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A Sensorimotor Map of Visual Space

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Abstract

The brain holds two representations of visual space: a cognitive representation that drives perception, and a sensorimotor representation that controls visually guided behavior. We separate spatial values in the two with the Roelofs effect: a target within an off-center frame appears biased in a direction opposite the offset of the frame. The effect appears for a verbal measure (cognitive) but not for a jab at the target (sensorimotor). Subjects might perform the jab by fixating the target during an exposure period, and jabbing where their eyes are aimed after the offset of target and frame. We show that normal humans use a context-free sensorimotor map even when they do not fixate the target: the motor map is a true 2-dimensional representation, not a 0-dimensional matching process.

Two Visual Systems

Common sense tells us that one must accurately perceive an object's location and properties to interact effectively with it. This intuition is in error, however: several experimental designs now show that humans can engage in accurate motor behavior despite inadequate or erroneous perceptual information. Accurate perception is not required to visually guide an action.

Early experiments on separation of cognitive and sensorimotor systems showed that normal subjects could not perceive jumps of targets that take place during saccadic eye movements (a cognitive-system function). But they could still point accurately to the new locations of the same targets (a sensorimotor-system function), even if their pointing movements were controlled open-loop (Bridgeman, Lewis, Heit & Nagle, 1979). This showed that information about the new location of the target was accurate. But it was not available to perception, defined here as sensory information that is experienced, or more operationally information that can be described and remembered. If a visual stimulus is masked so that an observer denies seeing it, according to this definition the stimulus is not perceived even if it can affect later perceptual judgments or actions.

If each pathway can be probed without affecting the representation in the other, then they must be coding spatial information independently. A more rigorous way to separate cognitive and sensorimotor systems, then, is by double dissociation, introducing a signal only into the sensorimotor pathway in one condition and only into the cognitive pathway in another (Bridgeman, Kirsh & Sperling, 1981). A fixed target was projected in front of a subject, with a frame surrounding it. When the frame was displaced left or right, subjects saw illusory induced motion -- the target appeared to jump in the opposite direction. After target and frame

were extinguished, the subjects pointed to the last target position. They pointed to the same location despite the stroboscopic induced motion. But the illusion did not affect pointing, showing that the displacement signal was present only in the cognitive system.

In another condition we inserted displacement information selectively into the sensorimotor system by nulling the cognitive signal. Each subject adjusted the real target jumps until the target appeared stationary, with a real displacement in phase with the background jump equaling the induced displacement out of phase with the background. Thus, the cognitive pathway specified a stable target. Nevertheless, subjects pointed in different directions when the target was extinguished in the left or the right positions, showing that the difference in real target positions was still represented in the sensorimotor pathway. This is a double dissociation because in the first condition the apparent target displacement affected only the cognitive measure, while in the second condition the real displacement affected only the sensorimotor measure.

A position-motion confound?

If a moving stimulus is sampled at different times for different functions, apparent dissociations might appear even though a unified visual representation underlies each function. Recently, methods have been developed, using static illusions, that can test dissociations of cognitive and sensorimotor function without possible confounding effects of motion. One method is based on the Ebbinghaus illusion, also called the Titchner circles illusion. A circle appears to be larger if it is surrounded by smaller circles than if it is surrounded by larger circles.

Aglioti, DeSouza and Goodale (1995) exploited this illusion by making the center circle into a 3-dimensional poker chip-like object and asking subjects either to judge the size of the circle or to grasp it. The grasp was adjusted closer to the real size of the circle than to its illusory size. Subjects were able to see their hands, however, so it is possible that subjects adjusted their grasp not to the non-illusory true size of the circle, but to the visible error between the grasp and the edge of the circle. The adjustments did not occur until just before the movement was completed, nearly 2 sec after it started.

Recognizing this problem, Aglioti et al. (1995) noted that calibration of grip aperture is largely refractory to visual information available during a movement, relying instead on motor programming that occurs before the movement begins. The experimental support cited for this open-loop

property, however, concerns movements to targets without illusory size modifications, so that visual recognition of grasp error and subsequent correction would not occur. The movements can be controlled open-loop because no correction is necessary. In a subsequent experiment that avoids the feedback confound, Haffenden and Goodale (1998) measured the illusion either by asking subjects to indicate the apparent size of a circle or to pick it up, in both cases without vision of hand or target. The illusion appeared for both estimations but was much smaller for grasp, indicating that the sensorimotor system was relatively insensitive to the illusion.

Another experiment contrasting grasp and perception, using the Müller-Lyer illusion, showed that while the illusion is significantly smaller when measured with grasp than with perception, there is some illusion under both conditions (Daprati & Gentilucci, 1997). Again, relatively slow grasp movements may be responsible, and vision of both hand and stimulus was allowed.

