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INFORMATION ABOUT SPATIAL LOCATION BASED ON KNOWLEDGE ABOUT EFFERENCE[1]

LEON FESTINGER AND LANCE KIRKPATRICK CANON
Stanford University

An experiment was designed to determine whether or not the human organism possessed "outflow" information derived from monitoring nerve impulses in motor pathways. The experiment focused on the extraocular muscles since proprioceptive input to the central nervous system from these muscles is poor. The results show that in the absence of good proprioceptive information, the presence or absence of "outflow" information makes a difference in accuracy of localizing an object in space.

The human being continually acquires and uses information about himself and his relation to the environment. We are accustomed to thinking of this information as having been acquired through input to afferent mechanisms. That is, we know about the environment through seeing, hearing, touching, and a variety of other means. Not the least of these sources of information is input from proprioceptors. For example, if I am led blindfolded into a room and I touch an object in that room with my hand, I know where that object is in relation to my body because, on the basis of proprioceptive feedback, I know where my hand is.

There is, however, another possible source of information about one's relation to the environment that has not been adequately explored. If, in the central nervous system, outgoing motor nerve impulses are monitored and recorded, then information would also exist concerning spatial location on the basis of this record of efferent impulses, that is, a record of the specific directions given to the musculature. This information, if it exists, need not rely on any current afferent input. To make this clear, let us illustrate by a loose analogy. Imagine there is a person who will unconditionally obey your orders. Let us also assume that you and the other person have had sufficient previous experience with the environment so that you can give him, and he can follow, clear directions. You tell this person to go to a certain specific place and to wait there for you. Even in the complete absence of any *current* sensory input you will know exactly where that person is because you know where you told him to go.

The question of whether or not such monitored efferent information exists is an old one in psychology although, of late, it has been rarely mentioned. Actually, a closely related speculation was vigorously debated many years ago. James (1950)[2] stated the issue clearly:

> There must, of course, be a special current of energy going out from the brain into the

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[2] We give the dates of the later editions from which we have quoted. The book by James was originally published in 1890, and the first edition of the book by Helmholtz was earlier than that.

> appropriate muscles during the act; and this outgoing current (it is supposed) must have in each particular case a feeling *sui generis* attached to it, ... This feeling of the current of outgoing energy has received from Wundt the name of the *feeling of innervation. I disbelieve in* its existence, and must proceed to criticise the notion of it, at what I fear may to some prove tedious length [p. 493].

If in this statement we replace the phrase "feeling of" by "information about," then this old controversy is exactly germane to our present question. While we do not intend to engage in an exhaustive review of the argument about "feeling of innervation," let us look at the principal data about which the disagreement centered.

One major piece of evidence at that time is summarized by Helmholtz (1925). He states:

> For instance, if the external rectus of the right eye is paralyzed or the nerve leading to it, this eye can no longer be pulled around to the right. As long as the patient continues to turn it inwards only it still makes regular movements, and he perceives correctly the directions of objects in the field of view. But the moment he tries to turn his eye outwards, that is, to the right, it ceases to do his bidding, and remains standing in the middle, while the objects appear to move to the right, although the adjustment of the eye and the positions of the retinal images in it have not varied [p. 245].

From this Helmholtz concludes that since there was absolutely no afferent change when the eye tried to move to the right, and since motion was perceived as if the eye *had* moved to the right with the retinal image remaining constant, there must be a feeling of (information about) innervation.

William James (1950) quotes other data in addition. He says:

> *Partial* paralysis of the same muscle, *paresis,* as it has been called, seems to point even more conclusively to the same inference, that the will to innervate is felt independently of all its afferent results. I will quote the account given by a recent authority, of the effects of this accident: "When the nerve going to an eye muscle, e.g., the external rectus of one side, falls into a state of paresis, the first result is that the same volitional stimulus, which under normal circumstances would have perhaps rotated the eye to its extreme position outwards, now is competent to effect only a moderate outwards rotation, say of 20 degrees. If now, shutting the sound eye, the patient looks at an object situated just so far outwards from the paretic eye that this latter must turn 20 degrees in order to see it distinctly, the patient will feel as if he had moved it not only 20 degrees toward the side, but into its extreme lateral position, ... The test proposed by von Graefe [1878], of localization by the sense of touch, serves to render evident the error which the patient now makes. If we direct him to touch rapidly the object looked at, with the fore-finger of the hand of the same side, the line through which the finger moves will not be the line of sight directed 20 degrees outward, but will approach more nearly to the extreme possible outward line of vision [p. 507]."

