

The Role of Brachial Muscle Spindle Signals in Assignment of Visual Direction

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SUMMARY AND CONCLUSIONS

1. In the oculobrachial illusion, a target light attached to the unseen stationary hand is perceived as moving and changing spatial position when illusory motion of the forearm is elicited by brachial muscle vibration. Our goal was to see whether we could induce apparent motion and displacement of two retinally fixed targets in opposite directions by the use of oculobrachial illusions.

2. We vibrated both biceps brachii, generating illusory movements of the two forearms in opposite directions, and measured any associated changes in perceived distance between target lights on the unseen stationary hands. The stability of visual fixation of one of the targets was also measured.

3. The seen distance between the stationary targets increased significantly when vibration induced an illusory increase in felt distance between the hands, both with binocular and monocular viewing.

4. Subjects maintained fixation accuracy equally well during vibration-induced illusory increases in visual target separation and in a no-vibration control condition. Fixation errors were not correlated with the extent or direction of illusory visual separation.

5. These findings indicate that brachial muscle spindle signals can contribute to an independent representation of felt target location in head-centric coordinates that can be interrelated with a visual representation of target location generated by retinal and oculomotor signals.

6. A model of how these representations are interrelated is proposed, and its relation to other intersensory interactions is discussed.

prevented, the physically stationary subject gets an illusion of falling forward (Lackner and Levine 1979). When the biceps brachii is vibrated, the forearm flexes, but restraining the forearm results in illusory extension (Goodwin et al. 1972a,b). Lackner (1988) has shown that virtually any illusory movement of the body or its parts, be it physically possible or not, can be elicited by vibrating the appropriate muscle or muscles.

Lackner and Levine (1978, 1979, 1981) studied how oculomotor control and visual localization could be influenced by vibratory myesthetic illusions involving a limb or the entire body. During vibration of Achilles tendons in darkness, immobilized subjects exhibited a nystagmus that was compensatory for their illusion of falling forward; if a head-fixed target was present, it would be steadily fixated but seen as moving in the same direction as the body and leading it somewhat. During vibration of the biceps brachii in darkness, many subjects could track the illusory extension of their restrained forearm with smooth pursuit eye movements; if a light-emitting diode (LED) were attached to the stationary finger of the vibrated arm, it would be perceived as moving with the finger. Lackner and Levine (1978) referred to the latter phenomenon as the "oculobrachial illusion" (OBI). During an OBI, if subjects pointed with their other hand to the LED they would indicate its seen rather than true location, although fixation of the true location could be maintained. Many subjects reported during physically stable fixation that they could feel their eyes tracking the LED's "motion."

In an OBI, the egocentric visual direction of a retinally fixed stimulus is remapped in the absence of a physical change in eye position. Lackner and Levine (1978) hypothesized that the stationary eyes were centrally registered as moving in their orbits during the OBI. Pursuit eye movement commands that are elicited during vibration-induced illusory arm movements in darkness could still be a source of efference copy signals about eye movement even when pursuit is suppressed by a retinally stationary stimulus during the OBI. Errors in visual localization during body motion, such as the oculogyral illusion (Graybiel and Hupp 1946), have been hypothesized to depend on copies of oculomotor signals generated to suppress reflexive eye movements (e.g., Ebenholtz, 1986; Post and Leibowitz 1985; Whiteside et al. 1965). This view has recently received strong experimental support (Evanoff and Lackner 1986, 1987, 1988). Thus muscle spindle signals need not participate directly in a retinotopic to head-centric transformation to elicit an OBI. They might do so indirectly by eliciting

INTRODUCTION

This paper describes how activity of skeletal muscle spindles can influence the assignment of visual direction to particular retinal loci. The discovery of vibratory myesthetic illusions, demonstrating a role of muscle spindles in kinesthesia (cf. Goodwin et al. 1972a,b), provided the background for our approach. To elicit such illusions, a manual physiotherapy vibrator oscillating at ~ 120 Hz is applied to the skin over a tendon. The vibration heightens spindle primary (Ia) and secondary (II) discharges, which excite the α -motoneurons innervating the extrafusal fibers of the vibrated muscle; consequently, the vibrated muscle contracts (Hagbarth and Eklund 1966). If mechanical restraint of the limb prevents full shortening of the vibrated muscle, the spindle firing level remains high and a change in limb or body position is perceived that is consistent with stretch of the vibrated muscle. For example, when the Achilles tendons are vibrated, a freely standing subject will tilt backward (Hagbarth and Eklund 1966), but, if backward tilt is

oculomotor commands that bias the representation of eye-head position, which, in turn, enters into the transformational remapping.

