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Brain Research 944 (2002) 56–64

BRAIN RESEARCH

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Research report

Multi-directional shifts of optokinetic responses to binocular-rivalrous motion stimuli

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Accepted 28 March 2002

Abstract

Previous dichoptic experiments showed that dissimilar stationary pattern stimuli resulted in the perception of binocular rivalry, whereas oppositely-directly moving grating stimuli resulted in alternating optokinetic nystagmus (OKN) and the perception of binocular motion rivalry. The present study extended these dichoptic motion experiments by introducing obliquely-oriented targets with the aim of probing further the cortical mechanisms underlying binocular processing of motion. Two-dimensional eye movements were recorded along with their subjective perceptual responses. The stimuli consisted of two tilted gratings, one moving diagonally upwards and to the right (UR, 45°) and the other diagonally upwards and to the left (UL, 135°), which were presented dichoptically to subjects under two stimulus modes. For the non-exchange mode, the OKN slow phases exhibited three types of directional shifts. Two of these directional shifts tracked the stimuli (i.e. UR or UL), whereas the third moved purely upwards (UP). Since physically there was no upward-moving target, the OKN and perceptual responses appeared to be associated with a perceptual interocular grouping of the two dichoptic stimuli in their reassembled vector-sum direction. The OKN shifts were also found to be highly correlated with the psychophysical responses of motion perception. For the rapid-exchange mode, in which the stimuli were rapidly exchanged between the two eyes, the OKN slow phases exhibited primarily two types of directional shifts, UR and UL, but no UP responses for most subjects. It also appeared that these two coherent motion percepts, UL and UR, were interocularly regrouped from the exchanged stimuli. Moreover, the lack of perceptual grouping to create an UP response in the rapid-exchange mode indicated that temporal integration of at least 200 ms was necessary for the development of a reassembled vector-sum-direction motion percept. The findings under both stimulus modes support the stimulus–feature rivalry hypothesis, in which higher cortical centers mediate interocular perceptual grouping and the associated motor response.

Theme: Motor systems and sensorimotor integration

Topic: Oculomotor system

Keywords: Binocular rivalry; Eye movement; Optokinetic nystagmus; Multi-directional OKN; Interocular grouping

1. Introduction

Previous studies have shown that stationary images presented dichoptically to the two eyes resulted in competition for perceptual dominance so that one image was visible while simultaneously the other was suppressed, and often the percept alternated between the two images [2]. Similarly, dichoptically-presented gratings moving in opposite directions resulted in both the perception of motion in one or the other direction, often alternating between the two directions, as well as optokinetic nystagmus (OKN), which is a series of involuntary eye movements that consist of slow phases for tracking the pattern and fast phases for resetting the eye position [4]. A high correlation was found between the direction of OKN slow phase and the perceived direction of motion [5,8,15,28,29]. For both stationary and moving stimuli, the resultant competition

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0006-8993/02/$ – see front matter
PII: S0006-8993(02)02706-3

between the two dichoptically-presented stimuli for perceptual dominance is called binocular rivalry [2,8,11–16].

Two primary hypotheses have been proposed to account for the findings. The *eye rivalry* hypothesis is based on the observation that interocular suppression occurred during binocular rivalry, where the suppressed eye suffered a general reduction in sensitivity [2,6]. Thus, under this hypothesis, binocular rivalry is considered to be due to competition for dominance between the two eyes, or two monocular-channel representations, with the signals from each monocular channel being represented in the ocular-dominance columns, or the monocular neurons, of the primary visual cortex. Support for this can be found in recent fMRI studies which showed that activity in the primary visual cortex (V1) was rivalry-related and that interocular competition mediated binocular rivalry [21,25].

The *stimulus–feature rivalry* hypothesis is based on the observation that the temporal characteristics of perceptual response were found to be the same under either normal rivalry with non-exchange stimuli or with rapid alternation of rivalry stimuli [14], indicating it is the stimulus features themselves, rather than the alternations of the stimulus patterns, that affected the perceptual response. In addition, two complementary patchworks of intermingled images presented dichoptically to the eyes resulted in two rivalrous coherent images that were reassembled from interocular groupings of portions of the stimuli [10,20]. Thus, under this hypothesis, binocular rivalry is considered to be due to competition between two perceived patterns, each being a coherent ensemble derived from various features in the two presented stimuli. Such processing would require higher cortical processing of the intermingled stimulus patterns. Indeed, this is supported by single unit recordings in monkeys and certain fMRI activity studies in humans that showed activities of many rivalry-related neurons in levels higher than V1 [12,17,24,26].

The purpose of this study was to extend the previous studies to explore further the cortical processing of binocular stimuli. Obliquely-moving grating stimuli were used under both non-exchange and exchange modes. Two-dimensional eye movements as well as psychophysical perceptual responses were recorded. The resultant triple-direction shifts in OKN and perceptual responses, with one of the responses being in the reassembled vector-sum direction, provided additional insight regarding the spatial and temporal requirements for interocular perceptual grouping, as well as higher-order cortical processing of complex dichoptic motion stimuli. These findings support the stimulus–feature rivalry hypothesis.