The theoretical relevance of this observation is stated succinctly by James:

> It appears as if here the judgment of direction *could* only arise from the excessive innervation of the rectus when the object is looked at. All the afferent feelings must be identical with those experienced when the eye is sound and the judgment is correct. The eyeball is rotated just 20 degrees in the one case as in the other, the image falls on the same part of the retina, the pressures on the eyeball and the tensions of the skin and conjunctiva are identical. There is only one feeling that *can* vary, and lead us to our mistake. That feeling must be the effort which the will makes, moderate in one case, excessive in the other, but in both cases an efferent feeling, pure and simple [p. 508].

James then proceeds to rebut the interpretations of these observations. Acknowledging that G. E. Müller was the first to propose the rebuttal explanation, he states:

> Beautiful and clear as this reasoning seems to be, it is based on an incomplete inventory of the afferent data. The writers have all omitted to consider what is going on in the

> *other eye.* This is kept covered during the experiments, to prevent double images, and other complications. But if its condition under these circumstances be examined, it will be found to present certain changes which must result in strong afferent feelings. And the taking account of these feelings demolishes in an instant all the conclusions which the authors from whom I have quoted base upon their supposed absence [p. 508].

James then proceeds to point out that the covered, healthy eye does rotate as directed by the efferent impulses and thereby provides the *afferent* stimulation necessary for the perception of motion in the Helmholtz (1925) example, or the misperception of direction in the Graefe (1878) example. Although James, in his explanation, never copes with the question of why the afferent impulses from the covered eye should completely dominate the afferent impulses from the open eye, nevertheless his "demolition" of the argument for feeling of (information about) innervation appears to have been very effective. So persuasive was the argument by James that Mach (1914), who in 1886 had argued strongly *for* the "feeling of innervation" and presented original experiments supporting it, almost completely reversed his stand in the fifth edition of his book, written in 1906. Here he says:

> The theory of James and Münsterberg fits these facts, as I think, without any straining, and we ought therefore to consider it as correct in essentials. The innervation is not felt, but the consequences of the innervation set up new peripheral sensible stimuli, which are connected with the execution of the movement [p. 176].

Rightly or wrongly, James apparently won the argument, and the issue has been a dead one in psychology for many years. Many dead issues do not stay dead, however, and this one has recently been revived by physiologists. Recently von Holst (1954), concerning himself with how the organism differentiates between self-generated movement of a part of the body and an identical movement generated by external forces, proposed the idea of "efference copy." His idea was that incoming afferent signals were matched against a temporary copy of outgoing efferent signals. If they matched perfectly, the motion involved was entirely self-generated. This, of course, is somewhat different from the idea that information from a record of efferent impulses is available and used all by itself. Nevertheless, it is related and served to revive the issue in other contexts.

The question has become particularly important to those who are concerned with understanding the control system for eye movements. Probably the major reason for this is that there is great doubt among physiologists that afferent signals from the extraocular muscles are used to any significant extent in the control of eye movements. If afferent feedback from the extraocular muscles is not useful for determining the position of the eye, then it becomes convenient for the theoretician to posit the existence of information obtained from a record of efferent impulses.

Thus, Fender (1964), discussing the possible role of afferent signals of position of the eye, says:

> There is experimental evidence that the positioned signal is not used, for if a subject views two similar but separately generated stabilized images, one with each eye, it is found that for a short period the two visual axes move in conjunction. However, this motion quickly breaks down, and the visual axes move independently, sometimes getting as far apart as 30 deg in the horizontal direction and 15 deg in the vertical. There is, of course, no binocular retinal-image disparity to act as a cue in this case, and it appears that any positional signal which might arise from the extraocular muscles is quite ineffective in maintaining the parallelism of the visual axes [p. 317].

Fender proceeds to incorporate an "efferent copy" feedback loop into his model of the physiological system controlling eye movements.

