PsyCh Journal
INSTITUTE OF PSYCHOLOGY Chinese Academy of Sciences
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PsyCh Journal **10** (2021): 499–507
DOI: 10.1002/pchj.438

The growing sensory suppression on visual perception during head-rotation preparation

Xue Dong ,[1,2] and Min Bao [1,2,3]

[1]CAS Key Laboratory of Behavioral Science, Institute of Psychology, Chinese Academy of Sciences, Beijing, China, [2]Department of Psychology, University of Chinese Academy of Sciences, Beijing, China, [3]State Key Laboratory of Brain and Cognitive Science, Institute of Psychology, Chinese Academy of Sciences, Beijing, China

Abstract: Sensory perception is often impaired by self-generated movements. This effect of sensory suppression has been commonly observed in voluntary hand-movement-induced tactile sensation during the period of motor preparation and execution. However, it remains unclear whether such suppression also occurs in the visual domain and if it can be induced by the preparation of other body movements. To extend our knowledge about sensory suppression, the present study investigated visual sensitivity during the preparation of head rotation. Participants wore virtual reality goggles and rotated their heads horizontally according to a visual cue presented on the goggles screens. Before the start of head rotation, a target of Landolt C was displayed at a peripheral location that was directed by the head-rotation cue or a symmetric location in the opposite visual field. After each head rotation, participants reported the target's orientation, allowing the measurement of the discrimination threshold. Besides, the discrimination sensitivity was also measured in two head-still conditions with or without the presentation of a visual cue. The results showed that the discrimination performance was largely impaired by the preparation of head rotation. This effect of sensory attenuation increased with the approach of head-motion onset. However, the attenuation was not found on the discrimination of auditory stimuli during the preparation of head rotation, thus excluding the account of general dual-task requirement. In contrast to the previous findings of improved perception by preparation of saccade or reach, our findings indicate that sensory suppression rather than attention shift plays a major role during the preparation of head movement.

Keywords: head rotation; motor preparation; sensory suppression; visual perception
Correspondence Dr. Xue Dong or Professor Min Bao, Institute of Psychology, Chinese Academy of Sciences, 16 Lincui Road, Chaoyang District, Beijing 100101, China. Email: dongx@psych.ac.cn (X.D.) or baom@psych.ac.cn (M.B.)
Received 26 April 2020. Accepted 20 January 2021.

Sensory changes induced by voluntary action are less intense than those caused by external stimulation. This phenomenon, known as sensory suppression, is explained by an internal model of motor control (Wolpert, Ghahramani, & Jordan, 1995). The model assumes that the efference copy of motor command to the muscles is used to predict the consequence of voluntary movements. If the prediction matches the sensory feedback, the sensory effect of self-motion is canceled (Wolpert, 1997), leading to the attenuation of sensation. Recent investigations suggest that sensory suppression occurs not only during voluntary movements but also in the preparation period (Baess, Widmann, Roye, Schröger, & Jacobsen, 2009; Bays, Flanagan, & Wolpert, 2006; Chapman & Beauchamp, 2006; Chapman, Bushnell, Miron, Duncan, & Lund, 1987; Gertz, Voudouris, & Fiehler, 2017; Juravle, Deubel, & Spence, 2011; Juravle & Spence, 2012; Timm, SanMiguel, Keil, Schröger, & Schönwiesner, 2014). However, the findings are primarily on tactile and auditory perception induced by hand movement or finger press. There are fewer studies in the visual domain.

Previous studies have revealed that the responses to visual stimuli during eye movements are inhibited (Castet & Masson, 2000; Duffy & Lombroso, 1968; Latour, 1962; Ross, Morrone, Goldberg, & Burr, 2001; Troncoso et al., 2015), which is considered to help maintain a stable perception when one moves (Wallach, 1987; Wurtz, Joiner, & Berman, 2011). This inhibition is consistent with the account of sensory suppression. However, the findings on the preparation period of eye movements display another pattern—discrimination of the targets of saccade is not impaired but even improved during saccade preparation (Deubel, 2008; Deubel & Schneider, 1996; Harrison, Mattingley, & Remington, 2013; Rolfs & Carrasco, 2012; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). This enhancement is often explained by the theory that attention shifts to the target location prior to saccade (Deubel, 2008; Rizzolatti, Riggio, & Sheliga, 1994; Rolfs et al., 2011; but see Rolfs & Carrasco, 2012).