2. Materials and methods

2.1. Stimuli

Two sets of orthogonally-oriented gratings within circular patches (18° in diameter), one tilted 135° that moved upwards and to the right (UR, 45°), and the other tilted 45° that moved upwards and to the left (UL, 135°) (see Fig. 1), were generated synchronously by two personal computers and displayed on two screens. The luminances of the gratings were 0.22 cd/m^2 and 13.8 cd/m^2 for the black and white stripes, respectively. The spatial frequency was 0.5 c/deg and grating velocity was 12 deg/s. The subject viewed the two moving gratings dichoptically via a four-mirror stereoscope with fine alignment. The optical distance between the subject's eye and the stimulus was 57 cm.

In the non-exchange stimulus mode, the tilt and motion direction of the grating stimuli presented to the two eyes were fixed during the experimental trial, e.g. rightward tilted gratings moving UL (135°) for the right eye and leftward tilted gratings moving UR (45°) for left eye. On the other hand, in the exchange stimulus mode, the two moving stimuli exchanged periodically between subjects' eyes with a cycle time of 400 ms, 800 ms, 2 s, or 10 s (i.e. the two stimuli exchanged between the two eyes every 200 ms, 400 ms, 1 s, or 5 s).

2.2. Measurement of OKN eye movements

Two-dimensional OKN responses were measured using the magnetic scleral search coil technique [3,22,29]. An annulus of silicone rubber with an induction coil (Skalar Medical BV, The Netherlands) was adhered to the subject's right eye. The horizontal and vertical eye movements can be obtained simultaneously from the voltage generated in the coil. Eye movement signals were sampled at 100 Hz and stored on a PC for off-line analysis. The OKN slow phase in UL, UR or UP direction was determined by both horizontal and vertical components.

2.3. Subjects

Six volunteer subjects with normal or corrected-to-normal visual acuity and normal stereopsis participated in the experiments. The experimental protocol was approved by the Institutional Review Board at the Shanghai Institutes for Biological Sciences and conformed with the Declaration of Helsinki.

2.4. Procedures

The subject sat on a stable chair with a chin rest to stabilize the head movement. Sixty trials, each lasting 30 s, were performed for each of two stimulus conditions: the non-exchange mode and the rapid exchange mode. Eye movement calibration was performed at the beginning of each trial. In the ancillary psychophysical experiments, the correlation between the OKN slow-phase direction and the subjective motion perception was examined, the subjects were instructed to press one of three buttons (UL, UR or

UP) when they perceived UL, UR or UP motion; otherwise, they did not press the button. These responses were converted into four-level voltage signals and recorded, along with the eye movements, in a computer.

2.5. Data analysis

The data were processed using a PC, and the eye-movement time courses were graphically displayed on a monitor. The phase transition boundaries were determined via visual inspection of the horizontal and vertical OKN eye movement time traces. These boundaries were usually quite clearly seen since they often occurred during the quick-phases of the OKN. When the transition did not occur precisely during a quick phase movement, the boundary was estimated based on the change in overall response shape. Phase changes between UR and UL were identified by a change in the average level of the horizontal eye movement response (see Fig. 5), followed by a change in direction of the slow phase. The amplitude of horizontal eye movement amplitudes remained approximately the same. On the other hand, phase changes from either UR or UL to a purely vertical OKN response (UP) were identified by a change in average level of the horizontal eye movement response (see Fig. 1), followed by a substantial diminution of the horizontal component amplitude (<1 deg), concomitant with a dramatic increase in the vertical component amplitude (nearly double the amplitude during UR or UL responses). The temporal dynamics of the multi-directional shift of OKN was examined using autocorrelation analysis. Also, the duration distribution for each direction was calculated [7,8,18]. To quantify the durations of OKN in each direction, two definitions were specified. The directional OKN time was defined here as the total cumulative time while the OKN eye movement tracked in a certain motion direction. The percentage time of directional OKN was defined as directional OKN time divided by total trial time. The data for each direction were averaged and then analyzed using ANOVA.

3. Results

3.1. Non-exchange stimulus mode OKN experiments

For the two dichoptically-presented stimuli in the non-exchange mode, in which the stimulus grating moved in the UL direction for the right eye and in the UR direction for the left eye, all subjects exhibited OKN slow phase tracking in any one of three directions (UL, UR, and UP) over a few tracking phases of OKN, with a stochastic occurrence in any particular direction. Fig. 1 shows a trace containing triple-directional shifts in OKN. For the UL or UR OKN responses, the horizontal and vertical OKN components were approximately equal in speed, but the horizontal components for UL and UR were opposite in