Whitteridge (1962) recently summarized the problem as follows:

> The role of extraocular afferent impulses in perception is very uncertain. It is self evident that we are not directly aware of the position of our eyes in the same sense in which we are aware of the position of our fingers even with the eyes shut. The question is whether the position of the eyes enters into judgments of position and movement, and if it does, how far proprioceptors are responsible. The alternative theories are that information from the volume of outgoing motor nerve impulses in the oculomotor pathways is centrally available—the *outflow* theory, or that impulses from proprioceptors directly signal the state of the eye muscles—the *inflow* theory. The strongest point against the inflow theory is that when a patient with a paralyzed and therefore immobile eye tries to turn it to one side, the observed visual field moves as though he had succeeded in moving the eye. This cannot be due to any conceivable change in proprioceptive discharge [p. 511].

As of 1962, among physiologists, the entire controversy seems to have revived. The issue is now more sophisticated from a theoretical point of view; but on the empirical side, Whitteridge (1962) seems to be back to Helmholtz (1925). There is, however, more empirical evidence on the issue today than there was 60 to 70 years ago. Brindley and Merton (1960) report a very direct attempt to settle the question as to whether or not there is usable proprioceptive feedback from the extraocular muscles. They anesthetized the surface of the eyes and the inner surface of the eyelids of subjects and covered the corneas with opaque caps so that the subjects received no visual information. They then mechanically moved a subject's eyeball by catching hold of the insertion of either the medial or lateral rectus muscle with toothed forceps. When the eye was moved in this manner through rotations of 20 degrees or more, sometimes even backward and forward quite rapidly, the subject did not know that his eye was moving.

Cognizant of the argument offered by James, they repeated these observations moving both eyes simultaneously and obtained the same result. Merton's (1964) paper, the main purpose of which is ". . . to reinstate the experiments of Helmholtz, which proved that no information about the position of the eyes is derived from sense endings in the eye muscles [p. 315]," comes to the conclusion: "A subject is only conscious of his intention to move his eye and does not know whether the movement has in fact taken place or not [p. 318]."

Considering these new data, it seems highly likely that Helmholtz (1925) was correct and that James (1950), in spite of having won the argument in his day, was wrong. It would be useful, however, to have additional data on the question. After all, the work of Brindley and Merton (1960) demonstrates the absence of a position sense in the eye based solely on proprioception from the extraocular muscles. To strengthen the argument one might well desire positive evidence that information obtained from a record of outgoing motor nerve impulses is available and useful.

Let us be specific. If it is true, as seems likely, that we know the position of the eye mainly in terms of knowing where the eye was directed to go, then it should be possible to show that when the eye is directed to go to a specific location, a subject knows where his eye is more accurately than if the eye arrived at the same position without directions concerning this specific location ever having been issued.

The technical problem in doing such an experiment is, of course, the problem of how to devise a method of having the subject move his eyes to a specific location without issuing efferent signals concerning that location. A plausible solution to this technical problem may be found in the work of Rashbass (1961). He reports a series of experiments designed to elucidate the relationship between the usual saccadic eye movements and the smooth eye movements that occur in tracking a target. Several of his findings are important to us here.

Rashbass reports evidence that saccadic eye movements and smooth tracking eye movements are controlled and generated independently of one another. Barbiturate drugs serve to almost completely disrupt smooth eye-tracking movements but do not interfere with precise saccadic movements. Thus, a subject who watched a target which moved horizontally at a rate of 3.5 degrees per second ordinarily showed a smooth eye movement before the administration of any drug. After administration of a barbiturate, Rashbass (1961) states:

> The first noticeable effect was the increase in the number of saccadic movements occurring during the first second of tracking. As the amount of drug given increased, the saccadic movements increased at the expense of the smooth movements, until, after 8 minutes, no smooth tracking movement could be detected [pp. 333–334].

From this and other data, he concludes that barbiturate drugs make the smooth tracking response inoperative but do not interfere with accurate saccadic eye movements. Hence the two types of eye movements must be separately controlled.

Rashbass also reports data from experiments designed to discover what produces smooth and saccadic eye movements. The specific question is "whether smooth movements are brought about by the position of the target's image on the retina, or by its movement over the retina [p. 331]." He tests this "by imparting to an initially stationary target a displacement to one side, and at the same time beginning a movement of uniform velocity toward the opposite side [p. 331]." The result is stated by Rashbass as follows:

> . . . after a reaction time during which the eye does not move, a smooth movement starts in the direction in which the target is moving. When this has been established, a saccadic movement occurs in the direction opposite to the smooth movement to counteract the lead which the eye has over the target. . . . This result indicates that the smooth movement is stimulated by the movement of the target irrespective of its position. The conclusion that the smooth movements are brought about by the movement of the target explains the apparently paradoxical observation that the first movement which the eye makes may take the point of fixation further from the target than if no eye movement at all were to occur [p. 332].