In summary, in normal subjects there is behavioral evidence for a distinction between processing in two visual streams, but we still know very little about processing in the sensorimotor pathway. With the exception of saccadic suppression and induced motion methods, all of the methods address the properties of objects rather than their locations.

A new method has produced large and consistent contrasts between cognitive and sensorimotor systems, differentiated by response measure. The dissociation is based on another perceptual illusion, the Roelofs effect: if a rectangular frame is presented off-center, so that one of its edges is directly in front of the subject, that edge will appear to be offset in the direction opposite the rest of the frame. A rectangle presented on the left side of the visual field, for example, with its right edge in the center, will appear less eccentric than it is, and the right edge will appear to the right of the subject's center (Roelofs, 1935).

We have extended and generalized this phenomenon to apply it to the study of the two-visual-systems theory. First, the frame need not have one edge centered in front of the subject; illusions occur whenever the frame is presented asymmetrically in the visual field. Second, if a target is presented within the offset rectangle, its location tends to be misperceived in the direction opposite the offset of the frame. Misperception of frame position induces illusions of target position; this is an induced Roelofs effect, but will be called simply a Roelofs effect here.

Roelofs effects can be observed reliably if subjects describe the target's position verbally, a task that addresses the cognitive system. If their task is to point to the target as soon as it disappears from view, however, they are not affected by the frame's position. This task addresses the sensorimotor system. Motor behavior for many subjects remains accurate despite the perceptual mislocalization (Bridgeman, Peery & Anand, 1997).

Though the motor task in our case is isomorphic with stimulus position, it is a communicatory act, and might be closely linked to cognitive representations. An alternative is to require an instrumental act, in which a subject must do something to the world rather than simply indicate a position

to another person. Behavior with a purely instrumental goal might be different from behavior with a communicatory goal, even if both the stimuli and the motor movements themselves are identical. Thus in our first experiment subjects jabbed a 3-dimensional target object, pushing it backward and making a clicking noise. Their intention was not to communicate anything, but only to do something to the world. With this improvement in our technique we achieve a cleaner separation of cognitive and motor systems. For a quick jab at a 3-dimensional target, rather than a pointing motion, almost all subjects show independence from Roelofs effects in immediate action, along with the previously observed robust Roelofs effects in verbal estimation of position.

Because this series of experiments follows up on earlier studies (Bridgeman et al., 1997), we were able to take advantage of the results of those studies to improve our experimental design. In the earlier data nearly all of the variance in responses as a function of target position was accounted for by a linear regression, so in the current experiments we did not need to present 5 target positions: two target positions would give us the same information, and allow us to increase the number of trials per condition.

Experiment 1

Using these improved techniques, we begin the job of characterizing the psychophysics of the sensorimotor system.

Method

Subjects Nine University of California undergraduates participated in the experiment, all right-handed with normal or corrected-to-normal visual acuity. Four were male and 5 female.

Apparatus Subjects sat with heads stabilized before a white hemicylindrical screen that provided a homogeneous visual field 180° wide x 50° high. A lever box located in front of the screen presented 5 white levers, each 1.8° wide, spaced 2.5° apart center-to-center (Figure 1). The center lever, marked with a black stripe, functioned as the target. Each lever was hinged at its base and spring-loaded. It activated a microswitch when pushed backward by 5mm. A long black baffle hid the microswitch assembly without revealing the position of the lever array. In the motor condition, the task was to jab the black target stripe rapidly with the right forefinger. The remaining levers served to record the locations of inaccurate responses.

A rectangular frame 38° wide x 1° in line width was projected, via a galvanic mirror under computer control, either centered on the subject's midline, 6° left, or 6° right of center. Inside the frame, the lever box occupied one of two positions, 3.5° left of center or 3.5° right of center. On each trial the frame and target were positioned in darkness during the intertrial interval. Then a computer-controlled shutter opened for one second. Stray light from the projected frame made the screen and the levers visible as well. As soon as

the shutter closed, the subject could jab the target or verbally indicate its position in complete darkness. Responses were recorded by the computer on an absolute scale (lever 1, 2, 3, 4, or 5).

