptation.

cross-over between monocular and binocular channels when in fact, binocular and monocular cues can show oppositely oriented SAEs when separated using computer generated stimuli.

In addition, the high level of variance in the data gathered with the manual rotation test demonstrates the rotation test stimulus' lack of reliability when compared to the short presentation staircase method.

5. Experiment 4

To ensure reliable slant rivalry, we were forced to use a reference surround. However, the influence of this surround on slant adaptation is unclear. We investigated how SAE magnitude and perceived slant magnitude are influenced by the surround.

5.1. Methods

5.1.1. SAE

Apparatus and stimulus/background dimensions were identical to those used in experiment 2, with the following exception: for efficiency no intermittent stimulus presentation was used and adaptation periods were shortened to 3 min, the net adaptation time of experiment 2. The adaptation stimulus was a random dot plane, slanted 55° using binocular disparity, presented either with or without the frontoparallel reference used in the previous experiments (see Fig. 1). Two staircase measurements were conducted per session. These staircases terminated after 12 reversals. Gaze measurement equipment and procedures were identical to those of experiment 1. Two subjects participated in this experiment.

5.1.2. Slant estimation

Separate from the adaptation sessions, we measured perceived slant. Subjects were shown a random dot plane, identical to the adaptation stimulus used for adaptation in this experiment. Since perceived slant depends on the presentation duration (Van Ee & Erkelens, 1996), we probed slant estimations at the moments that were used during the adaptation experiments. To mimick the slants perceived during a slant adaptation experiment, stimulus presentation periods were 3 min in the first trial, and 6 s in all subsequent trials. A session for this slant estimation experiment consisted of 20 repetitions per condition. After inspection of the stimulus, subjects were asked to report the perceived slant of the plane by use of a dial that could be set using a computer mouse (Van Ee & Erkelens, 1996).[1] Subjects performed 4 of these sessions, 2 with background and 2 without, for slants of ±55°.

5.2. Results

Fig. 7 shows the SAEs and slant estimates in the left and right column, respectively. Gaze measurements indicated that mean gaze position during the two conditions did not differ more than 0.75°, and that there were no excentric gaze shifts. Both subjects report greater SAEs when no reference was present ($p < 0.0001$). The effect for perceived slant is reversed, i.e., subjects perceive greater slant when the stimu-

[1] A sensible objection to this metrical slant-estimation method is that it is hard to interpret the data because a slant angle that is estimated at 35° in one trial might look like 40° in another trial. Previous work has demonstrated, however, that subjects have a relatively constant internal reference and that they do not regard this task as difficult. This estimation method has been used previously for real planes and when subjects wore distorting lenses (Adams et al., 2001). In addition, a similar metrical depth estimation method was successfully used for volumetric stimuli (van Ee & Anderson, 2001).

lus is surrounded by a reference plane ($p < 10^{-6}$). The surround's opposite influence on perceived slant and slant adaptation magnitude conflicts with the hypothesis that it is perceived slant that governs slant adaptation: although subjects perceive more slant during adaptation when the surround is included, the SAE is smaller.

6. Discussion

We examined whether slant perception, and its voluntary control, governs the SAE, leading to several main findings. First, there is no effect of voluntarily controlled perceptual state on the magnitude of the SAE for either of the cues used to invoke slant rivalry. Second, perspective-defined slant and disparity-defined slant adapt independently to a large extent. Third, the widely used standard method for examining slant aftereffects, i.e., the procedure of manual rotation of a test stimulus, is flawed. Fourth, the magnitude of binocular SAEs does not correlate with perceived slant. We will discuss each of these findings separately, commencing with the issue on methodology.

6.1. Flawed manual adjustment procedure

The standard way of quantifying slant aftereffects is the aforementioned manual adjustment procedure in which the subject rotates the test stimulus, thereby introducing spurious unadapted motion cues. (A notable exception here is Berends et al. (2005), who used a different method, see below.) We demonstrated that the adjustment procedure brings about reduced SAEs that are highly variable (experiment 3), which compares well with the variability and the size of the aftereffect for this procedure reported in the literature. Furthermore, we showed that the combination of binocular and monocular cues in the test stimulus results in a SAE that is biased towards the monocular SAE when using the manual rotation method. This bias could have led other studies to mistakenly conclude that there is considerable cross-cue adaptation. It is remarkable that the manual adjustment procedure has been widely used as there were early hints that the method is unreliable. Wenderoth (1970) reported a control experiment using a staircase method finding large SAEs (that were even parametrically dependent on the adapting slant). This finding was not reproduced by Poom and Borjesson (1999) using the adjustment procedure. Wenderoth went as far as noting that the adjustment procedure is unsatisfactory for studying SAEs.

