

VISUAL DIRECTION DEPENDS ON THE OPERATION OF SPATIAL CONSTANCY MECHANISMS: THE OCULOBRACHIAL ILLUSION

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SUMMARY

Subjects fixating a target light attached to their stationary hand saw it move when illusory motion of their arm was induced by muscle vibration. During the experienced visual motion and change in visual direction of the target light, their eyes maintained steady fixation. The existence of an 'oculobrachial illusion' provides evidence that visual direction depends on the operation of a spatial constancy mechanism interrelating sensory information about the external environment and the moment-to-moment postural configuration of the body.

Visual direction is known to depend on the pattern of stimulation at the retinae and on the position of the eyes in their orbits. A number of experiments, however, have also shown that visual direction can be influenced by abnormal changes in apparent body posture or apparent head-trunk articulation (cf. ref. 6). The oculogyral illusion [2] induced by vestibular stimulation and the illusory visual motion accompanying illusory body rotation elicited by vibrating tendons of hip muscles [8] represent two such examples. We now provide evidence that both visual motion and changes in visual direction are often forthcoming when a subject, whose head and eyes are stationary, fixates a target light on his stationary hand while his hand is undergoing illusory motion. Together with earlier observations, the demonstration of an oculobrachial illusion indicates that visual direction depends not only on eye posture and patterns of retinal stimulation but also on spatial information about the orientation of the entire body.

Illusory changes in limb position were elicited by vibrating muscles of the upper arm and then preventing the forearm from moving under the action of the resulting tonic vibration reflex [1]. Vibration of the biceps, for example, normally leads to reflex flexion but if the forearm is prevented from moving, then apparent extension is experienced; vibration of the triceps elicits the opposite pattern. Our approach was to determine (a) whether changes in apparent arm position elicited by muscle vibration would influence the visual

direction of a small target light attached to the hand, and (b) if so, whether changes in apparent target position would be associated with changes in actual or in registered eye position.

Six Brandeis students and the two investigators participated individually; they had been prescreened to ensure that they had brisk tonic vibration reflexes. During the experiment the subject was seated and his head was stabilized by a biteboard, his arms were strapped in padded counterbalanced goniometers. The upper arm was fixed at 90° of shoulder flexion and the forearm was set at 135° of elbow flexion. A fiber optic strand projecting 3 mm from the end of an opaque tube was taped on the subjects' right index finger and, when illuminated from a remotely controlled light source, served as a fixation target. A physiotherapy vibrator (120 pulses/sec) was used to provide mechanical stimulation of the biceps and triceps muscles of the right arm. Both horizontal and vertical eye position were monitored continuously with an infra-red sensing device (Narco Biosystems) and recorded on an ink-writing polygraph (Grass model 7). Eye position was calibrated by having the subject track the light on his finger while the arm was passively moved 20° into flexion and into extension from an arbitrary 'primary position' of 135° . The target light was the only object visible to the subject during the experiment.

Three procedures were followed with each subject: (a) the subject tracked the target light as his arm was passively moved 20° up and 20° down and noted the extent of the target displacement for comparison with subsequent conditions, (b) the subject fixated the target light on his stationary hand for 1 min and reported any changes in light position (i.e. autokinesis) or hand position, (c) the subject fixated the target light and received 4 separate vibration sequences each lasting 1 min, half the subjects received the vibration sequence, biceps-triceps-triceps-biceps; and half, triceps-biceps-biceps-triceps. During and after vibration, the subject reported any changes in arm or target position that had occurred, indicated whether these changes took place together, and related the extent and velocity of target movement to that which occurred in trial (a). In addition, the two investigators actively moved their arms to mimic the extent of target motion after each vibration trial.

Illusory arm movement elicited by muscle vibration was generally accompanied by apparent target motion of like latency and trajectory. The direction of the illusory arm movement corresponded to that reported by Goodwin et al. [1]. Vibration of the biceps of the restrained arm produced apparent extension and downward target movement; vibration of the triceps, apparent arm flexion and upward target motion. When the vibrator was turned off, subjects briefly experienced conjoint arm and visual target motion of opposite sign. The visual target motion was not related to eye movements. Within our recording sensitivity $\cong 0.5^\circ$ of visual angle, the eyes rarely changed position more than 1° during a vibration trial, and then never in a way correlated with the apparent visual motion. No subjects reported changes in the clarity of the visual stimulus.

