Exp. Brain Res. 36, 275–283 (1979)

Experimental Brain Research

Some Sensory and Motor Factors Influencing the Control and Appreciation of Eye and Limb Position

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Summary. Some aspects of the manner in which the central nervous system uses sensory information for the guidance of eye and arm movements were investigated. When subjects experience apparent motion of their restrained forearm, induced by vibration of their biceps muscle in the dark, they are able to pursue with their eyes at least part of this "motion" and to point with their nonvibrated limb to the apparent location of the vibrated arm. The presence of a small target light on the vibrated hand limits the extent of illusory change in limb position and results in illusory motion of the target light in the same direction as the arm motion. When asked to indicate the spatial position of the light or hand, subjects still point with their nonvibrated arm to the apparent locations. Although visual pursuit of the illusory motion of the forearm can still be elicited in the presence of the target light on the hand, the subjects' eyes remain steadily fixating the stationary target light when they are instructed to track its illusory motion. These findings demonstrate that sensory and motor factors affecting the perception of visual direction and the guidance of arm and eye movements can be differentially employed at several levels of central nervous control.

Key words: Spatial orientation – Visual direction – Motor control – Tonic vibration reflex – Myesthetic illusions

The apparent visual direction of an object with respect to the head is determined by patterns of retinal stimulation and the registered orientation of the eyes in their orbits (Helmholtz, 1962). Such retinal and oculomotor information about the spatial position of an object in relation to the body usually enables accurate arm movements to the object (Bowditch and Southard, 1880; Hanson and Skavenski, 1977; Woodworth, 1899). If one is holding the object, synergistic proprioceptive information about the position of the object in relation to the body will also be available to augment the visual specification of the object's spatial position (Lackner, 1974; Lackner and Zabkar, 1977). The present report examines the influence of such proprioceptive information from

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0014–4819/79/0036/0275/$ 1.80

non-oculomotor sources on the computation of visual direction. Its starting point is the recent demonstration that when a proprioceptive illusion of arm position is induced by muscle vibration, the apparent position of a stationary target light attached to the hand may also appear to change (Lackner and Levine, 1978). The existence of an *oculobrachial illusion* indicates that the assignment of visual direction can be influenced by positional information about body orientation other than that derived from retinal and oculomotor sources.

The elicitation of an oculobrachial illusion depends on the apparent motion of the stationary forearm experienced when the biceps or triceps muscle is vibrated and the forearm is prevented from moving under the action of the resulting tonic vibration reflex (Goodwin et al., 1972a, 1972b). Vibration of the biceps causes reflex flexion of the forearm but when the movement is checked, extension of the stationary forearm is experienced; vibration of the triceps elicits perceived flexion.

Lackner and Levine (1978) found that if a small target light was attached to a subject's hand when he was experiencing apparent motion of his stationary forearm, he would see the target light as moving in the same direction as the apparent motion of his arm. Recordings of eye position showed that the apparent visual motion was not accompanied by corresponding movements of the eyes. Some subjects, when experiencing the oculobrachial illusion, reported that the target light did not seem to move quite as fast as the hand and displaced a smaller apparent distance than the hand. Preliminary observations also suggested that the velocity and extent of arm motion elicited by muscle vibration might be diminished by the presence of the target light attached to the hand. These considerations raised the possibility that just as proprioceptive information about hand position can influence visual direction so might retinal and oculomotor factors influence the magnitude of the arm illusion evoked by muscle vibration. The experiments to be described evaluated this possibility.

Methods and Materials

Subjects

Two groups of six subjects (aged 19–36) participated individually in two experimental sessions. None had known oculomotor deficits and all were able to see the target light clearly with foveal fixation. Only subjects who experience vibration-induced illusory motion of the forearm were included ($\cong$ 75% of those sampled).

Apparatus

During an experimental session, the subject was seated and his head and upper torso were stabilized through the use of a biteboard. His arms were strapped in padded, contoured, counterbalanced arm supports constructed from thermoplastic sheets. These supports allowed free elbow flexion and extension. The right arm was fixed at an arbitrary elbow position of 100° during the experiment. Each arm support was attached to a potentiometer that provided a continuous signal indicating joint angle to an inkwriting polygraph (Grass model No. 7). A fiber optic strand projecting 5 mm from the end of an opaque tube was taped to the subject's right index finger which was held flexed at 90° flexion by the arm support. When illuminated from a remotely controlled light source, this strand served as the target light and was the only object visible to the subject during the experiment. A physiotherapy vibrator (120 pulses/s) was used to provide mechanical stimulation of the biceps muscle of the right arm.

