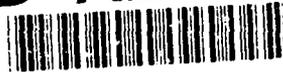




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Visual Functions Associated with Rhesus Visual Pursuit Tracking

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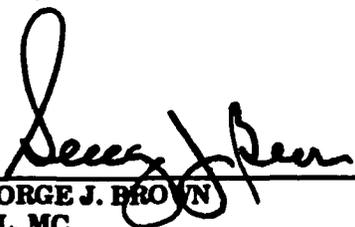
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Abstract

Although visual function and visual performance have both been investigated, the relationship between these measures is largely unexplored. In this study, we have evaluated the receptor input for visual pursuit motor tracking performance using the rhesus monkey as an animal model for the human visual system. Spectral sensitivity functions derived from rhesus spectral intensity tracking performance functions emphasize the role of photopic retinal mechanisms for high fidelity tracking performance criteria. Spectral sensitivity functions under these conditions appear photopic in shape and reflect central retinal long and intermediate cone systems. Scotopic intrusion may occur as performance decreases with lower fidelity performance criteria. Species differences previously reported between rhesus and human long wavelength foveal retinal mechanisms may be reflected in visual performance criteria as well.

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Visual Functions Associated with Rhesus Visual Pursuit Tracking -- H. Zwick, J. Calabrese, M. Cook, J. Molchany, and K.R. Bloom

Introduction

Numerous comparisons of human and rhesus visual function support the utilization of the rhesus monkey as a primary surrogate for human vision. The present investigation concerned the visual control of a complex visual motor task, pursuit motor tracking, and the utilization of the rhesus monkey as a viable human surrogate. The major question we asked was the extent to which the visual guidance provided by the rhesus monkey can be compared to the visual guidance mechanism employed by human observers.

Human visual pursuit tracking varies systematically with luminance level (1,2). Molchany et al. (3) showed that the absolute range of the photopic-mesopic luminance-rms error function in a pursuit motor tracking task compares favorably with that of the primate luminance acuity function (4). Although target size used in these tracking experiments exceeded the size of visual acuity targets by approximately a factor of 10, fine human pursuit tracking strategies under photopic luminance levels often seem to involve a high degree of fine acuity adjustment of target with tracking cross-hairs.

We have approached the problem of specifying the photopic mechanisms involved in visual guidance of visual motor tracking by determining the spectral sensitivity associated with this tracking task. In recent years, the photopic processes of the rhesus monkey have received considerable attention and generally match the human visual system extremely well. Microspectrophotometric (MSP) measurements of rhesus cone photopigments, measured indiscreetly from foveal and parafoveal retinal regions, compare favorably with psychophysical measurements of cone fundamentals (5). Measurements of rhesus photopic spectral sensitivity have been demonstrated to fit the human photopic functions with small departure in the short wavelength region generally attributed to differences in lens pigmentation (6-8). Human achromatic acuity is slightly better at high photopic luminance levels and rhesus acuity is better at scotopic acuity luminance levels (4). This species disparity can be attributed to differences in optical parameters between human and rhesus rather than retinal morphological or physiological factors.

On the other hand, spectral sensitivity functions measured for spatial grating and Landolt ring acuity criteria demonstrate a long wavelength insensitivity in the rhesus monkey relative to the human (9,10). In these investigations, target size is much more restrictive to the fovea, especially in the latter investigation in which Landolt rings less than 1 minute of arc produced the maximum long wavelength differences between human and rhesus subjects. Adams et al. (11) offered the possibility that foveal and parafoveal cones differ in either distribution or in neural interaction. No assumptions were made about differences between foveal and parafoveal cone photopigments, as separation of foveal and parafoveal cones in MSP investigations has not been technically feasible (5).

In the present investigation, we derived spectral sensitivity functions for a rhesus pursuit visual motor tracking task. We attempted a limited comparison of human and rhesus visual motor tracking with regard to spectral differences in the long and middle visible spectrum.