From this and other data, the conclusion is that "the smooth movement is stimulated by the direction of movement and the velocity of the target, and the saccadic movement is stimulated independently by the position of the target [p. 333]."

We have dealt at length with the results obtained by Rashbass because they are critical for us. They suggest that if the eye were brought into a given position by a saccadic movement, this movement would be a response to efferent signals concerning the position of the target. If, however, the eye were brought into that same position by a smooth tracking movement, the efferent directions would be concerned with velocity matching and not precisely with target location.

A possible experiment suggests itself to answer the question concerning the availability of information based on efference. The experiment would be conducted in a completely dark room with the subject's head fixed so that only eye movements could occur. In one variation, a light would suddenly appear within the visual field of the subject, then disappear, and the subject would be asked to point to the location where the light had been. In this variation, in order to fixate the light, a saccadic eye movement would occur, and "directions" would have been given to the extraocular muscles to move from "normal frontal" position to a specific location. If these directions to the musculature are monitored and recorded so as to be available as information, the person would know the location of the light on the basis of knowing where he had sent his musculature in order to fixate the light.

In another experimental variation, the light would appear and move slowly and smoothly across the visual field before coming to a stop. The subject would fixate the light when it first appeared and would then track the light across the visual field until it stopped moving. To the extent that *only* smooth tracking eye movements occurred, the musculature would, presumably, simply have been directed to "follow the light." Thus, in this experimental variation, the efferent information that existed would contain information about the direction of movement and the velocity of movement, but would not include information concerning the specifically designated position in which the light had stopped.

In both of the above variations, of course, there would be the same amount of proprioceptive information concerning where the light was. If the subject's head is clamped so that only eye movements are used to fixate the target, the only proprioceptive signals would come from the extraocular muscles. Since these signals are not useful, as Merton (1964) has shown, then subjects would know the location of the light more accurately when it suddenly appeared than when they tracked it across the visual field. We would, of course, expect more than zero knowledge of location in the tracking condition. The subject would have knowledge about direction and also some knowledge of eye position from afference from the eyelids. Also, it is well known that smooth tracking movements lag and saccadic movements occur periodically. These would also provide additional information. If, however, information based on efference is available, we would expect a difference between the two conditions.

Along with this, of course, one would want to set up another experimental condition in which the subject's head was not clamped so that head movements could be employed in helping to fixate the light. Useful proprioceptive input would be expected from the neck muscles, and to the extent that the position of the light could be adequately known on the basis of these proprioceptive signals from the neck muscles, the difference between the two experimental variations would be expected to vanish.

Such an experimental design, using two manners of presentation of the light and two degrees of adequacy of proprioceptive information, should provide data that would answer the question as to whether or not outflow information is available and is used.

PROCEDURE

Twenty-eight college students, 12 female and 16 male, were subjects in the experiment. Each subject volunteered and was paid $1.50 for participating.

The experiment was conducted in a lightproof room. The apparatus consisted of an overhead boom fastened to the ceiling with its pivot point slightly in front of a point directly over the subject's head. The boom extended 4 feet forward from the pivot point.

From the far end of the boom hung an illuminated rectangle that measured 2 × 3 inches. The experimenter, standing to the side of the seated subject, could move the boom noiselessly so that the light was at any desired lateral position. The height of the light was fixed approximately at the subject's eye level. Calibration at the pivot point of the boom enabled the experimenter to read the setting of the light in angular deviation from straight ahead of the subject.

On a table directly in front of the subject and at a suitable height was a pointer attached to a calibrated turntable. The pivot of the pointer was directly underneath the pivot of the boom. The subject, when pointing to where the light was, or had been, was instructed to lay his index finger along the pointer and move it so that he pointed in the proper direction. The measuring scales for both the boom and the pointer were very dimly illuminated and shielded from the subject. The illumination was sufficient, however, to allow the experimenter to read the scales in an otherwise totally dark room. The target light was also dimly illuminated so that there were no problems with afterimages, and the target light did not make other things in the room visible.

Fourteen of the subjects, seven male and seven female, were used in the "eye-movement-only" condition. These subjects had their head in a rigid clamp throughout the experiment so that fixating and tracking the target light could be done only with eye movement. The head and body were always in the directly forward position. The other 14 subjects, 9 male and 5 female, were used in the "head-movement" condition. This condition was identical to the other except that the head was not clamped. Thus, these subjects could and did rotate their heads, and even their bodies to some extent, in addition to moving their eyes in fixating and tracking the target light.

