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Manipulation of extraocular muscle afference has no effect on higher order perceptual judgments

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Abstract

Observers perceive targets as farther while performing the Jendrassik Maneuver (JM) suggesting that eye position is registered as more divergent. We examined the effects of the JM perturbation in three studies of perceptual judgment that rely on accurate registration of absolute distance: size constancy, stereoscopic depth, and the magnitude of the Pulfrich illusion. The data showed no significant differences between the JM and control conditions. The lack of an effect may be due to the fact that vergence is not a perfect cue to distance. Furthermore, the relative contribution of extraocular muscle afference to registered eye position may be less significant for higher order perceptual judgments.

Keywords: Extraocular muscles; Proprioception; Non-twitch motoneurons; Size constancy; Depth constancy

1. Introduction

Accurate estimation of egocentric distance is not only critical for the performance of reaching and grasping movements, but perceptual constancies, such as size and depth also rely on accurate registration of absolute distance. The central nervous system (CNS) can obtain depth information from static and dynamic monocular and binocular cues (Howard & Rogers, 2002). Ocular vergence is an extraretinal binocular cue which has been shown to provide crude but reliable distance information in a visually impoverished environment (for reviews see Collewijn & Erkelens, 1990; Foley, 1980).

Information about vergence eye position can come from two sources: the efference copy (outflow) and afferent feedback (inflow) from the eye muscles (Steinbach, 1987). There are at least two receptors in the extraocular muscles (EOM) that could provide proprioceptive information about eye position: muscle spindles and palisade endings (PE) (for review see Donaldson, 2000). Muscle spindles have been unequivocally shown to provide proprioceptive information from skeletal muscles; however, their role in EOM is not as clear. First, muscle spindles are only found the in the orbital layer of the EOM and they are morphologically different from the spindles found in skeletal muscle (for a review see Ruskell, 1989). Second, several species, such as cat, rabbit, horse, and mouse do not have muscles spindles in their EOM (Maier, DeSantis, & Eldred, 1974). In contrast, PE have been found in the EOMs of all the species tested to date, such as cat, rhesus monkey, sheep, rat, and human (Alvarado-Mallart & Pincon-Raymond,

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1979; Blumer, Lukas, Wasicky, & Mayr, 1998; Buttner-Ennever, Horn, Scherberger, & D'Ascanio, 2001; Eberhorn et al., 2005; Richmond, Johnston, Baker, & Steinbach, 1984). PE are also referred to as innervated myotendious cylinders (Ruskell, 1978) and they are uniquely associated with the multiply innervated non-twitch fibers (MIF) of the global layer of the eye muscles.

Neuroanatomical tracing studies by Buttner-Ennever and colleagues (2001) have shown that the MIF receive innervation from a distinct set of non-twitch motoneurons found in the periphery of the twitch motoneurons that control eye movements. The authors hypothesized that these non-twitch motoneurons could be involved in modulating the gain of sensory feedback from the extraocular muscles, analogous to the gamma (γ) fibers which control the sensitivity of muscle spindles in the skeletal muscles.

Our previous study (Niechwiej-Szwedo et al., 2006) tested the above hypothesis using a behavioral approach and a manipulation called the Jendrassik Maneuver (JM). The JM refers to a voluntary, forceful contraction of any muscle group. While the JM is performed, the amplitude of skeletal reflexes is facilitated (Delwaide & Toulouse, 1981; Murthy, 1978). One of the mechanisms proposed to explain the reflex reinforcement effect is that the muscle contraction has a general effect that results in up-regulation of the γ motoneuron activity which increases the baseline excitability of muscle spindles and, consequently, results in a larger response when the muscle is stretched. We hypothesized that the JM would also alter the gain of the afferent feedback from eye muscles which would result in misregistration of eye position and localization errors.

Altering the feedback from the eye muscles during vergence eye movements via the JM resulted in misregistration of eye position. In particular, when the JM was performed, eye position was registered as more divergent while the actual eye position did not change (Niechwiej-Szwedo et al., 2006). Based on these results we hypothesized that the JM would also alter higher order perceptual judgments that rely on accurate registration of absolute distance. This hypothesis was tested in three experiments.

In the first experiment, size constancy was examined while feedback from extraocular muscles was perturbed by the JM. Since the vergence angle of the eyes is an important source of extraretinal information contributing to size constancy, we hypothesized that participants would perceive the size of a constant retinal stimulus as larger when feedback from the eye muscles was altered via the JM.

