tion of the limb would be highly correlated with the position of the limb at any other point in time during the reaching trajectory; that is, early overshooting or undershooting errors would not be corrected by compensatory adjustments to the later trajectory. Because the visual control representation is assumed to decay following two seconds of delay, the PCM would predict that reaching movements involving a five-second delay would exhibit such a pattern

For the purposes of this commentary, we present the graphic result (Fig. 1) of an exemplar participant in three visual conditions (full-vision, 0-second delay, 5-second delay) while aiming to the 40-cm target. These figures quite nicely demonstrate the control characteristics of each reaching condition. Not surprisingly, R2 values for visually-guided trials (Fig. 1A) did not increase in the later stages (i.e., 50% and 75% of MT) of the reaching trajectory, indicating that the participant used direct visual input from the aiming environment for feedback-based corrections to their reaching trajectory. In contrast, the 0- (Fig. 1B) and 5-second (Fig. 1C) conditions exhibited robust R² values later in the movement trajectory (i.e., 50% and 75%). The magnitude and strikingly similar R² values associated with the 0- and 5-second delay conditions indicate that the movement endpoints for memory-guided reaching movements are largely determined by central planning processes operating in advance of movement onset. In other words, a visual control representation was not accessed for on-line control processing of very brief (0-second) or prolonged (5-second) delay intervals. These data are inconsistent with the PCM's position that a stored visual representation plays an important role in on-line reaching control when direct visual input is unavailable from the aiming environment.

Finally, although Glover presents a barrage of data supporting the PCM, both anatomically and behaviourally, our demonstration of the absence of a viable store for use by on-line control systems should not be surprising. According to the PCM representation view, brief delay conditions should behave in a very similar fashion to fully closed-loop conditions (i.e., full vision) – illusory bias should be corrected immediately based on the held veridical account of space. This prediction is at odds with a significant number of empirical papers demonstrating that illusory vigilance increases immediately upon removal of vision (e.g., Binsted & Elliott 1999; Westwood et al. 2000c).

ACKNOWLEDGMENTS

This work was supported by the Natural Sciences and Engineering Research Council of Canada, and the Canada Foundation for Innovation (Binsted); and by a Bell/Updyke Kinesiology Research Grant (Heath).

Defining visuomotor dissociations and an application to the oculomotor system

Bruce Bridgeman

Department of Psychology, University of California, Social Sciences 2, Santa Cruz, CA 95064. bruceb@cats.ucsc.edu http://psych.ucsc.edu/Faculty/bBridge.shtml

Abstract: The perception/planning—control conception has a direct predecessor in a cognitive/sensorimotor scheme, where the cognitive branch includes Glover's perception and planning functions. The sensorimotor branch corresponds to Glover's control function. The cognitive/sensorimotor scheme, like the perception/planning—control scheme, differentiates between motor planning and direct motor control, which is inaccessible to awareness or to long-term memory.

Distinguishing planning from control in visuomotor function is a useful step in interpreting the relationships between vision and action, but it is not a new step. Following the terminology of Paillard (1987), Bridgeman (1991b), and Bridgeman et al. (1997) divided visual perception, planning, and control into a cognitive and a sensorimotor pathway. The cognitive pathway groups to-

gether Glover's perception and planning functions, while the sensorimotor pathway corresponds to Glover's control function. In this context, Glover's additional contribution is a differentiation of the cognitive pathway into perceptual and action planning functions (Fig. 1).

The cognitive/sensorimotor mapping is consistent with Glover's demonstration that it is essential to differentiate planning, on the one hand, from control, on the other. In the cognitive/sensorimotor scheme, perception and planning are grouped into a single "cognitive" function because they share several key features. Both work over the long term, relying on memory to organize their content, and both rely strongly on context, thus exploiting the great power of contextual information but becoming vulnerable to visual illusions and to relatively slow operation. And both engage awareness, in the sense that a person can verbally describe their content in the present and in the past. That is, a person can describe both perceptions of the outside world and plans for action. The participation of the cognitive system in motor planning was made explicit: "It is at the cognitive level that symbolic decisions such as button pressing or verbal response are mediated" (Bridgeman et al. 1997, p. 457).

