

other object. Contrary to this prediction, Flanagan and Beltzner (1999) showed that a perceptual size-weight illusion (in which a larger object is consistently judged to weigh less than an equally massive but smaller object) does not influence the scaling of grip and load forces when the target objects are lifted a few times. This was true for force measurements taken well before proprioceptive and haptic feedback loops could modulate the grasping forces – in other words, the measured forces must have been programmed well in advance of contact with the object. In a similar vein, Westwood et al. (2000b) showed that a pictorial size illusion affected the perceived size of target objects, but not the force with which the objects were grasped when they were lifted. Importantly, all of the objects in that experiment had the same mass. Clearly, cognitive judgments about object size and mass are not always taken into account when programming grasping forces.

Grasping remembered objects: A rapid transition in control.

Glover suggests that a “control” representation of the target object gradually fades from memory when vision is taken away, leading to an increased influence of a “planning” representation for actions made to remembered objects. We have shown in several studies that the effects of pictorial illusions on action are exquisitely sensitive to the time at which vision of the target object is removed. In one recent study (Westwood & Goodale 2003) we show that a size-contrast illusion does not influence grip aperture when the target is visible during the reaction time interval, even if vision is removed at movement onset. However, the illusion reliably influenced grip aperture when vision was removed during the reaction time period (i.e., for the 250 msec between response cueing and movement onset). This finding is difficult to reconcile with a gradual transition from a “control” to a “planning” representation when vision of the target object is removed. The data are more consistent with a “real time” view of visuomotor programming in which retinal information about the target object is converted into a calibrated motor program at the time the action is actually required. Movement planning that takes place before this time likely accesses a visual representation of the target object that is laid down by the perceptual mechanisms in the ventral visual pathway (Goodale et al. 2004).

The “dynamic illusion effect”: A methodological illusion?

The key piece of evidence in favour of the PCM is the finding reported by Glover and Dixon (e.g., Glover & Dixon 2001a) that visual illusions have a greater influence on movement kinematics that occur earlier rather than later in the movement. Glover uses a *scaled illusion effect* to demonstrate this phenomenon. The scaled illusion effect is simply a ratio of the illusion’s absolute effect on a movement parameter (I) divided by the effect of a veridical change in an object’s features on the same movement parameter (O); this measure is calculated for a number of temporal points throughout the movement duration. Glover argues that this ratio is necessary to take into account the fact that visual object features do not have a constant influence on movement kinematics during execution: For example, the slope of the psychophysical function relating object size and grip aperture increases monotonically throughout the course of a grasping movement. When scaled illusion effects are plotted as a function of relative movement duration, Glover reports a gradual decrease over the course of the movement. This is interpreted as evidence that a “control” system that is impervious to visual illusions corrects spatial errors introduced by a “planning” system that is quite sensitive to visual illusions. The problem with this type of analysis is that the same effect would be obtained even if the absolute effect of the illusion were to remain stable over time (or even increase slightly), because of the monotonically increasing term in the denominator of the ratio. In this case, one would surely not wish to conclude that an illusion effect was being corrected as the response unfolded! If the PCM is correct, one should be able to demonstrate statistically that the absolute illusion effect decreases over the duration of the action. Such proof has not been provided in many of Glover’s key experiments. Moreover, at least one recent study has looked for but failed to find such statistical evidence (Danckert et al. 2002).

Summary. There is little empirical support for the notion that

separate visual representations underlie the planning and control of manual actions. Indeed, there is no good theoretical reason to suppose that separate representations would be necessary in the first place.

Planning differences for chromaticity- and luminance-defined stimuli: A possible problem for Glover’s planning–control model

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Abstract: We report data from an experiment using stimuli designed to differ in their availability for processing by the dorsal visual pathway, but which were equivalent in tasks mediated by the ventral pathway. When movements are made to these stimuli as targets, there are clear effects early in the movement. These effects appear at odds with the planning–control model of Glover.