Another kind of self-generated movement that may cause the change of visual perception is head movement. Bai, Bao, Zhang, and Jiang (2018) found a significant reduction of motion aftereffect from voluntary head-rotation-induced retinal motion. Moreover, similar suppression was also observed during passive head movements. This finding is different from sensory suppression, which is more profound during voluntary actions (Chapman et al., 1987; Juravle & Spence, 2012; Timm et al., 2014). Unlike eye movements, voluntary head movements require the cooperation of the motor system and several large muscles. In addition to the effect on vision and proprioception, head movements also stimulate the vestibular system, which makes it distinct from other body movements. What about the visual process during head-movement preparation? Unfortunately, except for a few studies testing reaction speeds to visual stimuli that appear in the preparation period of head movement (Cicchini, Valsecchi, & de'Sperati, 2008; Kaliuzhna, Serino, Berger, & Blanke, 2019), there is a lack of discovery on the perception of visual stimuli during head-movement preparation. Because of the important relevance of head movements to vision and the numerous differences between the motor control of head movements and other body movements, it remains to be tested whether one can deduce the effect of head-movement preparation on visual perception simply from the previous findings on eye movement preparation. For the first attempt, the present study aimed to address this issue.

One difficulty in exploring visual sensitivity during head-movement preparation is how to measure the latency of head movement and present visual stimuli in the preparation period accurately. A virtual reality (VR) approach developed by Bai et al. (2018) provides a solution. This VR system combines a head-mounted display (VR goggles) and a three-space sensor, allowing us to flexibly record head movements in real time and manipulate the presentation of visual stimuli accordingly. Wearing the goggles during the experiment, participants can rotate the head with relative freedom. The sensor fixed on the top of goggles can record head movements in pitch, yaw, and roll axis. Experimenters are thereby able to present stimuli on the screens of the goggles based on head-movement parameters using a customized computer program.

The current study thus adopted Bai et al.'s (2018) VR approach and a paradigm modified from the eye movement study of Deubel (2008) to investigate the effect of horizontal head-rotation preparation on visual sensitivity. Our experiments involved the most common head-rotation directions (leftward or rightward) and two corresponding target locations. Discrimination of stimuli presented on the left or right peripheral visual field was measured in the head-still conditions and prior to self-initiated leftward or rightward head rotations. If head-rotation preparation, like saccade preparation, can facilitate the perception at the destination location, better performance should be observed on discriminating targets appearing in the target visual field than in the opposite or in the head-still conditions. However, our results suggested that the head-rotation preparation did not produce extra attention shift to the cued location; rather, it led to a strong effect of sensory attenuation on visual discrimination. In addition, the closer it was to the onset of head rotation, the stronger the suppression was. Moreover, this impairment was not observed when participants were asked to discriminate the auditory stimuli during the head-rotation preparation, speaking against a general dual-task explanation.

Methods

Experiment 1

Participants

Eight volunteers (two males, six females, M_{age} = 22.13 years, age range: 19 to 26 years) participated in the experiment. Post hoc analysis using G*Power (Faul, Erdfelder, Buchner, & Lang, 2009) indicated that the current sample size provided a statistic power larger than 0.9. All the participants, except one of the authors, were naive to the experimental hypotheses. They all had normal or corrected-to-normal vision and provided informed consent. Experimental procedures were approved by the Institutional Review Board of the Institute of Psychology, Chinese Academy of Sciences.

Apparatus

The experiments were conducted using a VR device that Bai et al. (2018) developed. Stimuli were presented on Sony HMZ-T3 head-mounted goggles (60 Hz) which were fixed to a bicycle helmet (Figure 1B). Presentations on the goggles were controlled by a Dell XPS 8700 computer and programmed in MATLAB and Psychtoolbox-3 (Brainard, 1997). The goggle screen has a visual angle of 50° × 28° and a resolution of 1280 × 720 pixels. Before each session of the experiments, participants were asked to adjust the interpupillary distance and to position the goggles appropriately for the best clarity of viewing. Then they fastened the helmet and goggles to maintain constant visual clarity throughout the experiment. A three-space sensor (TSS-WL sensor, YEI Technology) was attached to the top of the helmet to record head movements in real time. Communications with the sensor were realized through a customized computer program.