Before data collection started, each subject was given practice at using the pointer with the target light at various positions. This practice was continued until the subject was familiar with the situation and the use of the pointer. The actual data collection consisted of 28 trials, 4 trials at each of 7 positions of the light. The positions used were +30, +20, +10, 0, −10, −20, and −30 degrees (+ referring to positions to the subject's right, −, to positions to the subject's left). For one trial in each position the target light was turned on in that position and stayed on. The subject pointed to the light while it was still visible. This was intended to yield a measure of the accuracy to be expected with optimal information. For another trial in each of the seven positions the light was turned on in that position, stayed on for 3 seconds, and was then turned off. The subject was asked to point, after the light was turned off, to where the light had been. In this condition, outflow information would presumably be available to the subject. When the light came on, the subject would have to direct a saccadic movement of his eyes to a specific location and would, hence, know this location at least with respect to a normal frontal reference point.

On the two remaining trials at each of the target-light positions, the light moved across part of the visual field. The light would appear, move slowly (approximately 10 degrees per second) across the visual field through an angle of 15, 20, 25, 30, or 35 degrees, and come to a halt at the desired position. The light then remained on in this final position for 3 seconds and was then turned off. The subject was asked to point to where the light had been after it was turned off. For each of the seven positions the light moved from right to left on one trial and from left to right on the other trials. These trials were, of course, intended to be trials on which outflow information concerning target position would be less available to the subject. To the extent that smooth tracking eye movements would have been involved, directions concerning target location would not have occurred.

The decision to keep the light on its final position for 3 seconds before turning it off was an arbitrary one. We wanted a period of time long enough so that in the tracking trials there would be no ambiguity about when and where the light had come to a stop. On the other hand, we wanted the period short enough so as to reduce the likelihood of blinking or moving the eyes to a forward position and refixating the light. Such eye movements would tend to vitiate the procedure. Certainly, in 3 seconds such movements can occur, but some compromise between allowing this and having an unambiguous final position was necessary.

The order of trials was arranged in a sequence so that the target light was never in the same position on any two consecutive trials, and the four different kinds of trials were distributed evenly through the series. The same order was used for all subjects. After the subject had pointed for a trial, he was asked to return his hand to his lap. The experimenter then recorded the setting of the pointer and moved the boom to the appropriate position for the next trial. The interval between trials was approximately 45 seconds. The subject's hand remained in his lap until the experimenter said, "All right, now point to where the light is (was)."

RESULTS

We are interested in the magnitude of the error made by the subject in pointing to the position of the target light. The less adequately the person knows the position of his eyes, or his head, when fixating the light, the less accurate should he be in pointing to its location afterwards. The simplest calculation is, of course, to take the absolute deviation of the pointer position from the target position for each trial. Thus, if the target was in position +20 and the subject set his pointer to +16, this would be an error of 4 degrees. Table 1 presents the results from the experiment based on this simple calculation.

Even a cursory look at the data in Table 1 reveals that the obtained data are of the kind one would expect if, indeed, proprioceptive input from the extraocular muscles is poor and the person has available, and uses, outflow information. When only eye movements are allowed, that is, when the head was clamped, the error of pointing when the light suddenly appeared at the designated position was only slightly worse than when the light was on while the person was pointing. However, when the subject tracked the light across the visual field, and thus would not have relevant outflow information, the error of pointing is considerably greater. It is also clear that when head movements are allowed, the results are very different. The "tracking" trials are then slightly superior to the "at position" trials.

TABLE 1

AVERAGE ABSOLUTE ERROR (IN DEGREES) OF POINTING TO TARGET LIGHT

Condition	Type of trial			
	Light on	Light off		
		At position	Tracked from right	Tracked from left
Eye movement only	3.06	3.54	5.24	5.55
Head movement	2.13	3.92	3.69	3.35

We have presented these data because some readers might consider this the proper measure to use. We will not engage in extended discussion of Table 1, however, nor present statistical analyses, since it seems to us that a more accurate measure should be used. The absolute error of pointing is, of course, affected by constant errors. One subject may consistently point somewhat to the right of the target, another consistently to the left. Such constant errors are probably due to coordinating the physical act of pointing with knowledge of location and probably should be disregarded in our calculations. Actually, there was an average constant error of pointing somewhat to the left of the position of the target. Over all types of trials, this average constant error was 1.6 degrees to the left in the "eye-movement-only" condition and .1 degree to the left in the "head-movement" condition. The probable reason for the direction of the constant error in the "eye-movement-only" condition is that, using the right hand, the hand position was more comfortable along the fixed pointer when pointing toward the left than when pointing toward the right. Apparently, head movements provided enough additional orientation to eliminate this constant error.