The interpretation of the ventral and dorsal visual processing streams (first identified by Ungerleider & Mishkin [1982]) as “what” and “how” systems, respectively (Milner & Goodale 1995), marked a turning point in understanding the functional role of this anatomical distinction. In his target article, Glover provides a compelling summary of the evidence supporting the planning–control model. By suggesting that initial planning and current control are functions of different parts of the parietal cortex, Glover’s model gives substance to a distinction first introduced by Woodworth (1899). Equally important, this model marks another stage in our developing understanding of the ventral-dorsal distinction.

Our aim in this commentary is to describe data, recently collected using a new procedure (Wright et al., submitted), which appears inconsistent with the planning–control model. Our goal in this experiment was not to test the planning–control model. Instead, the objective was to assess the relative sensitivity to luminance- versus chromaticity-defined targets of “how” tasks, in which the goal is to produce a movement to an object, and “what” tasks, in which the goal is to perceive some aspect of an object.

The impetus for this experiment was the what-how distinction (Milner & Goodale 1995) and a long line of evidence suggesting reduced color sensitivity in the dorsal stream. Although the evidence is far from clear-cut, it appears that the dorsal visual stream receives direct inputs from only the magnocellular pathway. In contrast, the ventral stream appears to receive projections directly from both pathways. Livingstone and Hubel (1988) have argued that these two channels differ physiologically in four major ways: color sensitivity, temporal resolution, contrast sensitivity, and acuity. Specifically, they suggest that the parvocellular system is highly color selective but the magnocellular system does not code color differences.

In one procedure of our experiment, subjects had to identify briefly presented, masked stimuli as one of four shapes. A given target was defined relative to the gray background by a difference either in luminance or in chromaticity. Luminance-defined targets had the same hue and saturation as the background, whereas saturation-defined targets were green and equiluminant with the background. Various luminances and saturations were used to define targets.¹ The results from this procedure identified levels of luminance and saturation that produced equivalent levels of performance in this identification (“what”) task.

In a second procedure, matched gray and green stimuli were used to define targets for rapid, high-accuracy, three-dimensional pointing movements. Consistent with our expectations, movements to green targets took longer and had larger endpoint errors