During one of the subject's two experimental sessions, his horizontal and vertical eye positions were monitored continuously with an infra-red sensing device (Narco Biosystems) and recorded separately on the polygraph. Eye position was calibrated by having the subject visually pursue the light on his finger while the arm was passively moved 20° into flexion and 20° into extension from the arbitrary primary position of 100°. In addition, subjects in group II tracked with their left arm this real motion of their right arm, once with the target light lit and once in the dark.

Procedure

Each experimental session consisted of blocks of four 20-s trials; the subjects in group I received five blocks of trials, those in group II, four blocks. Each block included in counterbalanced order the following conditions: A) the subject looked at the felt position of his right index finger in the dark and moved his left arm so that his index fingers were aligned; B) the subject fixated and pointed to the felt position of his right index finger while the target light was on; C) the subject fixated the target light and pointed to the felt position of his right index finger; and D) the subject fixated the target light and pointed to it. In all four conditions, after the subject indicated that he was satisfied with his pointing and fixation responses, the 20-s trial was begun and the subject changed his fixation or pointing as necessary to maintain apparent coincidence with the target light or the hand. During two of the blocks of trials, the right biceps muscle was vibrated; the onset of vibration was keyed to the subject's report that he was properly fixating and pointing to the target light or hand. The other three blocks from group I and two blocks from group II served as controls and monitors for autokinesis.

The subject was instructed to note what both the light and right arm were doing in addition to carrying out his fixation and pointing tasks. He was also asked to rate the extent of target and arm displacement for comparison with subsequent conditions and to indicate whether the target light had changed in brightness or clarity. The subject was told that it was possible to experience light or arm motion in a direction that was impossible to indicate with the constraints imposed by the apparatus. After each trial the subject reported what he had perceived, and compared the trial to others in the same block.

Results

Non-vibration Blocks

In trials not involving vibration, no subject reported a change in arm or target position, no subject showed a change in his pointing response to the target light or to his hand, and no subject exhibited pursuit eye movements or a change in fixation position.

Vibration Blocks

In vibration trials all subjects experienced illusory extension of their forearm; however, in Conditions B, C, and D when the target light was present the extent of illusory forearm extension was less than in Condition A without the target light (see Table 1). The perceived extensions of the forearm in Conditions B, C, D were reported as more or less equivalent although these conditions involved different combinations of pointing and fixation movements; similarly, the

Table 1. Character of illusory arm and target light motion during all trials with vibration of biceps. Chamber is in darkness and during Conditions B, C, and D a small target light is on the index finger of the vibrated arm

Conditions	Dark	Target Light on Hand		
	A Point Hand Look Hand	B Point Hand Look Hand	C Point Hand Look Light	D Point Light Look Light
Mean downward illusory motion (in degrees)[a]	16.5	12.0	12.3	8.5
Number trials with dissociations[b] (out of 48 per condition)		19	24	19
Number of trials with dissociations in which light was stationary[c]		14	11	5

[a] Overall ANOVA: $p < 0.001$; Condition A, B, C, > D: $p < 0.001$; Condition B > C: not signif.; Conditions B, C < D: $p < 0.01$
[b] Not signif.
[c] Overall ANOVA: $p < 0.02$; Conditions B, C > D: $p < 0.03$

extents of illusory light movement in Conditions B, C, and D were reported to be roughly equivalent. The onset of visual motion always corresponded with the onset of apparent arm extension although the extent of visual displacement was sometimes reported to be less than the magnitude of experienced arm extension. Such partial dissociations were distributed fairly equally among Conditions B, C, and D. Visual displacement greater than the apparent extension of the forearm never occurred.

An analysis of variance and planned comparisons were performed on the extent of arm and light illusions as measured by changes in pointing responses, number of trials in which the visual target did not seem to move as far as the arm, number of trials with some pursuit eye movements, and number of trials with no illusory light movement. The two experimental groups showed similar performance across conditions and their data were pooled.

In Condition A in which the subject, without a target light present, pointed to his hand, the mean extent of illusory arm displacement indicated was 16.5° (range 3–35°); accordingly mean apparent velocity was nearly 1°/s. Conditions B and C involving a target light but pointing movements to the hand while the subject fixated the hand (Condition B) or the light (Condition C) produced hand illusions of 12.0° and 12.3°. Condition A is significantly different from B and C ($p < 0.001$) but B and C are not different from one another.