There is also another source of constant error in the data. Two types of tracking trials, one from the left, one from the right, were used because of the possibility that the memory of where the light had stopped might be affected by the direction in which the light had moved. This, indeed, turns out to be the case. In the tracking trials, the subjects tend to point a bit more in the direction from which the light had come. Thus, in the "eye-movement-only" condition the constant error is −1.2 degrees when the light came from the right, but −2.2 degrees when the light moved from the left. Similarly, in the "head-movement" condition the corresponding constant errors are +1.1 and −.6. The difference between the two types of tracking trials is not quite significant statistically for the "eye-movement-only" condition ($t = 1.44$) but is significant at the 2% level for the "head-movement" condition ($t = 2.85$).

Clearly, we do not want to have our measure of accuracy of pointing contaminated by these various sources of constant error. We, therefore, computed a "corrected absolute error" of pointing by taking into account for each subject, for each type of trial, the constant error in the data. Thus, for example, a subject may have had a constant error of 2 degrees to the left on the seven trials on which the target was tracked in from the left. If this subject set his pointer at −24 degrees when the target light had actually stopped at −20 degrees, his corrected absolute error on this trial was 2 degrees. Table 2 presents the data using this measure.

TABLE 2

AVERAGE CORRECTED ABSOLUTE ERROR (IN DEGREES) OF POINTING TO TARGET LIGHT

Condition	Type of trial			
	Light on	Light off		
		At position	Tracked from right	Tracked from left
Eye movement only	2.58	3.11	4.38	4.50
Head movement	1.95	3.64	3.11	2.79

These corrected data show the same overall pattern of results as the data using the uncorrected absolute error. We will discuss these data in detail, presenting appropriate statistical analyses.

Eye-Movement-Only Condition

It is clear that when only eye movements are permitted, localization of the target light is better when the light suddenly *appears* at its final position than when it is *tracked* to its final position. An analysis of variance yields a highly significant F value (8.71, $df = 3/39$) for the variance among the means of the different types of trials. The variance among subjects is also significant ($F = 2.68$, $df = 13/39$). This latter, of course, simply means that some subjects are consistently more accurate than others in pointing to the target light.

The difference in accuracy between the "light-on" and "light-off-at-position" trials is not significant ($t = 1.10$). The mean for each is, however, significantly different from the mean for each of the "tracking" trials, the smallest t value being 3.86 between the "at-position" mean and the "tracked-from-right" mean. In short, with only eye movements permitted, pointing to the target when it suddenly appeared at its final position is not materially less accurate than when the pointing was done while the light was still on. In the tracking conditions, however, when relevant outflow information was presumably not available, accuracy is materially and significantly worse.

Head-Movement Condition

When head movements are allowed, the data present quite a different pattern, although significant differences still exist among the different types of trials. The variance of the means for the different types of trials and of the means for subjects both yield highly significant F values (7.30, $df = 3/39$; and 6.56, $df = 13/39$).

With head movements, the accuracy of pointing with the light still on is significantly better than each of the three conditions in which the pointing was done after the light was off. The important differences to us, however, are between the "at-position" trials and the "tracking" trials. Here we find that the "at-position" accuracy is no longer better, but is actually worse than the accuracy of pointing on the "tracking" trials. The two t values are 2.01 and 2.19 which, for $df = 13$, are each significant at about the 5% level. We had not anticipated this, and we are not certain of the reason for it. It may simply be that occasional inattention affected accuracy in the "at-position" trials. There was no warning of when the light would appear. In the "tracking" trials, the period of tracking could minimize the effects of any inattention. It is clear, however, that when head movements are allowed, thus making available good proprioceptive input concerning position, the availability of relevant outflow information no longer produces greater accuracy.

