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SEPARATE VISUAL REPRESENTATIONS FOR PERCEPTION AND FOR VISUALLY GUIDED BEHAVIOR

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SUMMARY

Converging evidence from several sources indicates that two distinct representations of visual space mediate perception and visually guided behavior, respectively. The two maps of visual space follow different rules; spatial values in either one can be biased without affecting the other. Ordinarily the two maps give equivalent responses because both are veridically in register with the world; special techniques are required to pull them apart. One such technique is saccadic suppression: small target displacements during saccadic eye movements are not perceived, though the displacements can change eye movements or pointing to the target.

A second way to separate cognitive and motor-oriented maps is with induced motion: a slowly moving frame will make a fixed target appear to drift in the opposite direction, while motor behavior toward the target is unchanged. The same result occurs with stroboscopic induced motion, where the frame jumps abruptly and the target seems to jump in the opposite direction.

A third method of separating cognitive and motor maps, requiring no motion of target, background or eye, is the "Roelofs effect": a target surrounded by an off-center rectangular frame will appear to be off-center in the direction opposite the frame. Again the effect influences perception, but in half of our subjects it does not influence pointing to the target. This experience also reveals more characteristics of the maps and their interactions with one another—the motor map apparently has little or no memory, and must be fed from the biased cognitive map if an enforced delay occurs between stimulus presentation and motor response.

In designing spatial displays, the results mean that "what you see isn't necessarily what you get." Displays must be designed with either perception or visually guided behavior in mind.

The visual world is represented by several topographic maps in the cortex (Van Essen, Newsome, and Bixby, 1982). This characteristic of the visual system raises a fundamental question for visual physiology: do all of these maps work together in a single visual representation, or are they functionally distinct? And if they are distinct, how many functional maps are there and how do they communicate with one another? Because these questions concern visual function in intact organisms, they can be answered only with psychophysical techniques. This paper presents evidence that there are at least two functionally distinct representations of the visual world in normal humans; under some conditions, the two representations can simultaneously hold different spatial values. Further, we are beginning to understand some of the ways in which the representations communicate with one another.

Experiments in several laboratories have revealed that subjects are unaware of sizeable displacements of the visual world if they occur during saccadic eye movements, implying that information about spatial location is degraded during saccades (Ditchburn, 1955; Wallach and Lewis, 1965; Brune and Lücking, 1969; Mack, 1970; Bridgeman, Hendry, and Stark, 1975). Yet people do not become disoriented after saccades, implying that spatial information is maintained. Experimental evidence supports this conclusion. For instance, the eyes can saccade accurately to a target that is flashed (and mislocalized) during an earlier saccade (Hallett and Lightstone, 1976), and hand-eye coordination remains fairly accurate following saccades (Festinger and Cannon, 1965). How can the loss of perceptual information and the maintenance of visually guided behavior exist side by side?

To begin a resolution of this paradox, we noted that the two kinds of conflicting observations use different response measures. The saccadic suppression of displacement experiments require a nonspatial verbal report or button press, both symbolic responses. Successful orienting of the eye or hand, in contrast, requires quantitative spatial information. The conflict might be resolved if the two types of report, which can be labeled as cognitive and motor, could be combined in a single experiment. If two pathways in the visual system process different kinds of information, spatially oriented motor activities might have access to accurate position information even when that information is unavailable at a cognitive level that mediates symbolic decisions such as button pressing or verbal response. The saccadic suppression of displacement experiments cited above address only the cognitive system.

In our first experiment on this problem (Bridgeman et al., 1979), the two conflicting observations (saccadic suppression on one hand and accurate motor behavior on the other) were combined by asking subjects to point to the position of a target that had been displaced and then extinguished. Subjects were also asked whether the target had been displaced or not. Extinguishing the target, and preventing the subjects from viewing their hands (open-loop pointing), guaranteed that only internally stored spatial information could be used for pointing. On some trials, the displacement was detected, while on others it went undetected, but pointing accuracy was similar whether the displacement was detected or not.

This result implied that quantitative control of motor activity was unaffected by the perceptual detectability of target position. But it is also possible (if a bit strained) to interpret the result in terms of signal detection theory as a high response criterion for the report of displacement. The first control for this possibility was a two-alternative, forced-choice measure of saccadic suppression of displacement, with the result that even this criterion-free measure showed no information about displacement to be available to the cognitive system under the conditions where pointing was affected (Bridgeman and Stark, 1979).