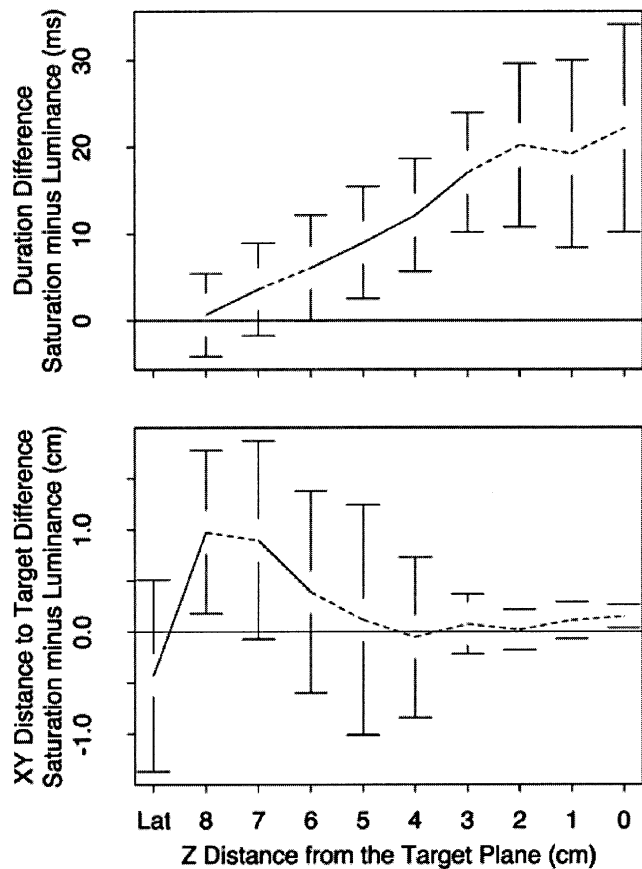


Figure 1 (Wright & Chubb). This figure summarizes differences in the trajectories of movements to matched gray and green targets based on more than 4,000 movements (~500 each for eight participants). The two panels of this figure share the same abscissa: Z distance. Z distance is the (perpendicular) distance separating the stylus (being moved by the subject) from the plane of the display containing the target. The movements begin with Z=10 cm and end with Z=0 cm, so decreasing values of the abscissa progress from the start of the movement (on the left) to the end (on the right). The ordinate in the upper panel is the mean difference (when pointing to green minus when pointing to gray targets) in the time required to reach the Z-distance given in the abscissa (with time measured from the start of the movement). The ordinate in the lower panel is the mean difference (when pointing to green minus when pointing to gray targets) in the X-Y distance (i.e., ignoring the Z dimension) of the stylus from the target point. This panel also includes a data point on the far left of the abscissa, labeled “Lat,” which shows this difference at the instant the movement began. The “Lat” point is absent in the upper panel because, by definition, movement duration is zero at this point in both conditions. In both panels, the error bars show 95% confidence intervals, computed based on the between-subject variability of that measure at that point. Points joined by solid lines differ at the .05 level of significance based on a paired *t*-test.

than movements to matched gray targets. This result is consistent with both the perception–action model (Milner & Goodale 1995) and the planning–control model outlined by Glover. To use this result to distinguish between these two models, we can, as Glover suggests, look at the full movements and not just their endpoints. Figure 1 displays the results of such an analysis.

We used targets defined by either their luminance or their chromaticity in this experiment, because the literature on the magnocellular versus parvocellular distinction suggests that there should be large differences in dorsal- but not ventral-stream sensitivity

for these stimuli. The planning–control model, as we understand it, suggests that the visual inputs to the movement planning process pass primarily through the ventral stream and therefore should not be affected by this manipulation. To reach this conclusion, we assume that the sensitivity of the movement-planning system to luminance- and chromaticity-defined target stimuli is roughly equal to the sensitivity of the system used to perform our shape identification (“what”) task.

The results shown in Figure 1 clearly contradict this expectation. For duration, the difference between the green and gray stimuli is evident one-third of the way into the movement and continues to grow until roughly two-thirds of the movement is complete. The difference in the XY-distance to the target starts out large and then falls to zero midway through the movement. At the end of the movement, however, a small but significant effect re-emerges.

A major contribution of the planning–control model is bringing the planning/control distinction, long central to the motor-control literature, into this arena. Although our results appear at odds with the predictions of the planning–control model, given the number of assumptions necessary to arrive at this conclusion, we hesitate to assert that they clearly contradict the model. The general approach that gave rise to these data is, however, one that we feel merits further exploration for the light it can shed on this and related questions.

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NOTE

1. Equiluminant greens differing in saturation were determined for each subject using a flicker-fusion procedure.

Planning and control: Are they separable in the brain? *Entia non sunt multiplicanda praeter necessitatem*

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Abstract: We argue that planning and control may not be separable entities, either at the behavioural level or at the neurophysiological level. We review studies that show the involvement of superior and inferior parietal cortex in both planning and control. We propose an alternative view to the localization theory put forth by Glover.

The distinction between planning and control has a long-standing history in neuroscience and robotics. It hinges on a scheme of serial organization of motor functions. For robotics, the separation may be justified by algorithmic and implementation constraints. In neuroscience, uncontroversial experimental evidence for separate neural implementation of planning and control is still lacking. Current notions favor the opposite view, that movement is organized over massively parallel distributed networks with coextensive and sometimes simultaneous processing of parameters once deemed to belong exclusively to either the planning or the control stage (Burnod et al. 1999; Kalaska et al. 1998; Lacquaniti 1997).

Psychophysics. Glover claims that the planning stage incorporates both spatial and nonspatial motor goals, whereas control deals only with spatial goals. His theory predicts that “the motor system should not be able to make a fast change to the force used in lifting the object, as this relies on a new computation of weight (a nonspatial characteristic)” (sect. 2.4.4). In fact this prediction is