The sensorimotor or control function, in contrast, operates only in the here-and-now, without sensitivity to context, but it is therefore invulnerable to illusions. Unlike the cognitive function, it manages real-time control of muscles without conscious awareness. During a complex action we are profoundly unaware of which muscle units, or even which muscles, are active, to what degree, and in what order. Further, this brain mechanism possesses a quantitative calibration of position that is unavailable to perception.

Further empirical studies have clarified this distinction: Apparently, the cognitive system can inform the sensorimotor system about which of two possible targets to approach, and the sensorimotor system can use its own egocentrically calibrated spatial information to guide the movement (Bridgeman et al. 2000, pp. 3549–50)

These two systems were first differentiated in the context of saccadic suppression (Bridgeman et al. 1979), and later in the context of induced motion (Bridgeman et al. 1981). Both of these methods, though, involved motion, and could also be interpreted as cognitive and motor systems picking up different spatial values from early vision at different times. The static Roelofs effect promised to more cleanly separate the two systems (the Roelofs effect is not a motion illusion, as Glover asserts). In the experiments, a static rectangular frame offset from the observer's centerline induces a misperception of a target's position in the direction opposite the frame's offset (Bridgeman 1991a). This is really a newly described, induced Roelofs effect. Nearly all observers show a large Roelofs effect in perception, but they point accurately to the target regardless of frame position (Bridgeman et al. 2000). Recent work, in collaboration with Paul Dassonville, has shown that the unconscious sensorimotor system has no visual map in this case, but possesses just what is missing from the cognitive system – a representation of the observer's own centerline, calibrating visual with personal space (Dassonville et al., in press).

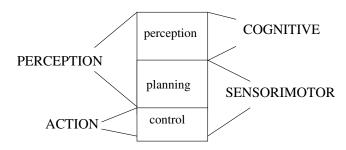


Figure 1 (Bridgeman). Three ways of parsing perception, planning, and control functions.

The cognitive/sensorimotor distinction or Glover's three-part distinction can be applied to the oculomotor system, as Glover notes. A first step in this analysis is to differentiate planning and control functions in the oculomotor system. Somewhat surprisingly, the planning function is very limited in the oculomotor system – of all the types of eye movements, only saccades, and only some of them, engage the planning function. All other movements, including vergence, pursuit, and optokinetic movements, are under real-time control of the visual stimulus and do not require planning. Saccades of the fast phase of optokinetic and vestibular nystagmus are also executed without intevention of a planning system. Voluntary saccades can be planned, but are usually executed in connection with the directing of attention.

Vision can be used to plan action, to execute action, or just to store information for future use. In the latter case, activities such as reading have a goal of collecting information about the world, rather than driving behavior directly. The sensorimotor interactions of reading involve the oculomotor system in the service of collecting information, not doing things to objects or moving through the world.

Using the same information for planning and control is compatible with the dynamic illusion effect

Anne-Marie Brouwer^a, Eli Brenner^b, and Jeroen B. J. Smeets^b

http://www.eur.nl/fgg/neuro/people/smeets/

^aMax Planck Institute for Biological Cybernetics, 72076 Tübingen, Germany; ^bDepartment of Neuroscience, Erasmus MC, 3000 DR Rotterdam, The Netherlands. anne-marie.brouwer@tuebingen.mpg.de e.brenner@erasmusmc.nl j.smeets@erasmusmc.nl http://www.kyb.tuebingen.mpg.de/~brouwer/ http://www.eur.nl/fgg/neuro/research/brenner/

Abstract: We argue that one can explain why the influence of illusions decreases during a movement without assuming that different visual representations are used for planning and control. The basis for this is that movements are guided by a combination of correctly perceived information about certain attributes (such as a target's position) and illusory information about other attributes (such as the direction of motion). We explain how this can automatically lead to a decreasing effect of illusions when hitting discs that move in an illusory direction, and when grasping objects of

which the apparent size or orientation has been changed by an illusion.

It is likely that more aspects of the available visual information are used to plan a movement than to control it. There are many attributes that normally cannot change during the short time that the movement is executed, such as the colour of a piece of fruit. Movements, therefore, usually need not be adjusted to such information. In this sense we agree with Glover that there are probably differences between the use of information for planning and for controlling movements. However, we doubt that the difference is more fundamental than this. In this commentary we argue that it is not necessary to assume that there are different visual representations for planning and control in order to explain the decreasing effect of illusions during human movements.