Fig. 1 shows the eye and arm position records of one of the investigators (M.L.) while she was experiencing relatively weak arm and visual motion during

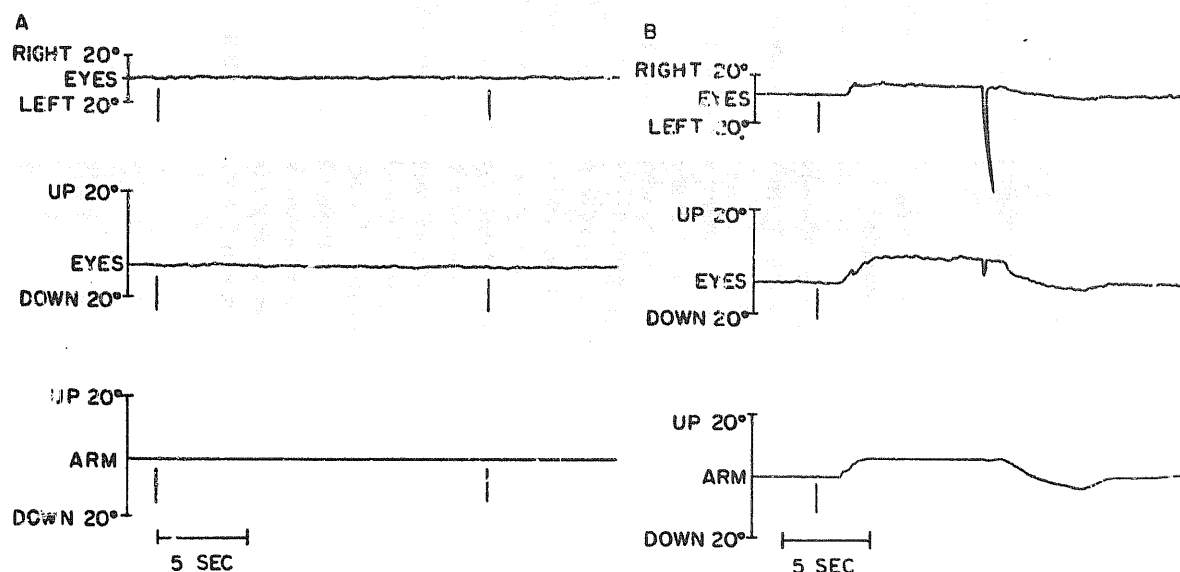


Fig. 1. A: the vertical bars under each trace indicate the onset and offset of vibration of the subject's right tricep muscle. A few seconds after the onset of vibration the subject felt her arm rise and saw the target light move upward keeping pace with her arm; the reverse illusion was experienced when the vibrator was turned off. The eyes and arm can be seen to remain stationary throughout the trial. B: the vertical bars indicate when the subject was instructed to mimic in extent the arm and target motion experienced in A. As can be seen considerable movement of eyes and arm occurs. The large momentary deflection in the eye movement traces approximately 10 sec into the trial represents a blink.

vibration of the triceps and was mimicking the extent of the illusory arm and target motion. We include this record because it illustrates that even when a subject has experienced a comparatively weak form of illusory arm and target motion, there is considerable movement of her arm and eyes when she attempts to mimic it.

Changes in both apparent arm and apparent target position usually began nearly immediately after the onset of vibration. Occasionally illusory arm motion did not occur: but, in such trials, the subjects reported that the vibrator had not been in proper contact with the muscle tendon; visual motion was not experienced in these cases. In several trials illusory arm motion was experienced without visual motion; and, occasionally, slight target motion in the expected direction without compelling arm motion. Autokinesis—as measured in condition (b)—was minor in extent, never more than a few degrees, and generally of irregular direction. In the vibration conditions, target motion was always upward or downward and always much greater in magnitude than the autokinesis experienced in condition (b). The experimental results are summarized in Table I.

The present observations support previous reports that factors in addition to local retinal stimulation and eye posture influence visual direction. They provide evidence that the apparent visual direction of an optical stimulus with respect to the body results from the operation of a spatial constancy mechanism that

TABLE I
CHARACTERISTICS OF THE ILLUSORY ARM AND TARGET MOTION INDUCED BY MUSCLE VIBRATION. THE ENTRY
'AUTOKINESIS' REPRESENTS THE CONTROL CONDITION WHERE MUSCLE VIBRATION WAS ABSENT