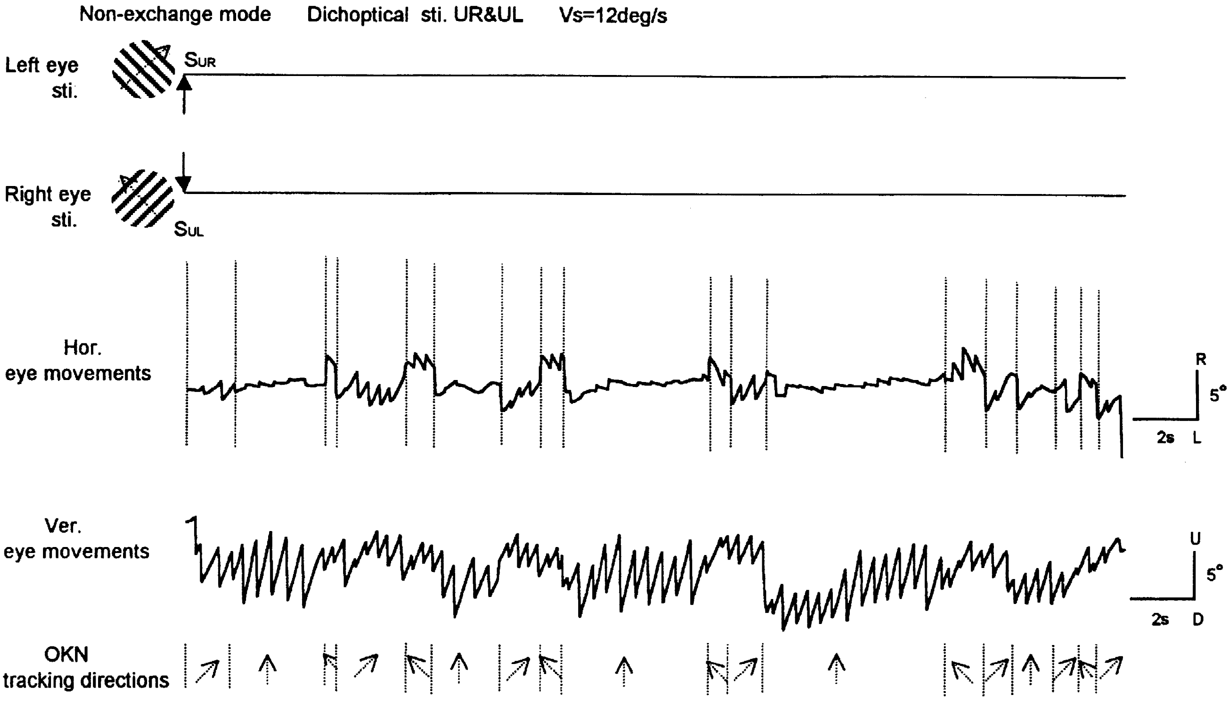

Fig. 1. Eye movement traces for non-exchange dichoptic motion stimuli. The circular patches show the stimuli that move upwards and to the right (S_{UR}) for the left eye and upwards and to the left (S_{UL}) for the right eye. Velocity, 12 deg/s. Sti, stimulus; UR, motion upward to the right; UL, motion upward to the left, and Vs, velocity of stimulus; Hor. and Ver. represent horizontal and vertical directions, respectively. R and L represent right and left, respectively, and U and D represent up and down, respectively. Time and eye movement calibrations are as indicated.

direction (as expected from the 45° and 135° stimuli motion directions). Whereas, in UP OKN response, the vertical component was approximately twice the speed compared to UL or UR OKN, while the horizontal component had zero amplitude.

The autocorrelation analysis of successive durations of slow phases was calculated for each subject, for lags 0–14 (where each lag represents one switching of the directional motion response during binocular rivalry). The correlation coefficients dropped to a small value (<0.1) even for one lag onward. The plot of autocorrelation coefficients, averaged for all subjects, is shown in Fig. 2A. These results indicated that the successive durations of the multi-directional shift of OKN were stochastically independent [7,8,14]. The normalized duration distribution for each directional OKN (UL, UR and UP) slow phase were fitted well with gamma distributions (Fig. 3). The cross-correlation coefficients between the experimental data and the theoretical curve of gamma distribution were greater than 0.98. The results from two statistical analysis procedures indicated that the successive durations of the multi-directional shift of OKN were stochastically independent, similar to the conclusion for the conventional binocular rivalry reported by previous studies [7,8,10,14].

The mean durations, relative frequency of occurrence and the percentage time of directional OKN, averaged for six subjects, are plotted in Fig. 4. Although the mean duration of UP was longer than UL or UR, due to the lower frequency of occurrence of UP than UL or UR, the percentage time of directional OKN turned out to be not significantly different for three directions, UL, UR and UP (F test, $F(2,15)=0.748$, $P>0.5$). These data demonstrated that the three directional components in the multi-directional shift of OKN have approximately equal contributions during binocular motion rivalry.

3.2. Exchange stimulating mode

For the shortest exchange period of 400 ms (stimuli exchanged every 200 ms), the directions of OKN slow phases tracked the two motion directions of UR and UL alternately, but it was difficult to elicit UP directional OKN (Fig. 5). For this rapid exchange cycle, the autocorrelation analysis of successive durations of slow phase OKN was calculated and shown in Fig. 2B. And the normalized duration distributions are plotted in Fig. 6. The cross-correlation coefficients between the experimental data histograms and the theoretical curve of gamma distributions were calculated (see Fig. 6, all $R^2>0.98$). The results of these two statistical analysis procedures indicated that the durations of directional OKN under rapid exchange stimulus mode were sequentially independent, similar to the characteristics of conventional binocular rivalry [7,8,10,14].

When the exchange cycle was 400 ms (stimulus changed every 200 ms), the UP motion response disappeared in nearly all the subjects, except one (JL), who had a residue UP component (less than 5 percentage time). When the exchange cycle was 800 ms (stimulus changed every 400 ms), the UP directional OKN were elicited in five of six subjects; when the exchange cycle was 2 s and 10 s, triple-directional shifts in OKN were elicited in all subjects. Mean duration and percentage time in different exchange cycles, averaged for the six subjects, are shown in Fig. 7. The percentage of UP directional OKN decreased with the shortening of the exchange cycle ($F(4,25)=33.58$, $P<0.001$). (Note that the very small residual decrease in percentage time of UP in exchange cycle of 400 ms resulted from only one of six subjects (JT).)