Procedure Cognitive Measure: For the cognitive system the subject verbally estimated the position of the target spot on the center lever. The choices were 'far left', 'left', 'center', 'right', or 'far right', so that the response was a 5-alternative forced choice. Choices were identified with the five lever positions, which were centered before the subject during the instruction period, when the screen was illuminated by general room lighting and the frame was not projected. The five levers, and nothing else, were visible when the five alternatives were defined. By equating the responses with the visible levers in the apparatus, we could assign estimations in degrees of angle to the qualitative verbal responses. Interpretation of the data depends upon presence or absence of Roelofs effects, however, not on absolute calibrations of the cognitive measure. In the present series of experiments the cognitive measure serves as a control to assure that a cognitive illusion is present, differentiating the cognitive and sensorimotor systems. All quantitative results are based on the motor measure.

Subject instructions in the verbal condition emphasized egocentric calibration. Quoting from the instructions that were read to each subject, "In this condition you will be telling the experimenter where you think the target is in relation to straight ahead." Further, "If the target looks like it's directly in front of you, you will indicate this by saying 'center'." Thus center was defined in terms of the subject's body rather than the apparatus or the frame.

Sensorimotor measure: the subject rested the right forefinger on a foam pad mounted on the centerline of the apparatus just in front of the chin rest, then jabbed the target with the forefinger as soon as the target disappeared. Thus both cognitive and sensorimotor measures were open-loop, without error feedback. Before the experimental trials began, subjects practiced jabbing the target -- some were reluctant to respond vigorously at first for fear of damaging the apparatus. Subjects then received at least 10 practice trials in the jab condition and 10 the verbal condition.

Trial Execution: A computer program randomly selected target and frame positions, with the exception that an identical set of positions could not occur on two successive trials. For verbal trials, the experimenter recorded the subject's response by typing a number (1-5) on the computer's keyboard corresponding to the subject's verbal estimate. The computer recorded motor responses automatically.

In each trial one of the two target positions and one of the three frame positions was presented, exposed for one second, and extinguished. Since the projected frame provided all of the illumination, target and frame exposure were simultaneous. A computer-generated tone told the subject to respond. For no-delay trials the tone sounded as the shutter extinguished the frame, while on other trials the tone began after a 1-sec or 2-sec delay. During the delay the subject sat in darkness.

Two target positions x three frame positions x two response modes x three delays resulted in 36 trial types. Each trial type was repeated 10 times for each subject, resulting in a data base of 360 trials/subject. There was a brief rest and a chance to light adapt after each block of 60 trials.

Data were collated on-line and analyzed statistically off-line. Two-way ANOVAs were run for each subject, each response mode, and each delay condition. Factors were frame position and target position. Summary statistics were analyzed between subjects.

Results

Cognitive The Roelofs effect, measured as a main effect of frame position, was significant under all delay conditions. Subjects tended to judge the target to be further to the left than its actual position when the frame was on the right, and vice versa. Six of 7 individual subjects showed a significant Roelofs effect ($F(2,5) > 8.43$, $p < 0.05$), and the magnitude of the Roelofs effect averaged across subjects was 2.23 deg (s.e. 0.86 deg).

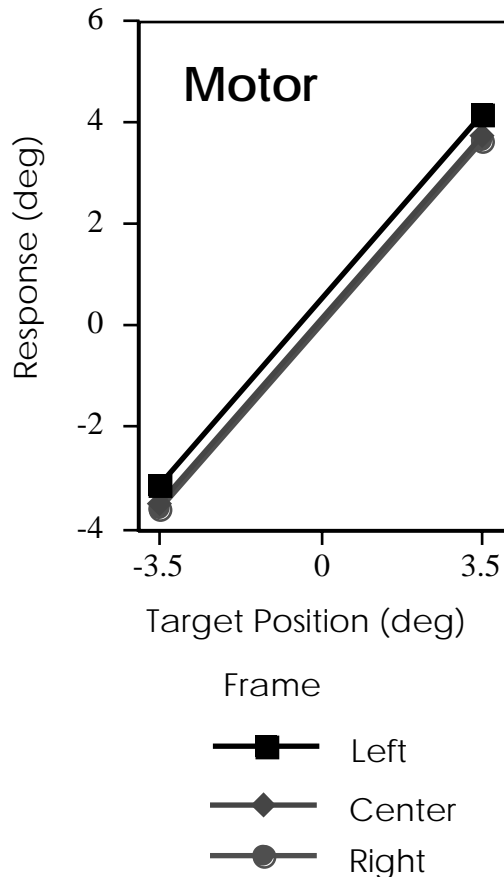


Figure 1. Motor responses, immediate action.

Sensorimotor The results can best be summarized with the generalization that subjects hardly ever missed the target, regardless of target position or frame position (Figure 1). Seven of 8 subjects showed no significant Roelofs effect (frame effect $p > 0.094$). Averaged across subjects, the magnitude of the Roelofs effect was 20 min. arc (s. e. 22 min. arc).