Methods

Two rhesus monkeys were trained on a pursuit motor tracking task which required continuous tracking of a horizontally moving annulus by maintaining a small spot of HeNe laser light in the center of this annulus. The rhesus monkeys were seated individually in a large primate cubicle. Their viewing condition was monocular, limited to only that portion of the screen across which the target moved, via monocular fiberglass face masks individually constructed for each animal. A viscous-damped tracking mount placed in front of the cubicle supported a video camera and HeNe laser. The HeNe laser served as the animal's aiming pointer. (The beam divergence of the HeNe laser equalled 1/2 milliradian and was attenuated in intensity by a 0.5 log unit filter.) A single lever arm with a vertical handle grip projected from the tracking head into the cubicle, serving as the control for the horizontal position of the laser pointer/video camera pair. The video camera was aligned so that the center of the video frame represented the aiming position of the HeNe laser. The horizontal position of the target in the field of view of a 100 mm lens mounted on the CCD video camera (Sony Corp. Mdl XC-37) was determined by a microcomputer-controlled video digitizing circuit. Target position was sampled at 21 Hz during the 20 second trial. Software controlled all experimental contingencies and provided on-

line determination of the aiming position and on/off-target status of each sample.

The task for the monkey began with the presentation of the stimulus target and the HeNe laser pointer. The animal was required to move the HeNe laser until it was in the center of the target ring. When the laser was correctly positioned within a window centered on the target's center of mass, a white background masking noise was terminated for 1 second as a cue for correct target acquisition. At the end of the 1-second cue, the noise was turned on, and the target began its horizontal track for 20 seconds. The monkey was required to maintain the HeNe laser on the target's center position until the target was extinguished. Positive reinforcement was used to reward the monkey for accurate tracking (12). The amount of liquid reinforcement (TangTM Orange Drink) was determined by aiming accuracy on each trial. Pursuit tracking targets consisted of reverse contrast annuli projected onto a curved high reflectance screen. The inner ring diameters of these stimuli varied from 18 min of arc to 3 min of arc. In this experiment, we employed a 6 min of arc target in obtaining all achromatic and chromatic intensity performance functions and spectral sensitivity functions derived from criterion performance. Stimulus intensity was varied by two continuously variable circular optical density wedges automatically moved in opposite directions over an optical density range of 3.8 log units. Narrow pass interference filters (± 10 nm half maximum bandwidth) were used to vary peak wavelength every 20 nm from 460 to 660 nm. An equal energy spectrum was constructed by normalizing the energy at each wavelength with the filter transmitting the maximum energy. Maximum energy was measured at 600 nm. Intensity performance functions at each peak wavelength were constructed from these measurements and spectral sensitivity functions derived for various criterion time-on-target performance criteria.

Three human subjects served in the same task under comparable conditions for measurement of achromatic and selective chromatic intensity performance functions (13). Rhesus and human achromatic and chromatic intensity performance functions were statistically evaluated using a general mixed-model Analysis of Variance (14).

Results

Sample tracking data from one rhesus subject during a 20 second trial period is presented in Fig. 1. The dashed lines indicate the inner diameter of the annulus which was 0.3 degree (18 min of arc) in this particular sample. The time-on-target, the total time the HeNe laser spot was maintained within the inner diameter of the annulus, exceeded 90 percent. As target luminance or intensity decreased, this measure of performance also decreased, as shown in the following figures employing a 6 minute of arc annulus.

