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# Localization in the frontal plane is not susceptible to manipulation of afferent feedback via the Jendrassik Maneuver

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## Abstract

We have previously shown that registered vergence eye position is altered while participants perform the Jendrassik Maneuver (JM). We proposed that the altered eye position signal registration is due to the effect of the JM which changes the gain of the sensory feedback from the eye muscles, possibly via the activity of non-twitch motoneurons. We conducted two studies to further extend and clarify one of our previous findings by examining whether the JM also affects registered eye position during localization in the frontal plane. Since the non-twitch motoneurons do not receive premotor input from areas involved in the programming of saccades, we hypothesized that localization responses associated with the saccadic system should not be affected by the JM. The data confirmed our prediction. We propose that the non-twitch motoneurons are involved in parametric adjustment of the proprioceptive feedback loops of the vergence but not the version eye movements.

*Keywords:* Extraocular muscles; Proprioception; Gain control; Non-twitch motoneurons; Localization; Saccades; Vergence

## 1. Introduction

Good eye-hand coordination is essential for accurate performance of daily activities. For example, reaching to pick up a cup of coffee is a simple movement and yet it requires a complex sensorimotor transformation of visual and somatosensory afference into a coordinated pattern of muscle activations. To perform this simple motor act, the central nervous system (CNS) has to process and integrate information from several receptors: the retinal location of the cup, the position of the eyes in the orbits, the position of the head, the arm and the hand.

In the case of skeletal muscles, it has been unequivocally recognized that muscle spindles provide the CNS with information concerning limb position and velocity (Matthews, 1981). In addition, a large body of research has addressed the structural properties, anatomical pathway, and central control of muscle spindles (for review see Hulliger, 1984). In contrast, eye muscle proprioceptors have not received similar attention. Although there is still controversy regarding the afferent pathway, a recent, elegant study by Wang and colleagues (Wang, Zhang, Cohen, & Goldberg, 2007) provided evidence that eye position is represented in the somatosensory area 3a in rhesus monkeys.

The CNS can obtain eye position information from two non-retinal sources: outflow (copy of the motor command)

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and inflow (signals from the eye muscles). Although, the contribution of inflow to eye position sense has been debated for years (for review see Donaldson, 2000), studies have shown that proprioceptive signals from the eye muscles in neurologically intact individuals 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; Roll, Velay, & Roll, 1991; Velay, Roll, Lennerstrand, & Roll, 1994) and adaptation of smooth pursuit (van Donkelaar, Gauthier, Blouin, & Vercher, 1997).

Extraocular muscles (EOM) contain at least two receptors which could provide eye position information: muscle spindles and palisade endings (PE). Muscle spindles are found in the orbital layer of the human EOM; however, their function has been questioned due to their unusual morphological characteristics (for review see Ruskell, 1989). In addition, muscle spindles have not been found in the EOM of some species, such as cats or rhesus monkeys. In contrast, PE have been found in the EOMs of all the species tested to date including humans, cats, rats, sheep, and rehsus monkeys (Alvarado-Mallart & Pincon-Raymond, 1979; Blumer, Lukas, Wasicky, & Mayr, 1998; Buttner-Ennever, Horn, Scherberger & D'Ascanio, 2001; Eberhorn et al., 2005; Richmond, Johnston, Baker, & Steinbach, 1984). PE are uniqe to the EOM and they are associated with the myotendious region of the global multiply innervated fibers (MIF). Several studies have considered that they might be the EOM proprioceptors based on their morphological characteristics (Alvarado-Mallart & Pincon-Raymond, 1979) and retrograde tracing studies (Billig, Buisseret Delmas, & Buisseret, 1997). However, recent histochemical examination of the musculotendinous junction in the cat and monkey has revealed that the region containing the PE is immounoreactive to markers for cholinergic nerve fibers and nerve terminals, which have been traditionally associated with motoneurons (Konakci et al., 2005a, 2005b).