Recent physiological studies suggest ways that visual localization could be influenced independently of a central misrepresentation of eye position. Cell ensembles in the superior colliculus, posterior parietal cortex, and other areas that represent object location in motor-error (Mays and Sparks 1980) or head-centric (Andersen et al. 1985) coordinates received retinal signals and extraretinal eye movement signals (Andersen et al. 1987; Cohen and Buttner-Ennever 1984; Kunzle 1978; McCrea and Baker 1985; Sparks and Mays 1983) as well as limb proprioceptive signals (Andersen et al. 1990; Clemo and Stein 1984; Edwards et al. 1979; Pandya and Kuypers 1969), among others. Such physiological convergence provides a way that limb muscle spindles might contribute to visual localization independently of feedback about eye position. If such an influence exists, errors in visual localization could be elicited without a misrepresentation of eye position.

Our approach to evaluating this possibility was to induce vibratory myesthetic illusions of the two forearms in opposite directions and to measure the perceived separation of LEDs attached to the two index fingers. Our specific goals were 1) to determine the character of the LED and arm movements that subjects experienced during vibration of the two arms and 2) to measure the stability of visual fixation. We conducted two experiments. The first optimized the measurement of perceived movement of the LEDs and the arms. After we had demonstrated that illusory separation of the LEDs and arms could be elicited, we assessed fixation stability in a second experiment. A combination of monocular and binocular viewing conditions was used across both experiments to evaluate the contribution of size-distance mechanisms.

The results of this work have been presented in part at the annual meeting of the Association for Research in Vision and Ophthalmology in Sarasota, Florida, May 1992.

METHODS

Subjects

Fifteen individuals with normal or corrected vision participated in our first experiment. They consistently experienced OBIs with either arm. For the second study, in which we measured eye movements, we retested 5 of the 15 and added 3 naive subjects. The apparatus for monitoring eye movements could not be worn with eyeglasses, so the subjects who participated had to be able to see clearly, without correction, an LED at arm's length. The subjects gave informed consent and were paid for their time.

Apparatus

The subject was seated at a table with both forearms strapped in arm holders and with his or her head stabilized by an individually molded bite bar. An LED was taped to the tip of each index finger, and dimmed until it did not illuminate any part of the finger when the room lights were extinguished. The arm holders could pivot in a plane parallel to the table top. Potentiometers on their shafts provided readouts of elbow joint angles, which were recorded on a polygraph (model 7; Grass), calibrated in degrees of visual angle at the fingertips (resolution = 0.5°). The physiotherapy vibrators were distributed by Sears (model 273.2250).