Stereoscopic depth constancy was examined in the second experiment. Horizontal disparities must be scaled by viewing distance in order for depth constancy to be preserved and the vergence angle of the eyes can be used to calibrate horizontal disparities for different viewing distances. We hypothesized that for the same disparity, the perceived depth would be greater when the JM is performed compared to the control condition without JM.

In the third experiment, we examined whether perceived depth during the Pulfrich illusion was affected by the JM. In the Pulfrich effect a pendulum objectively swinging in the frontal plane appears to move in an elliptical orbit in depth. The effect results from the cortical time delay, interpreted as a disparity induced when one eye views it through a neutral density filter. It has been shown that the perceived depth (i.e., the short axis of the ellipse) is dependent on the viewing distance, so we hypothesized that the perceived depth would be greater while participants perform the JM.

All participants in the three studies had normal or corrected-to-normal visual acuity of 20/20 and stereopsis of at least 40 s of arc as measured with the Titmus test (Titmus Optical Co., Inc., Petersburg, VA 23805). All experimental protocols were approved by the Ethics Review Boards at the University of Toronto and the University Health Network and participants gave their informed consent prior to participating.

2. Experiment 1: The effect of JM on perceived size

Even though the size of the image projected on the retina changes substantially over a range of viewing distances, observers perceive the size of an object as relatively constant. This is referred to as size constancy. There are three laws which describe the relationship between the object size, image size and distance: (1) for a constant object size, the image size varies inversely with distance, (2) for a constant image size, object size is proportional to distance, and (3) image size is proportional to object size for an object presented at a fixed distance (Howard & Rogers, 2002).

Observers are remarkably good at judging object size accurately in natural environments where the CNS can use multiple cues to distance. As depth cues are reduced so is the degree of size constancy and observers tend to rely more on the retinal image size to make judgments (Ono, 1966). Ocular vergence and accommodation are the only cues that the CNS can use in an unstructured visual environment to judge the size of unfamiliar objects; however, vergence is only reliable when the distance to the stimulus is less than 2 m (Harvey & Leibowitz, 1967; Leibowitz & Moore, 1966; Wallach & Floor, 1971).

The contribution of oculomotor cues to size perception within near visual space was shown by Wallach and Zuckerman (1963). Participants were asked to judge the size of a wire-form pyramid while vergence and accommodation were altered using mirrors and lenses. The size estimates obtained experimentally varied accordingly with the changes in oculomotor cues, thus confirming that the perception of size relies on these cues.

More recently, Mon-Williams and colleagues (Mon-Williams, Tresilian, Plooy, Wann, & Broerse, 1997) examined the role of vergence in explaining the illusory size change of an afterimage (i.e., Emmert's law, which states that the perceived size of an afterimage is dependent on the perceived distance to the surface). Participants judged the vertical size of an afterimage in two conditions. In the control condition, the card on which the afterimage was created was moved by the participant but fixation was maintained on a stationary light emitting diode (LED). In the experimental condition participants made converging or diverging eye movements when judging the size of the afterimage. The experimental results clearly supported the hypothesis that vergence is necessary and sufficient to explain the illusory change in the size of the afterimage. Specifically, converging eye movements were associated with a smaller perceived size of the afterimage whereas diverging eye movements led to reports of a larger afterimage.

Experiment 1 was designed to examine whether the perceptual phenomenon of size constancy was affected by the JM which has been shown to affect the registered vergence eye position. We employed a two-alternative forced choice paradigm (2 AFC) and the method of constant stimuli. The perturbation (JM) occurred when either the standard or the comparison stimuli were shown. We hypothesized that the order of the JM would affect the size judgment. Two specific predictions were made for the case when both the standard and comparison stimuli had the same retinal size: (1) if the JM were performed while participants viewed the standard stimulus, the comparison would be perceived as smaller, and (2) if the JM were performed while viewing the comparison stimulus, participants would report it as larger. Eye movements were not recorded in this study because our previous work had shown that the actual vergence eye position was not affected by the JM (Niechwiej-Szwedo et al., 2006). In addition, a pilot study using the current methodology measured the eye movements of three participants and found no differences between the JM and control conditions.

2.1. Methodology

2.1.1. Participants

Twenty healthy adults (9 males) with no history of ocular disorders and a mean age of 28 ± 13 years participated.

2.1.2. Stimuli

The initial fixation stimulus was a green LED controlled by a custom-made trigger box. The LED was placed at a distance of 25 cm in front of the participant in the midline. The height of the LED placement was adjusted for each participant individually to prevent obstruction of the stimulus.