Although the question of whether PE have a sensory or a motor function has yet to be resolved, several authors have proposed the possibility that PE, along with the MIF, might have a proprioceptive role in the control of eye movements. Robinson (1991) was the first to use the term 'inverted muscle spindle' to suggest that the non-twitch MIF and the PE might be comparable to the gamma ($\gamma$)-spindle system found in the skeletal muscles. This hypothesis has been further extended by Buttner-Ennever and colleagues (Buttner-Ennever, Horn, Graf, & Ugolini, 2002) based on their neuroanatomical tracing studies which demonstrated that the MIF receive innervation from separate groups of ocular motoneurons (Buttner-Ennever et al., 2001).

The goal of the present studies was to test the above hypothesis using a psychophysical approach and the Jendrassik Maneuver (JM). The JM is a forceful voluntary muscle contraction of any muscle group. Previous studies have shown that the JM alters the excitability of tendon reflexes. Specifically, the amplitude of the reflex is enhanced and the facilitation is dependent on the strength of the reinforcing maneuver (Delwaide & Toulouse, 1981). One hypothesis that has been proposed to explain the reinforcing effect is that the JM increases the excitability of the gamma system (Murthy, 1978). Since the gamma system regulates the baseline activity of spindles, the JM increases the baseline activity of spindles which become more sensitive to the upcoming stimulus resulting in a larger response when the muscle is stretched.

JM not only affects the excitability of reflexes but also the perceived position of the arms and eyes. In a recent study, Yasuda and colleagues (Yasuda et al., 2006) examined the upper limb position sense while participants performed a reinforcing maneuver with their quadriceps muscles. Data showed that the arm was perceived in a more extended position when the JM was performed and the error increased with the intensity of the quadriceps contraction.

The effect of JM on registered vergence eye position was shown in our previous study (Niechwiej-Szwedo et al., 2006). In short, while the JM was performed, targets were perceived as farther while the actual eye position was not affected. In the current investigation we conducted two studies to examine whether the JM affects localization responses associated with saccadic eye movements. Manual pointing responses were examined in the first study and perceptual localization was investigated in the second study.

Although version and vergence share a final common pathway, different pre-motor areas are involved in programming of these eye movements (for a review see Buttner-Ennever, 2005). In addition, conjugate and disconjugate eye movements are differentially susceptible to manipulations of afferent feedback. For example, saccades do not seem to be affected by sectioning of the ophthalmic branch of the trigeminal nerve (deafferentation) whereas vergence is disrupted by the same procedure (Guthrie, Porter, & Sparks, 1982). Additionally, the accuracy of pointing to targets arranged along the horizontal axis was not affected by deafferentation (Lewis, Gaymard, & Tamargo, 1998). In contrast, binocular depth discrimination was impaired in cats following the same procedure (Fiorentini, Mafei, Cenni, & Tacchi, 1985). Given the differences between the saccadic and vergence systems, our studies were designed to further explore the hypothesis that version and vergence are differentially susceptible to manipulations of afferent feedback using the JM.

The current studies also help to extend and clarify the findings from one of our previous experiments (Niechwiej-Szwedo et al., 2006). First, we showed that the JM affected pointing responses to targets in depth, but it is possible that the pointing error was due to the effect of the JM on the upper limb muscles instead of the eye muscles. Thus, in the first experiment of our current examination, participants pointed to targets presented along the frontal plane. It was hypothesized that if the JM affects the activity of non-twitch motoneurons which do not receive premotor monosynaptic input from areas involved in the programming of saccades (Wasicky, Horn, & Buttner-Ennever, 2004), the pointing responses should not be affected by the JM. Alternatively, pointing responses might be affected if the result that we have previously observed was due to the effect of the JM on the limb muscles.

Secondly, we showed that the JM does not affect the actual vergence or saccadic eye movements; however, the perceptual localization of eccentric targets was not explicitly examined. Therefore, in the second experiment we asked participants to localize briefly flashed targets after they made a saccadic eye movement. We hypothesized that if the JM acts through the activity of non-twitch motoneurons then perceptual localization associated with saccadic eye movements should not be affected. Alternatively, if the effect of the JM occurs via a different neural mechanism then we might see increased localization errors during saccades similar to the overshoot errors found in the case of the vergence system. Eye movements were recorded in experiment 1 in order to replicate our previous findings and verify that the JM does not affect activity of the twitch motoneurons.