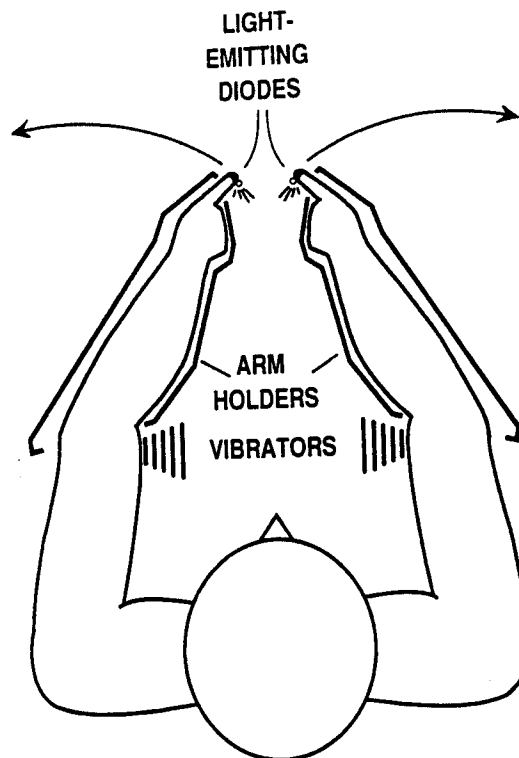


FIG. 1. Schematic illustration of experimental setup. Fairly extended configuration of forearms (elbows set at $\sim 145^\circ$) was used so that vibration would induce apparent motion of fingers in arcs that involved mainly lateral motion relative to head (arrows). Apparatus for measuring movements of the right eye is not depicted.

To monitor eye movements, we used a photoelectric technique (model EM130 ACS Applied Research Developments) for tracking the iris-sclera border. An array of infrared light emitters and detectors through which the fingertips were visible was positioned in front of the right eye on a specially constructed headset worn by the subject. The headset was stabilized by both a headband and the biteplate. The eye position signal was recorded on the polygraph, DC coupled, through a 35-Hz low-pass filter. The output of the entire system had an accuracy and resolution of $\geq 0.5^\circ$. Figure 1 illustrates a subject in the apparatus.

Procedure

In the first experiment, we vibrated both immobilized forearms simultaneously and measured the perceived separation of the fingertips and LEDs. The room was dark except for the LEDs, and the subjects were permitted binocular vision. The arm holders were locked in position with the finger LEDs 4° of visual angle apart, 2° to either side of the median plane. This was the maximum separation possible without a Troxler effect, that is, without the nonfixated LED perceptually fading. Before the start of each 30-s trial the subject was told which LED to fixate and to remember the largest visual distance between the two LEDs and the largest felt distance between the fingers during the trial. Vibrators were then placed against both biceps brachii and held there for 30 s by two highly experienced experimenters. In some trials the vibrators were activated; in others they were not. Next, the arm holders were unlocked and the subject, with the LEDs still visible and attached to the fingers, attempted to reproduce 1) the greatest lateral distance seen between the LEDs during the trial, 2) the greatest distance felt between the finger tips during the trial, and 3) the original distance between the LEDs just before the vibrators

TABLE 1. Perceived distance between LEDs and between fingers, as indicated by post-trial reproductions, in subjects who reported illusory separation of LEDs

Condition	Remembered distance between LEDs before a 30-s trial	Perceived distance between LEDs during a 30-s trial	Perceived distance between fingers during a 30-s trial
Vibration			
mean	5.6	8.5	24.7
SD	1.15	2.71	13.86
No vibration			
mean	5.3	5.3	6.5
SD	1.42	1.61	3.43

$n = 9$. Units are degrees of visual angle. LEDs, light-emitting diodes.

had been placed on the arms. The subject's arms were passively displaced by random amounts between settings. Finally, the subject gave a verbal description of what had been experienced.

The procedure was modified slightly for the second experiment, in which eye movements were monitored. Subjects wore the headgear described above, and eye position was calibrated before every trial. The left eye was occluded. During each 30-s trial, the subject's tasks were to fixate monocularly the specified LED and to note any change in the seen distance between the two LEDs. After 30 s, the vibrators were taken away and the subject made saccadic eye movements between the two LEDs, which were still physically 4° apart. Then the arm holders were unlocked, the arms were passively displaced, and the subject set the LEDs to the maximum visually perceived distance during the trial and then made saccadic eye movements between them.

In both experiments, subjects each completed eight trials, including four control trials in which the vibrators were held against the biceps brachii but not turned on and four experimental trials in which the vibrators were actuated. In one-half the trials the right LED was fixated, in one-half the left, in a counterbalanced order.

Only ~70% of individuals tested have strong tonic vibration reflexes. Those who do also have strong OBIs (Levine and Lackner 1979). Our approach in the present experiments was to test a substantial number of individuals and to analyze in detail the results of only those who experienced apparent motion of the forearms. We vibrated both arms to improve the likelihood of such motion being experienced.