A more rigorous way to separate cognitive and motor systems was to put a signal only into the motor system in one condition and only into the cognitive system in another. We know that induced motion affects the cognitive system, because we experience the effect and subjects can make verbal judgments of it. But the above experiments implied that the information used for pointing might come from sources unavailable to perception. We inserted a signal selectivity into the cognitive system with stroboscopic induced motion (Bridgeman, Kirch, and Sperling, 1981). A surrounding frame was displaced, creating the illusion that the target had jumped, although it remained fixed relative to the subject. Target and frame were then extinguished, and the subject pointed open-loop to the last position of the target. Trials where the target had seemed to be on the left were compared with trials where it had seemed to be on the right. Pointing was not significantly different in the two kinds of trials, showing that the induced-motion illusion did not affect pointing.

Information was inserted selectively into the motor system by asking each subject to adjust a real motion of the target, jumped in phase with the frame, until the target was stationary. Thus the cognitive system specified a stable target. Nevertheless, subjects pointed in significantly different directions when the target was extinguished in the left or the right positions, showing that the difference in real target positions was still available to the motor system. The visual system must have picked up the target displacement, but not reported it to the cognitive system, or the cognitive system could have ascribed the visually specified displacement to an artifact of frame movement. Thus a double dissociation occurred: in one condition the target displacement affected only the cognitive system, and in the other it affected only the motor behavior.

Dissociation of cognitive and motor function has also been demonstrated for the oculomotor system by creating conditions in which cognitive and motor systems receive opposite signals at the same time. Again the experiment involved stroboscopic-induced motion; a target jumped in the same direction as a frame, but not far enough to cancel the induced motion. The spot still appeared to jump in the direction opposite the frame, while it actually jumped in the same direction. Saccadic eye movements followed the veridical direction even though subjects perceived stroboscopic motion in the opposite direction (Wong and Mack, 1981). If a delay in responding was required, however, eye movements followed the perceptual illusion, implying that the motor system has no memory and must rely on information from the cognitive system under these conditions.

All of these experiments involve motion or displacement, leaving open the possibility that the dissociations are associated in some way with motion systems rather than with representation of visual space per se. A new series of experiments in my laboratory, however, has demonstrated dissociations of cognitive and motor function without any motion of the eye or the stimuli at any time. The dissociation is based on the Roelofs effect (Roelofs, 1935), a tendency to misperceive target position, in the presence of a surrounding frame presented asymmetrically, in the direction opposite the offset of the frame. The effect is similar to a stroboscopic induced motion in which only the final positions of the target and frame are presented (Bridgeman and Klassen, 1983).

METHOD

Subjects

The subjects were nine undergraduate volunteers and the author. Six of the subjects were naive with respect to the purposes of the experiment; the others assisted with the experiments, as well as serving as subjects.

Apparatus

Subjects sat with stabilized heads before a hemicylindrical screen that provided a clear field of view 180° wide x 50° high. A rectangular frame 21° wide x 8.5° high x 1° in width was projected, via a galvanic mirror, either centered on the subject's midline, 5° left, or 5° right of center. Inside the frame, an "x" 0.35° in diameter could be projected via a second galvanic mirror in one of five positions, 2° apart, with the middle "x" on the subject's midline (Fig. 1). A pointer with its axis attached to a potentiometer mounted near the center of curvature of the screen and its tip near the screen gave a voltage proportional to the tip's position, with a simple analog circuit. The voltage was fed into an A/D converter of a laboratory computer that controlled trial presentation and data collection. Perceived target position was recorded from a detachable computer keyboard placed in front of the subject. All keys except the five keys corresponding to the five target positions were masked off.

PROCEDURE

Training

Subjects were first shown the five possible positions of the target in sequence on an otherwise blank screen. Then they saw targets exposed for 1 sec and estimated their positions with the five response keys ("judging trials"), until they were correct in five consecutive trials. Next, they were trained on pointing, with the same stimuli ("pointing trials"), until they spontaneously returned the pointer to its rightmost position (as initially instructed) for five consecutive trials. In both conditions, subjects were instructed to wait until the offset of the stimulus before responding. Presentation of the target alone forced the subjects to use an egocentric judgment, and the long display time reduced the possibility of target onset eliciting a spurious motion signal that might affect responses.

