

also implemented in separate neural structures running on the basis of different internal representations. Although Glover's model is remarkably successful in accounting for a large body of data, it seems to us that other results remain problematic in the light of a sharp planning/control distinction.

One of us (Battaglini) has described arm-movement related neurons in area V6A of the macaque superior parietal lobe (SPL). Comparing neural activity with arm electromyographic recordings clearly showed that several of these neurons discharged prior to the onset of movement (Galletti et al. 1997b). Further analyses suggested that as many as 30% of these V6A neurons may be activated before the onset of a reaching movement (Fattori et al. 2001). In a lesion study, small bilateral lesions in the same area (V6A) of the green monkey produced deficits in fast, ballistic reaching and grasping. When presented with food (raisins) at specific egocentric distances, in initial trials, lesioned monkeys misreached the targets several times and only in later trials reached correctly from the start. Moreover, lesioned monkeys failed to generalize their training to other egocentric distances, as one would expect if they suffered from a planning deficit (Battaglini et al. 2002a; 2003). Contrary to Glover's predictions for humans, these data suggest that the monkey SPL may be involved in both planning and control. Although these results may reflect functional differences between the human and monkey brain structures (but see Galletti et al. 1997a), in EEG studies of reaching in humans Battaglini also found a clear activation at the SPL before the onset of movement (Battaglini et al. 2002b). These findings suggest that Glover's identification of the human SPL as the site of on-line control may be too schematic.

Similarly, human studies from the second of our laboratories (Bruno) may be interpreted as evidence that Glover's conception of the internal representations used by planning and control is also too schematic. In a study of bimanual, fast reaching to the endpoints of a surface subjected to Kanizsa's compression illusion (Bruno & Bernardis 2002), Bruno measured performance in two motor conditions. In the first of these conditions, blindfolded actors extended their arms until their hands were in the position where they had seen the endpoint of the surface. Results showed no hints of compression, although visual discrimination data showed the usual 5% compression reported in previous studies (Kanizsa 1975). Given that these actions were performed quickly and without visual feedback, in the planning-control framework they should have reflected a greater influence of the "cognitive" representations used for planning. However, the results failed to show the "cognitive" effect of the illusion. Even more convincingly, in a second condition actors simply placed their hand in front of their chest, in spatial alignment with the surface endpoint, without extending their arms completely. Given that this second action corresponded to the early part of bimanual reaching, in the planning-control framework it should have reflected an even greater influence of the cognitive representation. However, the results again failed to show any cognitive effect. In fact, there was no difference with the full reaching condition. Comparable results were found in a pointing study, which also generalized them to a variant of Müller-Lyer's illusion (Bruno & Bernardis 2003).

Can the motor system utilize a stored representation to control movement?

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Abstract: This commentary focuses on issues related to Glover's suppositions regarding the information available to the on-line control system and the behavioral consequences of (visual) information disruption. According to the author, a "highly accurate," yet temporally unstable, visual representation of peripersonal space is available for real-time trajectory corrections. However, no direct evidence is currently available to support the position.

Glover's planning-control model (PCM) suggests that an unfolding visual representation (of the aiming environment) gradually assumes control of goal-directed action. Certainly, this view is consistent with a number of investigations suggesting that "control" builds throughout the time-course of visually-guided movements, culminating in a smooth transition between preplanned and on-line control processes (Elliott et al. 1999; Heath et al. 1998). But what happens to on-line control processes when vision of the aiming environment is occluded at some point prior to the movement (i.e., so-called memory-guided reaching movements)? Glover's PCM assumes that a visual representation persists and is available to the motor system to rapidly modify the *memory-guided* reaching trajectory. Because this visual representation is assumed to be transient in nature, delays of greater than two seconds purportedly lead to near-complete decay of the visual representation, resulting in an action executed *without the benefit of on-line control*. The inference here is that a stored visual representation may serve as a valid, albeit temporally unstable, spatial referent for executing (error-nullifying) corrections to the movement (<2-seconds delay). Undoubtedly, this account of the PCM is rooted in Elliott and Madalena's (1987) position that "highly accurate" sensory information about the aiming environment is available for "on-line error reduction during the movement." Specifically, Glover suggests that:

movements made after delays much longer than two seconds will be executed entirely 'as planned' (i.e., without the benefit of on-line control). (target article, sect. 1.1.3, para. 5)

