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Separate visual representations in the planning and control of action

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Abstract: Evidence for a dichotomy between the planning of an action and its on-line control in humans is reviewed. This evidence suggests that planning and control each serve a specialized purpose utilizing distinct visual representations. Evidence from behavioral studies suggests that planning is influenced by a large array of visual and cognitive information, whereas control is influenced solely by the spatial characteristics of the target, including such things as its size, shape, orientation, and so forth. Evidence from brain imaging and neuropsychology suggests that planning and control are subserved by separate visual centers in the posterior parietal lobes, each constituting part of a larger network for planning and control. Planning appears to rely on phylogenetically newer regions in the inferior parietal lobe, along with the frontal lobes and basal ganglia, whereas control appears to rely on older regions in the superior parietal lobe, along with the cerebellum.

Keywords: action; apraxia; control; illusions; optic ataxia; PET; planning; reaching

1. Introduction

This article explores the evidence for a distinction in human performance between the planning and on-line control of actions. The planning–control model is put forth as an explanation for human action production. A review of studies from healthy subjects reveals differences between the visual and cognitive processes involved in planning and control. Brain imaging studies support the dichotomy, in that planning in humans is linked with activity in a distributed network including a visual representation in the inferior parietal lobe (IPL), whereas control is linked with activity in a separate network including a visual representation in the superior parietal lobe (SPL). Studies of brain-damaged populations also support the thesis that separate brain regions support planning and control, respectively. A review of evidence from brain and behavior studies suggests that the planning–control model provides an account of the data better than a model based on a distinction between perception and action (Milner & Goodale 1995).

1.1. The planning–control framework

Woodworth (1899) was the first to propose a distinction between the planning and control stages of action, based on his seminal study examining the use of visual feedback in on-line control. Since Woodworth's time, the distinction between planning and control has been the subject of much investigation (e.g., Beggs & Howarth 1970; 1972; Carlton 1981; Fitts 1957; Keele 1968; Meyer et al. 1988; Vince 1948; see Elliott et al. 2001, for a review), and the existence of these two stages has generally become accepted as an underlying principle of human motor behavior (Jeannerod 1988; Rosenbaum 1991).

We have expanded on the planning and control distinction (Glover 2002; Glover & Dixon 2001a; 2001b; 2001c; 2002a; 2002b; Glover et al. 2004) to include separate visual representations in each stage of action. In our "planning–control" model, body movements are selected and executed by means of two temporally overlapping systems. Prior to a movement's initiation, a motor program is selected based on a broad range of cognitive factors coupled with a visual "planning" representation in the IPL. During execution of a movement, the action comes increasingly under the influence of a "control" system, using a limited but quickly updated visual representation in the SPL, coupled with visual and proprioceptive feedback, and an efference copy of the movement plan.

1.1.1. The need for separate planning and control systems. In the planning–control model, the planning system generally operates prior to a movement, whereas the control system operates during execution. The quasi-separa-

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tion of these two stages is hypothesized to reflect the need of each system to fulfill distinct purposes. For planning, the requirement is to select an adaptive motor program given the environment and the goals of the actor. This will depend on a number of factors related to the object of the action, the surrounding environment, and the internal state of the actor. Conversely, for control, the requirement is the minimization of the spatial error of the movement. This requires a relatively simple but quickly updated analysis of the spatial characteristics of the target and actor. The next two sections expand on the characteristics of the planning and control systems.

1.1.2. The planning system. The planning system has the goal of selecting and initiating an adaptive motor program, given the environment and the goals of the actor. At a high level, planning is responsible for such things as selecting an appropriate target, or choosing to grasp an object in a certain manner. Beyond these selection processes, however, planning also determines the initial kinematic parametrization of the movements, including their timing and velocity.

To fulfill its aims, planning must take into account a wide variety of visual and cognitive information. This information can be classified into four basic aspects of the environment and actor: (1) the spatial characteristics of the actor and the target, including such things as the size, shape, and orientation of the target, as well as the spatial relations between the actor and the target; (2) the nonspatial characteristics of the target, including such things as its function, weight, fragility, and the coefficient of friction of its surfaces; (3) the overarching goal(s) of the action; and (4) the visual context surrounding the target. This information is integrated with memories of past experiences (cf. Rosenbaum et al. 1995). Table 1 lists object characteristics important for action as belonging to either the spatial or nonspatial class, as well as the movement parameters most dependent on each characteristic. The position of the effector is always considered to be a spatial characteristic.