Subject	Autokinesis	Vibration order ^a	Direction of primary illusion		Direction of afterillusion		Comments
LW	none	BTTB	arm target	- ↑ - ↓ - - ↑ ↑	arm target	- ↓ ↓ ↑ - ↓ ↓ ↑	illusion, afterillusion slow steady motion; unsure extent 1°/sec motion during trial
JV	bouncing	BTTB	arm target	↑ - - ↑ ↑ - - ↑	arm target	↓ - - ↓ ↓ - - ↓	afterillusion slower very fast motion; greater than 20° displacement
BS	down and to. right	TBBT	arm target	↑ ↓ ↓ ↑ ↑ ↓ ↓ ↑	arm target	↑ ↑ ↑ ↑ ↑ ↑ ↑ ↑	faster motion than the standard trial; unsure extent
JS	toward 4:00	TBBT	arm target	↑ ↓ ↓ ↑ ↑ ↓ ↓ ↑	arm target	↑ ↓ ↓ ↓ ↑ ↓ ↓ ↓	slow steady motion for first half of trial; no further displacement after
RN	none	BTTB	arm target	- ↑ ↑ ↑ - ↑ ↑ -	arm target	- - - - - - - -	slow steady motion, not full extent of standard motion: 2°/sec trial 2, 1°/sec others; about 25° displacement all trials
EG	at end down	BTTB	arm target	↓ b ↑ ↓ ↓ - ↑ ↓	arm target	↑ - ↓ - ↑ - ↓ -	slow steady motion; between 5 and 15° extent
JRL	lateral	BTTB	arm target	↑ ↑ ↑ ↑ ↑ ↑ ↑ ↑	arm target	↑ ↑ ↑ ↑ ↑ ↑ ↑ ↑	
ML	bobbing	TBBT	arm target	↑ ↓ ↓ - ↑ ↓ ↓ -	arm target	↑ ↑ ↑ - ↑ ↑ ↑ -	

^a B = biceps; T = triceps.

^b Light moving as it did during autokinesis trial.

interrelates information about the external environment and information about the moment-to-moment configuration of the body. One consequence of this interrelationship is that if there is an error in the registration of body posture, then errors in sensory localization of related magnitude and time course will result (cf. ref. 7).

Information about body posture is derived from many sensory modalities. Normally the patterns of input from these sources are synergistic in specifying the relative orientation of the body and its relation to the environment. When, for example, the gaze is directed at a part of the body, eye position and retinal information are consonant with postural or body schema information about the locus of that part. Actually, in such a situation, the positional specification of the body part is sufficiently refined that it can be utilized to stabilize fixation when the eyes are directed at a target light attached to that part of the body [9]. This latter fact indicates that proprioceptive information about hand position can influence oculomotor control and also accounts for why only nominal autokinesis was experienced by our subjects when they fixated the target light attached to their hand in control condition [b].

Although patterns of sensory afflux signalling body position are normally synergistic, it is commonly found that one input dominates when they are in antagonism. For instance, when there is a conflict between the visual and proprioceptive specifications of limb position, the felt position of the limb will correspond to its seen position. Our experiment shows, however, that if the visual input is reduced to a point of light attached to the hand, then visual localization can be influenced by the apparent position of the hand. Consequently, the representation of eye position with respect to the head must be being overridden by the proprioceptive specification of arm position. This means that when a subject in our experimental situation is experiencing illusory arm and visual target motion that at some level of representation his eyes are being interpreted as moving even though they are stationary. Nevertheless, the veridical eye position signal available from monitoring commands to the extraocular muscles [4,10] is not 'lost' when a subject is experiencing illusory visual motion. It is still potentially available because sporadically the position of the target light became dissociated from that of the hand, with the light either not following the illusory motion of the arm or not following its full motion. Furthermore, informal observations suggest that when a target light is attached to the subject's hand, the maximum velocity and extent of illusory arm motion elicited by muscle vibration are diminished*.

* Visual illusions of movement associated with changes in body posture have sometimes been attributed to an outflow monitoring of voluntary refixation movements [11]. The voluntary innervations are thought to be necessary to counteract compensatory eye movements associated with postural reflexes. The visual illusion of motion that we have described cannot be accounted for in this manner. It might be thought that the subject in our experimental situation 'reflexly' attempts to track the apparent motion of his arm because it is known that this can be done in complete darkness[5]; and, that to maintain fixation of the target light he provides a voluntary counterinnervation to these eye muscles. However, monitoring of this counterinnervation would predict visual motion in the opposite direction to that experienced by our subjects.

Several times the proprioceptive signal about hand position was strong enough to elicit visual motion but below threshold for evoking perceived arm motion. This observation is not unexpected because it is also characteristic of a related illusion, the oculogyral illusion [2]. In the oculogyral illusion, the threshold for detection of visual motion is much less than that for detection of body rotation although their cupolograms are parallel [3].

In conclusion, our findings support the notion that the assignment of visual direction depends on the operation of a spatial constancy mechanism. This mechanism utilizes in its operation not only retinal and oculomotor signals but also a continuous spatial representation of the entire body.

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