RESULTS

In the first experiment, 10 of the 15 subjects reported that the apparent separation between the LEDs increased during vibration. In vibration trials, the perceived distances between the LEDs and between the fingers, as indicated by posttrial reproductions, were 1) significantly larger than the perceived distances in the no-vibration condition, 2) significantly larger than the actual 4° distances during the trial, and 3) significantly larger than the remembered pretrial LED distances (see Table 1 and Fig. 2). In the no-vibration trials there was a nonsignificant tendency for the posttrial reproductions to be larger than the true and remembered distances both between the LEDs and between the fingers. Table 1 summarizes these data. These statistical comparisons were made with correlated, two-tailed t -tests, and differences reported as significant achieved alpha levels of $\geq P < 0.002$. Nine rather than 10 subjects are included in the quantitative analysis. One subject was omitted because he made errors ≥ 3.5 SD units greater than the other sub-

jects on the posttrial task of resetting the LEDs to the remembered pretrial distance, irrespective of whether it was an experimental or control trial.

The experiences reported by all 10 subjects were consistent. In vibration trials, they initially felt lateral motion and displacement of both forearms, and 10–15 s later continued to feel apparent motion but no further apparent displacement. Their forearms seemed to rotate at the elbows. The index fingers were perceived as moving in arcs involving mainly lateral motion but also some motion in depth. (This is consistent with the fairly extended, 145° , starting angles of the elbows.) The two LEDs seemed to follow the same paths as the fingers, but to displace only about one-third as far, almost exclusively laterally. Thus the LEDs seemed to dissociate from the fingers. Eight subjects perceived symmetrical motion and displacement of the two arms and LEDs, and two perceived one LED to displace more than the other.

The other five subjects, who failed to report an apparent increase in lateral distance between the LEDs, fell into two categories. Three reported apparent motion of both arms and both LEDs in opposite directions but without apparent displacement through space. The other two felt illusory extension of only one of their arms during vibration and an increase in the felt distance between the fingertips; however, neither reported an increase in the seen distance between the LEDs. Instead, the LED on the perceptually nonmoving arm seemed to dissociate from the finger and to move as a visual unit with the other LED.

In the second experiment, seven of the eight subjects reported seeing an increase in the lateral distance between the two LEDs during vibration without an increase in depth, yet they accurately maintained fixation throughout the trial. Figure 3 presents eye and arm movement records from a typical vibration trial. The largest error in LED fixation during each trial was measured to the nearest one-half

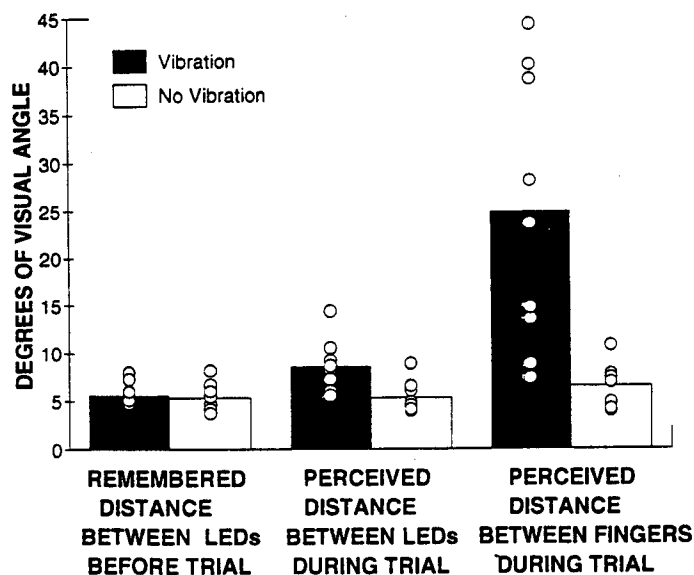


FIG. 2. Bar graph of mean ($n = 9$) posttrial reproduction of remembered distance between light-emitting diodes (LEDs) before a 30-s trial and perceived maximum distance between LEDs and fingers during a trial. Open circles, some of which overlap, are individual data.