No Delay Condition

The 30 types of judging and pointing trials were mixed in a pseudorandom order. Each trial type was repeated 5 times, for a total of 150 trials/block. Trial order was restricted so that pointing trials and judging trials with the same target and frame positions would alternate in the series. At stimulus offset, subjects heard a short "beep" tone to indicate a judging trial or a longer "squawk" tone to indicate a pointing trial. There was a rest period after each 50 trials.

Trials were collated by the computer and a separate two-way ANOVA was run for each response type (assessing target main effect, frame main effect, and interaction).

Delay Condition

Procedures were the same except that a 4-sec interval was interposed between stimulus offset and the tone that indicated the type of response.

RESULTS

No Delay Condition

For all subjects, there was a significant main effect of target position in both trial types and a significant main effect of frame position for judging trials. Thus, all subjects showed a Roelofs effect (Fig. 2).

The main effect of frame position in pointing trials showed a sharp division of the subjects into two groups: 5 of the 10 subjects showed a highly significant Roelofs effect ($p < 0.005$), while the other 5 showed no sign of an effect ($p > 0.18$). Thus, responses to pointing and judging trials were qualitatively different for half of the subjects, showing a Roelofs effect only for judging.

Four of the five subjects who showed a Roelofs effect in pointing were females. Thus, a sex effect is possible in this condition, with females more likely to code the target position in a symbolic form. The number of subjects, however, is too small to draw firm conclusions on this issue.

Delay Condition

With a 4-sec delay interposed between display offset and tone, 9 of the 10 subjects showed a significant Roelofs effect for the judging task ($p < 0.01$) and 8 of the 10 showed a significant effect for the pointing task. One of the two remaining subjects showed no significant effect of frame position for either task. The other subject whose pointing behavior still showed no effect of the frame (Fig. 3) was retested with an 8-sec delay between display offset and tone. A Roelofs effect was found for both pointing and judging trials ($p < 0.001$) (Fig. 4).

In summary, interposting a long enough delay before the response cue forces all subjects to use pointing information that is vulnerable to bias from the frame position, even though half of the subjects were not vulnerable to this bias when responding immediately.

DISCUSSION

These experiments show that perception of a Roelofs effect is robust, being seen by nearly all subjects under all delays. The Roelofs effect in visually guided behavior, though, depends much more strongly on the subjects and conditions. Half of the subject showed an effect of a surrounding frame on pointing behavior. The remainder showed the effect only when a long enough delay was interposed between target presentation and response.

The appearance of the Roelofs effect with a delay between stimulus and motor response is reminiscent of the results of Wong and Mack (1981): saccadic eye movements followed a veridical motion with a short delay, but followed a perceived motion in the opposite direction after a longer delay. If eye movements and visually guided behavior of the arm were controlled by a single motor-oriented internal map of the visual world, then we would expect the effects of delay to influence eye and arm similarly, and the Wong and Mack results and our results could be explained in the same way.

There is now some evidence that oculomotor and skeletal motor systems do indeed share one map of visual space (Nemire and Bridgeman, 1987). Normally, eye and hand behavior are not correlated (Prablanc et al., 1979), in our interpretation because eye and hand motor systems read their information from the same visual map through separate, independent noise sources. To show the identity of visual information driving these two systems, we disturbed the normally veridical mapping process by having subjects make repeated saccades in darkness. This resulted in saccade undershoot, but equally great undershoot of manual pointing.

Our conclusion is that the normal human possesses two maps of visual space. One of them holds information used in perception: if subjects are asked what they see, the information in this "cognitive" map is accessed. The other map drives visually guided behavior, for both eye and arm. The "motor" map is not subject to illusions such as induced motion and the Roelofs effect. In this sense it is more robust, but as a result it is less sensitive to small motions or fine-grained spatial relationships. It also has no memory, being concerned only with the here-and-now correspondence between visual information and motor behavior. If a subject must make motor responses to stimuli no longer present, this system must take its spatial information from the cognitive representation, and brings any cognitively based illusions along with it.