Subjects often reported that the illusory arm motion in Condition D (during which they were indicating target light position) was equal to that of Conditions B and C and generally reported that the extent of visual motion in the three conditions with the target light was about the same. In 62 of 144 trials, subjects

Table 2. Character of illusory arm motion, eye movements and illusory target light motion during trials with biceps vibration and eye position monitored. Chamber is in darkness and during trials in Conditions B, C, and D a small target light is on the index finger of the vibrated arm

Conditions	Dark	Target Light on Hand		
	A Point Hand Look Hand	B Point Hand Look Hand	C Point Hand Look Light	D Point Light Look Light
Trials with some pursuit eye movements (%)[a]	63	37	0	8
Trials with eye movements		9	0	2
Hand moving with light		3	0	0
Hand and light dissociated		6	0	2
Hand and light dissociated with light stationary		3	0	0
Trials without eye movements		15	24	22
Hand moving with light		9	10	14
Hand and light dissociated		5	14	7
Hand and light dissociated with light stationary		2	6	1
No illusory motion of arm or light		1	0	1

[a] Overall ANOVA: $p < 0.001$

reported that the light moved less than the hand. These reports of dissociations were nearly equally distributed across the three conditions. Consequently, in Condition D, the only one in which subjects tracked the light illusion with their left arm, the *average* extent of the illusion was only 8.5°, a value which is significantly less than the arm motion illusions of B and C when the target light was also present ($p < 0.01$).

Subjects in total darkness were able to pursue with their eyes at least part of the illusory arm motion in 63% of the trials in Condition A; Lackner (1975) earlier had found a value of 57% under comparable conditions. Subjects in Condition B (fixate hand, point hand) were able despite the presence of the target light to pursue at least part of their illusory arm motion in 37% of the trials. However, in Conditions C and D, involving fixation of the target light, subjects usually remained steadily fixating the position maintained before the onset of vibration although in two trials there were downward eye deflections greater than the perceived light motion. Table 2 summarizes the eye movement recording data for the four experimental conditions.

Representative eye movement tracings from one subject's four conditions are presented in Fig. 1. It is obvious that the visual motion experienced in Conditions B, C, and D is not correlated with eye position or changes in eye position.

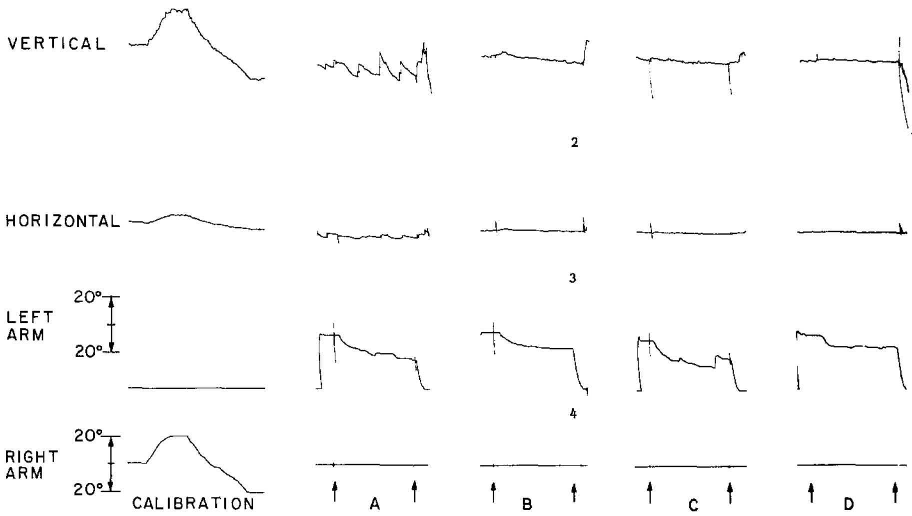

Fig. 1. Representative eye and arm traces from one subject's experimental session. The calibration traces show the vertical eye movements that resulted when the subject fixated a target light on her right index finger while her arm was moved 20° up and 20° down. During the experimental conditions (**A–D**) the biceps muscle of the subject's restrained right arm was vibrated; the subject was indicating the apparent position of her stationary right arm with her left arm. In Condition **A** (no target light, fixate hand and point to hand), the subject had an illusory arm extension of 17° and there is evidence of pursuit-like eye movements. In Condition **B** (target light on hand, fixate hand and point to hand), the subject pursued a fraction of her 12° arm movement illusion while the light appeared to move with her hand. In Conditions **C** (target light on hand, fixate light and point to hand) and **D** (target light on hand, fixate light and point to light), the subject's eyes did not change position although the larget light appeared to follow the full 18° apparent displacement of the arm in **C** and the 9° displacement in **D**