Comparison of the Two Conditions

If we compare the accuracy between the condition in which only eye movements were allowed and the condition in which head movements were also allowed, we see that in the latter condition there is a general tendency to be more accurate. When the light is on while pointing, the average corrected error decreases from 2.58 to 1.95, a difference significant at the 10% level ($t = 1.73$, $df = 26$). The data for the "tracking" trials also show much less error with head movement allowed. The two t values here are 2.11 for "tracking from the right" and 2.98 for "tracking from the left," significant at the 5% and 1% level respectively.

Only for the "light-off-at-position" trials is there no improvement from the "eye-movement-only" to the "head-movement" condition. The actual difference is slightly in the opposite direction but is negligible ($t = .81$). Indeed, it seems as though the presence of relevant outflow information about eye position in the "eye-movement-only" condition is just as good as the presence of the same outflow information plus good proprioceptive input in the "head-movement" condition. It is clear also that, when there is good proprioceptive input and no relevant outflow information, as in the tracking trials with head movements, accuracy is at least as good as when relevant outflow information is also present. This would tend to imply that, in this situation, there is some redundancy of information.

DISCUSSION

The main conclusion we would like to draw from the results of the experiment is that information based on some kind of record of efferent impulses (i.e., outflow information) is available to the organism. The major result on which we wish to base this conclusion is the finding that, when only eye movements were permitted, target localization was more accurate when the target suddenly appeared at its final position than when it was tracked to that position.

Let us review the line of reasoning involved in coming to this conclusion.

Accuracy of localization of an object in space with respect to one's body depends on knowledge of body, head, and eyeball position. If the head and body are fixed, the only variable is position of the eyeball.

There is evidence that the position of the eyeball is *not* adequately known on the basis of proprioceptive signals from the extraocular muscles. Hence, with head and body in a fixed position, accuracy of localizing an object in space would be poor if the only information about eyeball position came from such proprioceptive signals.

There is evidence that smooth tracking movements of the eye are controlled and directed by the direction and velocity of movement across the retina and *not* by target location. Saccadic eye movements, on the other hand, are directed on the basis of target location on the retina. Hence, if a target is fixated by means of a saccadic movement, efferent signals relevant to target location would have been issued. If a target is tracked by a smooth eye movement, however, efferent signals concerning direction and velocity of movement would have been issued—information not optimally useful for knowing the target location.

Consequently, if a record of efferent signals is available, localization in space of a target should be better following fixation by a saccadic eye movement than following a smooth tracking eye movement. Having found this result, we regard it as evidence for the existence of information based on this hypothesized record of efferent signals.

It is, of course, possible that there are alternative interpretations of the data we have presented. No such plausible alternatives occur to us, however. It does not, for example, seem possible to maintain any alternative interpretations in terms of confusion introduced by the tracking procedure, since it is clear, in the "head-movement condition," that the tracking procedure, in and of itself, does not interfere with accuracy.

Another possible alternative explanation could be elaborated as follows. Presumably, during the period of darkness between trials, the subject's eyes revert to some "normal" frontal position. Such a normal position is probably a reference point for location in the visual field, and, presumably, directions are issued to the extraocular muscles with respect to some such reference point. The eyeball then moves, in accordance with the efferent directions, in a saccadic, ballistic movement. Under such circumstances the initial movement of the eye to fixate the target is *not* a continuously controlled movement. Once started it proceeds to its destination. The saccadic movement, hence, must have a complete set of directions issued at the beginning.

It thus becomes clear that, in order to issue directions that are relatively accurate for the initial ballistic movement of the eye, information as to the location in space of the target must exist before the directions are issued. And indeed, this information must be obtained on the basis of the stimulation of the periphery of the retina when, with the eyes in frontal position, the target light suddenly appears. It is on the basis of this information that the initial ballistic eye movement is more or less accurately directed.

Why, then, is it necessary to say that the differences obtained between the "eye-movement-only" conditions are due to a record of the efferent impulses *actually* sent out to the muscles? Why could we not simply maintain that the information the person has as to the location of the target light is simply the information on the basis of which the efferent directions were issued? After all, on the tracking trials the subject did not see the target light at its final position in peripheral vision. The results of the "head-movement" conditions rule out this explanation of the results. If seeing the target light in peripheral vision were important, the tracking conditions should still be inferior even with head movements allowed.

One must admit, however, that information based on a record of the efferent signals is not likely to be better than the information on the basis of which those efferent signals were sent. Our present data cannot answer questions concerning the relation between these two things. Our experiment does, however, confirm the existence, and usefulness, of outflow information.

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