kind which have shown nonrandomness in matching by mammals failed to give positive results; that is, there was no evidence of reward-following or of any relation at all between choice on any trial and the events of the immediately preceding trial.

Six turtles were trained in spatial problems (both targets the same color, the reward depending on the position of the target). The reward ratio was 70 : 30 for three of the animals (one position rewarded on a random 70 percent of trials, the alternative position on the remaining trials) and 50 : 50 for the other three (each position rewarded on a random 50 percent of trials). One of the animals trained on the 70 : 30 problem maximized, and two of the animals trained on the 50 : 50 problem developed strong positional preferences. The other three animals showed some tendency to match (the asymptotic choice-ratios were 67 : 33 and 64 : 36, respectively, for the two animals trained on the 70 : 30 problem, and 55 : 45 for the animal trained on the 50 : 50 problem), but sequential analysis gave clear evidence of reward-following in each case. The first of the animals trained on the 70 : 30 problem chose the more frequently rewarded side on 82 percent of trials subsequent to reward on that side, but on only 33 percent of trials subsequent to reward on the opposite side, while the corresponding values for the second animal were 88 percent and 7 percent; the animal trained on the 50 : 50 problem chose the rewarded side of the previous trial on about 90 percent of all trials.

Eleven turtles were trained on confounded visual-spatial problems (the two targets differing in color, but with the spatial placement of the colors remaining the same from trial to trial). Five animals were begun at 100 : 0, shifted to 70 : 30, and later shifted to 50 : 50. Six other animals were trained throughout at 70 : 30. In Fig. 2, their performance is plotted in terms of the mean percentage of trials on which the more frequently reinforced alternative was chosen. Of the five turtles trained at 100 : 0, two continued in 180 trials at 70 : 30 to show an exclusive preference for the more frequently reinforced alternative; but the preference of the other three shifted rapidly to about 70 percent, and later, when the reward-ratio became 50 : 50, shifted to about 50 percent. All turtles trained from the outset at 70 : 30 matched approximately, their asymptotic preferences for the more-frequently reinforced alternative ranging from 66 to 75 percent. For none of the eight matching animals was there a significant relation between the choices made and the events of immediately preceding trials. Apparently, then, the confounded problem functions as a visual problem for the turtle except where previous 100 : 0 training has established a strong set for position.

These results for the turtle—random matching in visual problems and maximizing or reward-following in spatial problems—are like those obtained for the pigeon (*7*) and for adult rats that had been extensively decorticated in infancy (*8*). They support the inference from the earlier results that random probability-matching is a precortical phenomenon which tends to be suppressed by cortical development, more effectively in the spatial modality than in the visual. It will be interesting to see whether cortical ablation in the turtle produces random matching in spatial problems.

KATHLEEN L. KIRK
M. E. BITTERMAN

Department of Psychology,
Bryn Mawr College,
Bryn Mawr, Pennslyvania

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9. Work supported by ONR contract Nonr 2829(01).

4 March 1965

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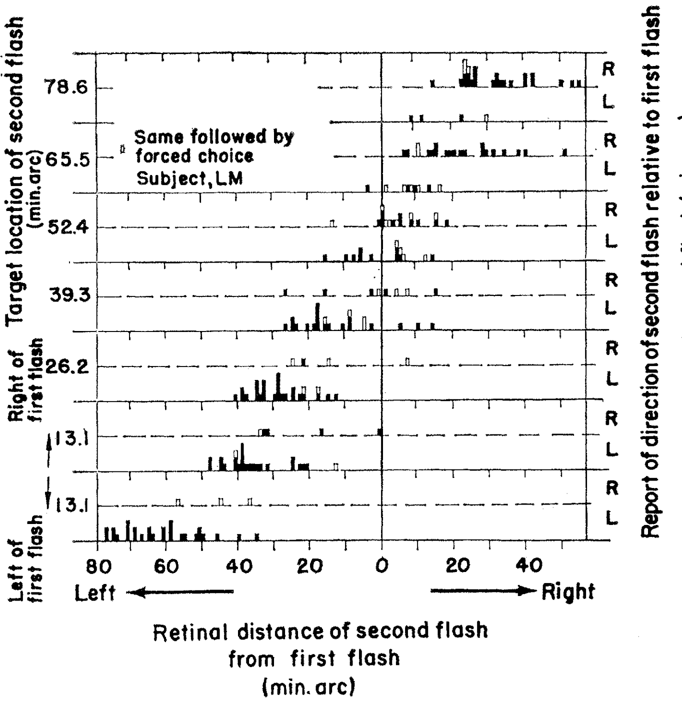
Visual Perception of Direction for Stimuli Flashed During Voluntary Saccadic Eye Movements