An alternative explanation of the results has been suggested (Ian Howard, personal communication, Sept. 2, 1987); presentation of an off-center frame might bias the subject's subjective straight-ahead in the same direction as the frame's offset. Judging of point position would then be biased in the opposite direction because the subject bases his or her judgments on an offset straight ahead direction. Pointing, however, would remain the same because the subject has not in fact moved, and arm position must be egocentric. This alternative can be tested empirically by having subjects point to the center of the apparatus when the frame is presented in center, left, or right position. Preliminary data from three subjects indicate that frame position has no effect on pointing straight ahead.

Finally, we can apply this conception of two maps of visual space to design of spatial displays. Any display where perception is the primary goal, such as displays of the status of instruments, is subject to induced-motion illusions, Roelofs effects, and other cognitive biases. The designer can take advantage of these effects in designing such displays, but must beware that they do not distort the data displayed.

Displays which guide real-time behavior, on the other hand, are not subject to such illusions. The designer need not worry, for instance, about background motions affecting visually guided behavior toward a target (Bridgeman, Kirch, and Sperling, 1981). But information must be available continuously, for the internal map guiding these behaviors has no significant memory.

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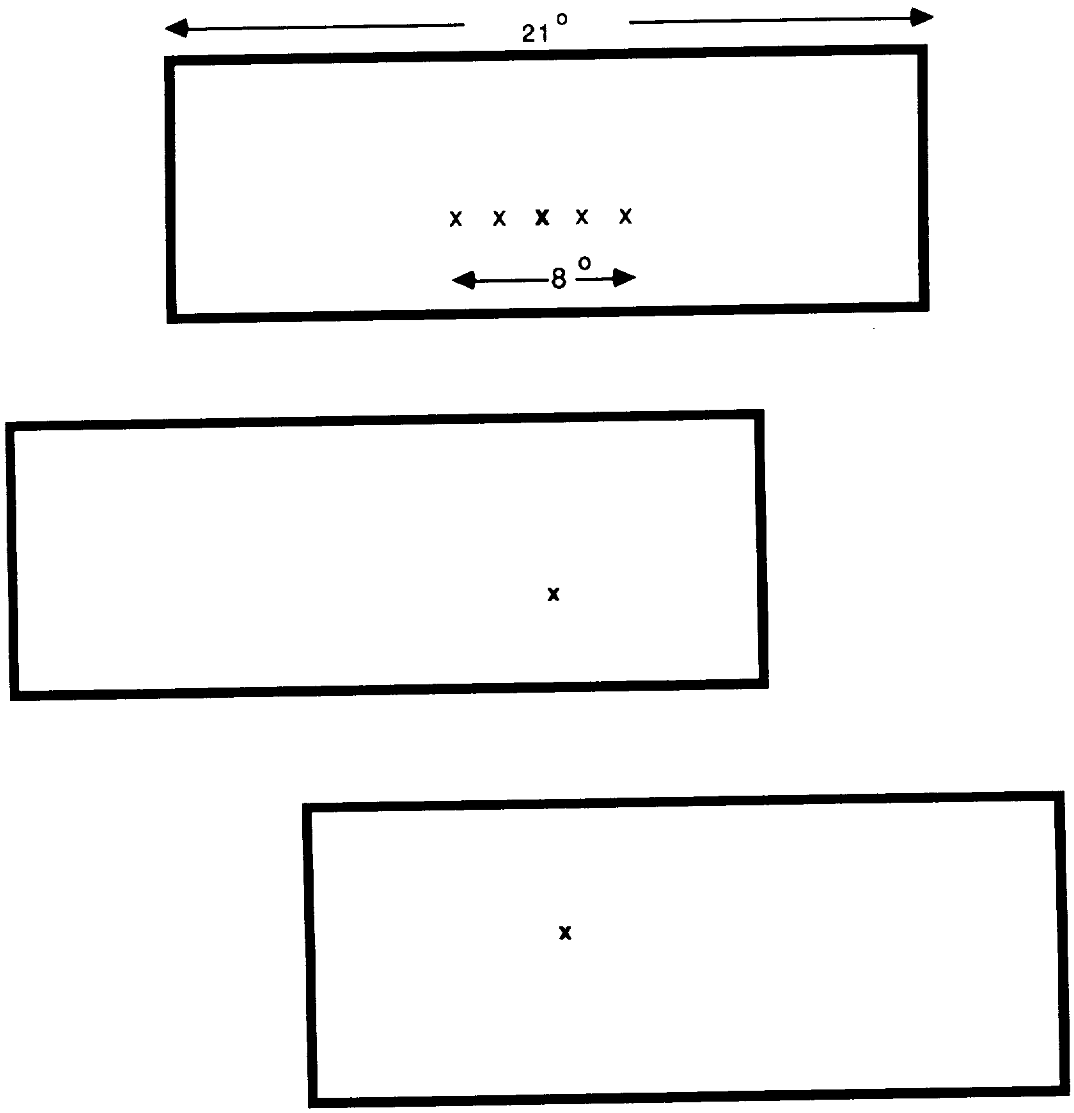