3.3. Psychophysical experiments

The subjective motion direction reported psychophysically was found to be highly correlated with the objectively recorded OKN directions. Fig. 8 shows a sample record from the non-exchange mode, where the horizontal and vertical eye movements are shown in the upper and middle traces, respectively. The dashed arrows

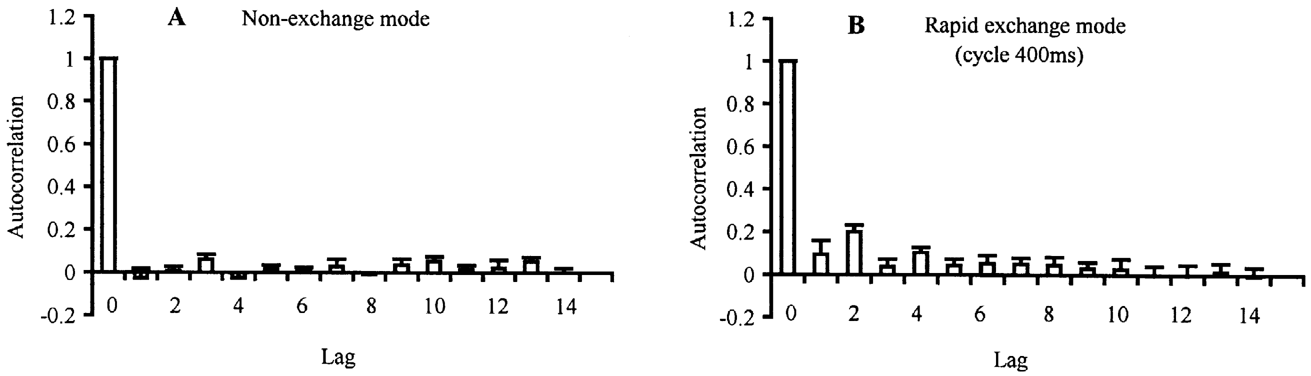

Fig. 2. Autocorrelation of the successive durations vs. lag (where each lag represents one switching of the directional response during the OKN shifts). All autocorrelation coefficients averaged for six subjects, error bars represent 1 S.E. (A) Data for dichoptic non-exchange motion stimuli; (B) data for rapid exchange stimuli in the cycle time of 400 ms.

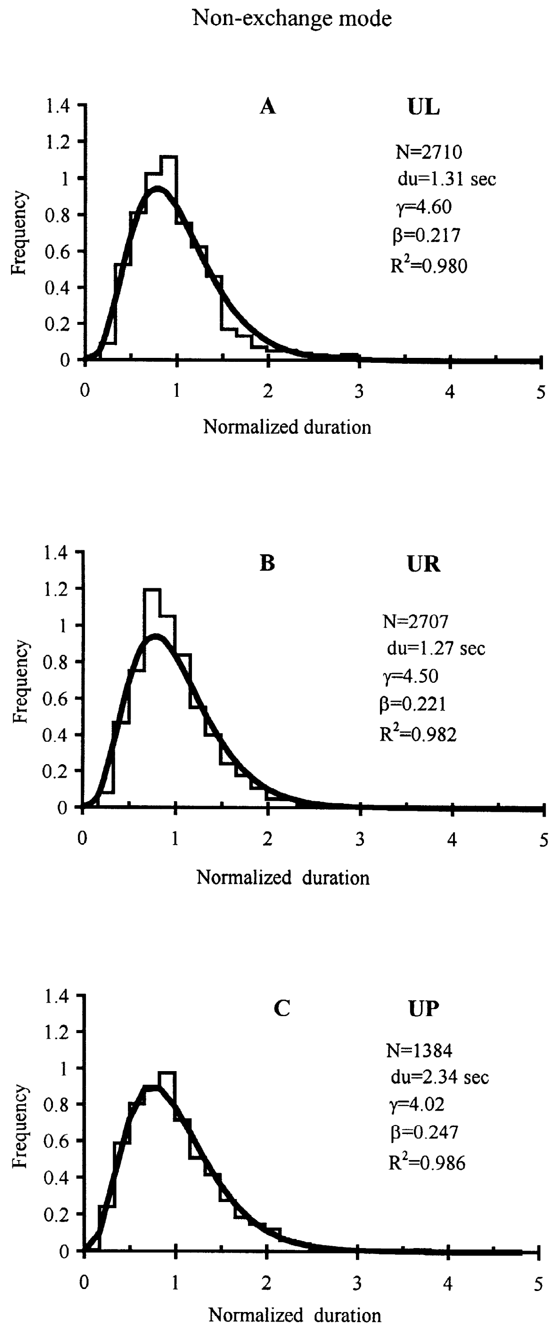

Fig. 3. Normalized duration distribution of non-exchange stimulus experiments compared with theoretical gamma distribution. The frequency histogram represents experimental data collected from six subjects. The smooth curve shows the theoretical gamma distribution, $f(x) = (\lambda^{\gamma}/\Gamma(\gamma))\, x^{\gamma-1} \exp(-\lambda x)$, where $\Gamma(\gamma) = (\gamma - 1)!$; UL, UR and UP marked in each plot are motion directions; parameters listed on the right corners: N, the number of durations in each motion direction; Du, the averaged duration in seconds; γ and λ (gamma and lambda), the parameters in the gamma distribution function; R^2, the crosscorrelation between the experimental data and the theoretical gamma distribution.