Abstract. *In two different experiments, subjects reported on the visual direction of a flash presented during a voluntary saccade relative to the visual direction of a stimulus viewed prior to the saccade. Under the conditions of the first experiment the report given by the subject was primarily determined by the relative retinal positions of the two stimuli. In the second experiment evidence was obtained for precisely timed shifts in local signs which are due to proprioceptive compensation for changes in ocular position during the saccade.*

As we move our eyes from place to place in a visual field, stationary objects do not normally appear to change their locations, in spite of the changed locations of images of these objects on the retina. It was suggested at least as far back as 1866 that this result is due to a proprioceptive signal regarding the change in eye position which is taken into account in "interpreting" the changed locations of the retinal images (*1*). However, no clear-cut direct evidence bearing on this position has ever been presented. We have now obtained such evidence by recording eye movements in perceptual situations devised to yield separate measures of the retinal and proprioceptive stimuli. In combination with psychophysical reports these measurements yield information on whether or not (or how much) proprioceptive compensation is involved in the visual perception of direction. Previously we described experiments in which no evidence was found for the operation of proprioceptive compensation for involuntary eye movements in the judgment of visual direction in the dark (*2*). In this report we describe two experiments bearing on the existence of proprioceptive compensation during voluntary saccades. The unexpected finding that clear evidence for the operation of such a mechanism was obtained under the conditions of one experiment but not under the conditions of the other opens the entire problem for further detailed parametric investigation.

On each trial of each experiment, the subject, who was in a completely dark room, first viewed a circular 3.5-minute target for 4 seconds with the left eye (the right eye was covered with an eye patch); 300 msec after the