Comparing the two measures Overall, ANOVA showed a significant difference between cognitive and motor measures ($F_{1,43} = 12.45$, $p = 0.001$), as expected from the robustness of Roelofs effects with the cognitive measure and the absence of Roelofs effects at short delays with the motor measure.

The sizes of the Roelofs effects under various conditions can be compared by measuring the difference between average response with the target on the right and with the target on the left. The cognitive measure shows a large and

consistent deviation, replicating Bridgeman et al. (1997), while the sensorimotor measure shows no deviation.

Discussion

This experiment showed that the sensorimotor pathway can maintain veridical information about target position, unaffected by visual context, even when perception shows an illusion of position. The rules are different for the two systems. Cognition is conscious and must use context, even when that leads to errors of localization. The sensorimotor system does not use context, and its spatial values are held unconsciously. Conflicting spatial values can exist in the two systems simultaneously.

A possible mechanism of the sensorimotor store is that subjects might fixate the target visually when it is visible, then point where they are looking when the target is extinguished. This would mean a 0-dimensional storage of information of spatial information limited to the location of a single point, held in gaze position rather than in an internal register. If this interpretation is correct, subjects will be unable to perform the motor task if they are prevented from ever fixating the target. In the next experiment, extending the Roelofs effect paradigm, we seek to control for possible attention and fixation effects by preventing our subjects from fixating the target.

Experiment 2

We hypothesize that if subjects cannot fixate the target, the motor system cannot use spatial information from gaze position and will be forced to call upon the cognitive system for spatial location information. Further, we prevent covert orienting to the target by requiring subjects to perform a continuous oculomotor task throughout the exposure period.

Method

Subjects Seven University of California undergraduates participated in the cognitive condition, and 7 in the motor condition, all right-handed with normal or corrected-to-normal visual acuity. Each subject was run in only one condition, cognitive or motor.

For this experiment we need fixation points that define eye movements, but give the subject no information about target or frame positions. A pair of fixation points is added to the display, in positions statistically uncorrelated with target or frame positions, to elicit horizontal saccades.

Apparatus In order to present the target, frame and fixation points simultaneously, and also to improve the accuracy of our jab recordings, we move to an electronic apparatus with all stimuli displayed on a CRT screen. The screen is mounted with its face down and is viewed through a mirror mounted at 45 deg in front of the eyes, so that the display appears to be directly in front of the subject. A touch pad mounted vertically in the apparent plane of the display records jab responses made with a stylus. The frame's width is 24 deg, and the saccade targets are 23 deg apart, displayed above the frame. As before, targets are at 6 deg. left, center, and 6 deg. right.

Results

Results were analyzed in the same manner as experiment 1. The cognitive subjects showed an effect of target position, frame position and fixation point position, all significant at $p < 0.0001$.

The motor subjects, in contrast, showed no Roelofs effect (no significant frame effect), but had a target significant at $p < 0.0001$ and a fixation point effect significant at $p < 0.0011$. There were no significant interactions in either set of results.

Discussion

Since the subjects in the motor condition showed no Roelofs effect, while those in the cognitive condition did, we can conclude that the sensorimotor representation was controlling the jab for the motor subjects. The representation is at least 2-dimensional, a true map and not a simple matching of gaze and jab positions. The single most important finding of the experiments reported here is that preventing direct fixation on the target, even when multiple targets must be discriminated, does not cause a Roelofs effect. These experiments show that oculomotor fixation and spatially selective attention are not responsible for accurate pointing behavior in an illusory visual context.

Conclusions

Once again, the evidence can be interpreted in terms of two visual systems, one based on egocentric coordinates to govern motor behavior and another that uses information from visual context to represent spatial relationships in perception. Also, these experiments lend support to the claim that the price in performance the cognitive system must pay in order to take advantage of visual context information is a susceptibility to illusions of spatial context. While it has been shown that direct fixation driven by attentional selection is not the mechanism responsible for accurate pointing behavior in a visual context that creates illusory perceptions in the cognitive system, this shows only that fixation is not responsible. Other aspects of attention may be responsible for the continued accuracy of motor behavior in these experiments.

The visual mechanism by which motor behavior is governed has been shown to be extremely robust, both by these and previous studies. Indeed, the reappearance of a Roelofs effect for motor responses after a delay (Bridgeman et. al., 1997) shows that the cognitive system can provide information to the motor system when necessary, and this so far appears to be the only form of communication between the two systems. To date there is no evidence that the cognitive system can access spatial location information in the motor system, supporting the inference that spatial information can flow in only one direction, from cognitive to motor. In normal visual conditions, however (motor interactions with still-visible targets), spatial information in the two systems remains segregated.

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