indicate the directions of OKN slow phase. The bottom trace shows the subjective perceived motion direction, in which the different levels represent the different directions as illustrated by the solid arrows. The cross-correlation function, $R(\tau)$, for UP directional OKN and the UP motion perception response was calculated. Its maximum correlation coefficient was higher than 0.93 at the delay value, τ_0, approximated to 0.42 s. The 0.42-s delay is consistent with the latency of the manual push button response [9]. The correlation functions for UR and UL motion were similar. Thus, there is a direct correspondence between the triple-directional shift of OKN and the multiple-state perceptual response. In the exchange mode, the directional OKN (UL or UR) was also highly correlated with the corresponding motion perception, where the maximum correlation coefficient was greater than 0.94 at about 0.20 s time delay.

4. Discussion

It was known previously that when oppositely-directed moving gratings were presented to the two eyes dichoptically, the eye movement response consisted of bi-directional alternating OKN that tracked the two opposite motion directions [5,8,15,28,29]. In the present experiments, we found that, in contrast to the previous binocular rivalry results, triple-directional shifts in the OKN response were elicited that corresponded with the shifts in motion perception. The directions of OKN slow phases that alternately tracked the three motion directions were: the two stimulus motions, UR and UL; and the vector sum direction, or pure upwards, motion (UP). The statistic analysis results (auto-correlation, and gamma distribution) for the OKN shifts are similar to those reported by previous studies on conventional binocular rivalry [7,8,10,14]. Therefore, the present OKN responses, characterized as stochastic triple-directional shift of OKN, reflect a multi-state competition in the binocular motion rivalry.

The results demonstrate that OKN eye movements track not only the original motion stimuli but also their combined motion (UP), which had not existed previously as a part of the physical stimulus. The explanation for the UP motion response is that there must have been an interocular grouping, or reassembling, of the two physical motion stimuli to provide a third coherent percept. The significance of such spatially interocular grouping is that this suggests higher cortical centers may be involved in processing the binocular signals. Such higher-order processing, in turn, supports the stimulus–feature rivalry rather than the eye rivalry hypothesis.

It is clear that switching of perceptual states occurs, but it is not so clear what causes the switching to take place. Lumar et al. [17] found that fMRI activity related to rivalrous perceptual transitions take place in the extrastriate visual area 19 and in the inferior and superior parietal and inferior frontal cortex of the right hemisphere. Thus, the right frontoparietal cortex may play a role in the selection of neuronal responses that lead to conscious perception [17]. The notion that the two hemispheres play

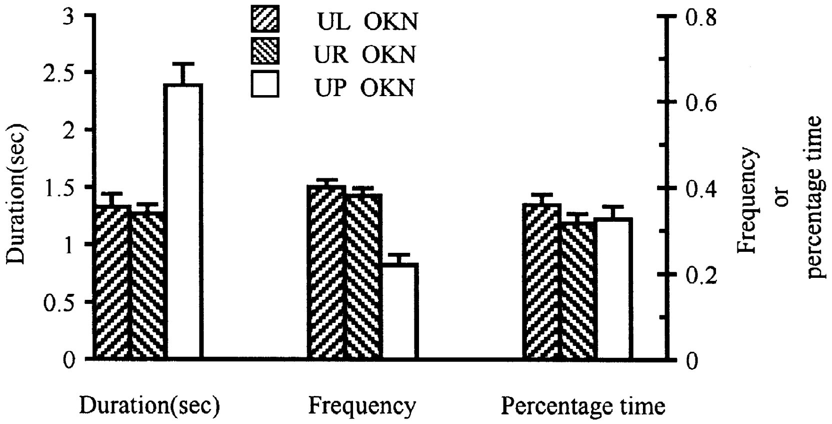

Fig. 4. The mean duration, occurring frequency and percentage time for UL, UR and UP directional OKN under the non-exchange stimuli. Data averaged for six subjects. Bars with rightward-tilted hashes for UL motion, and leftward-tilted hashes for UR; empty bar for UP; error bars for 1 S.E.

different roles in perception was further demonstrated in the cortical stimulation experiments by Miller et al. [19]. They found that left cortical stimulation using either right-ear caloric or direct left-cortical transcranial magnetic stimulation resulted in a significant change in the predominance ratio of the V/H, or the vertical-leftward tilted grating (left eye target) to the horizontal-rightward tilted grating (right eye target). On the other hand, right cortical stimulation as well as non-stimulation control experiments showed no significant change. Miller et al. [19] have proposed that perceptual views are held separately in the two hemispheres, and that interhemispheric switching results in changes in the perceptual state. However, their hypothesis does not address the crucial question of how a hemisphere adopts one of the two dissimilar stimuli, which are both available in each hemisphere [23]. Also, it does not explain our results, in which a third direction of motion (UP) is perceptually seen instead of one of the two rivalrous motion percepts (UL or UR) that would have been expected to be represented in the two separate hemispheres.