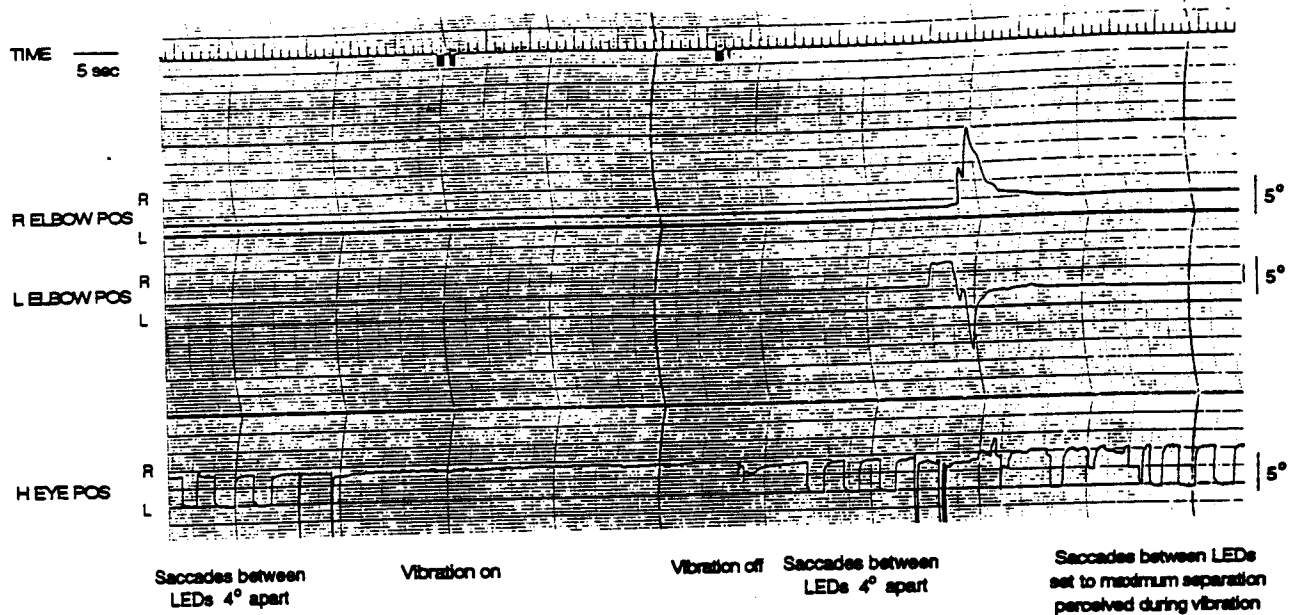


FIG. 3. Typical record of position of both arms and of right eye during a vibration trial in which subject was attempting to fixate LED on his left finger.

degree and given a positive sign if it was in the same direction as illusory movement of the LED and arm (extension). The average fixation errors in the control and vibration conditions were not significantly different from each other ($P > 0.05$). Posttrial saccades between the LEDs that had been positioned to reproduce the maximum visually perceived distance between them during the trial were larger in the vibration than the control condition. The former were significantly greater ($P < 0.01$) than the actual per-trial separation (4°); the latter were not ($P > 0.05$). There was no significant correlation between fixation error and perceived increase in LED separation in either the vibration or the control trials. The amplitude of posttrial saccades between the actual per-trial LED positions was not significantly different between the vibration and control conditions, and neither was significantly different from the actual LED separation ($P > 0.05$). Table 2 and Fig. 4 summarize these results.

TABLE 2. Error in LED fixation and perceived distance between LEDs during trials, as indicated by posttrial saccades to reproduced positions, in subjects who reported illusory separation of LEDs and arms

Condition	Maximum fixation error during a 30-s trial	Magnitude of saccades between LEDs 4° apart	Magnitude of saccades between LEDs at their perceived positions during a 30-s trial
Vibration mean	0.46	4.05	6.86
SD	0.101	0.120	0.915
No vibration mean	0.367	4.01	4.35
SD	0.14	0.07	0.545

$n = 7$. Units are degrees of visual angle.

The subjective descriptions and reproduction responses of all seven subjects were qualitatively and quantitatively similar to those of subjects in the first experiment. The eighth subject reported that his arms had moved laterally outward but that the LEDs had maintained a constant lateral separation and had moved upward together without changing in depth.