It is important to point out that nonspatial object characteristics are not entirely visual. That is, whereas the spatial characteristics of objects tend to be geometric properties that can be gleaned from low-level visual processes alone, the nonspatial characteristics invariably necessitate reference to stored memories. For example, knowing that a tomato is more fragile than an apple requires that each be identified and that these properties be called up from memory. The identification process may require the incorporation of spatial information, such as the target's shape and size, with other information such as color. Similarly, knowing that an iron bar is heavier than a wooden bar of the same size requires not just being able to identify the material, but also to judge the similarity in size of the two objects. Thus, an integration of spatial characteristics with information about an object's identity is usually required to compute a nonspatial characteristic. However, the reverse is not also true: Nonspatial characteristics are not required to compute spatial characteristics.

Table 1. Spatial and nonspatial object characteristics

Spatial	Most salient effect	Basic reference
Orientation	Hand orientation	Jeannerod (1981)
Position	Hand trajectory	Jeannerod (1981)
Shape	Hand shape	Klatzky et al. (1995)
Size	Grasping aperture	Jeannerod (1984)
Velocity	Hand trajectory	Brenner et al. (1998)
Nonspatial	**Most salient effect**	**Basic reference**
Fragility	Grasping force	Klatzky et al. (1989)
Function	Hand shape	Klatzky et al. (1987)
Temperature	Grasping force?	—
Texture	Movement time	Fikes et al. (1994)
Weight	Grasping/lifting force	Gordon et al. (1991)

As mentioned, the planning system specifies the majority of the macroscopic and microscopic aspects of the action before initiation. Specifically, planning is responsible for: selecting the target; for all movement parameters relating to nonspatial target characteristics; for the initial determination of the movement parameters relating to spatial target characteristics (although these can be modified on-line by the control system); for determining the timing of movements (including reaction times, movement times, and acceleration/velocity parameters); and for the selection of macroscopic (i.e., postural) aspects of the movement.

The integration of such a broad range of information and the computation of a broad range of movement parameters by the planning system requires a relatively long processing time. Further, these varied sources of information can interact, sometimes interfering with the selection of adaptive motor programs. For example, contextual figures can induce visual illusions (Coren & Girgus 1978; Gregory 1968) that will impact the computation of both spatial and nonspatial target characteristics in the planning system. This means that visual illusions will have large effects on spatial parameters early in a movement, and large effects on nonspatial parameters over the entire course of the movement. Further, as planning relates closely to cognitive processes, the planning representation will rely on and be subject to interference from processes such as language and memory. Again, interference effects of these variables will be evident when they interact with the computation of characteristics of the target. Further, because planning relies on a store of memories of past experiences in selecting an appropriate plan, it will be less able to plan precise movements when the situation is unfamiliar, such as when a novel object is the target, as compared to when the target is familiar or the movement is well practiced. Finally, the interaction of planning with cognitive processes will result in planning being at least somewhat susceptible to conscious influence.

The general operation of the planning system can be illustrated with an everyday example. Imagine an actor with the aim of satisfying his thirst. To achieve this goal, the planning system may select a reach-to-grasp movement directed towards a glass on a shelf. It will first select a glass of an appropriate size depending on how thirsty the actor is (overarching goals). The action of grasping the glass will serve the ultimate purpose of filling it with water and drinking out of it (overarching goals). The planning system will choose to grasp a thin glass with less force than a thick glass because the former is more fragile (nonspatial characteristics of the target). It will determine a path that will avoid contacting obstacles along the way to the glass (visual context). It will plan a fairly accurate movement towards the glass, taking into account its position relative to the effector, its size, its shape, and so forth (spatial characteristics of

the actor and target). Finally, planning will time the movement such that a sufficient period of time is available for the control system to operate. When a motor program is selected that satisfies these constraints, the planning system will determine when to initiate the movement. Once the movement has been selected and initiated, it will come increasingly under the influence of the control system.