Previous investigations showed that viewing dichoptically stationary dissimilar patterns within a large visual field results in alternating periods of exclusive visibility of one

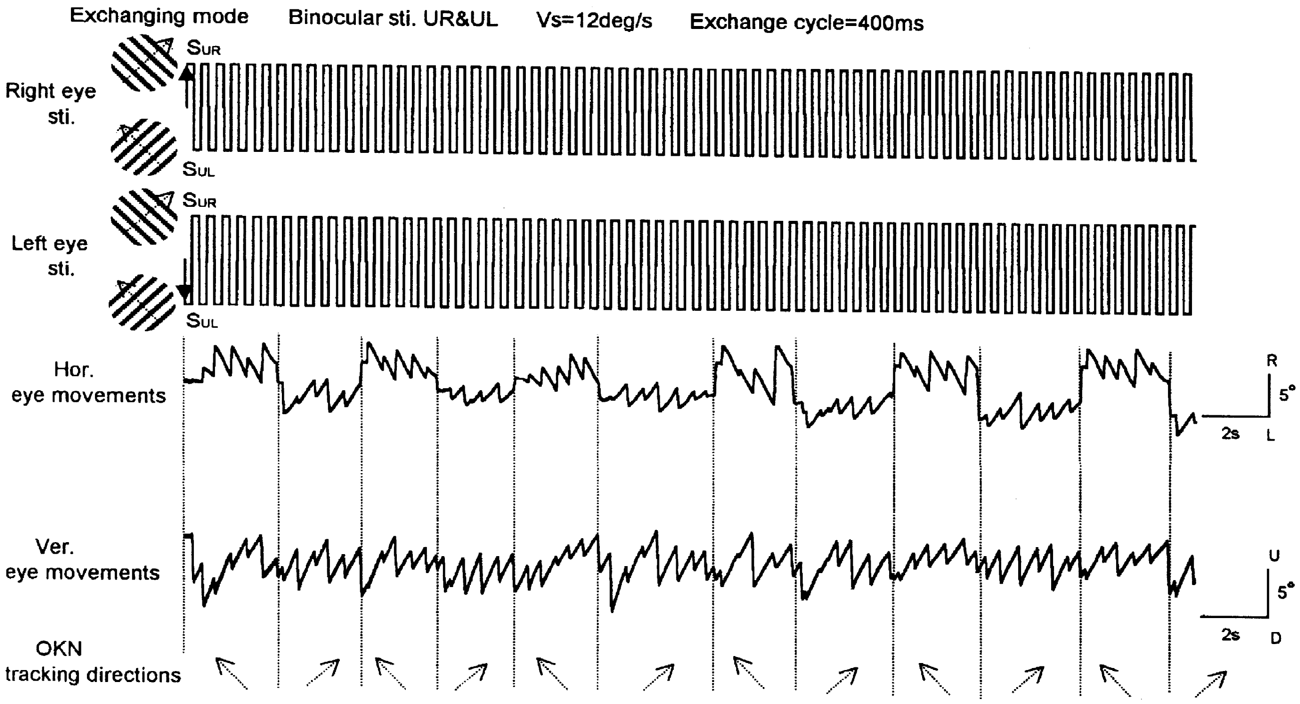

Fig. 5. Eye movement traces for rapid exchange stimuli experiments (in the cycle time of 400 ms). The circular patches represent stimuli that move upwards and to the right (S_{UR}), and upwards and to the left (S_{UL}). The two stimuli are presented to the subject's eyes dichoptically, and exchanged periodically between the subject's two eyes. Velocity, 12 deg/s. Bold arrows indicate the start of the stimuli. All labels are the same as in Fig. 1.

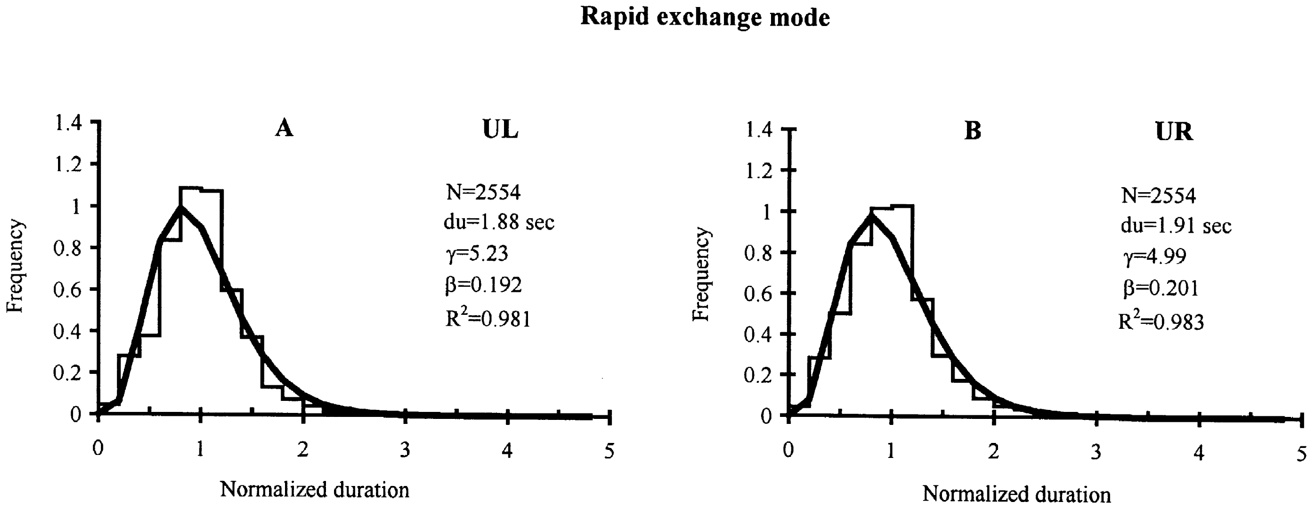

Fig. 6. Normalized duration distribution of rapid exchange stimuli experiments compared with theoretical gamma distribution. The exchange cycle time is 400 ms. All labels are the same as in Fig. 3.