Discussion

The experimental findings here described confirm the earlier report of an oculobrachial illusion (Lackner and Levine, 1978) and provide insight into some of the complex oculomotor, retinal, postural, and attentional factors that influence its precise form. During the oculobrachial illusion, the apparent motion of the target light attached to the stationary limb always coincides temporally with the illusory limb motion and is always equal or less in velocity and extent, never greater. When subjects are instructed to indicate the spatial position of either the vibrated arm or target with their other arm, they indicate the illusory location of the limb and target light; that is, they show systematic and large pointing errors consistent in direction and magnitude with their verbal reports.

Just as the illusory motion of the forearm influences the apparent spatial position of the target light so does the presence of the target light affect the illusory motion of the vibrated arm. When the target light is present, there is an approximately 25% decrement in the magnitude of the illusory arm motion

(16.5° vs. 12.0° and 12.3°). The magnitude of the decrement is the same whether the subject is "attending" to his hand or to the target light on his hand. The presence of this interaction indicates that spatial information related to retinal and oculomotor activity is affecting the spatial representation of arm position at the same time that the latter is affecting the interpretation of visual direction; the existence of some experimental trials in which hand position and target light position became dissociated illustrates the lability of this interrelationship. This reciprocal interaction underscores the complexity of the sensory and motor factors that are utilized in assigning visual direction, deriving position sense representation of the body parts, and ultimately guiding eye and arm movements.

This complexity is also evident in the finding that the pattern of eye movements elicited during illusory motion of the arm and target light is partly a function of where the subjects were instructed to fixate. When subjects attempted to maintain fixation of their hand, they often exhibited some pursuit eye movement during the trials: in 63% of the trials without a light (Condition A) subjects were able to pursue in part the illusory motion of their forearm; in 37% of the trials in Condition B subjects attempting to fixate their hand could pursue in part the apparent motion of their forearm. This latter situation is notable because it reveals that pursuit eye movements can be elicited in response to a changing proprioceptive stimulus even when a stationary target light is present at the true position of the hand. By contrast, in trials for which the subjects were instructed to fixate the target light and point to the target light, or vibrated hand, with their other arm, their eyes generally maintained steady fixation of the stationary target light which in turn maintained its clarity and appeared to move downward in keeping with the apparent motion of the forearm. These cases are of especial significance because they demonstrate that perceived target motion alone is not necessarily a sufficient condition for eliciting pursuit eye movements despite several recent suggestions to this effect (Lackner and Evanoff, 1977; Steinbach, 1976; Yasui and Young, 1976).

In those trials in Conditions C and D in which eye position was recorded there were two instances, both in Condition D, in which pursuit-like eye movements were present. In these cases there was a dissociation between apparent target position and apparent hand position with the target remaining stationary while apparent extension of the forearm was experienced. Pursuit eye movements occurred in nine of the trials in Condition B. Three times the target light and hand seemed to move together, three times the target light seemed to move less than the hand, and the remaining three times the target light appeared stationary while the forearm was felt to extend. Thus, in eight of the 11 trials, across Conditions B, C, and D, in which there were pursuit-like eye movements there was a dissociation between hand and target motion with the target appearing to move less than the hand or to remain stationary. It appears, therefore, that eye movements tend to produce dissociations and attenuate apparent target motion. By contrast, in trials not involving eye movements partial or complete dissociations occurred less frequently, although still in 33% of the trials in Condition B, 58% of the trials in Condition C, and 32% in Condition D.

A misinterpretation of eye position related to the abnormal proprioceptive signal about arm position would appear to be responsible for the apparent visual motion experienced in trials in which the target light seemed to move. That is, it is our hypothesis that the eyes are being interpreted as moving downwards even when they remain steadily fixating the target. Consequently, because the target light is retinally stable, the non-changing pattern of retinal activity is attributed to the target light moving with the eyes. When the target light and hand seem to move at the same velocity the interpreted velocity of the eyes is equal to that of the hand, during partial dissociations the eyes are interpreted as moving more slowly than the hand. When the target light appears stationary the eyes are being correctly interpreted as being stationary.