Stimuli

A black circle fixation on the center of the screen and two peripheral gray circles (0.5° larger than the maximum size of target, 20° eccentricity) were presented throughout the experiments on a white noise background (see Figure 1A). Two black bars were displayed above and below each gray circle. The noise background and black bars moved at the same speed and amplitude but in the opposite direction with head rotation. The moving speed and visual angle were manipulated according to the head-motion parameters recorded by the sensor. These simulated the head-movement-induced retinal motion. The target was a Landolt C that was presented randomly in one of the peripheral gray circles.

Procedure

Reaction time measurements

To accurately present the visual target during the preparation period of head rotation, we first measured the reaction time (RT) of head rotation after a motion cue was presented and then estimated the average duration for head-rotation preparation. Participants wore the goggles and gazed at the central fixation where a cue would be presented. They were instructed to rotate the head to the cued direction.

At the start of a trial, participants faced forward and kept the head static. They could then press SPACE to start a trial. Simultaneously, the sensor recording (60 Hz) and the checking of head movements started. Normally, after a 700-ms interval of no head movement was detected in the last 333 ms, a white triangle, pointing to the left or right, would be presented on the center of the screen for 200 ms. Participants were required to rotate the head towards the cued direction for an amplitude of about 20° immediately

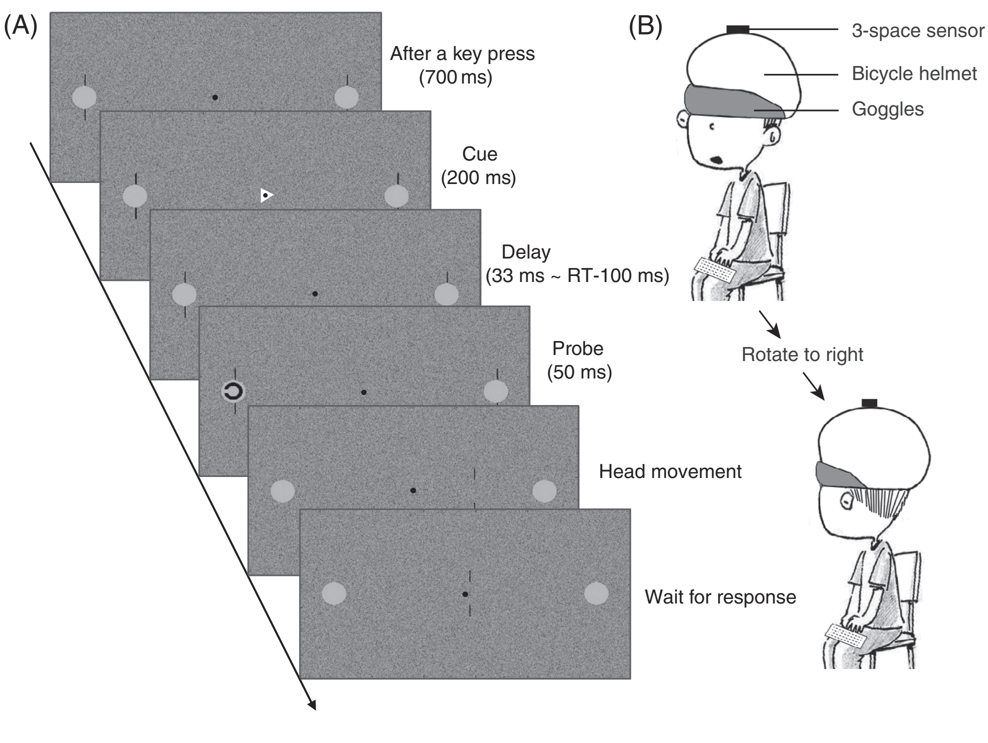

Figure 1. The procedure of a trial in head-rotation conditions of Experiment 1. (A) Stimuli presented on the goggles. (B) Participants wore the goggles during the experiments. A three-space sensor fixed to the top of the goggles recorded the head movements in real time. Participants pressed a key to start a trial. Immediately after the cue disappeared, they were required to rotate the head towards the cued direction. A response to the target orientation was collected after the head rotation.

after the triangle cue had disappeared. One hundred milliseconds after the cue offset, a Landolt C target (1.4°) was presented for 50 ms. Participants pressed the arrow key to indicate in which gray circle the target was presented once the head rotation was completed. Then the sensor recording stopped and participants could rotate the head back to face forward. One hundred trials were tested.