DISCUSSION

The seen distance between two LEDs attached to the stationary index fingers increased when brachial muscle vibration induced an illusory increase in felt distance between the two forearms. Two stationary points subtending a fixed

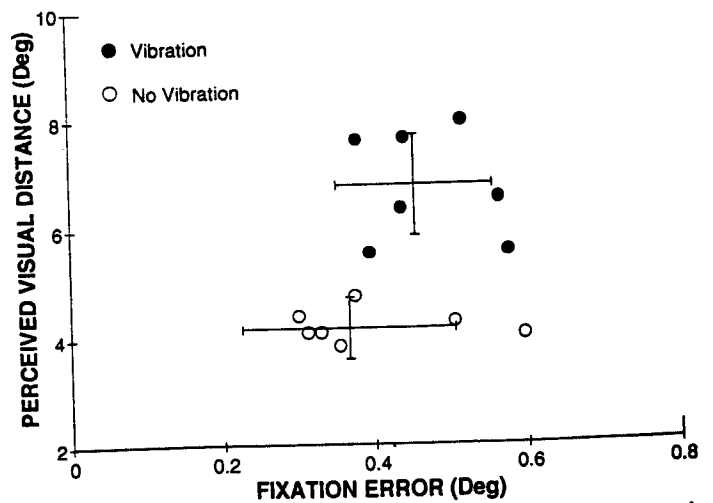


FIG. 4. Scatterplot ($n = 7$) of maximum error during 30 s of attempted fixation of an LED on stationary left index finger vs. maximum perceived distance between LEDs on left and right index fingers during same period, as indicated by post-trial reproduction. Error bars indicate means \pm SD.

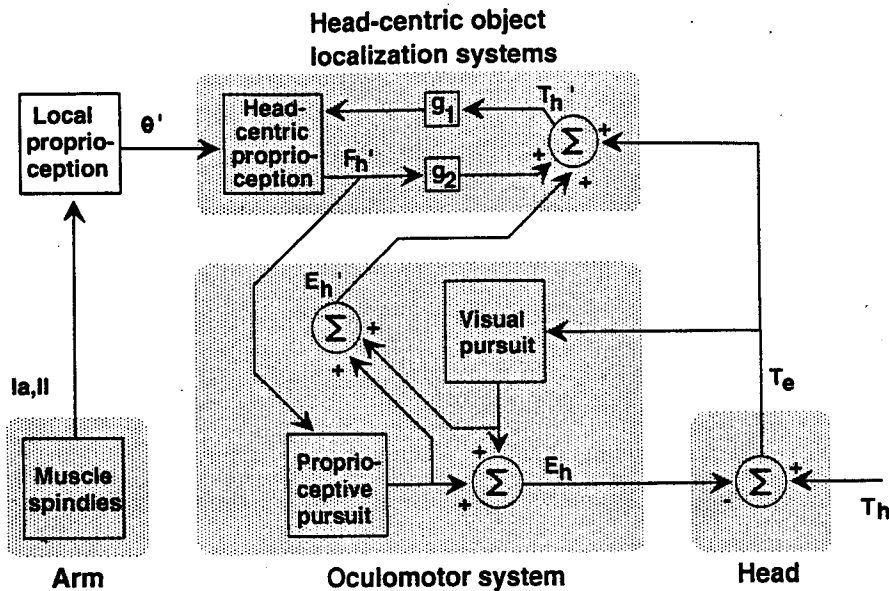


FIG. 5. Block diagram of flow of muscle spindle and visual information contributing to assignment of visual direction and maintenance of foveation. See text for explanation.