1.1.3. The control system. Whereas the planning system is generally adept at selecting an appropriate motor program, given the environment, the control system allows the added benefit of monitoring and occasionally adjusting motor programs in flight. These adjustments are limited to the spatial characteristics of the target, as these are the most likely to change or to be erroneously planned. Specifically, spatial errors may arise either from how the movement was planned (e.g., from interference as a result of cognitive influences), or during execution of the plan (e.g., because of noise in the neuromuscular system). Also, the spatial characteristics of the target may change in unanticipated ways (e.g., a fruit on a branch blowing in the wind). In contrast, the nonspatial characteristics of the target (such as its weight or function) are almost completely unlikely to change after the movement is planned.

The vicissitudes of the spatial characteristics of the actor and target, along with interference from cognitive or perceptual variables, will make it difficult to always plan a spatially accurate movement. Yet this is of little consequence to the overall adaptiveness of the action. This is because the ultimate success of the movement depends much more on how accurate it is at its end, not on how accurate it was when it was planned. In other words, errors in planning can still be corrected given sufficient time; errors in control are much more likely to cause the act to fail.

To ensure that the movement is spatially accurate, the control system requires a quickly computed visual representation. The speed of processing in this representation is gained by limiting it to the spatial characteristics of the target. This control representation is coupled with visual feedback, proprioception, and efference copy (i.e., a "blueprint" of the movement plan obtained from the planning system prior to initiation). The limit of the control representation to spatial characteristics naturally limits its influence to the spatial parameters of the movement. These include such things as grip aperture, hand trajectory, and hand orientation (see Table 1). As planning and control overlap in time, the influence of control on the spatial parameters becomes increasingly larger as the movement unfolds.

Being limited to the spatial characteristics of the actor and target has the benefit of allowing for fast processing and similarly fast on-line adjustments by the control system. Further, the spatial analysis that takes place in the control representation is immune to the interference of such variables as the visual context or cognitive processes. The independence of the control system from such cognitive processes as goal formation and conscious perception also means that control operates outside of conscious awareness and influence.

The visual representation guiding control is transient in nature. This allows for it to be quickly updated as a movement unfolds, but it also means that its memory is of short duration. When visual information regarding the effector or target is removed either prior to or during a movement, the control representation will begin to gradually decay over a period of roughly two seconds (cf. Elliott & Madalena 1987). The decay of the control representation is gradual rather than instantaneous, and during delay periods of less than two seconds, a less dramatic reduction in the influence of control will result (Westwood et al. 2001a). However, when the delay is more than two seconds, the decay will be nearly complete, and movements made after delays much longer than two seconds will be executed entirely "as planned" (i.e., without the benefit of on-line control).

Completing the above example of grasping a glass illustrates the operation of the control system. After the planning system has selected and initiated an appropriate movement directed towards the glass, the control system will be responsible for minimizing any spatial error in the movement itself (spatial characteristics of the target and actor). These might include the scaling of the hand to the size of the glass or the orienting of the wrist to the appropriate angle. Control will generally ignore any objects surrounding the glass (visual context), the intention to use the glass to drink from (overarching goals), and the fragility of the glass (nonspatial characteristics of the target). Put simply, the control system is focused on the on-line correction of the spatial parameters of the action.

1.1.4. The time course of planning and control. As mentioned above, the two stages of action are temporally overlapping (cf. Desmurget & Grafton 2000; Wolpert & Ghahramani 2000; Wolpert et al. 1995; but see Crossman & Goodeve 1983; Meyer et al. 1988). Prior to movement initiation, planning is entirely responsible for the initial determination of all movement parameters, and continues to be highly influential early in the movement. As movements progress, however, the influence of control on the spatial parameters of the action increases. Such a gradual crossover between planning and control systems has the benefit of allowing for smooth rather than jerky corrections (cf. Wolpert & Ghahramani 2000).

As planning is generally operative early in a movement and control late in a movement, the influence of each will rise and fall as the movement unfolds. For example, peak grip acceleration, a size-dependent parameter that occurs at roughly 35% of movement duration (Jakobson & Goodale 1991; Jeannerod 1984), will reflect planning more than control. In contrast, maximum grip aperture, a size-dependent parameter that occurs at roughly 70% of movement duration (Jakobson & Goodale 1991; Jeannerod 1984) will reflect control more than planning. Similar applications can be made to other parameters dependent on spatial characteristics: The orientation of the hand early in a reach should reflect mainly planning, late in a reach it should reflect mainly control, and so forth.