Since the background noise and black bars always moved in the opposite direction to head rotation (at the same speed), participants were also told to stop head rotation until the black bars on the cued location moved to the center of the screen, which corresponded to a rotation amplitude of 20°. Offline analysis on the rotation amplitudes showed that participants followed the instruction well. The mean amplitude of the rotation condition in the formal experiments was 20.48 ± 2.01°.

The RT was defined as the duration between the cue offset and the onset of head rotation. To identify the start of head rotation, we first calculated the velocity and acceleration of the head movement at each frame from the start of sensor recording. Movements at a velocity larger than 15°/s and acceleration larger than $50°/s^2$ (Fang, Nakashima, Matsumiya, Kuriki, & Shioiri, 2015) were then defined as "large movements." The onset of head movement was detected only when there were at least four successive large movements to the cued direction. This criterion was determined according to experiences and some preliminary analysis. If less than four successive large movements were detected, they were more likely to be slight quivers of the head. If a movement to the opposite direction was detected, the trial would be discarded. Finally, we calculated the mean RT from all the remaining trials.

Test of individual discrimination sensitivity

In some pilot experiments of this study, we found large individual differences in discrimination sensitivity. Thus, we asked participants to discriminate the Landolt C target and measured the individual discrimination threshold in a head-still condition before the formal experiments. During the test, participants kept the head stable and there were no motion cues. The target presentation was similar to that of RT measurements. The discrimination threshold was measured with a constant stimuli method. The maximum (2.5°–3.5°) and minimum (0.5°–1°) sizes of the target were predetermined and equally divided to seven levels. Each level was tested for 48 trials, half of which were presented in the left circle and the rest in the right one. Participants reported the orientation of the Landolt C target by pressing one of the arrow keys. The discrimination threshold at a correction rate of 71% was achieved by fitting a Weibull function.

Formal experiments

The individual discrimination threshold was then used in the formal experiments to estimate the discrimination performance when head rotation was required or not.

The test procedure was similar to the discrimination sensitivity experiment with the following differences. The test levels were determined with the thresholds measured in the sensitivity experiment, with twice the threshold as the maximum size and half the threshold as the minimum size. To present the target in the preparation period in a head-rotation trial, the probe was delivered 33 ms – RT-100 ms after the cue offset (Figure 1A). The RT used in the first session was acquired from the RT test. For the other sessions, the RT was calculated from the former one session. In addition, targets in half of the trials were presented in the gray circle to which the triangle cue pointed (congruent condition) and the others were presented in the opposite one (incongruent condition).

Participants completed the formal experiments in 2 days, with five sessions each day. A baseline session without head rotation and motion cues was performed first. Each level was tested for 24 trials in a session, resulting in 48 trials per level from all sessions. Then, four sessions with motion cues were finished. Each of these four sessions included two rotation and two non-rotation blocks. The two kinds of blocks were tested in the sequence of ABBA or BAAB. Each level was tested for six trials in a block and there were 96 trials/level from all sessions for each condition. Before every block, a message on the screen would remind participants whether they should rotate the head to the cued direction or ignore the cues. Participants had short breaks between each block and each session.

The threshold of the baseline condition and those in the congruent and incongruent conditions for the non-rotation trials were acquired by fitting the data with Weibull functions. As to the rotation conditions, we calculated the RT of each trial first. The trials were excluded from further analysis if participants rotated the head before the end of target presentation or to the false direction. On average, 4.67 ± 2.89% of the trials were discarded. Then we estimated the threshold for the congruent and incongruent conditions from the remaining trials. Moreover, the trials of two rotation conditions were also divided into three equal time bins to investigate the change of task performance with the approach of rotation onset. The time bins were individually determined for each participant according to the longest interval between target offset and head-rotation onset. There were about 30.63 ± 3.77 trials/level for the estimation of discrimination threshold of each time bin.