## 2. Experiment 1

### 2.1. Methodology

#### 2.1.1. Participants

Participants in both studies had normal or corrected-to-normal visual acuity of 20/20 or better and stereopsis of at least 40 s of arc as measured with the Titmus test (Titmus Optical Co., Inc., Petersburg, Virginia 23805). All experimental protocols were approved by the Ethics Review Boards at the University of Toronto and the University Health Network. The research adhered to the tenets of the Declaration of Helsinki, and all participants gave their written informed consent prior to participating. Ten healthy adults (8 females) with no history of ocular disorders and a mean age of 34 ± 16 years, participated in the first experiment. Five of the participants also participated in the experiment that involved pointing in depth which was reported in our previous paper (Niechwiej-Szwedo et al., 2006).

#### 2.1.2. Stimuli

The stimuli were three red light-emitting diodes (LEDs) placed on a custom-made black board and controlled by the experimenter via a trigger box. The fixation stimulus was aligned with the participant's midline and the other two LEDs were located 8° to the left and right of fixation. All LED's were presented slightly below eye level. The two eccentric targets were located 51 cm from the participants so everyone could point to the target comfortably. The board was positioned so that participants could not see their arms and they had no feedback about the accuracy of their pointing. The only difference between the stimuli presented in this experiment and those used in the previous study (Niechwiej-Szwedo et al., 2006) was the fact that the two LEDs were presented eccentrically in the frontal plane and not in depth.

#### 2.1.3. Apparatus

Horizontal and vertical position of both eyes was monitored and recorded using an infra-red eye-tracker system (El-Mar series 2020, Toronto, Ont., Canada). Horizontal and vertical eye positions were obtained from the relative positions of two corneal reflections and the center of the pupil. Prior to data collection, the eye tracker was calibrated. The system accuracy is 0.5° with a linear visual range of ±40° horizontally and ±30° vertically, the resolution is 0.1°, and it is free from drift. Eye position data were sampled at 120 Hz and stored on a computer for further analysis. Arm movement data were recorded at 60 Hz with a resolution of 0.5 mm using an electromagnetic device (Flock of Birds, Ascension Technology Co., Burlington, Vermont, USA). The receiver was placed on the thumb of the participant's dominant hand, which was used for pointing.

JM involved an isometric, voluntary muscle contraction which was performed with the abductor muscles of the legs against resistance. The device used for resistance was a Thigh Master™. Participants were asked to perform each contraction at 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 tied around the Thigh Master™ was 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 total darkness while performing an open-loop pointing task. During the experimental procedure participants were instructed to look and point by raising the thumb to be exactly underneath the target (red LED) as accurately as possible when cued by the experimenter. Participants initiated the pointing movements from the same starting position which was identified by a tactile cue placed on a table at their midline. All extraneous visual cues were removed to ensure that participants had to use a non-visual source of information to localize the target. There were three experimental conditions randomized as to order: (a) control: look and point to the target; (b) task 1: look and point to the target while performing the JM; (c) task 2: look at the target while performing the JM and point 2–3 s after the contraction had been released (see Fig. 1 for illustration of the protocol). Participants completed 15 trials in each condition.