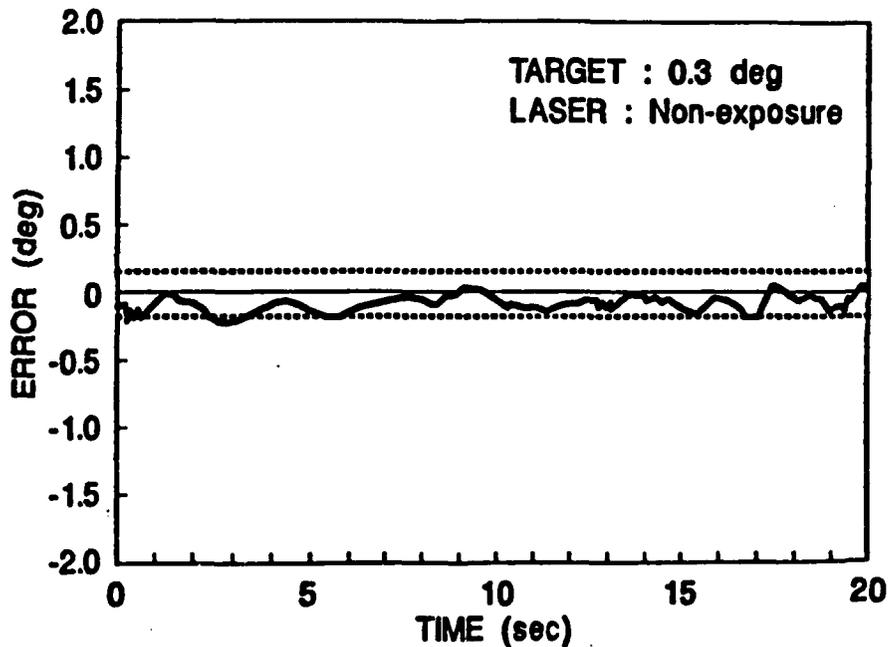


Figure 1. Sample visual tracking data from one rhesus subject. This trial began after initial target had been successfully acquired; i.e., after subject has placed the HeNe laser spot within the inner diameter of the annulus.

In Fig. 2, human and rhesus mean achromatic intensity performance functions are shown for 2 human and 2 rhesus subjects. The human function is superior for the higher luminance targets but the rhesus function becomes slightly more sensitive at the lower target intensities. Over the high intensity range, differences between the human and the rhesus were statistically significant ($p < 0.05$) using a general mixed model Analysis of Variance (14). Although the rhesus was slightly superior in time-on-target scores for the dimmer luminance levels, differences at the three lower luminance levels were not statistically significant.

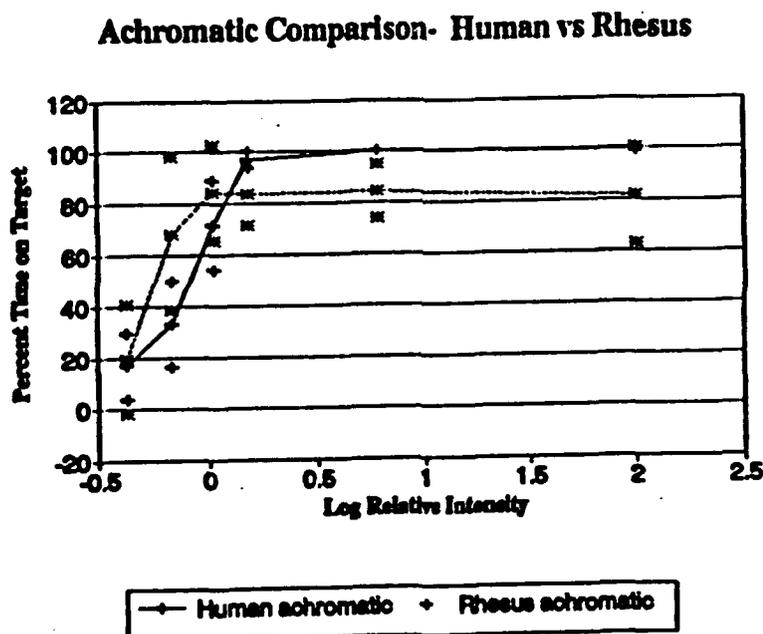


Figure 2. Comparison of mean human and rhesus intensity performance functions for achromatic (white) targets. The human achromatic intensity performance function is superior to the rhesus function at the upper luminance levels. Plus and minus one standard deviation scores are shown for each function. Standard deviations do not overlap at all for the highest three luminance levels. At lower luminance levels, the rhesus function becomes superior, and standard deviations tend to overlap.