- T_h - Visual target relative to head
- T_h' - CNS representation of visual target relative to head
- E_h - Eye relative to head
- E_h' - CNS representation of eye relative to head
- T_e - Visual target relative to eye (retinal slip/offset)
- Ia,II - Muscle spindle afferent activity
- F_h' - CNS representation of finger relative to head
- θ' - CNS representation of joint angles

retinal angle may be remapped as expanding or contracting in the frontal plane if the eyes diverge or converge, respectively (Collewyn et al. 1986; Heinemann et al. 1959). If the vibration-induced, apparent motion of the fingers in depth (see Fig. 1) induced divergence of the eyes, it could have led to an increase in apparent separation of the LEDs. However, our monocular recordings revealed no significant vergence and no correlations were present between eye movements and illusory movements of the LEDs. Moreover, identical patterns were obtained under binocular (Exp. 1) and monocular (Exp. 2) viewing conditions. Thus what our subjects experienced was not solely mediated either by proprioceptively induced version or vergence.

Our findings indicate that muscle spindle information about body configuration can be interrelated with visual signals to influence visual direction independently of the oculomotor system. Figure 5 is a simple block diagram model of how brachial muscle spindle information could influence the assignment of visual direction. It has four functional blocks representing 1) muscle spindles from the arms contributing to limb position sense; 2) the eyes and a target relative to the head, which yield a retinal slip/offset signal; 3) the oculomotor system; and 4) a system for head-centric localization of seen and felt objects.

Ocular pursuit and perception of a moving visual target that is not being touched are handled as in most models (cf. Henn et al. 1980 for reviews). Retinal slip/offset (T_e) is the difference between target (T_h) and eye (E_h) movements relative to the head. The pursuit system has sufficient gain at low velocities (Koerner and Schiller 1972; Robinson

1965) for pursuit to approach target motion, reducing retinal slip/offset (T_e) virtually to zero. A copy of the visual pursuit signal contributes to a central representation of eye movement in the orbit (E_h'), and E_h' and T_e are summed to yield a head-centric representation of the visual target (T_h').

In this model, ocular pursuit and perception of one's unseen finger depends on input from muscle spindles (Ia and II) in the muscles of the arm or other motile appendage of the body. Muscle spindle activity must be transformed in a process requiring at least two steps. The first, conversion of muscle spindle activity to signals for joint angles (θ'), is beyond the scope of this paper but has been addressed by others (Matthews 1981, 1988) and involves comparisons with patterns of voluntary muscle innervation and limb loading. The second step, conversion of joint angles to head-centric felt position, has also been dealt with by others and probably requires experience with objects that are seen and touched (Burnod et al. 1992; Caminiti et al. 1990). The result of these two transformations of spindle input is a signal for felt finger (or other appendage) position (F_h') in head-centric coordinates compatible with other (retinotopic and oculomotor) signals involved in assignment of visual direction and generation of eye movements. Felt finger position, F_h' , influences seen target position, T_h' , by converging on the summation point in the system for head-centric visual localization. F_h' also can generate eye movements. Such proprioceptive pursuit is modeled separately from visual pursuit because it is inherently open loop and does not exhibit high gain at low velocities like visual pursuit. The velocity of pursuit eye movements during at-

tempts to pursue illusory movement of the unseen finger during brachial vibration is lower than the perceived velocity of the finger (Lackner 1975), and proprioceptive pursuit of the unseen physically moving hand has a lower gain than visual pursuit (Mather and Lackner 1980). Ocular pursuit of seen and felt targets can each be voluntarily generated or withheld.

Importantly, when one's seen hand is the target, accurate pursuit is possible to much higher frequencies for both passive and active movements of the hand than for an external visual target undergoing comparable motion (Mather and Lackner 1980; Steinbach 1969; Steinbach and Held 1968). This behavioral evidence indicates that the proprioceptive and visual pursuit mechanisms can act synergistically to enhance the range of pursuit eye movements even when vibrations are not involved. That is, T'_h and F'_h are both important for eye-hand coordination.