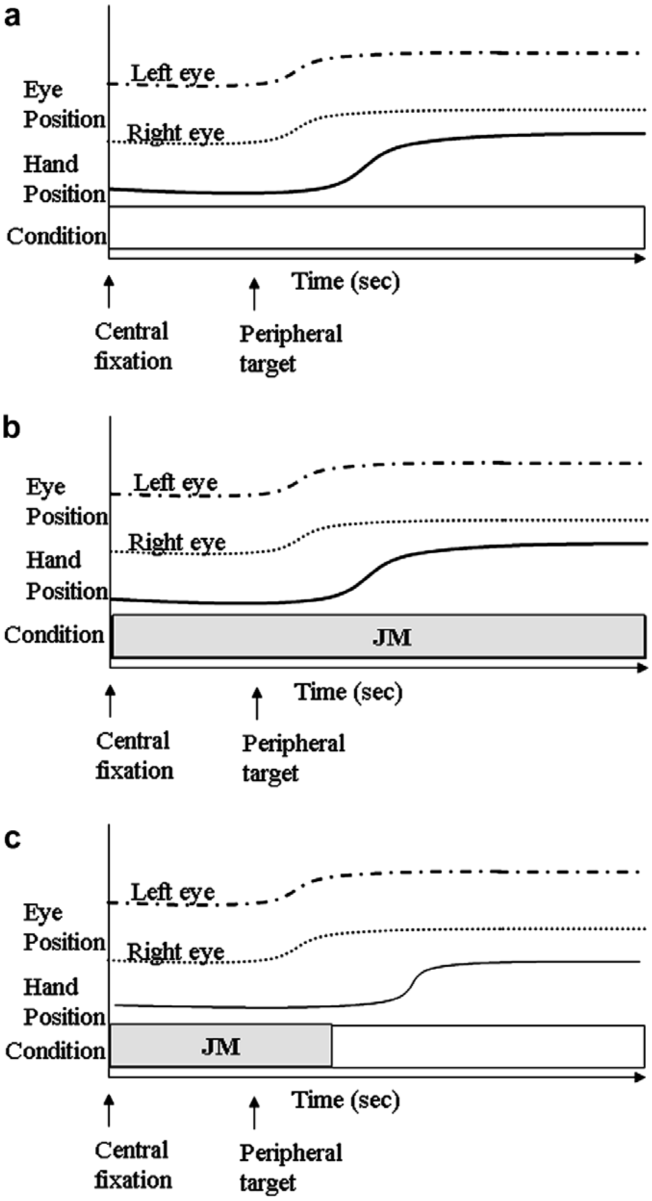

Fig. 1. Schematic illustration of the experimental protocol used in experiment 1: (a) control: no JM; (b) task 1: JM performed during saccade and pointing; (c) task 2: JM performed during saccade, but not during pointing.

### 2.1.5. Data analysis

Data analysis was conducted using custom software and focused on the end-point accuracy of the hand and saccadic eye movements. The pointing data for each trial were examined visually. The end of the pointing trajectory was established from the position and velocity traces. The end point was the position of the hand when it came to rest and it was calculated as the mean of 50 ms when the hand velocity was 0°/s. The calibration of the hand position performed at the end of the experiment for each subject could not be used to calculate the errors due to a noisy signal. We have, however, relative error measures that allowed us to compare the two experimental conditions.

Pointing data, saccade amplitude and saccade peak velocity were submitted to repeated measures, two-way analyses of variance (ANOVA) with condition (control, task 1, task 2) and target position (left, right) as the independent variables.

## 2.2. Results

The data from individual participants for each condition were plotted and visually inspected for trends to determine if participants were more likely to overshoot or undershoot the target in the experimental condition in comparison to the control condition. No trends were evident: half of the participants overshot the target regardless of the experimental condition. The lack of a reliable effect was confirmed by the statistical analysis. Results from the ANOVA for the pointing response showed no significant interaction effect between the task and pointing to the left or right targets ($F(2,18) = 0.66$, $p > .05$). The mean pointing responses to the right sided targets were 8.95 ± 2.66 cm for the control condition, 9.57 ± 2.79 cm for task 1 and 9.10 ± 2.56 cm for task 2. The mean pointing responses to the left sided targets were 9.74 ± 2.50 cm for the control condition, 9.79 ± 2.85 cm for task 1 and 9.56 ± 2.90 cm for task 2. There was no difference in pointing accuracy between the conditions ($F(2,18) = 1.33$, $p > .05$). The distribution of pointing responses to both targets for each task is shown in the boxplots in Fig. 2.

The data showed no significant differences between the conditions for the amplitude of saccadic eye movements ($F(2,18) = 0.67$, $p > .05$). The mean amplitude of the first saccade to the right sided target was 6.73 ± 1.4° for the