Moreover, one out of a series of experiments by Poom and Börjesson shows a clear decrease in the amount of SAE cross-over between monocular and binocular slant cues when using a 2AFC task, as opposed to the adjustment procedure that they used in the rest of their paper. These authors even proposed that "the motion in the test conditions interfered with the adaptation effect", but they did not reinterpret their other results obtained with the adjustment procedure. Initially, the cross-cue adaptation had been taken in the literature as evidence for either an influence of texture cues or for slant adaptation. After Balch et al. (1977) and Ryan and Gillam (1993) had provided evidence that it is not texture of a surface patch that subjects adapt to, cross-cue adaptation found with the adjustment procedure had been alleged commonly as evidence for perceived slant adaptation.

6.2. Cross-cue slant adaptation

We quantified the amount of SAE that can be measured by testing one slant cue when adapted to the other slant cue (experiment 2). The magnitude of SAE crossover was small (about 20%) compared to the SAE measured for a cue that is adapted. We reasoned that adaptation to a bistable slant rivalry stimulus could hamper the development of a SAE for either cue because of the other cue's oppositely oriented slant information. One would then predict to find greater aftereffects when adapting to single-cue or congruent-cue stimuli. We found, however, no significant differences in SAEs across single-cue, congruent-cue, and conflicting-cue slant adaptation for either cue. From this latter result, we conclude that adaptation to the cues used in our stimuli occurs mainly independently.

Balch et al. showed full SAE crossover between slant cues employing line drawings and textured paper, which was again taken as evidence for perceived slant adaptation. A few years earlier, however, Epstein and Morgan-Paap (1974) reported a SAE crossover of approximately 50% when subjects adapted to a trapezoidal shape and set a binocularly shown luminous line. These latter results are more in line with the 20% cross-over that we found. A difference between our stimuli and that of the precursors discussed here is that the stimuli used before were based on physical apparatuses with physically slanted planes as slant stimuli. When stimuli are drawn on paper the shape of the drawn stimulus outline can be contradicted or reinforced by the texture of the paper on which the outline is drawn, giving rise to larger cross-cue aftereffects.

6.3. Stable perception of slant rivalry stimuli

Subjects have a limited degree of voluntary control over their perceptual state during slant rivalry and can increase the preponderance of the desired interpretation to approximately 70% (van Ee et al., 2005). Using the intermittent stimulus removal (Orbach et al., 1963) as a psychophysical technique (Leopold et al., 2002; Maier et al., 2003), the amount of control observers could successfully exert was increased considerably, to approximately 90% in the present study. We demonstrated that subjects were able to exert this influence without resorting to the aid of specific eye movement patterns or gaze positions, see Fig. 2. This is in accordance with recent results which demonstrate that both (micro-)saccades and blinks are necessary for neither the occurrence of (van Dam & van Ee, 2005) nor voluntary control over (van Dam & van Ee, 2006) perceptual alternations in slant rivalry.

6.4. Effect of perceived slant on SAE

If slant adaptation occurs at a stage where slant information is represented in a high-level, cue-independent fashion, influence on the generation of SAEs through voluntary control would be more likely than when slant adaptation occurs at a cue-dependent low stage. We demonstrated (experiment 1) that perceptual state and selective attention to cues during adaptation do not influence the magnitude of the SAE for both perspective and disparity slant cues, suggesting that slant adaptation is a low-level process. We are able to discount most of the findings that were responsible for the idea of perceived slant adaptation, as those were all based upon a flawed method (experiment 3).