The standard stimulus for the psychophysical procedure was a grey square (4.7° visual angle) presented on a black background and displayed on a flat CRT monitor (refresh rate 85 Hz). The viewing distance was 100 cm. There were five comparison stimuli: 4.5°, 4.6°, 4.7°, 4.8°, and 4.9°. The display was programmed using VPixx (VPixx Technologies, Inc., Montreal, QC), a graphics generation and psychophysics testing software, controlled by a Macintosh iBook computer.

2.1.3. Apparatus

The JM consisted of an isometric voluntary contraction against resistance with the abductor muscles of the legs. The device used for resistance was a Thigh Master™. Participants were asked to perform each contraction at a 75% level of their maximal voluntary contraction, which was determined prior to the initiation of the experiment. To ensure that the isometric contraction was performed at a consistent level throughout the experiment, a string was tied around the Thigh Master™ which pulled taut when the muscle contraction was executed. Participants were instructed to hold the string taut while performing the JM.

2.1.4. Procedure

Participants were seated in complete darkness. At the beginning of each trial they fixated on the LED for 2.5 s in order to standardize the initial vergence eye position. As soon as the LED was switched off, the standard stimulus was presented for 2.5 s and participants were asked to fixate on it and to remember its size when it disappeared. The comparison stimulus was shown at the same location 1.5 s after the standard had disappeared. Five sizes of the comparison stimulus were tested and their presentation order was determined randomly by the computer. On each trial participants were asked to report whether the comparison stimulus was ‘smaller’ or ‘larger’ than the standard. The comparison stimulus disappeared after participants made the judgment. There were three experimental conditions: control: the judgment task was performed without the JM; task 1: participants performed the JM while viewing the LED and the standard stimulus and relaxed the contraction before the comparison stimulus was presented (verbal judgment was made without the JM); task 2: participants fixated the LED and the standard stimulus without the JM and started the JM when the standard stimulus disappeared (verbal judgment was made with JM). The protocol is illustrated in Fig. 1. The five comparison stimuli were tested 10 times in each experimental condition for a total of 150 trials. All experimental conditions were completely randomized.

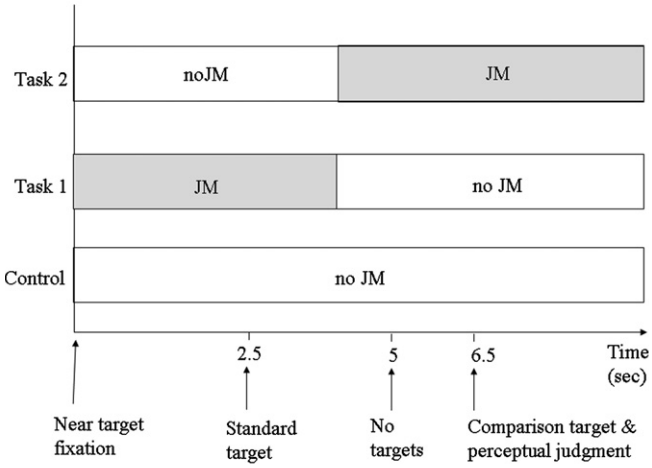

Fig. 1. Schematic illustration of the experimental protocol used in Experiment 1.

2.1.5. Data analysis

The proportion of 'smaller' responses was calculated and plotted for each participant and condition for the five sizes of the comparison stimuli. Data were visually inspected for trends and then fitted with a psychometric function using a logistic regression (SAS, Ver. 8.1). The goodness of fit of the model was tested using the Hosmer–Lemeshow statistic and a non-significant result was used to verify that the logistic model was appropriate. Subsequently, an overall psychometric function based on the means of all participants was fitted for each task.

For each participant, the point of subjective equality (PSE) and the just noticeable difference (JND) were calculated using the estimated parameters (slope and intercept) from the logistic model. The PSE is the point at which the logistic function yields a probability of 0.5 (i.e., the comparison stimulus is perceived as smaller than the standard stimulus 50% of the time) and it reflects the accuracy of the judgment. The JND is the smallest possible physical difference that can be detected reliably and it reflects the precision of the judgment. The PSE, JND, intercept, and slope were submitted to a one-way repeated measures ANOVA each with condition (control, task 1, and task 2) as the independent variable.

The magnitude of the illusion (i.e., the proportion of 'smaller' responses) was examined for the condition in which the comparison stimulus was the same size as the standard. Data for each participant and condition were submitted to a one-way repeated measures ANOVA each with condition (control, task 1, and task 2) as the independent variable.

2.2. Results

Preliminary inspection of the individual psychometric curves did not reveal consistent differences between the conditions. The data were collapsed and the mean performance of all participants in each condition is shown in Fig. 2. The mean psychophysical curves clearly show that participants were able to judge the size of the comparison square accurately in each of the conditions.