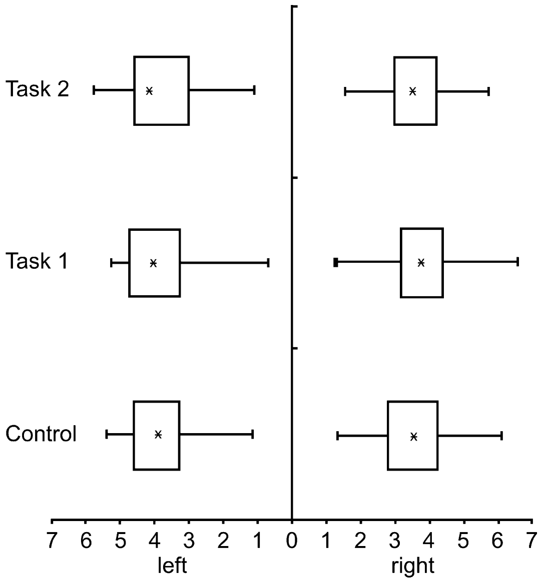

Fig. 2. Distribution of pointing responses obtained in experiment 1. The boxplot contains the middle 50% of the data (the upper edge is the 75th percentile and the lower edge is the 25th percentile), the line in the box represents the median. The lines extending from the boxplot (whiskers) indicate the 1st and 99th percentile.

control condition, 6.62 ± 1.8° for task 1 and 6.65 ± 1.1° for task 2. The mean amplitude of the first saccade to the left sided target was 6.08 ± 1.3° for the control condition, 6.15 ± 1.3° for task 1 and 5.97 ± 2.4° for task 2. Statistical analysis also showed no significant differences between conditions for the velocity data ($F(2,18) = 1.19$, n.s). The mean velocity of the first saccade to the right sided target was 234 ± 1.49°/s for the control condition, 228 ± 67°/s for task 1 and 231 ± 44°/s for task 2. The mean velocity of the first saccade to the left sided target was 220 ± 67° for the control condition, 226 ± 52°/s for task 1 and 215 ± 84°/s for task 2.

### 2.3. Discussion

Results from this study showed that the accuracy of pointing responses associated with a saccade is not affected by the JM. These data help to clarify our previous findings which showed that the JM affected pointing responses to targets presented in depth (Niechwiej-Szwedo et al., 2006). Since the JM has a general effect on the gamma system, presumably affecting all muscles (Delwaide & Toulouse, 1981), the pointing error obtained in the previous study could have been due to the effect of JM on the limb muscles instead of the EOM. Given that the non-twitch motoneurons do not receive monosynaptic input from premotor areas involved in the programming of saccades (Wasicky et al., 2004), the results from the current study support the hypothesis that the pointing error obtained in the previous study was due to the effect of the JM on the EOM muscles and not on the limb muscles.

As expected, we found that the JM did not affect the actual eye movements as shown by the lack of significant differences in saccadic parameters between the control and experimental conditions. Again, the negative findings from this experiment provide additional support to our hypothesis that the JM acts via the activity of non-twitch motoneurons and has no effect on the twitch motoneurons.

## 3. Experiment 2

### 3.1. Methodology

#### 3.1.1. Participants

Eleven healthy adults (8 females) with no history of ocular disorders and a mean age 34 ± 16 years participated in the second experiment.

#### 3.1.2. Stimuli

The stimuli were 0.25° white dots displayed on a black background on a flat CRT monitor (refresh rate 160 Hz). The display was programmed using VPixx (VPixx Technologies, Inc., Montreal, QC), a graphics generation and psychophysics testing software, controlled by a Macintosh G4 computer. The fixation stimulus was presented in the participants' midline and the other two targets were presented randomly at a 10° eccentricity to the left or right of fixation. The comparison stimulus was also a 0.25° white dot and it was presented on the same side as the target in one of five locations: 8°, 9°, 10°, 11° and 12° away from the fixation stimulus.

#### 3.1.3. Apparatus

The JM manipulation procedure was the same as described in the methods section of experiment 1.

#### 3.1.4. Procedure

Participants were seated in total darkness and performed a two-alternative forced choice task (2-AFC) using the method of constant stimuli. At the beginning of each trial participants were instructed to look at the fixation dot, which was shown for a variable time ranging from 1.5 to 2 s. The target was flashed briefly for 50 ms to the left or the right of fixation which was determined randomly by the computer. Participants were instructed to move their eyes as quickly as possible to the location were they saw the target appear and to keep fixating on that location. The comparison target was shown after 2.5 s at 1 of 5 possible locations and participants had to report whether the comparison target was to the left or to the right of their current fixation.

There were three conditions: (a) control: participants executed the eye movement and made the judgement without the JM; (b) task 1: participants performed the JM while the target was shown and during the eye movement, but not during the perceptual judgment; (c) task 2: participants performed the JM during the perceptual judgements but not during the eye movement (see Fig. 3 for illustration of the protocol).