or the other eye's view, interspersed by a mosaic-like collage ('piecemeal rivalry') consisting of different portions of each eye's stimulus pattern [10,20]. In our experiments (stimulus gratings moving at the speed of 12°/s), subjects perceived mosaic-like motion only in rare instances. Besides UL and UR stimulus motion gratings, there was the perception of an upwards-moving pattern shaped like a stack of 'Λ' or 'V' during the period of UP OKN. This indicates that motion perception in binocular rivalry may be ruled by the global spatial characteristics either from the full- or half-visual field. Considering that the percentage of cumulative time for each directional OKN (UL, UR and UP) is approximately equal to one third of the total time (see Fig. 4), the resultant global percept (UP) is strong enough to compete equally with the physically moving stimuli (UL and UR). In contrast, the perception of stationary images in binocular rivalry appears to be controlled by localized spatial features, resulting in piecemeal rivalry between mosaic images [10,20]. This suggests that different neural control strategies may be used to process global (form and motion) as compared to local (form alone) features.

Further evidence can be found in the exchange stimulus mode: when the rapid exchanging of UL and UR stimuli (in 400 ms cycle time) between two eyes resulted in the alternation of UL and UR motion responses. This indicated that interocular grouping occurred to cluster two temporal-intermingled motion stimuli into two coherent motion percepts (UL and UR) for competition. Thus, this result further supported the hypothesis of stimulus–feature rivalry.

On the other hand, the percentage time for the UP response decreased with the shortening of the exchange cycle, and finally the UP response disappeared for the

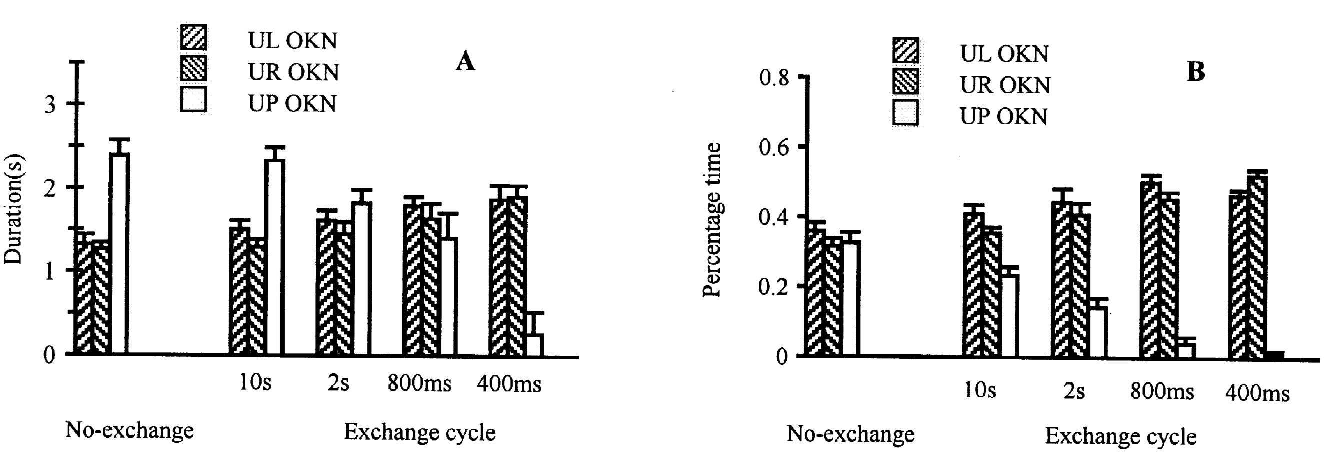

Fig. 7. The mean duration and percentage time for UL, UR and UP directional OKN for the experiments of the exchange stimulus mode (A) for mean duration; (B) for percentage time. The exchange cycle time, 10 s, 2 s, 800 ms and 400 ms marked below the abscissa; the non-exchange data are plotted on the left panel for comparison. All data averaged for six subjects. All labels are the same as in Fig. 4.