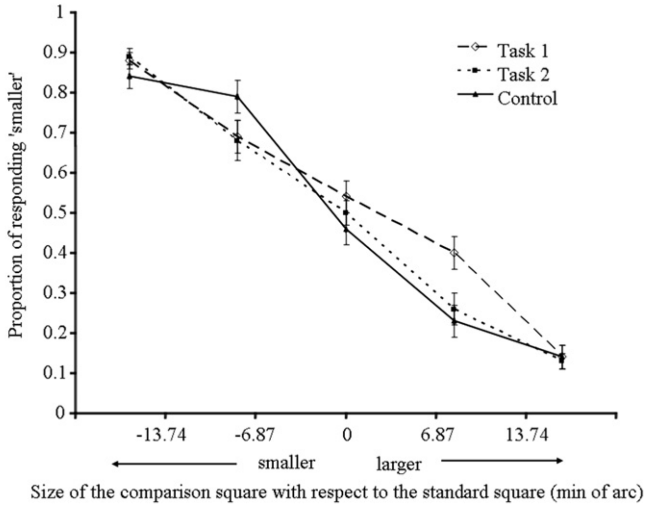

Fig. 2. Mean proportion of responding 'smaller' for each of the five sizes of the comparison square (at 0 both the standard and comparison squares were the same physical size, negative values indicate that the comparison square was smaller). Bars show ±1 standard errors.

The logistic model fitted the experimental data well for the majority of the psychometric curves (59 out of 63), which was supported by the non-significant result from the Hosmer–Lemeshow test. Although in four cases (one in task 1 and three in task 2) the test was statistically significant, the logistic model was still used to fit the data. In contrast to the hypothesis, no significant differences were found for any of the variables: PSE ($F(2,38) = 2.61$, *ns*), JND ($F(2,38) = 1.52$, *ns*), slope ($F(2,38) = 1.53$, *ns*), *y*-intercept ($F(2,38) = 1.21$, *ns*). The magnitude of the illusion was not significantly different at the point where both the standard and comparison stimuli were physically the same ($F(2,38) = 1.20$, *ns*).

2.3. Discussion

It was expected that the order of JM would affect the size judgments; however, neither the accuracy nor the precision of the perceptual judgment were affected by the perturbation. A potential weakness of the experiment is that participants were aware that the stimulus was always presented on a flat monitor screen at a fixed distance. Previous research has shown that observers tend to make judgments of distal (object) or proximal (image) size depending on the experimental conditions. For example, when no specific instructions were given and with unrestricted viewing, observers tended to judge the distal size. In contrast, when all visual cues were eliminated and viewing was monocular, observers judged the proximal size (Ono, 1966). When only binocular cues were present, observers also tended to judge the distal size and size constancy was preserved, at least up to 30 feet (Chalmers, 1952). Although the current experiment was conducted in the dark and no other visual cues were available, participants could have relied on the oculomotor cues of vergence and accommodation. Thus, it is likely that participants used distal size to make judgments in the current study.

3. Experiment 2: The effect of JM on stereoscopic depth judgments

The perceptual phenomenon of depth constancy is conceptually similar to size constancy and refers to the ability of the observer to judge the linear extent of a stimulus in the saggital plane accurately despite changes in viewing distance (Ono & Comerford, 1977). Depth constancy depends on the accurate registration of disparity and fixation distance. When two images are separated in depth, they fall on non-corresponding or disparate retinal points, which is the bases of stereopsis. By convention, points that are nearer to the observer than the fixation point have crossed disparity, conversely, points farther than the fixation point have uncrossed disparity. Stereopsis is one of the cues contributing to depth perception but it can only provide relative information. Specifically, a given disparity can be associated with different depth intervals depending on the fixation distance. For example, a disparity of 50 min arc will be interpreted as a depth interval of 5 cm when viewed at 50 cm or a depth interval of 20 cm if viewed at 100 cm. Likewise, a 5 cm depth interval viewed at 100 cm will have disparity of 12 min of arc and the disparity will be 4 times larger when viewed from 50 cm away. To sum up, for a constant physical depth, retinal disparity decreases in proportion to the square of the absolute distance (Ono & Comerford, 1977). Therefore, in order for depth constancy to occur, the CNS must take into account the fixation distance or, in other words, horizontal disparity must be calibrated for different fixation distances.