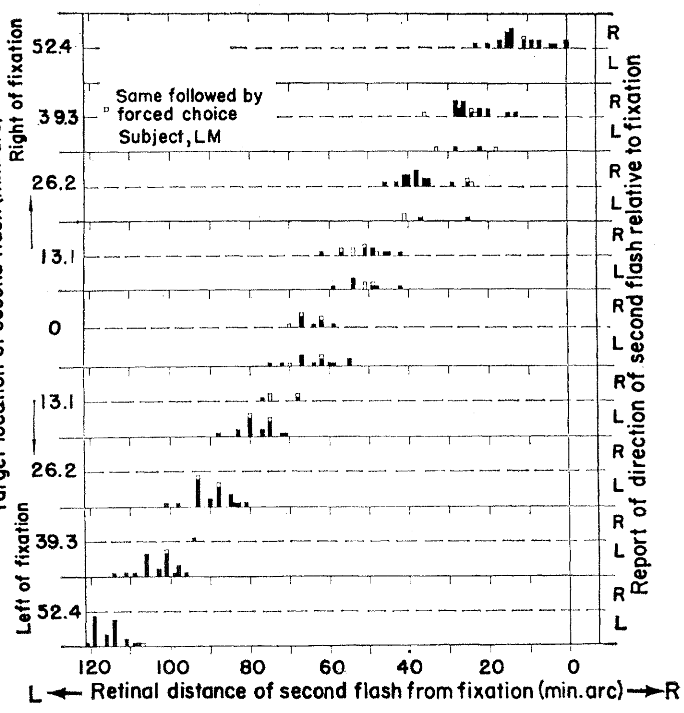


Fig. 1 (left). Results of experiment in which the subjects report the direction at which the second flash (presented during the saccade) appears relative to the first flash (presented before the saccade). The psychophysical direction report (right ordinate: *L*, left; *R*, right) is displayed as a function of the retinal distance between the two targets (abscissa) for each target location used for the second flash (left ordinate). Height of bar in legend at upper left indicates a single trial. Fig. 2 (right). Results of experiment in which the subject reports the direction at which the second flash (presented during the saccade) appears relative to the fixation target (viewed prior to the saccade). The report of direction (right ordinate: *L*, left; *R*, right) is displayed as a function of the retinal distance between the second flash and fixation target (abscissa) for each target location used for the second flash (left ordinate). Height of bar in legend at upper left indicates a single trial.

offset of this target, a 70-msec flash was presented from another 3.5-minute target located at 2°11′ to the right of the fixation target. The subject turned his eye to the flash as soon as he saw it. (Reaction time was sufficiently long so that the flash was over before the saccade began.) On each trial, at a precisely known point near the center of the saccade (*3*), another 3.5-minute target was flashed; this target had been randomly selected from a horizontal array of targets in which adjacent members were separated from each other by 13.1 minutes of arc (*4*). This final flash was triggered from an electrical signal monitoring eye position (*5*). Eye movements were measured by means of a contact-lens technique (*6*) in which an invisible (infrared) measuring beam was used; variations in the intensity of the beam, after reflection from a plane, front-surfaced mirror embedded in the tightly fitted contact lens, was measured by a photocell and resulted in a voltage (corrected for spurious variations by the use of a reference system) that was linear with variations in horizontal ocular rotation.

In the first experiment the subject reported the direction at which the second flash appeared relative to the first flash (left, right, same). In the second experiment the subject reported the direction at which the second flash appeared relative to the fixation target (left, right, same) (*7*). Two subjects were used in each experiment. Since the results were similar for both subjects, data for only one subject are shown here.

It is clear from Fig. 1 that in the first experiment the subject tended to report "left" when the retinal locus struck by the second flash was to the left of the retinal locus struck by the first flash, and to report "right" when the retinal locus of the second flash was to the right of the retinal locus of the first flash (that is, the distribution of variability of the psychophysical reports appears compatible with a *retinal* point of subjective equality at zero) (*8*). The data are not compatible with a simple hypothesis of proprioceptive compensation which requires that, regardless of retinal distance and direction between the second and the first flash, all of those flash targets to the right of the first flash be reported as "right" and the flash target to the left of the first flash be reported as "left" (that is, "compensation" requires a point of subjective equality at a physical target location of zero, which is clearly not the case in Fig. 1).

In the second experiment (Fig. 2) the subject tended to report that the second flash appeared to the left of the fixation target when the flash target in fact was to the left of the fixation target and to report "right" when the second flash target in fact was to the right of the fixation target in spite of the fact that the second flash was always to the left of the average retinal position of the fixation target (that is, zero on the abscissa). The results of this experiment thus support a hypothesis of proprioceptive compensation—they are in fact difficult to interpret otherwise. Since the room was in complete darkness, stable relative retinal relations between surrounding objects normally present in illuminated environments could not serve to mask changes in subjective visual directions relative to the subject during eye movements. In addition, no two of the three stimuli in each trial were simultaneously present. Further, except during the 1 msec occupied by the second flash, during the saccade the usual continuous movement across the retina of images of stationary objects was not available as a possible cue.