In Fig. 3 mean spectral intensity performance functions at 520 and 640 nm are compared for the three human and two rhesus subjects. At 520 nm the human function was slightly superior for the high target intensity levels, whereas, the rhesus displayed better time-on-target scores as target intensity decreased. The human 640 nm function is superior to the rhesus over the entire target intensity range. The difference between human and rhesus time-on-target scores at 640 nm over intensity was statistically significant ($p < 0.05$). A similar ANOVA between human and rhesus time on target scores at 520 nm was not statistically significant.

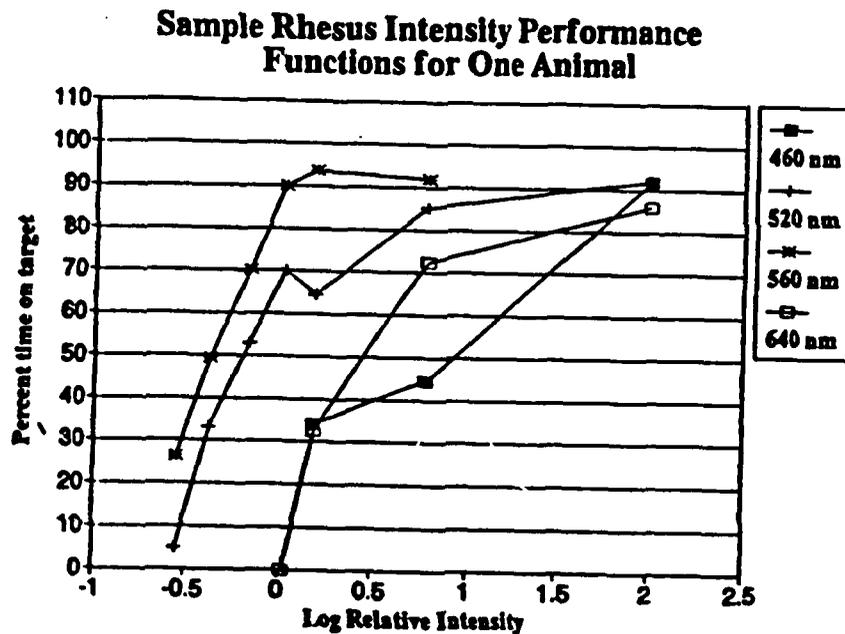


Figure 3. Comparison of human and rhesus intensity performance functions for two chromatic targets are presented in this figure. At 640 nm, the average human function (3 subjects) is superior to the average rhesus function (2 subjects). At 520 nm the average human function is initially superior to the rhesus but crosses over, becoming less accurate, as target intensity decreases.

Fig. 4 displays rhesus intensity performance functions sampled over the visible spectrum for one rhesus subject. Systematic variation in slope is evident from the shorter to the longer wavelength functions; slopes become steeper as wavelength increases.