Wallach and Zuckerman (1963) were among the first to empirically examine whether changes in vergence and accommodation contribute to depth constancy. In their experiments the oculomotor cues were altered by optical means and the obtained depth estimates approximated those that were predicted by the inverse square law. A detailed examination of vergence contribution to depth constancy was reported by Ritter (1977). All distance cues except for convergence and accommodation were removed and participants viewed a stereoscopically presented image of a pyramid at different viewing distances. Results showed that in the case of vergence–accommodation conflict, the depth interval was perceived based on the convergence distance.

Experiment 2 was designed to examine whether the perceptual phenomenon of depth constancy could be modified by the JM. Participants were asked to judge the separation in depth between two lines when the registered vergence eye position was perturbed by the JM. Since during the JM eye position is registered as more divergent, we hypothesized that participants would perceive the depth interval as larger while the JM was performed as compared to the control condition. Vertical lines were used instead of random dot stereograms to reduce the likelihood of participants using vertical disparities to judge depth.

3.1. Methodology

3.1.1. Participants

Five healthy adults with no history of ocular disorders, mean age 27.2 ± 6.6 years, participated.

3.1.2. Stimuli

The stimuli consisted of two vertical white lines subtending 1.5° by 0.1° of visual angle, which were presented on a black background inside a white square outline subtending 5° × 5° of visual angle. The stimuli were viewed on a flat CRT monitor (Viewsonic, refresh rate 60 Hz) at a viewing distance of 57 cm. The stereo images were displayed with 5 crossed disparities: 1.17, 2.34, 3.51, 4.68, and 5.85 min of arc. A rating scale consisting of 10 horizontal lines ranging in length from 1 to 10 mm was displayed at the end of each trial and numbers from 1 to 10 were displayed above the corresponding horizontal line.

3.1.3. Apparatus

The stimulus presentation was controlled by VPixx (VPixx Technologies, Montreal, QC), a graphics generation and psychophysics testing software, controlled by Macintosh G4 computer. The stereo images were seen using liquid crystal glasses (CrystalEyes Workstation, Stereographics, San Rafael, CA). The JM procedure was the same as in Experiment 1.

3.1.4. Procedure

Participants saw the display with the room lights turned off. At the beginning of each trial, they fixated on a standard vertical line presented for 1 s. A second, or comparison, vertical line appeared to the left of the first one with a variable crossed disparity and for a 2-s duration. Participants were instructed to remember the separation in depth between the two vertical lines. After the comparison stimulus disappeared, participants were shown 10 horizontal lines and were asked to estimate the distance in depth between the two vertical lines by choosing one of the horizontal lines. Participants made a verbal response indicating the number (1–10) corresponding to the depth interval that they saw between the two vertical lines. They were not informed that only five disparity stimuli were used. Participants completed 10 trials for each stimulus disparity with and without the JM for a total of 100 stereoscopic depth judgments. For the JM trials participants started the isometric contraction prior to seeing the stimulus with the disparity and held it while viewing it. Prior to data collection, all participants completed 20 practice trials to become acquainted with the task.

3.1.5. Data analysis

For each disparity value the mean perceived depth was calculated and plotted for all participants. Data were fitted using a linear regression model. The slope and y-intercept parameters obtained from the model were submitted to a paired Student's t-test with condition (control, JM) as the dependent variable.

3.2. Results

The mean responses of all participants ranged in values from 2 to 7; thus, participants used the middle range of the scale and responses at the limits were not frequent. The individual curves showed that participants could judge the depth difference reliably, which is evident in the slope values and the measure of goodness of fit of the model (Table 1). A paired samples t-test showed no significant differences between the control condition and the JM condition for the slope or y-intercept values. The lack of difference is illustrated in Fig. 3 which shows the mean data of all participants.

Table 1
Parameters obtained from the linear regression model for individual participants in Experiment 2

Participant	Model fit (R^2)		Slope		y-Intercept value	
	Control	JM	Control	JM	Control	JM
1	0.92	0.90	1.11	0.99	0.59	1.47
2	0.87	0.75	0.78	0.58	2.46	3.36
3	0.97	0.97	0.67	1.04	2.21	0.94
4	0.85	0.71	1.02	0.94	1.30	1.76
5	0.88	0.55	1.36	0.86	0.60	0.76

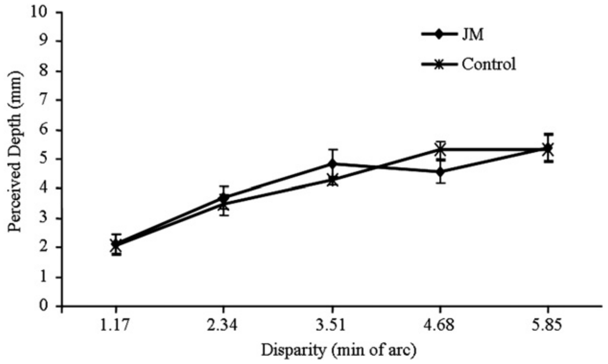

Fig. 3. Mean perceived depth for stereoscopically presented stimuli in Experiment 2. Bars show ±1 standard errors.