It is worth noting that proprioceptive compensation, which seemed to occur in the second experiment, needs to be timed with extreme precision to be effective, as indicated by the following example. In Fig. 2, the target 13.1 minutes to the right of the fixation target was presented at 52.8 minutes to the left of the fovea at a moment when the eye had traveled 65.9 minutes from fixation position (average of 24 trials); the target 13.1 minutes to the left of fixation was presented at 78.7 minutes to the left of the fovea at a moment when the eye had traveled 65.6 minutes from the fixation position (average of 24 trials). The eye was traveling at a rate of about 6.5 minutes of arc per millisecond during the flash. In order that the directions of the two flash targets relative to the fixation target be discriminated reliably (as they were), it is necessary that the region at which a "same" judgment would be given should shift retinal position as the eye turns so that this region falls reliably between 52.8 minutes and 78.7 minutes to the left of the fovea within a "moment" whose span is about 4 msec. But this in itself is not sufficient. We may expect that the proprioceptive information converges with the retinal information at some point in the nervous system. It would thus be necessary that the shift in local signs at this point of convergence lag the actual turning of the eye by an interval equal to the interval occupied in the visual nervous system between the moment of flash presentation during the saccade and the moment at which the retinal signal reaches this point of convergence; such a result would ensue if this latency for the retinal signal were to equal the latency for the proprioceptive signal at the point of convergence.

The results of the two experiments considered jointly yield the following interesting conclusion which we have found to hold in a further single experiment. The point of subjective equality for the fixation target as measured by a flash presented during the saccade is at the fixation target itself, whereas the point of subjective equality for the first flash as measured by a flash presented during the saccade is at a point to the right of the first flash. Such a "contraction of visual space in the direction of ocular motion" could be due to proprioceptive compensation occurring at different rates at different regions of the visual field. In turn, such a differential rate could be due to the proprioceptive signal reaching points of convergence with signals from different retinal regions at different times or to differences in latency for retinal signals at different retinal loci arriving at points of convergence with the proprioceptive signal, or to both. Such a latency mismatch would result in the retinal signal regarding flash occurrence meeting a proprioceptive signal corresponding to an earlier position of the eye. It is also possible, however, that inappropriate magnitudes of the proprioceptive signal could arise from causes other than inappropriate latency (*9*). An alternative to variations in the accuracy of latency or magnitude matching or both as the basis for the difference between the results of the two experiments lies in the fact that the temporal interval between termination of the first flash and presentation of the second flash was 370 msec shorter than the interval between termination of the fixation target and presentation of the second flash. It is possible that the phenomenal impression of the first flash persisted (for example, as an afterimage) up to the moment of comparison with the second flash, providing a basis for judgment based on relative retinal location sufficiently strong as to result in failure of compensation.

While the second experiment required a judgment against a foveally presented standard (the fixation target) and the first experiment required a judgment against a peripherally presented standard (the first flash), it should be noted that the foveal-peripheral difference does not appear to be the critical factor accounting for the different results. In other experiments involving different temporal relations between the three stimuli we have found "proprioceptive compensation" in judgments against peripherally located standards and "no proprioceptive compensation" against foveally located standards; "partial compensation" has also been obtained. Although the data from the present experiments as well as data from these other studies do not yet permit a full picture of the situation, we suggest that proprioceptive compensation is subject to important restrictions related to the temporal and spatial characteristics of the visual presentation and is more limited than heretofore thought (*10*). We also suggest that a sizable portion of the normal stability of visual directions during eye movements results from purely visual factors such as continuously stable relative retinal positions of stationary objects and from the continuity of movement across the retina of the images of stationary objects during eye movements—both of these factors serving to mask the frequent transient distortions resulting from the brief voluntary saccades which would otherwise be noticeable.

LEONARD MATIN
*New York University,
Bronx 53, New York*
DOUGLAS G. PEARCE
*Defense Research Medical
Laboratories, Toronto, Ontario, Canada*