Experiment 2

As participants had two tasks (one perceptual task and one motor task) in the rotation condition but only one perceptual task in the non-rotation condition in Experiment 1, one may argue that the difference in the visual discrimination performance between the two conditions was likely caused by the dual-task requirement or divided attention in the rotation condition. We thus adopted an auditory task to test this alternative explanation as in Juravle and Spence (2011). A discrimination task to auditory stimuli rather than visual stimuli was performed during the preparation of head rotation. According to the internal model of motor control, if the deterioration of visual perception in Experiment 1 was due to sensory suppression applied on the information causally related to the head movement, we would expect no deterioration of auditory performance in Experiment 2 since self-generated head rotation would not induce causal changes on auditory perception in most cases of everyday life. However, if the general dual-task requirement or divided attention is responsible for the deterioration of visual perception, we would expect a similar attenuation on other perceptual tasks, such as the auditory task.

Participants

Eight volunteers (three males, five females, M_{age} = 22.88 years, age range: 19 to 28 years) participated in the experiment. All participants had normal hearing and were naive to the experimental hypotheses. Experimental procedures were approved by the Institutional Review Board of the Institute of Psychology, Chinese Academy of Sciences.

Apparatus

The experimental devices were the same as those in Experiment 1. Additionally, two loudspeakers were placed in front of the participants at a distance of 70 cm for the presentation of auditory stimuli. The volume of loudspeakers and the system were fixed the whole time.

Stimuli

The visual presentations in the goggles were same as those in Experiment 1 except that there were no visual targets. For the auditory task, we selected 72 Chinese characters based on four different tones in Chinese Mandarin. There were 18 characters for each tone. The Mandarin pronunciations of these characters were obtained through an online text-to-pronunciation app. Each character was pronounced by a female and a male reader, resulting in 144 auditory stimuli. The amplitude of each stimulus was normalized, and the duration was normalized to 183 ms.

Procedure

Practice of head rotation

The task was similar to the RT measurement in Experiment 1 except that an auditory stimulus would be presented 200 ms after the cue offset and participants responded to the gender of the voice after the head rotation. Seventy-two trials were finished.

Test of individual discrimination sensitivity

At first, participants practiced the auditory discrimination task for one session. Fifty trials were finished. The auditory stimuli were randomly selected from all the 144 lexical tone stimuli. Participants kept the head static and judged the tone by pressing a corresponding key. Since they all performed well when the lexical tone stimuli were presented alone (80.75 ± 3.54% correction, given that the chance level was 25%), we then added a white noise to the audio spectrum of each stimulus to increase the task difficulty. One or two sessions of the discrimination task with noise were finished. In the first session, the strength of noise was the same as the lexical tone stimuli. If the individual correction rate was around 50%, the participant would not take Session 2. Otherwise, he/ she would have to finish another session with adjusted noise strength. The adjustments were made by the experimenter according to the experience and the correction rate in Session 1. In this way, we roughly obtained a noise strength to which the participant could discriminate the tone with a medium correction rate when it was presented with the lexical tone stimuli. The individually determined noise strength would be used in the formal experiments, allowing us to observe any improvement or attenuation of the discrimination performance during head-rotation preparation.