The notion that a stored, visual representation of the aiming environment is available for "on-line error reduction" represents an intriguing possibility; we wonder, however, whether there is empirical evidence to support this view. Indeed, our examination of the memory-guided reaching literature indicated that it is largely unclear whether stored visual information about the aiming environment is used for movement planning, on-line movement control, or both. This primarily reflects a limitation of previous work and emphasis on the endpoint characteristics of memory-guided reaches (e.g., Elliott 1988; Elliott & Madalena 1987; Westwood et al. 2001a; 2003); no direct evidence (i.e., movement corrections or kinematics) is available to support the position that stored target information is used for on-line movement control following brief delays. Hence, the reported residual accuracy of memory-guided reaches might simply reflect the use of a stored representation of the aiming environment for movement planning processes; that is, stored information is not used for error-nullifying limb/target corrections – regardless of the length of the memory delay (Flanders et al. 1992; Plamondon 1995).

In an attempt to reconcile this issue, we (Heath & Binsted 2003), present very recent data in which participants (N=15) completed a number of reaching movements (450) to three mid-line targets (20, 30, 40 cm) in three visual conditions: a visually-guided one and two delay intervals (0 and 5 seconds of delay, respectively). To infer movement control, we implemented a

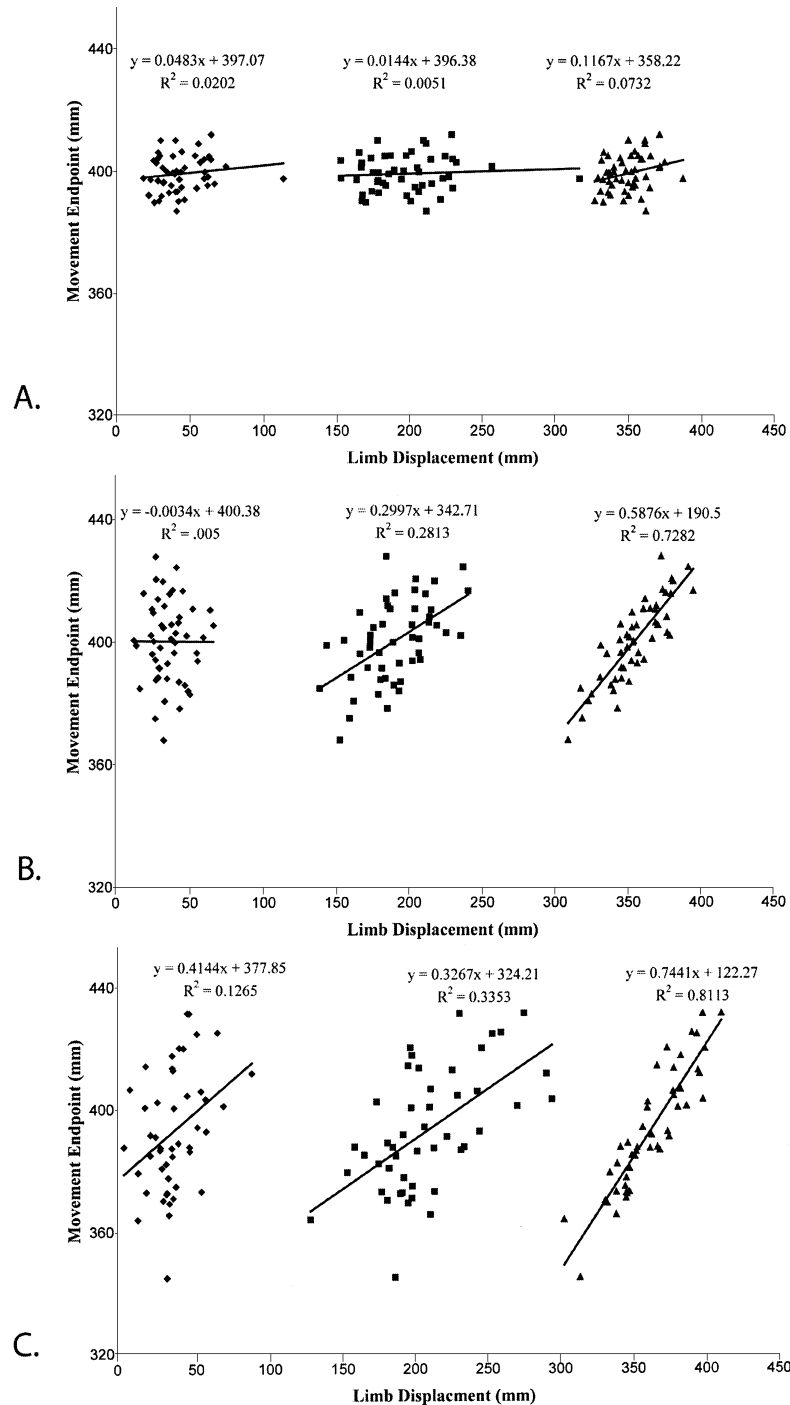


Figure 1 (Binsted & Heath). Predictability of movement endpoint from mid-trajectory limb positions. The proportion of endpoint variance (R^2) in movement endpoints (primary movement axis) explained by the limb position at three positions (25% \diamond , 50% \blacksquare , and 75% \blacktriangle of movement time) is presented for an exemplar participant. Note that R^2 in Full Vision trials (Fig. 1A) do not increase in the later stages of the trajectory (50% and 75% of MT). In contrast, 0-second (Fig. 1B) and 5-second (Fig. 1C) delay trials demonstrate larger R^2 values later in the movement trajectory.