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2. L. Matin, D. G. Pearce, G. Kibler, *J. Opt. Soc. Amer.* **54**, 1398 (1964), abstr. The first experiment in the present report was described there.
3. The saccade itself occupied about 25 msec—time between 10 and 90 percent of the saccade took about 15 msec—with very little variability among trials.
4. The locations of the triggered flashes employed in each experiment are shown along the left ordinates of Figs. 1 and 2. The set of stimuli used was chosen from preliminary work so as to be approximately centered within the subject's uncertainty range for each experiment. A randomized block design for flash location was used in each experiment; 32 measurements per flash location were obtained over four sessions in the first experiment; 24 measurements per flash location were obtained over three sessions in the second experiment.
5. The electrical signal monitoring eye position was fed to a d-c comparator whose output in turn was fed to a differentiator. When the signal monitoring eye position crossed a preset voltage the comparator changed states; the differentiator responded to this change at the comparator's output with a pulse which triggered the circuitry controlling flash occurrence. A flash only occurred when the eye traveled from left to right *and* crossed the trigger point at greater than some minimum velocity. Hence, when the eye drifted across the trigger point in either direction no flash was produced. In addition, if the eye drifted too far from fixation position before beginning the saccade, no flash was produced since ocular velocity is maximum about halfway through a saccade and was not great enough to trigger a flash if the saccade began too close to or too far from the trigger point. In

fact the eye very frequently did drift *toward* the trigger point in the interval between fixation-target offset and saccade beginning; this is of general interest with regard to suggesting that ocular drift in the dark can be influenced by a pattern of expectancies.

6. L. Matin, *J. Opt. Soc. Amer.* **54**, 1008 (1964); L. Matin and D. G. Pearce in *Biomedical Sciences Instrumentation*, W. E. Murry and P. F. Salisbury, Ed. (Plenum, New York, 1964), vol. 2, p. 79–95.
7. When a "same" report was given, a forced-choice was then obtained.
8. The scales on the abscissa in both Figs. 1 and 2 neglect the fact that image inversion is produced by the dioptrics of the eye. The abscissa value of a trial in Fig. 1 is obtained, for example, as follows: If on a given trial the eye had moved 64 minutes to the right from fixation position at the time the second flash was presented, and if the second flash was 65.5 mlnutes to the right of the first flash, it would be 1.5 minutes retinal distance to the right of the first flash (abscissa plotted to the nearest minute). The values shown in Fig. 2 were similarly obtained.

   Abscissa values for a given location of the flash target varied among trials for the following reason. (i) The voltage setting for the electrical signal monitoring eye position was not set at exactly the same value in different sessions when the eye was on the fixation target. Since the voltage at which the second flash was triggered was always the same, the eye traveled different distances from the fixation target at the time the triggered flash was presented in different sessions; hence the triggered flash from a given target location struck different retinal loci. (ii) After the offset of the fixation target the eye was in complete darkness for 300 msec until the occurrence of the first flash. Although the subject attempted to maintain the fixation position during this interval, considerable drifts of variable magnitude did occur (see *2*) so that at the time the first flash occurred the eye was in different positions from trial to trial with the result that the first flash struck different retinal loci from trial to trial. (iii) Trial-to-trial variation in average fixation position or slippage of the contact lens from fixation period to fixation period, or both, resulted in trial-to-trial variation in the difference in retinal loci between fixation and first flash, and variation in the distance which the eye traveled to the trigger point for the second flash.
9. The latency of the retinal response to the flash may be expected to vary with flash intensity and state of adaptation of the eye. In our present state of knowledge, however, we have no reason to expect the lag between the turning of the eye (either actual turning or "effort" to turn) and the proprioceptive signal's arrival at the point of convergence to vary with either flash intensity or adaptation level. The latency-mismatch interpretation would thus predict a variation with flash intensity and adaptation level in amount of compensation as measured in experiments of the type reported here. While it appears difficult to handle the results of the present experiments without a precise neural timing mechanism which takes latency differences into account, it seems unlikely that the specific intensities and adaptation levels which were used (and which were chosen without any forethought) would fortuitously result in compensation of the accuracy observed in the second experiment if only the specific latency-matching (or mismatching) approach described above was involved.
10. Errors of localization relative to a continuously present background for flashes presented during voluntary saccades have been reported. G. Sperling and R. Speelman, paper read at convention of American Psychiatric Association, September 1964.
11. This research was supported by NSF grants G-18120, GB-944, and GB-2899. The experiments were performed at the Department of Psychology, Johns Hopkins University.