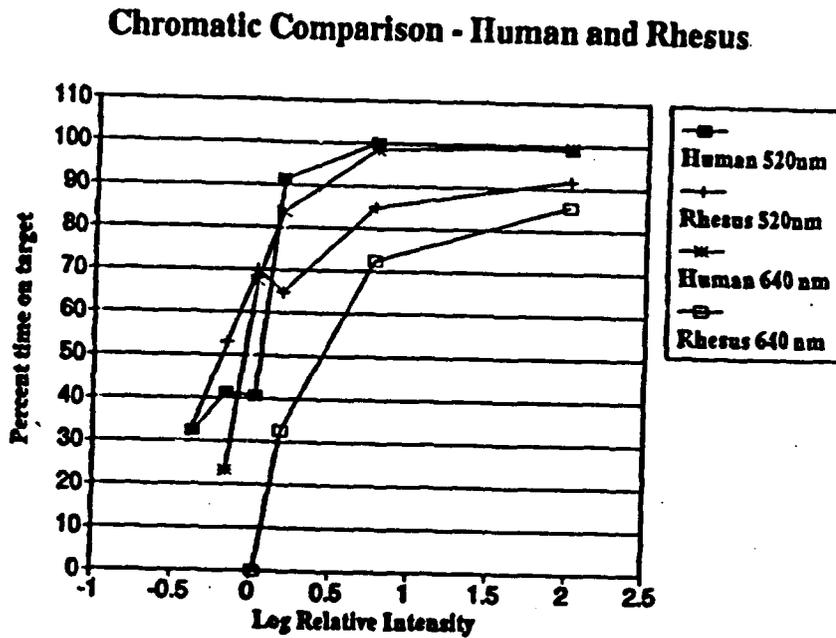


Figure 4. Rhesus spectral intensity performance functions for one rhesus subject. These functions were measured at 20 nm intervals between 460 and 660 nm.

Spectral sensitivity functions derived for constant percent time-on-target performance criteria are shown for two rhesus subjects in Figs 5 and 6. In Fig. 5, the subject's spectral sensitivity at the 40 percent time-on-target criterion peaks between 500 and 520 nm with a shoulder between 540 and 580 nm. As the time-on-target criterion increased from 40 to 70 percent, overall sensitivity decreased by at least 1 log unit at 500 nm with a relative plateau and a slight depression at 560 nm between the 70 and 80 percent time-on-target criteria.

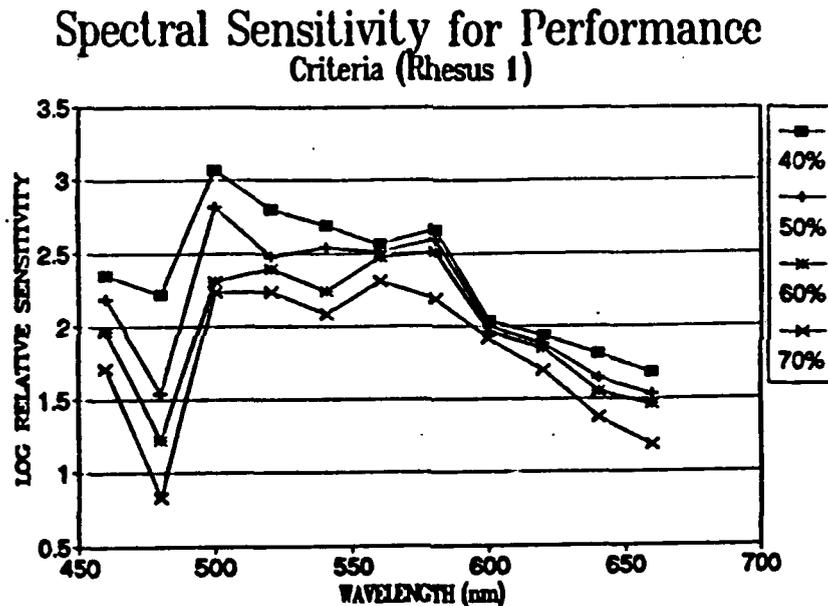


Figure 5. Spectral sensitivity functions for percent time-on-target criteria are presented for the first rhesus subject. Spectral sensitivity functions for constant time-on-target criteria were derived by relative intensity values for constant percent time-on-target criteria at different spectral intensity performance functions from 460 to 660 nm. Relative intensity values were then adjusted for equal energy by normalizing each value to the spectral filter that transmitted maximum energy, the 600 nm filter, and then, by plotting them as reciprocal relative sensitivity values vs. wavelength for various equal performance criteria. As time-on-target decreases, maximum spectral sensitivity shifts from a shallow peak at 560 nm to a peak at 500 nm.

A similar set of functions was derived for the second rhesus subject shown in Fig. 6. At 40 percent time-on-target, the spectral sensitivity function peaked at 500 nm and displayed a shoulder between 540 and 580 nm. As time-on-target increased from 40 to 80 percent, peak sensitivity at 500 nm decreased by about 1 log unit with a broad plateau from 520 to 580 nm.