A recent study (Berends et al., 2005) demonstrated that adaptation to disparity-defined slant occurs at relatively high levels, i.e., after eye posture is incorporated into the disparity processing stream. These researchers used the aforementioned feature that perceived slant from a gradient of disparity depends critically on the viewing distance (Domini et al., 2001). Here we took non-disparity cues into account that also influence perceived slant. We also used the frontal surround, which facilitates the generation of slant rivalry, to investigate the hypothesis that perceived slant governs the SAE. We demonstrated that the surround influences perceived slant and SAE magnitude oppositely; perceived slant increases by the introduction of a surround whereas the SAE decreases (experiment 4). Thus, perceived slant magnitude does not determine SAE magnitude. The effect of the surround on the generation of the SAE can be seen in light of recent results by Taya, Sato, and Nakamizo (2005) who reported that binocular SAEs are not retinotopic, and that the magnitude of the SAE is dependent on the size of the adapting stimulus. In our experiments, the inclusion of the frontoparallel reference surround induces non-retinotopic slant adaptation to the frontoparallel plane, thus diminishing the SAE due to the center stimulus for conditions in which the background was presented. Also, the adaptation stimulus we used was far smaller than used elsewhere in literature (Adams et al., 2001; Berends et al., 2005; Taya et al., 2005), leading to a smaller binocular SAE.

The SAE data of Berends et al. (2005) have sometimes been interpreted as showing that it is perceived slant that adapts. Our results, combined with those of Berends et al. (2005), show that it is not perceived slant that adapts, and position the site of disparity-slant adaptation after eye posture incorporation, but before slant signals are integrated for the awareness of slant: multiple slant signals adapt independently. It remains to be seen whether similar reasoning applies to the results of Domini et al. (2001).

6.5. Physiology

We found that monocular perspective and binocular disparity cues were simultaneously adapted in opposite directions after viewing a slant rivalry stimulus (Fig. 4). This suggests the separation of the different cues' channels as distinct from a putative high-level cue independent slant channel. We reasoned that the switch between the two percepts would occur before information reaches the cue-independent slant channel, but after slants based on either cue alone have been resolved. In slant rivalry the slant information based on the two cues separately is relatively well elaborated before it enters the process of slant rivalry. A division of stimulus-related and percept-related channels is supported by recent physiological findings. Welchman, Deubelius, Conrad, Bulthoff, and Kourtzi (2005) have used a stimulus akin to ours, and found that fMRI signal in lower visual cortical areas correlates well with the stimulus parameters, whereas higher visual cortical areas such as lateral-occipital (LOC) and medial temporal (MT+/V5) cortex show higher correlations with perceived slant or depth structure. Brouwer, van Ee, and Schwarzbach (2005) reported that during slant rivalry fMRI activation correlating with alternations towards the disparity-dominated percept was found in a number of visual areas, including dorsal visual areas V3A, V7, V4d-topo and visual areas MT+ and LO. No activation was found for alternations towards the perspective-dominated percept. Two relatively high areas have been targeted by neurophysiologists using single-cell recordings in macaque. These areas are located in parietal and temporal cortex, part of the dorsal and ventral stream, respectively. The caudal intraparietal area (CIP) was found to contain neurons that are selective for slant from both monocular and binocular cues by Tsutsui, Jiang, Yara, Sakata, and Taira (2001), Tsutsui, Sakata, Naganuma, and Taira (2002), Tsutsui, Taira, and Sakata (2005). The same role was found to be played by neurons in the inferior temporal (IT) cortex (Liu, Vogels, & Orban, 2004). In both these areas, activity correlates with the presentation of slant independent from the cues that produce it. Of these two areas, IT is likely more involved in the use of disparity gradients (Janssen, Vogels, Liu, & Orban, 2001; Janssen, Vogels, & Orban, 1999, 2000) and monocular depth cues as a means to establish object selectivity. CIP, being part of the dorsal stream, is more involved in the appreciation of depth as a means to guide action and visual field segregation.

Interesting questions remain, for instance how these areas interact, and how different stimulus cues serve to stimulate them differentially. Investigating these areas under conditions of mentally selected slant (such as possible in the slant rivalry paradigm) might reveal answers to these open questions.

7. Conclusions

Slant perception and its voluntary control did not govern the SAE for either monocular or binocular signals. There was relatively small cross-cue SAE. We conclude that slant specified by single cues is elaborated at relatively low and cue-dependent levels, and that perceptual switching between the two possible slant rivalry percepts occurs above these levels in the visual processing hierarchy.

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