16 February 1965

Warm Interstadial Interval in Wisconsin Stage of the Pleistocene

A summary of Atlantic deep-sea stratigraphy of Pleistocene sediments by Ericson, Ewing, and Wollin (*1*) includes a conclusion that there was a marked, but brief, warm interval within what is generally regarded as the Wisconsin (Würm) glacial stage, some 80,000 years ago. This date was obtained by assuming fairly uniform rates of sedimentation in the deep Atlantic over a large span of time. Charles Stearns and David Thurber (*2*) have determined from the ratio of thorium-230 to uranium-234 that some of the Tyrrhenian and Ouljian low terrace deposits of Mallorca and Morocco record a nonglacial interval of high sea level 75,000 to 90,000 years ago. This is considerably more recent than usual dates given for the elevated low coral reefs, shore dunes, and marine platforms of the western Atlantic and elsewhere, apparently formed somewhat more than 100,000 years ago in the Sangamon (Riss-Würm) interstadial interval (*3*).

Recently I collected well-preserved hermatypic coral rubble of species now absent in immediately adjacent waters. These were welded by calcareous caliche to a marginal platform cut in an eolianite ridge on the northwestern side of Lignum Vitae Cay, Berry Islands, Bahamas. This narrow bench slopes seaward from about 3 meters to less than ½ meter. One of the corals, *Montastraea* sp., was dated at 80,000 years by Broecker and Thurber, at the Lamont Geological Observatory, by uranium, thorium, and radium ratios (*4*).

It is becoming apparent that sea level stood appreciably higher than the present level for a brief interval about the middle of Wisconsin time. Evidence for this higher level was recognized at a number of places on Andros Island, Bahamas, by Newell and Rigby (*5*), and it was their opinion that this high level might date from the last interglacial stage. Elevated sea caves occur at the same level a mile or so west of Nassau, and about a mile south of Nicholl's Town (Andros). Probably these caves also date from the 80,000-year-old sea level. Certainly, this 2- to 3-meter level does not date from the post-Pleistocene "hypsithermal" interval, as often postulated by students of Pacific coral reefs. Where are the fringing coral reefs and elevated marine sediments of mid-Wisconsin age? They should be widely distributed.

NORMAN D. NEWELL
American Museum of Natural History
and *Columbia University,*
New York 10027

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4. W. S. Broecker and D. Thurber, personal communication.
5. N. D. Newell and J. K. Rigby, in "Regional Aspects of Carbonate Deposition—a Symposium," *Soc. Econ. Paleontol. Mineral Spec. Publ. No. 5* (1957), p. 68.

5 May 1965

Sap Pressure: Addendum

The following scientific names pertain to Fig. 3 in the article "Sap pressure in vascular plants" [*Science* **148**, 339 (1965)] by P. F. Scholander, H. T. Hammel, E. D. Bradstreet, and E. A. Hemmingsen. I am indebted to Reid Moran, of the Museum of Natural History, San Diego, for identification of several species.

From left to right: *Rhizophora Mangle, Avicennia nitida, Laguncularia racemosa, Batis maritima, Distichlis spicata, Salicornia pacifica, Populus Fremontii, Platanus racemosa, Chilopsis linearis, Dalea spinosa, Prosopis juliflora, Tamarix aphylla, Fouquieria splendens, Salvia apiana, Encelia farinosa, Acacia Greggii, Atriplex polycarpa, Larrea divaricata, Juniperus californica, Pseudotsuga Menziesii, Sequoia sempervirens, Tsuga heterophylla, Acer macrophyllum, A. circinatum, Darlingtonia californica* (flower stalk), *Cypripedium californicum* (flower stalk), *Thuja plicata, Oxalis oregana, Dryopteris Linnaeana, Pteris aquilina, Blechnum spicant, Adiantum pedatum, Spiraea Douglasii, Cornus californica, Salix lasiandra, Myrica Hartwegii, Comarum palustre, Cicuta Douglasii, Menyanthes trifoliata, Veronica scutellata, Polygonum punctatum.*

P. F. SCHOLANDER
Scripps Institute of Oceanography,
University of California, San Diego

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