#### 3.1.5. Data analysis

For each participant, the proportion of 'left' responses was calculated for each, target presentation side and task at the five locations where the comparison target was shown and a psychometric function was fitted. All psychometric curves were visually inspected for trends. Subsequently, an overall psychometric function based on the mean of all participants was fitted for each task.

Data for each participant, target side and task were fitted 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. The point of subjective equality (PSE) was 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 target is perceived to the left of the standard target 50% of the time). The PSE, intercept and slope were submitted to repeated measures ANOVA each with task (control, task 1 and task 2) and target side as the independent variables.

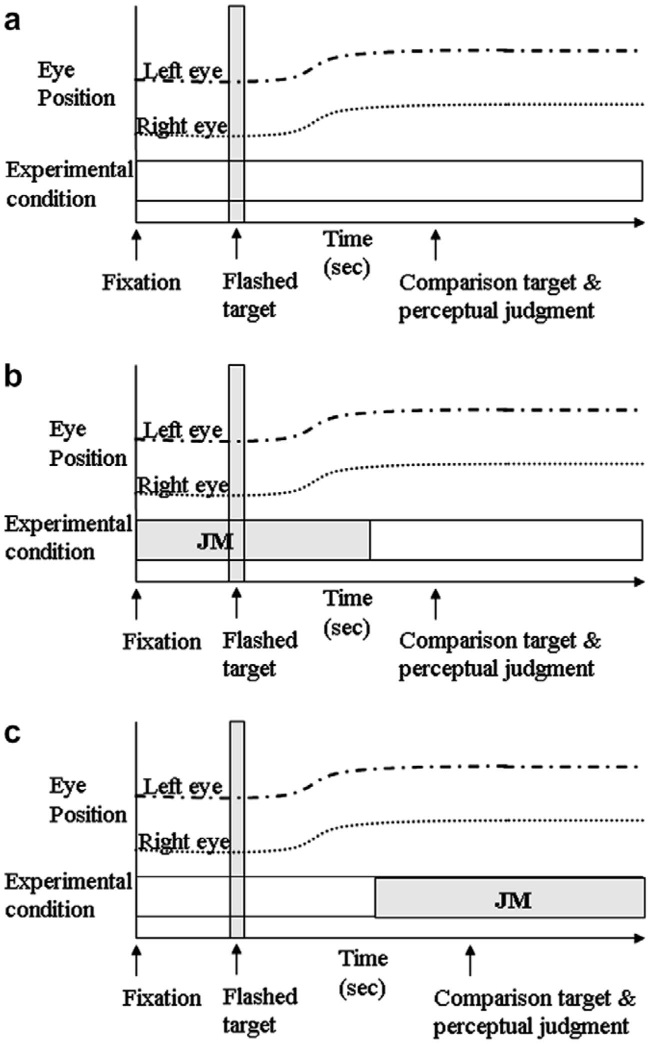

Fig. 3. Schematic illustration of the experimental protocol used in experiment 2: (a) control: no JM; (b) task 1: JM performed during the presentation of the standard target and saccade; (c) task 2: JM performed during perceptual localization.

### 3.2. Results

Preliminary inspection of the individual psychometric curves did not reveal any consistent trends in differences between the conditions. The logistic model fitted the majority of the psychometric curves well (62 out of 66). Although in four cases (two in the control condition, one in task 1 and one in task 2) the Hosmer–Lemeshow test was statistically significant (i.e., the data did not fit the model), the logistic model was still used to fit the data.

The mean psychometric curve is shown in Fig. 4. Results from the statistical analyses showed no significant interaction effect between the experimental conditions and target side: PSE ($F(2,19) = 3.28$, $p > .05$), slope ($F(2,19) = 0.19$, $p > .05$), intercept ($F(2,19) = 0.54$, $p > .05$). The main effect of condition was also not significant: PSE ($F(2,20) = 1.01$, $p > .05$), slope ($F(2,20) = 0.26$, $p > .05$), intercept $F(2,20) = 0.13$, $p > .05$).