Figure 1.– Stimulus array used in pointing/judging experiments. The frame could be centered (top), biased 5° left (middle), or biased 5° right (bottom). A target appeared in one of the five positions indicated in the top frame. Other frames show the position of the center target.

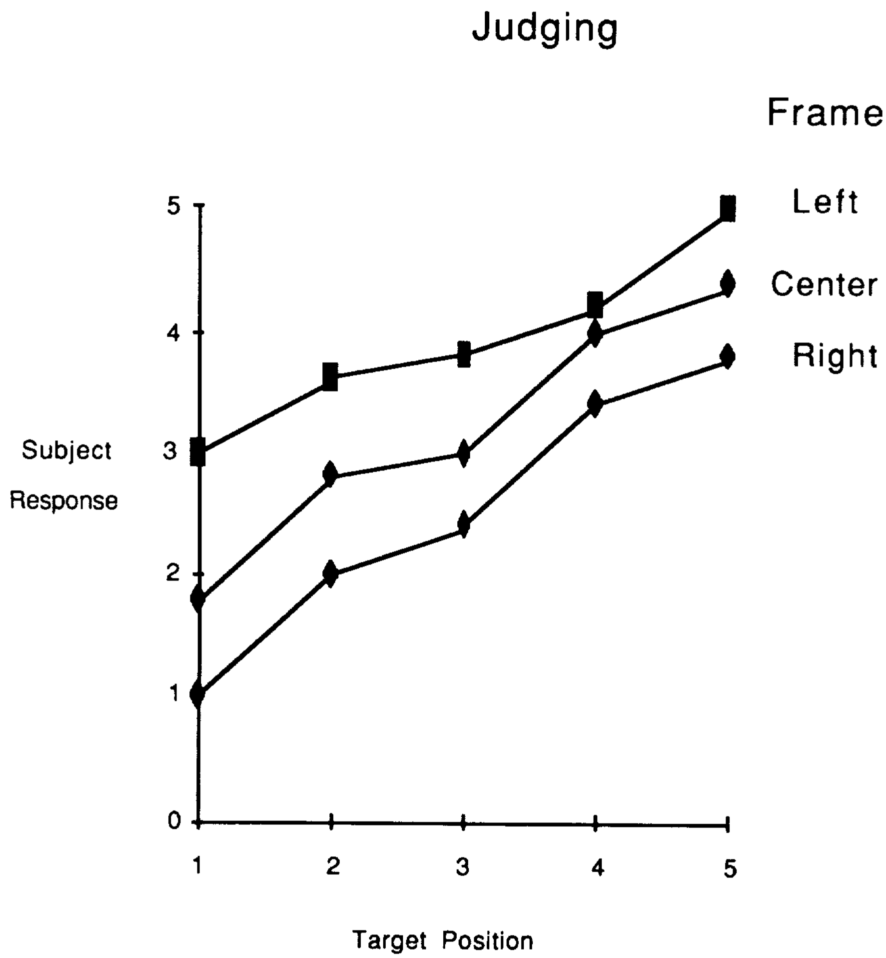


Figure 2.– Judging and pointing behavior immediately after stimulus offset. a) Judging target position with a five-alternative, forced-choice procedure. The separation of three curves corresponding to the three frame positions is due to the Roelofs effect.