The main conclusion of the present experiment is that the spindle-based representation of finger location, F'_h , has direct access to the model node where retinal slip/offset, T'_e , and registered eye position, E'_h converge in the head-centric visual localization system. We will illustrate how this model can explain the original OBI as well as the present results. In the OBI the stationary arm and a visual target attached to the hand are perceived as moving and displacing when the biceps brachii or triceps brachii are vibrated in darkness. Vibrating the biceps of the restrained right arm generates a proprioceptive representation of the arm and finger moving and displacing rightward. Cutaneous contact cues establish a link between the finger and the LED that the subject is attempting to fixate. Proprioceptively induced pursuit drives the eyes rightward, generating leftward retinal slip and eliciting visual pursuit to preserve foveation of the target (cf. Levine and Lackner 1979). Because the proprioceptive pursuit and visual pursuit (suppression) commands are in opposite directions, the sum of their efference copies tends toward zero, and little or no misregistration of eye position is predicted. As a result, the summing point in the system for head-centric visual localization receives signals indicating a stationary or nearly stationary eye and negligible retinal slip/offset. The F'_h input to the summing point indicating rightward finger displacement would explain why rightward visual motion and displacement, T'_h , are perceived.

The results of a prior investigation demonstrating proprioceptive influences on assignment of auditory direction can be modeled in an analogous way. In that experiment (Lackner and Shenker 1985) muscle vibration was used to induce illusory motion of the hand to which a small speaker emitting clicks was affixed. Subjects heard the sound source moving in the same direction as the apparent displacement of their hand but they did not experience any head turning. Illusory head displacement might have been expected because constant binaural arrival times at the ears are physically consistent with auditory motion only if the head is moving. The lack of perceived head displacement means proprioceptive information about hand position led to a remapping of auditory direction independent of the head-neck sensorimotor system, just as it can lead to remappings of visual direction independently of the oculomotor system.

In the present experiment, proprioceptive mislocalizations of the two hands oppositely biased the assignment of visual direction to two retinally fixed stimuli simultaneously. A single signal conveying information about eye version or vergence could not explain this; however, a spindle-based signal indicating leftward motion of the vibrated left arm could influence localization of the left LED and simultaneously the right arm could influence the right LED. This would require the model to have a F'_h signal for each finger, a T'_h signal for each LED, and a means of determining which seen target corresponds to which felt target.

The model contains separate representations of seen and felt target location, which is consistent with the common observation that the target LED and finger often become perceptually dissociated during the OBI. An LED seems to move in the direction of the hand but often not as far. These two representations are separate but not independent. The spatial representation of the finger influences visual direction, as described above, but the representation of visual direction also captures the perception of finger position (cf. Hay et al. 1965; Stratton 1987). For example, when a target light is attached to the arm, biceps vibration induces less perceived movement of the finger than in total darkness (Levine and Lackner 1979). To account for such interactions the model includes reciprocal connections between the head-centric representations of visual direction and finger location. These reciprocal pathways contain gain elements because the bidirectional perceptual and oculomotor interactions depend on context (as described above) and instructions (cf. Levine and Lackner 1979). The gain elements are controlled by supraordinate spatial constancy mechanisms, which are not explicitly represented in the model. These mechanisms continuously evaluate the internal spatial representations of the fingers and targets as well as of the head, the body, and the contact surface of support, among others, to best evaluate new afferent and efferent information within current physical constraints (Lackner 1981, 1992, 1993). For example, breaking cutaneous contact between the finger and the target reduces the certainty that the signal for felt finger position, F'_h , is a good representation for felt target position; in this case, the visual illusion is eliminated during muscle vibration. Variability in these complex mechanisms may account for intersubject variability.

In summary, we have demonstrated that providing proprioceptive misinformation about the spatial location of two retinally fixed stimuli can independently and simultaneously influence assignment of their perceived visual directions. The model we have presented makes predictions about visual and auditory localization and oculomotor control in a variety of other situations in which the target, a limb, or the whole body is moving. It is open to inputs from supraordinate mechanisms involved in adaptation to sensorimotor rearrangements and is consistent with existing ideas about eye-limb coordination, including recent studies concerning the convergence of visual, eye position, and limb proprioceptive signals in the posterior parietal cortex (Andersen et al. 1990; Zipser and Andersen 1988).

We thank Dr. Nikos Logothetis for pointing out the need to address the issue of binocular size-depth illusions. C. E. Lathan gives special thanks to her undergraduate thesis advisor, Don Reynolds.

This work was supported by National Aeronautics and Space Administration Grant NAG 9-515.

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Received 4 January 1993; accepted in final form 7 June 1993.

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