3.3. Discussion

The experimental results did not confirm our hypothesis and showed that JM did not affect judgments of stereoscopic depth. The CNS must use oculomotor cues or vertical disparities in order for stereoscopic depth constancy to be preserved. The disparity stimulus in the current study consisted of vertical lines presented at the midline so no vertical disparities were present in the field of view and the CNS must have relied on the only available cues, which were the vergence and accommodative state of the eyes.

We chose to examine the effect of JM on depth constancy by presenting the stimulus using stereoscopic goggles, which allowed us to precisely control the disparity. However, stereoscopic presentation has a disadvantage: the oculomotor cues of vergence and accommodation are in conflict (Ono & Comerford, 1977). The disparity stimulus which drives the vergence system creates an illusion of depth, but there is no retinal blur and the cue of accommodation informs the system that both stimuli are at the same distance. Ritter (1977), however, showed that in a case of vergence–accommodation conflict the judgments of perceived distance are based on the cue of convergence so it is unlikely that the mismatch between these cues contributed to the present findings. The next study was designed to further examine the effect of JM on depth constancy using the Pulfrich phenomenon for which there was no conflict between oculomotor cues.

4. Experiment 3: The effect of JM on perceived depth during the Pulfrich illusion

In the Pulfrich illusion, a pendulum moving sinusoidally in the frontoparallel plane appears to move along an elliptical path plane when viewed through a neutral density filter placed over one eye. Placing the filter in front of one eye creates a luminance difference between the two eyes which leads to a temporal delay in transmitting visual information to the cortex. The cortical time delay is interpreted by the CNS as binocular disparity of the moving object between the images seen by the two eyes (Howard & Rogers, 2002).

The effect of fixation distance on the magnitude of perceived depth during the Pulfrich illusion was studied by Lit and Hyman (1951). They systematically investigated whether variables such as differences in illumination, distance to target, and velocity of the target influenced the magnitude of the stereoscopic depth effect. Their results clearly showed that for any given illumination difference value, the pendulum's motion depended on the fixation distance with the largest depth interval observed for the largest fixation distance and greater illumination difference between the two eyes. These results were later replicated by Wallach and colleagues (Wallach, Gillam, & Cardillo, 1979).

More recently, Nakamizo and Lei (2000) examined the magnitude of the illusion at larger viewing distances raging from 1 to 4 m for stimulus velocities of 0.2, 0.4, and 0.6 Hz. Two procedures for measuring depth were used: participants had to match the perceived depth interval using a probe or to reproduce the depth interval using a tape measure. Although there were no significant differences between the two response methods (matching and reproduction), the matching response produced depth estimates that were closer to those that would be expected if the Pulfrich effect increased in direct proportion to viewing distance.

In summary, previous studies have shown that the perceived depth of the Pulfrich effect depends on the viewing distance and the vergence angle of the eyes; therefore, Experiment 3 was designed to examine whether the perceived depth during the Pulfrich illusion is also affected by the JM. Participants viewed the moving stimulus through a pair of different filters placed in front of the two eyes: one of the filters was constant while the other was adjusted by the participant. Participants were asked to null the apparent depth by adjusting one of the filters. We hypothesized that during the JM the depth interval would be perceived as larger and that in order to null the illusion participants would compensate by over-adjusting the variable filter.

4.1. Methodology

4.1.1. Participants

Five healthy adults with no history of any ocular disorders, mean age 47.2 ± 13.5 years, participated in Experiment 3.

4.1.2. *Stimuli*

The fixation stimulus was a 0.25° black dot and the target stimulus was a black vertical 1.5° bar both displayed on a white background on a flat CRT monitor (Viewsonic, refresh rate 85 Hz). The target stimulus moved sinusoidally in the frontoparallel plane at a peak velocity of 15°/s. The display was programmed using VPixx (VPixx Technologies, Inc., Montreal, QC) and controlled by Mcintosh G4 computer.