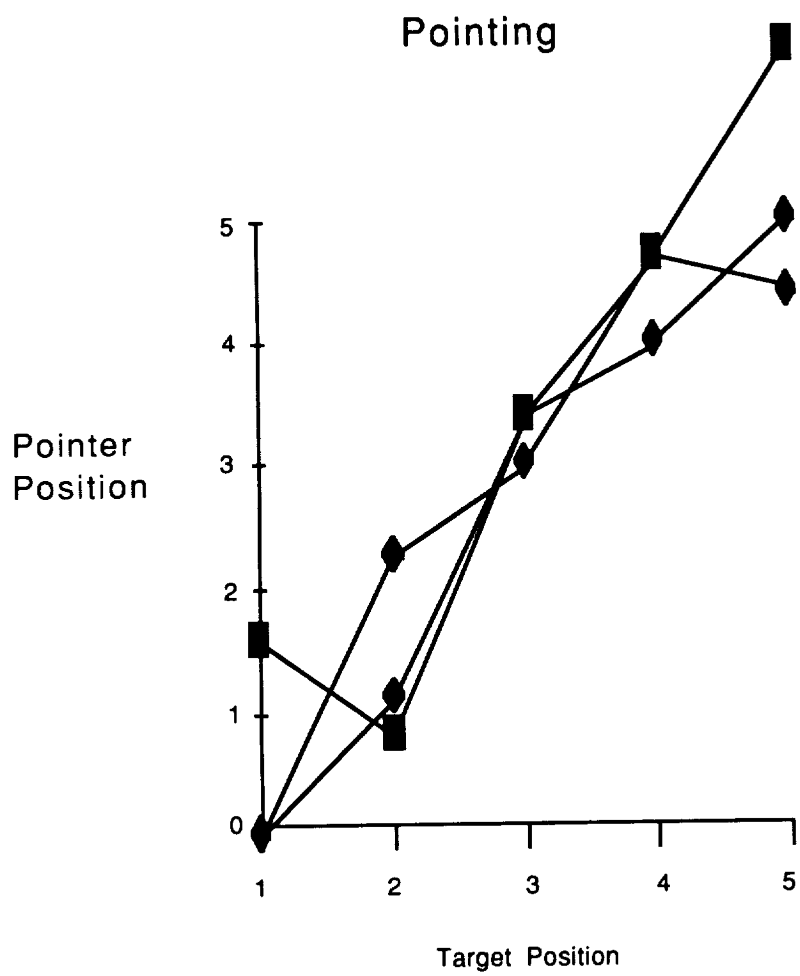


Figure 2.– Concluded. b) Pointing to targets under the same perceptual conditions, in trials intermingled with the judging trials. Overlap of the three curves indicates lack of influence of frame position on pointing behavior. Data are from one subject.