Because control relies to a significant degree on visual and proprioceptive feedback loops, the more time in which these loops can operate, the greater the influence control will exert. That is, whenever actions take longer or shorter than a stereotypical reach-to-grasp movement, the influence of control will be extended or shortened, respectively. In long-duration movements such as manual tracking or catching a long fly ball, for example, almost the entire movement will be under the influence of control. In contrast, for short-duration movements such as keyboarding, practically the entire movement will be executed as planned.

The planning–control model can also be applied to more complex and continuous movements, such as playing tennis

or running over rough terrain. In these movement sequences, planning and control processes would alternate with each other in succession. For example, the intention to swing at a ball in tennis and the initial parametrization of the muscle contractions underlying the swing will be preplanned, whereas the execution of the swing will be controlled on-line. The ensuing movement of rushing towards the net to anticipate the opponent's return will require a different set of muscle movements, and a new plan. The planning of this action may begin even while the control process is monitoring and adjusting the initial swing at the ball. In this way, the planning system can use the times in which control is operating to select and parametrize the next movement in the sequence.

Running over rough terrain would similarly engage both planning and control mechanisms. Whereas each step or series of steps could be preplanned, the execution of the steps would be controlled on-line. Given the difficult nature of the task, and the need to make adjustments based on unanticipated events (such as stepping on a rock that throws the actor off balance), such a task would most likely tax the control system quite heavily. Generally speaking, the more the outcome of a given movement or series of movements is predictable, the more it will rely on planning and the less on control. Conversely, when the consequences of movements are unpredictable, or when unanticipated forces act on the body or target, planning will give way more and more to control processes.

1.1.5. Limitations of the planning–control model. The planning–control model is designed to predict and explain body movements. It is not meant to generalize to eye movements. This limitation is necessary because of the very different constraints that apply to each type of movement. For example, body movements involve complex physical transitions through three-dimensional space. These transitions require consideration of objects in the visual context as potential obstacles. Conversely, eye movements involve relatively simple (in terms of muscle activations) rotations of the eyes in the orbits in which collisions with the visual context are extremely unlikely, if not impossible. Because of these different constraints, the planning–control model is limited to movements of the body, although how eye and body movements are coordinated is undoubtedly an important issue.

1.2. Neural components of planning and control

In the planning–control model, the two stages of action utilize distinct neural networks in the human brain. Planning involves the use of a visual representation located in the IPL, coupled with motor and related cognitive processes in the frontal lobes and basal ganglia. Control, on the other hand, involves a visual representation located in the SPL, coupled with motor processes in the cerebellum.

1.2.1. Evolution of the parietal lobes and a greater separation of planning and control in humans. The evolutionary divergence of humans and monkeys has coincided with a significant relative enlargement of the parietal lobes in humans (Fig. 1). According to the planning–control model, this expansion has allowed humans to integrate a vast array of visual and cognitive information into an action plan. While both planning and control appear to exist (though not necessarily together) in the IPL of monkeys, I contend that in humans planning is largely the province of the phylogenetically newer cortex in the IPL, whereas control is largely the province of the phylogenetically older SPL.

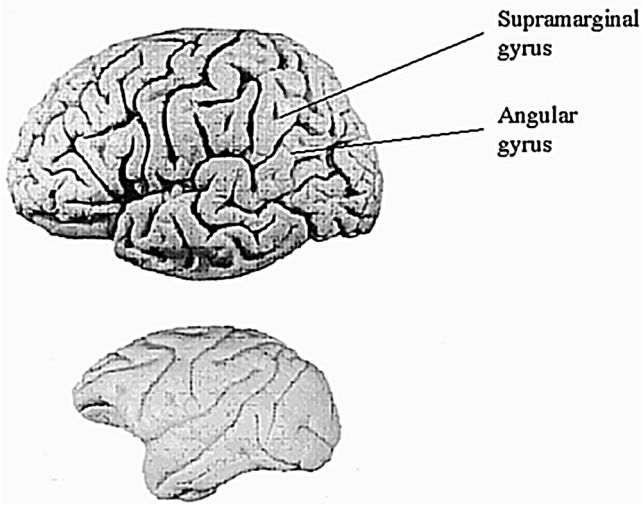

Figure 1. Comparison of the human (top) and macaque (bottom) brains. Cortical surfaces of the left hemispheres of both species are shown. Note the large area of expansion within the parietal lobes of the human brain compared to the monkey. Labeled in the figure of the human brain are the two regions of the parietal lobe unique to humans, the supramarginal and angular gyri. Not to scale.