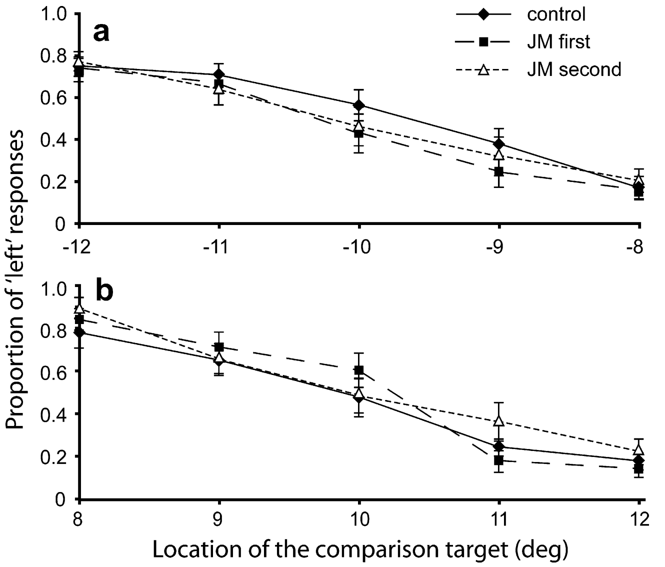

Fig. 4. Mean proportion of 'left' responses for the five comparison targets (at ±10° both the standard and comparison target were presented at the same location). (a) Standard target presented in the left hemifield; (b) standard target presented in the right hemifield. Bars show ±1 standard errors of the mean.

## 4. Discussion

We conducted two studies to examine whether the JM affects the saccadic system similarly to the vergence system, which would help us to elucidate the potential neural mechanism involved in mediating the effect of the JM on the vergence system. We have previously proposed that the JM acts through the activity of non-twitch motoneurons (Niechwiej-Szwedo et al., 2006) which receive monosynaptic input from premotor areas involved in the programming of vergence eye movements but not from areas involved in the programming of saccades (Wasicky et al., 2004). Thus, we hypothesized that if the JM acts through the non-twitch motoneurons then the localization associated with saccades should not have been affected by the manipulation. In contrast, if we had found that responses associated with saccades were affected by the JM, then it would have been more likely that a different neural mechanism was involved in mediating the effect. Overall, the results from both experiments showed that the JM did not affect pointing or perceptual localization of targets presented in the frontal plane. Our data support the first hypothesis and our earlier proposal that the JM affects the gain of the proprioceptive feedback from EOM via the non-twitch motoneurons.

One of the limitations of our studies is the fact that our hypotheses are based on neuroanatomical tracing studies which were conducted in sub-human primates. At the present time it is unknown whether the human EOM fibers also receive dual innervation from ocular motor nuclei (Buttner-Ennever, Horn, Scherberger, & D'Ascanio, 2001). Nonetheless, human EOM do contain similar fiber types to those found in primates and other mammals (Wasicky, Ziya-Ghazvini, Blumer, Lukas, & Mayr, 2000) and the PE are found in the global MIF in humans (Richmond et al., 1984) and monkeys (Ruskell, 1978). Overall, the human and primate EOM are remarkably similar in their organization, histochemical properties and repertoire of eye movements, thus, we believe that it is likely that the dual innervation hypothesis can be extended to humans as well.

A longstanding question in oculomotor physiology concerns the functional significance of the MIF. It has been proposed that the MIF might participate in fine foveation eye movements or might be part of a proprioceptive feedback loop (Buttner-Ennever, Konakci, & Blumer, 2005; Spencer & Porter, 2005). These two possibilities are not mutually exclusive as it is certainly possible that very fine eye adjustments rely on proprioceptive feedback. Moreover, the fact that the global MIF are associated with the PE, the putative EOM proprioceptors, makes the proprioceptive hypothesis viable. Two questions that remain are: (1) why is proprioceptive feedback subject to gamma modulation when the localization response is associated with the vergence but not with the saccadic system? and more generally (2) what is the role of the gamma system in oculomotor control?