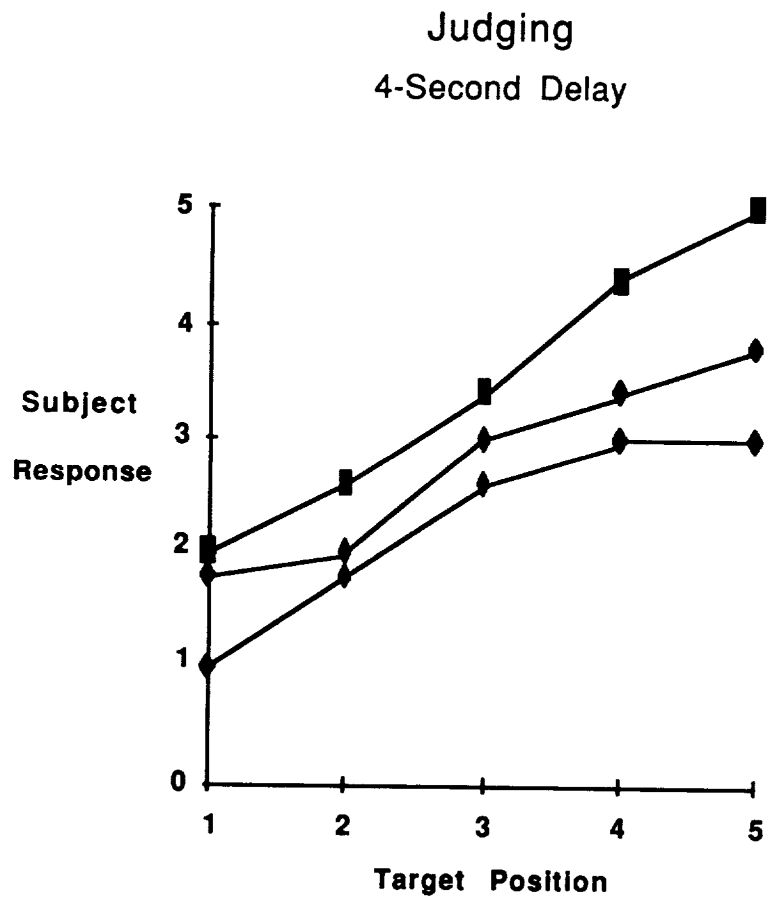
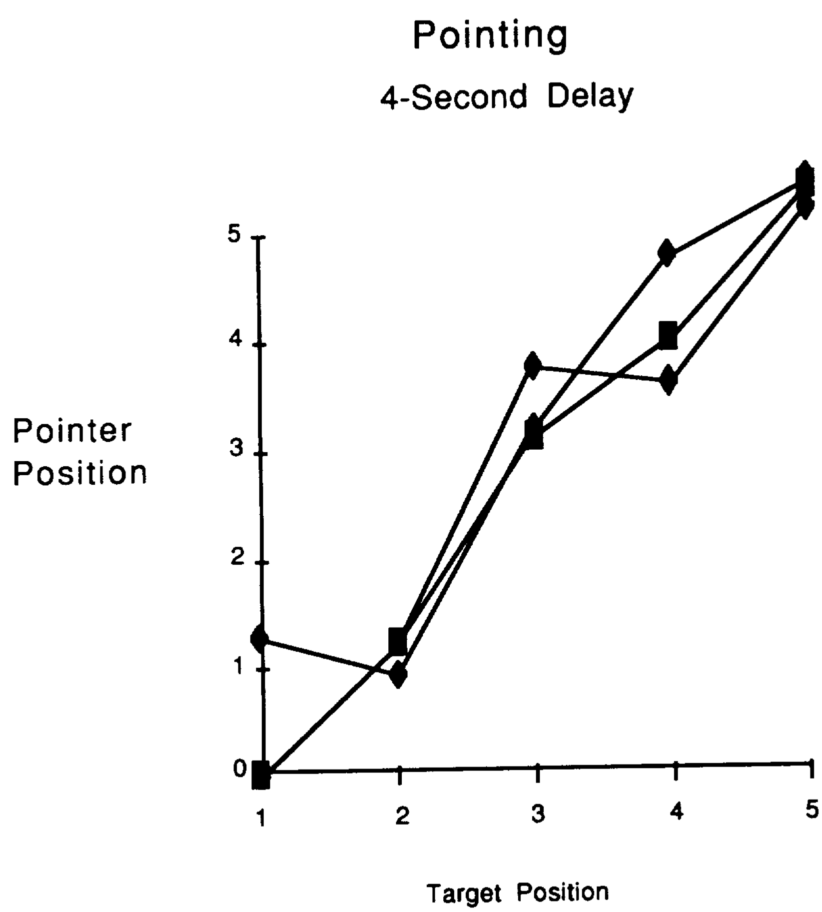


Figure 3.– Judging and pointing after a 4-sec delay. In this subject, no Roelofs effect is evident for pointing; the other subjects showed an effect at this delay.