4.1.3. *Apparatus*

Participants viewed the vertical bar through a custom-made apparatus that contained two round apertures. Participants were seated behind the apparatus and the height of the chair was adjusted so that they could see the stimulus through the apertures. A variable neutral density (ND) filter (luminance values ranging from 2.5 to 102.5 cd/m^2) mounted on a movable wheel, was placed over the right aperture. The density of the variable filter could be adjusted by turning a knob. A 360° protractor was attached to the movable wheel so that the responses could be read out with an accuracy of 1/10 of a degree. Three constant, non-adjustable ND filters (0.2, 0.7, and 1.0 log units) were used during the experiment and placed over the left aperture.

The JM procedure was the same as in Experiments 1 and 2.

4.1.4. *Procedure*

At the beginning of each trial participants closed their eyes. The experimenter spun the wheel with the variable ND filters to vary the initial value of the filter between trials. One of the three ND filters, randomly determined prior to the experiment, was placed to cover the left aperture. Participants opened their eyes when cued by the experimenter and viewed the moving bar while fixating the dot. The moving target was viewed through different filters over each eye which produced an illusion of elliptical movement (Pulfrich effect). Participants were asked to null the illusion by adjusting the variable ND filter with the movable knob. They were allowed as much time to make the adjustment as they needed to make sure that the elliptical movement of the target stimulus disappeared. Once the participant indicated that the illusion had disappeared, the experimenter recorded the response which was the number indicated by the protractor. The task was performed while participants performed the JM and without the JM and these two conditions were randomized prior to the experiment. Participants completed five trials in each experimental condition for a total of 30 trials.

4.1.5. *Analysis*

Data for individual participants were plotted for the three values of ND filters for the two JM conditions and inspected visually for trends. Subsequently, data were submitted to two-way repeated measures ANOVA with two factors: condition (control, JM) and filter value (0.2, 0.5, and 1.0 log units).

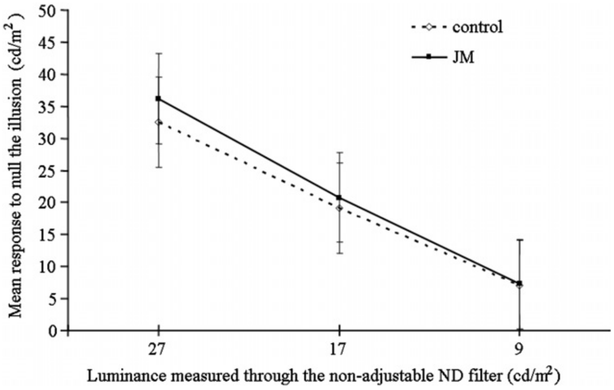

Fig. 4. Mean values obtained when participants were asked to null the Pulfrich illusion by adjusting the value of the variable filter. Bars show ±1 standard errors.

4.2. *Results*

Preliminary inspection of the individual response curves did not reveal consistent differences between the experimental and control conditions. The data were collapsed and the mean performance of all participants in each condition is shown in Fig. 4. As expected, the main effect of filter was significant ($F(2,140) = 541.68$, $p < .0001$) showing that the perceived depth interval varied across the three filter values. Specifically, the largest depth interval was perceived with ND filter 1.0 which created the largest luminance difference between the two eyes. In contrast to our hypothesis, there were no significant differences between the control and the JM condition ($F(1,140) = 3.43$, *ns*) and the interaction effect was also not significant ($F(2,140) = 0.36$, *ns*).

4.3. *Discussion*

Although the Pulfrich effect has been shown to depend on viewing distance, the current study showed that it was not affected by the JM perturbation. Overall, the results from Experiments 2 and 3 showed that the JM had no effect on the perceptual phenomenon of depth constancy.

5. General discussion

The purpose of our studies was to examine whether higher order perceptual judgments which require accurate registration of absolute distance are affected by a manipulation which we have shown alters the gain of the proprioceptive feedback from the EOM. Contrary to our hypotheses, we found that the JM manipulation did not significantly affect judgments of size, depth or the Pulfrich illusion. These are important findings as they help to establish that proprioceptive feedback plays a negligible role in maintaining the perceptual phenomena of size and depth constancy.

Previous studies have shown that proprioceptive signals from the eye muscles play a significant role in the programming of eye movements (Knox, Weir, & Murphy, 2000;

Weir & Knox, 2001), during egocentric localization tasks (Bridgeman & Stark, 1991; Gauthier, Nommay, & Vercher, 1990; Lewis & Zee, 1993; Roll, Velay, & Roll, 1991; Steinbach, 1987; Velay, Roll, Lennerstrand, & Roll, 1994) and adaptation of smooth pursuit (van Donkelaar, Gauthier, Blouin, & Vercher, 1997).