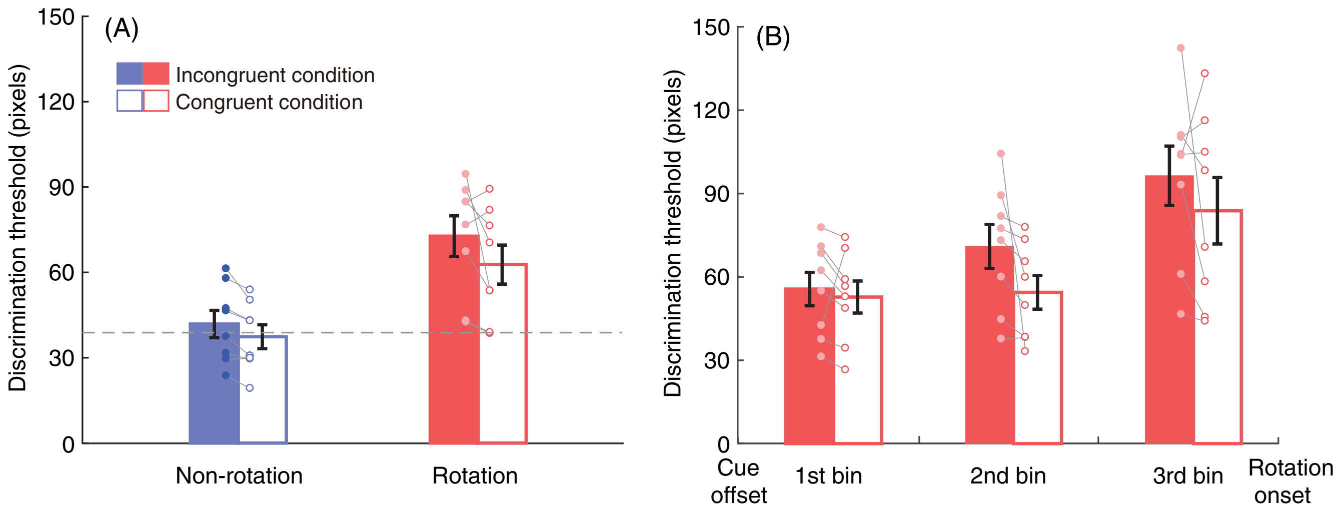

Figure 2. Results of Experiment 1. (A) The discrimination threshold of each condition. Dotted line represents the baseline threshold. (B) Trials of two rotation conditions were divided into three time bins. Thresholds of the first to third bin represent the discrimination of targets that appeared from the cue offset to the head-rotation onset. Error bars represent standard error of the mean.

Formal experiments

In the formal experiments, participants finished four blocks, two for the head-rotation condition and two for the non-rotation condition. Each block contained 72 trials. Each of the 144 lexical tone stimuli was presented once in a random order in the two blocks of rotation and non-rotation trials. All auditory stimuli were presented 200 ms after the cue offset. The task procedure was similar to that in the head-rotation practice session except that the perceptual task was to discriminate the tone of each auditory stimulus, which was presented with white noise.

Results

Experiment 1

When head rotation was not required, participants had a better discrimination sensitivity for the targets presented on the cued location than those on the uncued location, $t(7) = 3.79$, $p = .007$, Cohen's $d = 0.35$ (Figure 2A). However, there was no significant difference between the baseline condition and either of these two conditions: baseline versus congruent condition (non-rotation), $t(7) = 0.55$, $p = .596$, Cohen's $d = 0.11$; baseline versus incongruent condition (non-rotation), $t(7) = 0.97$, $p = .364$, Cohen's $d = 0.21$.

When head rotation was needed, the preparation of head rotation significantly impaired task performance. The discrimination thresholds were much higher than baseline in both head-rotation conditions: baseline versus congruent condition (rotation), $t(7) = 2.93$, $p = .022$, Cohen's $d = 1.39$; baseline versus incongruent condition (rotation), $t(7) = 5.15$, $p = .001$, Cohen's $d = 1.91$. We also performed a repeated-measurements analysis of variance (ANOVA) on congruency (congruent vs. incongruent) and motor preparation (rotation vs. non-rotation). The results disclosed significant main effects of congruency, $F(1, 7) = 8.50$, $p = .022$, $\eta^2 = .55$, and motor preparation, $F(1, 7) = 30.72$, $p < .001$, $\eta^2 = .81$, but no significant interaction between these two factors, $F(1, 7) = 0.91$, $p = .372$, $\eta^2 = .12$. Thus, the preparation of head rotation had a strong impairment on visual discrimination, but it did not produce extra attention shift.

Further, we analyzed how the performance changed as the time approached the onset of head rotation (Figure 2B). The 2 (congruency) × 3 (time bins) repeated-measurements ANOVA revealed a significant main effect of time bins, $F(2, 14) = 31.06$, $p < .001$, $\eta^2 = .82$. The discrimination sensitivity became worse for the time bin closer to the onset of head rotation. However, the main effect of congruency did not reach significance, $F(1, 7) = 2.64$, $p = .148$, $\eta^2 = .27$, which might be due to fewer data after the trials were divided into different time bins. The interaction between two factors was also not significant, $F(2, 14) = 1.29$, $p = .307$, $\eta^2 = .16$.