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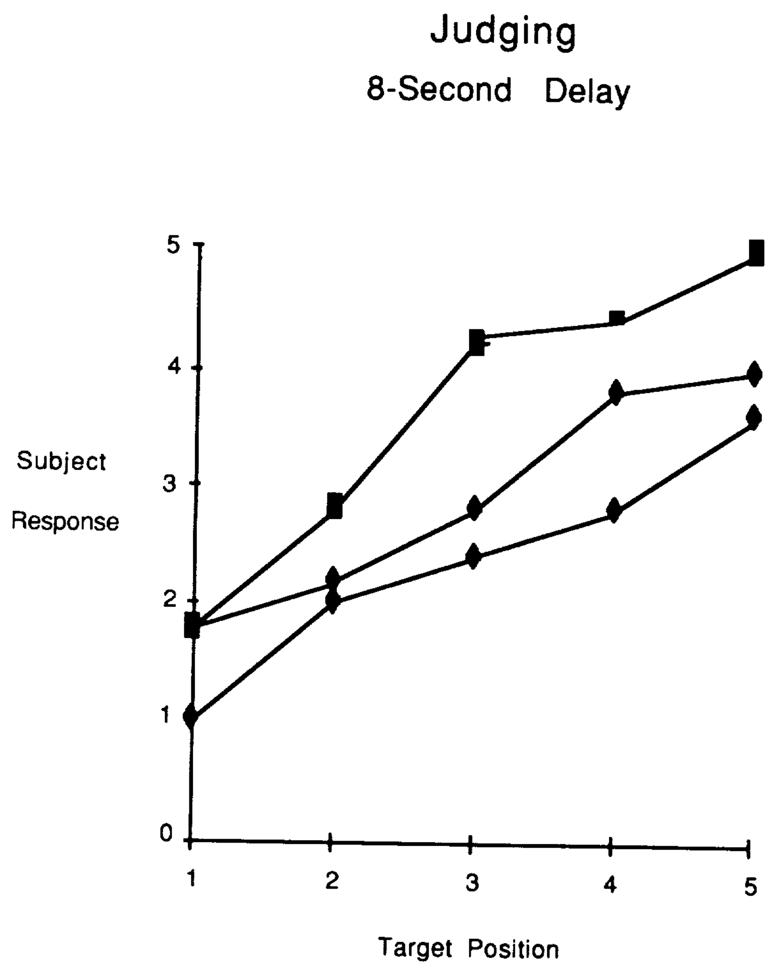

Figure 4.– Judging and pointing after an 8-sec delay. A Roelofs effect for pointing has appeared.

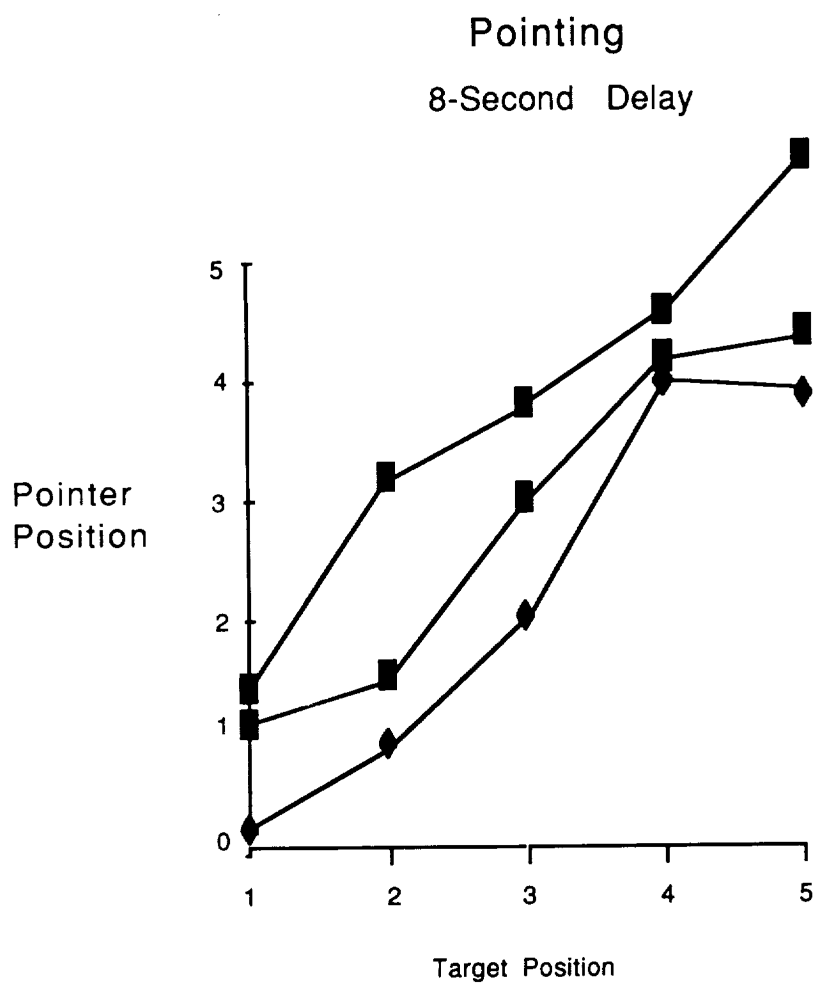

Figure 4.– Concluded.