The fact that the saccadic system was not affected by the JM perturbation in our study is analogous to the findings of Guthrie and colleagues (1982) who reported that cutting the monkeys' ophthalmic branch of the trigeminal nerve (i.e., deafferentation) altered their vergence responses but had no effect on their conjugate eye movements. Fusional vergence involves disjunctive eye movements which are driven by disparity (i.e., the eyes move in opposite direction when the stimulus falls on non-corresponding retinal points in order to avoid double vision); thus, vergence eye movements require precise adjustment of both eyes to foveate the target and maintain single vision. The CNS might monitor proprioceptive feedback from the EOM for optimal performance in this task. In brief, our results reinforce the previous findings and emphasize the importance of the EOM proprioceptive feedback loop for binocular function.

The modulation of proprioceptive feedback by the gamma system has been studied extensively in the case of the skeletal system; in contrast, only one study, to our knowledge, examined the gamma system in the EOM. Whitteridge (1959) demonstrated that proprioceptive feedback from the EOM in the ungulate is modulated by the gamma system. Direct experimental evidence of the gamma system in other species has been precluded by the lack of information about the afferent pathway and location of the cell body. Nonetheless, we have used an indirect method to change the excitability of the gamma system by using the JM manipulation. Using this proxy method we have provided evidence to support the notion that proprioceptive feedback from the human EOM is also subject to gamma modulation.

It has been proposed that the gamma system is important for parametric adjustment of the proprioceptive feedback loops to match the demands of different tasks (Prochazka, 1989). For example, in the case of the skeletal system an increase in the sensorimotor gain is associated with the performance of difficult or novel tasks in contexts that evoke generalized arousal and vigilance. In other words, the gamma system allows state-dependent adjustment of proprioceptive feedback which can be adjusted to address the specific sensorimotor requirements predicted for the upcoming movement. An example of the parametric feedback adjustment for the jaw muscles has been provided by Taylor and Gottlieb (1985). They suggested that the gain of proprioceptive feedback might depend on the phase of the jaw movement. For instance, the control of the velocity and displacement of the jaw are critical until the moment of tooth contact whereupon the control of the force becomes critical. Moreover, they suggested that the CNS can use proprioceptive feedback to determine the nature of the controlled variable (i.e., velocity or force).

The requirement for gamma modulation of feedback from the EOM might be different for saccades and vergence eye movements. Saccades are fast, ballistic eye movements ranging in amplitude from 3 min arc to 90° and lasting between 15 and 100 ms. Programming of a saccade involves a pulse and a step, which are related to the velocity and the amplitude of the eye movement. In contrast, fusional vergence responses are slow (up to 1 s) and generally small. Vergence angle changes about 14° when gaze is moved from infinity to approximately 25 cm (Howard, 2002). Even though horizontal saccades and vergence are both driven by the medial and lateral recti muscles, the differences in neural control for version and vergence eye movements are reflected in the premotor input and the activity of the motoneurons. For example, for conjugate adduction the premotor excitatory input comes from the abducens internuclear neurons. In contrast, premotor input for convergence eye movements comes from supraocular motor area (Mays, 1984). In addition, Mays and Porter (1984) reported that the relationship between eye position and motoneuron firing rate is dependent on whether the eye movements are conjugate or disconjugate. In their study, recordings were made from the abducens nucleus during conjugate adduction and during convergence. Data showed that for a given eye position the firing rate was greater for convergence compared to conjugate adduction suggesting that there would be greater co-contraction in convergence.

Miller, Bockisch, and Pavlovski (2002) tested this hypothesis by measuring the oculorotary forces in the medial and lateral recti muscles during both types of eye movements. In contrast to the hypothesis, they found decreased forces in both muscles (Miller et al., 2002). These results showed that the innervation of the EOM is much more complex than previously acknowledged and that the motor commands sent to the eye muscles differ during convergence and adduction. Given our results, we propose that the CNS can also set the gain of the proprioceptive feedback differently for vergence and saccades via the gamma system.

In conclusion, we have examined whether registered eye position during saccadic eye movements is affected by the JM manipulation which alters the excitability of the gamma system. We have shown that the JM does not affect manual or perceptual localization of targets presented in the frontal plane. Overall, data from the present study help to clarify findings from our previous study which examined pointing in depth and strengthen our hypothesis that the JM affects the activity of the non-twitch motoneurons. We propose that that the non-twitch motoneurons might be involved in the parametric adjustment of the proprioceptive feedback loops to match the demands of different types of eye movements.

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