Experiment 2

We then tested the auditory sensitivity when head rotation was required or not (Figure 3A). The accuracy of

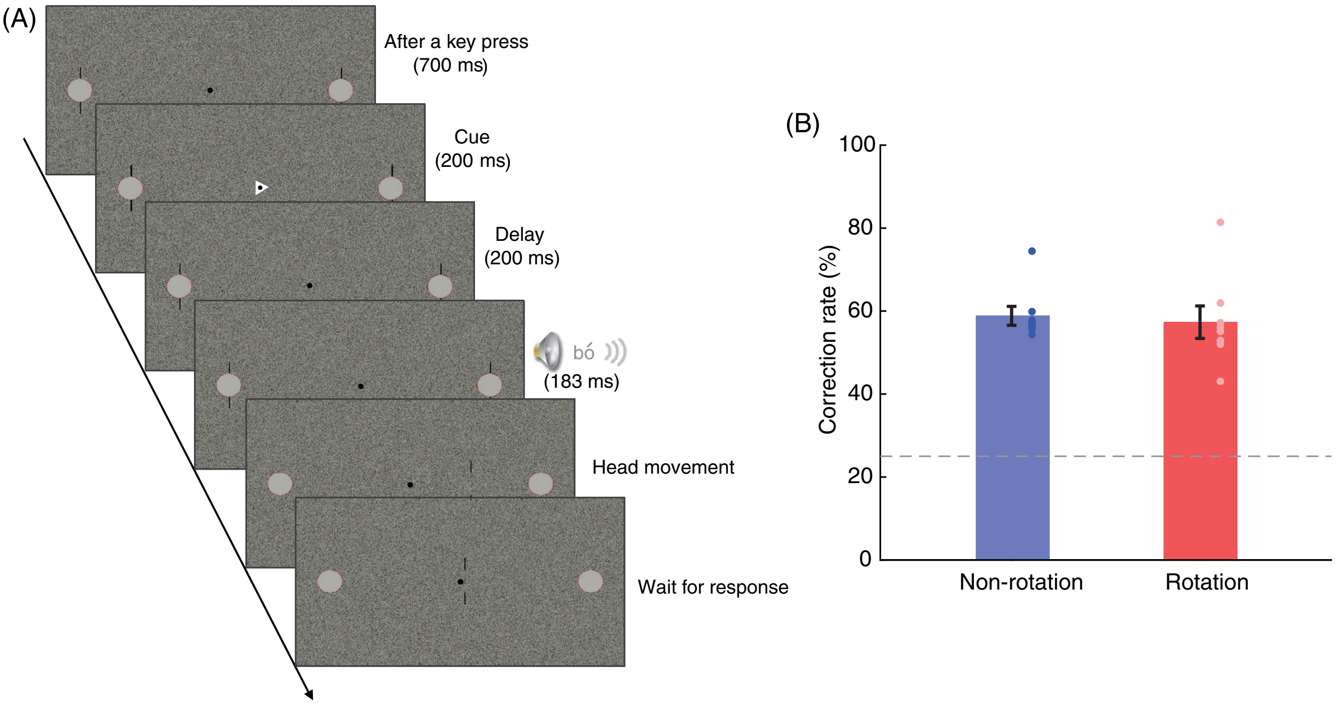

Figure 3. The procedure and results of Experiment 2. (A) An example of the sequence of a trial in the head-rotation condition. Participants were asked to discriminate the tone stimulus that was presented with white noise during the preparation period of head rotation. (B) The correction rates of discriminating lexical tone in non-rotation and rotation conditions. Dotted line represents the chance level (25%).

discriminating lexical tone was 58.85 ± 6.45% in the non-rotation condition and 57.32 ± 11.07% in the rotation condition (Figure 3B). Both were much higher than the chance level (25%), non-rotation: $t(7) = 14.85$, $p < .001$, Cohen's $d = 7.42$; rotation: $t(7) = 8.26$, $p < .001$, Cohen's $d = 4.32$. Comparison of the accuracies of the two conditions revealed no significant difference, $t(7) = 0.71$, $p = .503$, Cohen's $d = 0.17$. Therefore, head-rotation preparation did not affect auditory sensitivity.