When participants grasp objects that are presented in illusion-inducing contexts, the effect of the illusion on the movement appears to decrease over time. Glover argues that this dynamic illusion effect is caused by the increasing influence of on-line control (using information about the target that is independent of the context), which eliminates the errors that are made when the movement is planned (using context-dependent information). Recently, we found a very clear decreasing effect of an illusion within a study in which participants hit discs that moved downwards across a structured background on a screen (Brouwer et al. 2003). The background could move to the right or the left, or it could remain static. A moving background affects the perceived direction of the

target's motion (Smeets & Brenner 1995b). In accordance with the misperceived direction, we observed an effect of background motion on the direction in which the participants' hands started to move. This effect of the illusion had disappeared by the end of the movement, as indicated by a lack of effect of background motion on the hitting error.

Although this dynamic illusion effect is consistent with Glover's model, it can also be explained without assuming that different sources of information are used in the planning and the control phase of the movement. The basis for this explanation is the observation that the illusion does not affect the target's apparent position (Smeets & Brenner 1995b). We propose that participants use the same (misjudged) direction information and (correct) position information for planning and controlling the movement. If this information is used to extrapolate the target's movement during the time until impact, there will be a large effect of the illusion at the start of the movement, because the trajectory of the target that has to be extrapolated is still long. Near the end of the movement, the effect of the illusion will be negligible, because there is only a short distance from the most recent (correctly) perceived position across which the target's trajectory has to be extrapolated.

To illustrate how continuous extrapolation results in a dynamic illusion effect, we simulated the lateral movement of a hand hitting three moving discs. One disc moved straight down, one disc moved at an angle of 9.5 degrees from the vertical, and one disc moved straight down but had an illusory direction of motion of 9.5 degrees. For the latter case, as illustrated in Figure 1A, a new prediction is made at every point in time, based on the present target position and the (in this case, incorrectly) perceived direction of motion. We assume that the hand always moves straight towards the most recent prediction of the disc's final position. The resulting directions of hand movement are shown in Figure 1B. If the disc's direction of motion is perceived correctly, the predicted final position of the disc is correct from the moment that the hand starts to move; thus, the hand follows a straight path to that position. If the disc moves straight down but appears to move in a different direction, the hand follows a curved path. Figure 1C depicts the strength of the illusion according to the scheme of Glover and colleagues. This is the ratio between the effect of a disc that is actually moving at an angle of 9.5 degrees and the effect of a disc that only seems to move at an angle of 9.5 degrees (both relative to the vertical). At the start of the movement, the lateral movements of hands hitting these discs are very similar. During the movement, the lateral position of the hand hitting the disc with the illusory direction moves toward that of the hand hitting the disc that is (correctly) perceived to move straight down.

Examples of a dynamic effect of illusion on action that were provided to support Glover's model (cf. target article; Glover 2002), are focused on grasping: grasping the central disc in the Ebbinghaus illusion (Glover & Dixon 2002a), the central bar of the Müller-Lyer illusion (Westwood et al. 2000c; 2001b), and a bar affected by an orientation illusion (Glover & Dixon 2001a; 2001b). These results can also be explained without assuming that different information is used for planning and control if one realises that related physical attributes (such as a target's size and the positions of its edges) might be processed independently (Smeets et al. 2002).

To explain the dynamic illusion effect for the examples above, we can look at the predictions of a model for grasping (Smeets & Brenner 1999; 2001). This model describes the movement of the digits by the intended contact positions, which are assumed to be perceived correctly, and the approach parameter, which describes how much of the digits' final trajectories is orthogonal to the surfaces around the intended contact positions. The approach parameter increases with required accuracy. A larger approach parameter results in a larger maximum grip aperture.

Smeets et al. (2003) have demonstrated that the influence of the Ebbinghaus illusion on grasping could be caused by considering the grasp to require a higher accuracy (and therefore to have a larger approach parameter) if the target circle is surrounded by small circles than if it is surrounded by large circles. The dynamic