regression analysis to examine the proportion of variability (R^2) in endpoint position that can be explained by the position of the limb at early (25% of movement time [MT]), middle (50% MT), and later (75% MT) stages of a reaching trajectory (see also Heath et al. 2004). We reasoned that if the motor system used on-line control processes, early undershooting or overshooting errors should be detected and eliminated by adjusting the later reaching trajectory. As a result, position of the limb during the middle and latter stages of the reaching trajectory need not predict the ultimate

movement endpoint. According to the PCM, visually guided reaches and the 0-second delay condition should demonstrate such a pattern of results. Either direct visual input from the aiming environment would serve as the basis for executing corrections or a stored visual control representation would provide the basis for on-line and feedback- and feedforward-derived, corrections to the reaching trajectory. Conversely, if movements are executed without on-line control, then the limb trajectory should unfold according to a programmed spatiotemporal pattern; the final posi-

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, R^2 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 R^2 values later in the movement trajectory (i.e., 50% and 75%). The magnitude and strikingly similar R^2 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).

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Defining visuomotor dissociations and an application to the oculomotor system

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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).

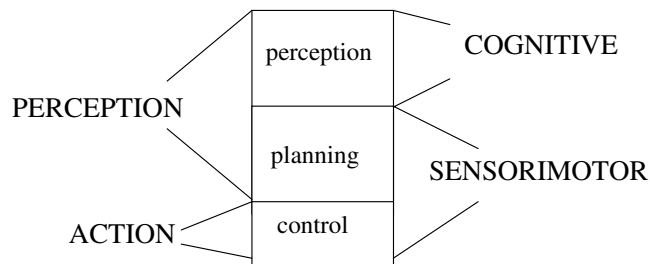


Figure 1 (Bridgeman). Three ways of parsing perception, planning, and control functions.