Discussion

Using a VR device, our first experiment investigated visual perception during the preparation of head rotation. The results showed significant impairment on discrimination sensitivity in the rotation conditions. The findings can be well explained by the phenomenon of sensory suppression that voluntary action causes suppression of the information causally related to the movement itself. Alternatively, the impaired performance in the rotation condition might be due to the dual-task paradigm since participants had both a visual discrimination task and a head-movement task in the head-rotation conditions but only a visual discrimination task in the non-rotation conditions. However, this alternative explanation is not supported by the results of Experiment 2 where head-rotation preparation did not affect the performance of auditory discrimination. Besides, in Experiment 1, we found a better performance when the target was presented at the visually cued location (Posner, 1980), which, however, was regardless of whether the head was going to rotate or not.

By analyzing the time course of discrimination threshold during the head-rotation preparation, we found that the impairment became stronger with the approach of rotation onset. This pattern further supported that visual perception was suppressed by motor intention and preparation. However, our results were inconsistent with some findings on saccade preparation (Deubel, 2008; Deubel & Schneider, 1996; Harrison et al., 2013; Rolfs et al., 2011; Rolfs & Carrasco, 2012) and reach movement preparation (Rolfs, Lawrence, & Carrasco, 2013; Stewart & Ma-Wyatt, 2015), since those lines of research generally report improved sensitivity during motor preparation. This effect is often explained by attention shift to the target prior to motion onset. What causes the distinct influences on visual sensitivity between the saccade (or reach) preparation and head-movement preparation? One detail should be noted. The target location of the motor task was identical to that of the perceptual task in the studies that found enhanced perception during the motor preparation. However, this is not the case in the studies where sensory suppression was observed (Chapman & Beauchamp, 2006; Juravle et al., 2011; Juravle & Spence, 2012). Deubel and Schneider (1996) revealed that the discrimination performance was the best when the target of motor action and perceptual tasks coincided. Thus, it is possible that the representations of visual targets could be largely spared from sensory suppression due to the precise coincidence of the targets for motor and perception in the saccade and reach preparation studies (Deubel, 2008; Deubel & Schneider, 1996; Harrison et al., 2013; Rolfs & Carrasco, 2012; Rolfs et al., 2011; Rolfs et al., 2013; Stewart & Ma-Wyatt, 2015). In our experiments, when preparing a head rotation, the location of the visual target did not necessarily match the destination location of the planned head rotation, possibly because head rotation, as a gross motor skill, mainly involves movements of several large muscles, and thus may not be as precise as fine movements of eyes and hands. In daily life, we seldom rely on head rotation alone to bring a peripheral target accurately onto the foveola. What happens more often is that eye movements co-work with head movements to capture as wide a visual scene as possible, so we can efficiently fixate any object in the scene we want to inspect in detail. Therefore, when only head rotation is prepared, attention might not be able to accurately shift to the target location. As a result, the effect of attention cannot overcome the effect of sensory suppression induced by motor control signals.

Ross et al. (2001) suggested that the suppression induced by saccade is specific for magnocellular function, indicating that the motion signals might be selectively suppressed for a sense of stability. Similarly, Bai et al. (2018) found that motion aftereffect was reduced when it was caused by head-rotation-induced retinal motion. By contrast, our work studied the discrimination sensitivity. The impaired task performance may indicate that parvocellular function was suppressed during the period of head-rotation preparation. However, in order to have an extended understanding of visual perception in the process of head movement, it is necessary to further examine the magnocellular function during head-movement preparation and the parvocellular function during head movement. The VR device provides us with a flexible approach to study the effect of self-generated head movement on visual sensation. Future work may take advantage of this device for more investigations.

In conclusion, our study revealed that the preparation of head rotation induced a strong sensory suppression on visual perception, extending our knowledge of sensory suppression in the visual domain and the motor control of head movement.

Disclosure of conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgments

This research was supported by the National Natural Science Foundation of China (31571112, 31871104 and 31830037) and the Scientific Foundation of Institute of Psychology, Chinese Academy of Sciences (Y9CX152005).

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