Two methods have been used to manipulate EOM afference in binocularly intact observers: a vibration stimulus applied over the muscle and passive deviation of the eye using a suction lens. Vibration provides a good stimulus for activating the Ia afferents which in skeletal muscles activate the tonic vibration reflex (i.e., contraction of the vibrated muscle). Roll and colleagues (1991) applied vibration over the inferior rectus muscle while subjects were fixating a single light in the dark. During the vibration trials subjects reported that the target moved up and they also pointed above the target. Similar results were obtained by Velay et al. (1994) where vibration of the right lateral rectus muscle resulted in an illusory movement of the target to the left. Overall, results from these studies suggest that vibration of an EOM muscle leads to the perception that the muscle is lengthening, and participants report that the target is moving in a direction opposite to that of the vibrated muscle.

The afferent signals from eye muscles can be also altered by passively moving the eye using a suction lens. This method, introduced by Gauthier and colleagues (1990), offers a way of distinguishing the contributions of inflow and outflow to registered eye position. The paradigm involves subjects fixating a target with one eye while the other eye is occluded. In the first experimental condition the fixating eye is deviated, thus, the amount of innervation sent to the muscles must be increased in order to maintain fixation. Since both eyes receive the same amount of innervation during conjugate eye movements (Hering's law), the occluded eye should deviate by an amount corresponding to the efferent signal sent to the fixating eye. In this condition, the efferent signal to the eye muscles must be increased to compensate for the perturbation, but the afferent feedback from the fixating eye is not changing because the eye is not changing position. Therefore, this task allows one to examine the effect of efference on registered eye position. The second experimental condition involves passive deviation of the occluded eye. In this case, the amount of innervation does not change, but the afferent feedback from the deviated eye does change. Therefore, the second condition allows one to examine the contribution of afference to registered eye position.

The current study is the first examination of the role of afference in higher order perceptual phenomena using the JM manipulation to alter the feedback from the eye muscles. The JM has been used extensively to alter the excitability of spinal reflexes (Dowman & Wolpaw, 1988; Gregory, Wood, & Proske, 2001; Murthy, 1978; Zehr & Stein, 1999) and limb position information (Yasuda et al., 2006). Our previous studies (Niechwiej-Szwedo & Steinbach, 2007) were the first to show that the JM can also be used to alter proprioceptive feedback from the EOM. Specifically, we showed that participants made consistent perceptual errors when localizing targets in depth during the JM while the actual eye position was not affected. Thus, we expected that perceptual judgments that require accurate registration of depth would be also affected by the JM. This was not confirmed by the results from the three experiments.

The perceptual phenomena of size and depth constancy depend on the *preceived distance*, which is an internally generated estimate of the viewing distance. In the real world, the neural estimate of viewing distance is based on multiple visual and oculomotor cues. In the present experiments most visual cues were removed and oculomotor cues provided the only input for distance estimation; nontheless, the perturbed vergence signal was not taken into account by the CNS. This result could be explained by considering the relative contribution of efference and afference to registered eye position examined by Gauthier and colleagues (1990) and Bridgeman and Stark (1991). Both studies used the passive eye deflection paradigm (described above) and found significant localization errors with open-loop pointing responses, which were always correlated with the direction of the deviated eye. However, the localization errors were only found when the occluded eye was deviated by a large amount (>10°). Based on the localization errors and using a regression analysis, these authors calculated that the contribution of proprioception from the eye muscles to the registered eye position was approximately 30%, under their experimental conditions. It is possible that the afferent contribution from the EOM to judgments involving size and depth constancy or the Pulfrich illusion is even less significant and is not actually used for higher order perceptual judgments by the CNS. Alternatively, it is also possible that the perturbation that we are using, i.e., the JM, is not large enough to disrupt perceptual constancies.[1] In short, the lack of significant effect was most likely due to a combination of factors, such as the fact that vergence is not a perfect cue to distance and the JM manipulation is not a strong peturbation of the feedback from the extraocular muscles. In addition, perceptual constancies rely on multiple cues and are not easily perturbed, therefore, a strong manipulation might be necessary to definitively determine whether the afferent feedback from the eye muscles plays a role in maintaining perceptual constancies.

In summary, results from the present study showed that altering feedback from the EOM via the JM did not affect perceptual judgments of size or depth. The lack of a significant effect might not be surprising given that the JM manipulation affects the registered vergence eye positions, but vergence itself is not a perfect cue to distance. Overall, the role of afference in oculomotor control and visuomotor behavior is not well understood yet; however, the current study is the first to report that perturbations of afferent

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[1] We thank an anonymous reviewer for this suggestion.

input from the extraocular muscles do not affect higher order perceptual judgments.

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