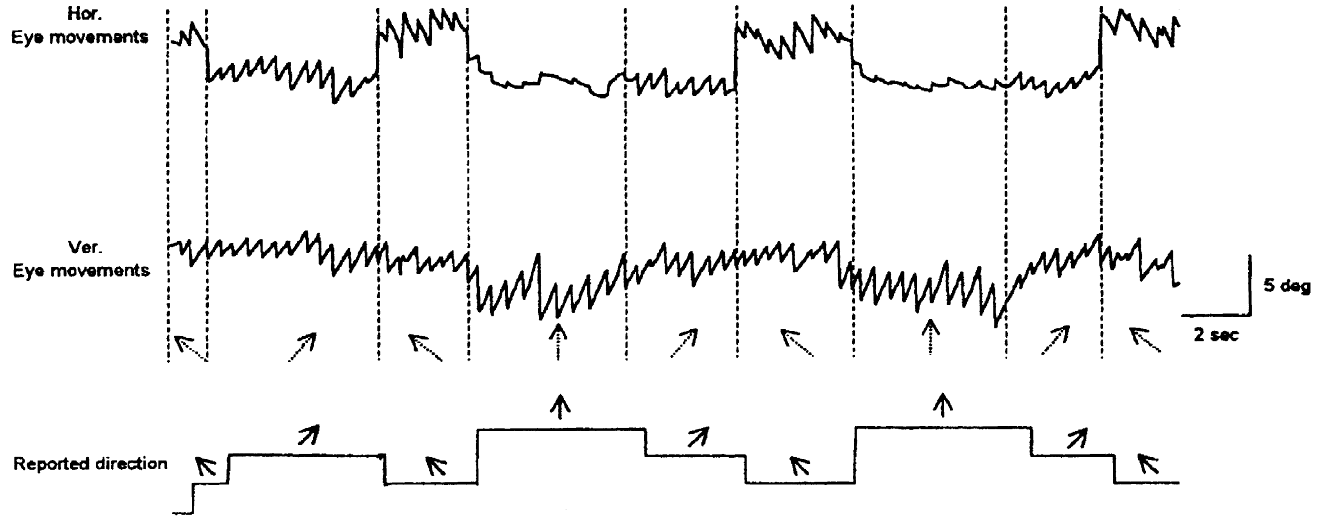

Fig. 8. A sample record of the subjective motion perception and objective OKN shifts for dichoptic motion stimuli. The grating moving upwards and to the right (S_{UR}) is presented to the left eye, while the grating moving upwards and to the left (S_{UL}) is presented to the right eye; horizontal and vertical eye movements are shown in the upper and middle traces, respectively; the dashed arrows show the directions of OKN slow phase; the bottom trace shows psychophysical responses (via push button signals) pressed by subject to report the perceived motion directions, where the different levels represent different directions as illustrated by the solid arrows.

cycle time of 400 ms (stimulus duration of 200 ms) (see Fig. 7). The lack of the UP response suggests that a minimum temporal integration time (about 200 ms) was required for reassembling two directional motion stimuli into a third coherent motion percept (UP).

Summing up the phenomena obtained from two stimulus modes, it could be supposed that, during binocular rivalry, interocular grouping involves two different processes. One is the spatial reassembling, or regrouping, of two non-exchange obliquely-moving stimuli (UL and UR) into a third motion percept (UP) that is in a different direction. The other is the temporal clustering, or regrouping, of two rapid-exchange motion stimuli into two coherent motion percepts (UL and UR). This implies that the brain has different schemes to group possible coherent percepts from rivalrous stimuli according to the stimulus features. To probe the fine spatial and temporal characteristics of this interocular grouping would require further experimental investigations with manipulated stimulus design, such as the rivalrous moving stimuli constructed by intermingled mosaic patterns (reference to the stationary rivalry experiment [10,20]).

Previous psychophysical study has found an approximately equal distribution of perceived combined (~50%) and non-combined individual stimuli (~50%) [1]. This is different from our results, which showed a nearly equal distribution for perception of each stimulus motion and the combination motion (UL, UR and UP). This discrepancy probably comes from differences in experimental designs. For instance, a short time (1.5 s) of presentation was employed in their experiment trial, whereas we employed 30 s for each trial, in which the binocular rivalry responses would occur more naturally. In addition, the velocity of moving gratings in their experiment was very low (0.25 deg/s) as compared to ours (12 deg/s, which is easier for evoking OKN eye movements). Moreover, such a difference in stimulus velocity may evoke different motion channels (slow and fast, respectively) to result in different binocular rivalry effects [27].

Significantly, in contrast to previous studies, our stimuli were able to elicit triple-directional shifts in the OKN and perceptual responses that provided new insights regarding binocular visual processing. This suggests that our new spatial and temporal stimulus configuration can serve as a paradigm for eliciting important aspects of the response under binocular rivalry.

The complex processing of stimuli under binocular rivalry may be conceptualized as a multiple-state control model. For example, the processing may proceed as follows: for the dichoptic stimuli, the visual perceptual system clusters and reassembles all inputs into several possible coherent percepts according to the stimulus features, and perhaps also to different perceptual experiences. Also, moving stimuli need to be processed by the cortical motion centers (e.g. MT). When a perceived candidate emerges, a match is made between this candidate and the visual stimuli. If the discrepancy, or error, between the candidate and dichoptic stimuli is above a certain threshold, the perceptual system removes this candidate and switches to another. On the other hand, if the discrepancy is below the threshold, then binocular fusion would take place without rivalry. This successive control process, and the switching in conscious perception, is what we have come to know as binocular rivalry. Therefore, this multiple-state control model provides a systematic scheme for processing the stimulus features at various cortical areas and producing the stimulus–feature dependent rivalry in the final percept.

Acknowledgements

The authors are grateful to Lingyu Chen, Xinzhen Zhao and Cunguo Wang for their help in the data processing. This study was supported by the National Natural Science Foundation of China and the National Basic Research Program of China (G1999054000).

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