In the six trials of Condition B involving both apparent downward target motion and downward eye movements a second factor would appear to be involved as well. Compensation is being made for the interpreted change in eye position resulting from the abnormal position sense signal from the arm as well as for the physical deviation of the eyes which displaced the retinal image of the target light. The latter compensation normally occurs during pursuit or saccadic eye movements that change the position of the eyes in relation to stationary objects in the visual field and accounts for visual stability during eye movements (cf. Helmholtz, 1962; Mach, 1897). Compensation for the additional aberrant change in registered eye position then produces an oculobrachial illusion just as in those trials in which the eyes remain steadily fixating.

The present findings provide further support for the notion (Lackner and Levine, 1978) that the computation of visual direction involves the operation of spatial constancy mechanisms that utilize information from retinal, oculomotor, and postural sources in assigning the apparent direction of an object in relation to the head and body (Brandt et al., 1977; Lackner, 1978). The complex nature of this operation is shown by the fact that the interpretation of the ongoing position of the eyes in their orbits can be influenced by spatial information about the orientation of the body and limbs and that the reciprocal pattern of interaction is also present. The observations here reported and the results of studies involving vibration of skeletal muscles related to postural stability (Lackner and Levine, in press) lead to a common conclusion. Computation of the apparent spatial orientation of the body depends on the monitoring and interrelating of information from exteroceptive and interoceptive sources – and internal motor feedback – about the moment-to-moment configuration of the body.

Acknowledgements. This study was supported by the National Aeronautics and Space Administration, Contract NAS 9-15147. The authors wish to thank Garrick Kwan for technical assistance.

References

Bowditch, H. P., Southard, W. F.: A comparison of sight and touch. J. Physiol. (Lond.) **3**, 232–245 (1880)

Brandt, T. H., Büchele, W., Arnold, F.: Orthokinetic nystagmus and egomotion sensation. Exp. Brain Res. **30**, 331–338 (1977)

Goodwin, G.M., McCloskey, D.I., Matthews, P.B.C.: Proprioceptive illusions induced by muscle vibration: Contribution to perception by muscle spindles? Science **175**, 1382–1384 (1972a)

Goodwin, G.M., McCloskey, D.I., Mathews, P.B.C.: The contribution of muscle afferents to kinaesthesia shown by vibration-induced illusions of movement and by paralysing joint afferents. Brain **95**, 705–748 (1972b)

Hanson, R.M., Skavenski, A.A.: Accuracy of eye position information for motor control. Vision Res. **17**, 919–926 (1977)

Helmholtz, H. von: Treatise on physiological optics. New York: Dover 1962

Lackner, J.R.: Proprioceptive facilitation of open loop visual pointing. Percept. Motor Skills **39**, 263–265 (1974)

Lackner, J.R.: Pursuit eye movements elicited by muscle afferent information. Neurosci. Lett. **1**, 25–28 (1975)

Lackner, J.R.: Some mechanisms underlying sensory and postural stability in man. In: Handbook of sensory physiology, Held, R., Leibowitz, H.W., Teuber, H.-L. (eds.), Vol. VIII, pp. 805–845. Berlin, Heidelberg, New York: Springer 1978

Lackner, J.R., Evanoff, J.: Smooth pursuit eye movements elicited by somatosensory stimulation. Neurosci. Lett. **4**, 43–48 (1977)

Lackner, J.R., Levine, M.S.: Visual direction depends upon the operation of spatial constancy mechanisms: the oculobrachial illusion. Neurosci. Lett. **7**, 207–212 (1978)

Lackner, J.R., Levine, M.S.: Changes in apparent body orientation and sensory localization induced by vibration of postural muscles: vibratory myesthetic illusions. Aviat. Space Environ. Med. (in press)

Lackner, J.R., Zabkar, J.J.: Proprioceptive information about target location suppresses autokinesis. Vision Res. **17**, 1225–1229 (1977)

Mach, E.: Contribution to the Analysis of the Sensations (Transl. C.M. Williams). Chicago: Open Court Publishing 1897

Steinbach, M.J.: Pursuing the perceptual rather than the retinal stimulus. Vision Res. **46**, 1371–1376 (1976)

Woodworth, R.S.: The accuracy of voluntary movement. Psychol. Rev. Monogr. Suppl. **3**, 1–114 (1899)

Yasui, S., Young, L.R.: Eye movements during afterimage tracking under sinusoidal and random vestibular stimulation. In: Eye movements and psychological processes (ed. R.A. Monty and J.W. Senders). New Jersey: Lawrence Erlbaum Association 1976

Received September 14, 1978