Spectral Sensitivity for Performance Criteria (Rhesus 2)

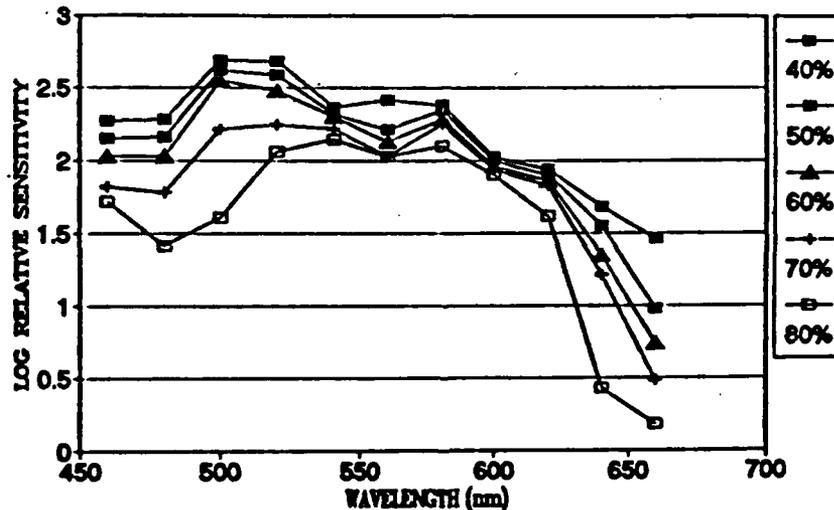


Figure 6. Spectral sensitivity functions for percent time-on-target criteria were derived as described above for the second rhesus subject. A similar shift in spectral sensitivity function occurs for this animal from a maximum sensitivity near 560 nm to a peak between 500 and 520 nm as criterion time-on-target decreases along with a similar overall increase in sensitivity as observed in the first rhesus subject.

In Fig. 7, we have compared the spectral sensitivity functions obtained for the 40, 70 and 80 percent time-on-target criteria for rhesus 1 with the Smith and Pokorny (15) cone fundamentals normalized at 580 nm. In general, the long wavelength cone fundamental provides a better fit at the long wavelength region for all time-on-target criteria, whereas the intermediate cone fundamental provides a better fit in the intermediate and shorter wavelength spectral regions. However, it is also apparent that the peak of the 40 percent time-on-target function is not well accounted for by either fundamental. A similar situation is apparent in rhesus 2, in which a similar shift in peak spectral sensitivity occurs as the time-on-target criterion is decreased.

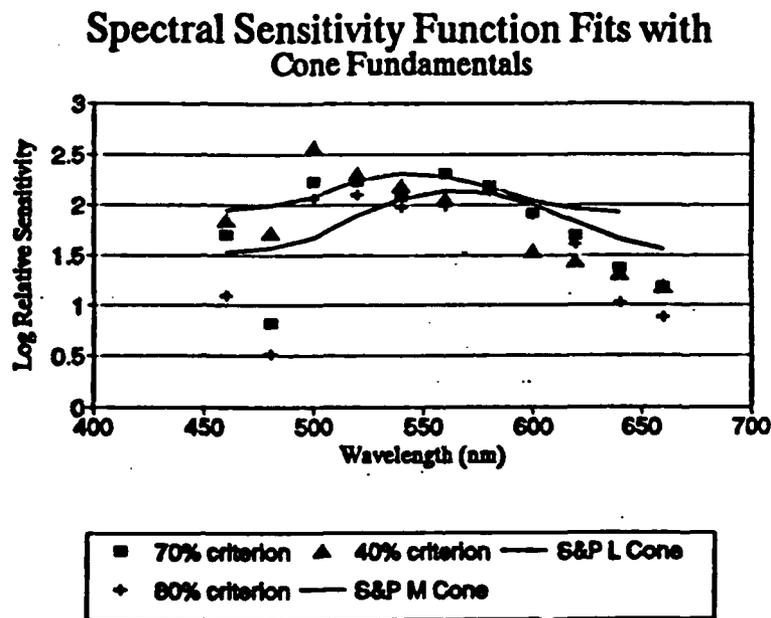


Figure 7. Comparison three spectral sensitivity functions from rhesus 1 at 40, 70 and 80 percent time-on-target which were normalized with the Smith and Pokorny cone fundamentals at 580 nm.

Discussion

Our major objective in this paper was the derivation of rhesus spectral sensitivity for a complex visual motor task. Although rhesus spectral sensitivity has been assessed in numerous investigations, to our knowledge, no investigation has evaluated a complex visual motor task with regard to the visual guidance provided by visual mechanisms. The spectral sensitivity functions derived from rhesus spectral intensity performance functions obtained in this study provide a relationship between rhesus visual motor performance and visual mechanism guidance of pursuit motor tracking in the rhesus monkey.

For high performance criteria, the rhesus spectral sensitivity functions in both subject animals compare favorably with other investigations of rhesus photopic spectral sensitivity. These functions have a broad maximum sensitivity from 520 to 580 nm and appear to make a good, although not perfect, fit with the long and intermediate cone fundamentals of Smith and Pokorny (15). Encroachment of shorter wavelength receptor mechanisms is suggested by the shift in the peaks of these spectral sensitivity functions with decreasing time-on-target criterion from 80 to 40 percent, as demonstrated in both rhesus subjects. We have added the intermediate cone fundamental to fit the 40 percent function (Fig. 7). Although this fit is not perfect, it provides a better fit to the shorter wavelength end of the lower criterion spectral sensitivity functions than that of the long wavelength cone fundamental alone.

Although we have not fitted a rod spectral sensitivity function to the lower criterion spectral sensitivity function, we do not preclude the intrusion of rods as criterion time-on-target decreases. However, evidence from previous measures of visual motor pursuit tracking performance and target luminance suggests that pursuit tracking performance may operate into the mesopic luminance range but not into the fully scotopic luminance range (3). Human observers report a shift in their response strategy under dim luminance conditions from a continuous tracking strategy involving fine adjustments to a grosser tracking strategy involving discrete target "bracketing" or estimation of center of target mass (1). Such strategies may involve both peripheral and central retinal receptor processes. Similarly, in the present study, both rhesus and human achromatic intensity tracking functions (Fig. 2) fall off abruptly at the lower target intensities.

In addition to supporting the accepted status of the rhesus monkey as a viable surrogate of human photopic function, we have also demonstrated species differences reminiscent of previous rhesus and human comparisons (4). Human tracking at the high intensity levels (Fig. 2) exceeded that of the rhesus, whereas rhesus time-on-target scores tend to exceed those of human observers at the dimmer target intensity levels.

Even more significant was the dramatic difference between human and rhesus intensity performance functions at 640 nm, as compared to statistically non-significant differences between human and rhesus functions at 520 nm. This result is consistent with target sizes used in studies in which rhesus long wavelength sensitivity was suppressed relative to the human (9,10,16-18). In other rhesus and human comparisons of photopic spectral sensitivity, much more agreement exists between human and rhesus in the spectral sensitivity range from 580 to 640 nm (6-8). However, all of these studies utilized test targets many times larger than the test target limits which we used for observing rhesus long wavelength insensitivity. Yet, in at least two studies (7,8) a small deficit in rhesus long wavelength sensitivity either appeared without comment or was noted and dismissed as incidental experimental variation.

In summary, we have derived spectral sensitivity functions for complex rhesus visual motor performance. These spectral sensitivity functions indicate domination of cone mechanisms, although rod function may interact at lower photopic luminance levels. Furthermore, these functions are consistent with data derived from afferent visual response criteria as well as providing consistency with possible species differences between the rhesus monkey and the human regarding foveal visual processing in the visible long wavelength spectral region.

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