The role of the human IPL in action planning may have arisen quite recently in evolution and may be manifest in the uniquely human population lateralization in hand preference (Hacean & Ajuriaguerra 1964; Harris 1993; Hopkins 1996). This human hand preference may have evolved from the need to have at least one highly coordinated limb that could accomplish fine unimanual manipulatory acts.

1.2.2. Distinct neural systems subserving planning and control. Figure 2 represents a schematic of the neural bases of planning and control. Prior to a plan being formed, visual input travels to the IPL via the temporal lobe and a "third" visual stream (Boussaoud et al. 1990). The temporal lobe input includes both the spatial (e.g., size, shape, orientation) and nonspatial (e.g., weight, function, fragility) characteristics of a target, as well as the visual context surrounding the target (it is less clear what the third stream contributes). Information relating to the overarching goals of the action is provided by the frontal lobes, and the frontal lobes also exert executive control (i.e., they are heavily involved in selecting the target, and in deciding "what" to do as well as "how" to do it). The visual and cognitive information used in planning is integrated with proprioceptive input from somatosensory association areas in the selection of an appropriate motor plan. Simple movements such as reaching and grasping tend to rely more on the IPL for movement selection and parametrization. Complex movement sequences rely more heavily on frontal lobe sequencing and timing mechanisms.

After a movement has been planned, an efference copy of the plan is forwarded to the SPL and cerebellum. This efference copy represents a "blueprint" of an upcoming action. Once the action is initiated, the control regions begin to integrate visual and proprioceptive feedback with the ef-

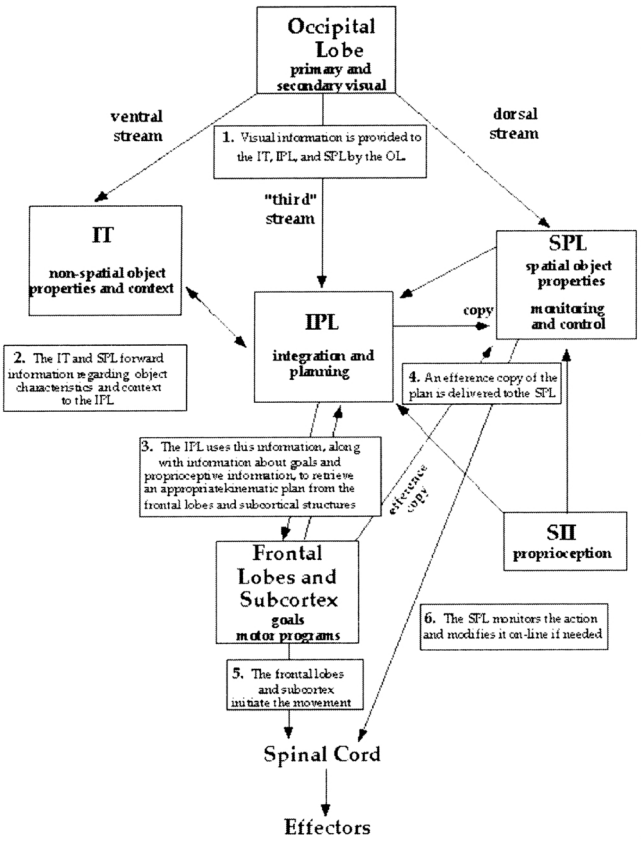

Figure 2. Schematic of the planning–control model showing the hypothesized connectivity and functions of the human visuomotor, cognitive, and somatosensory regions involved in action planning and control. Connections between early visual regions, and between visual and cerebellar regions are putative human homologues of connections in the macaque brain (Boussaoud et al. 1990; Glickstein 2000; Mishkin et al. 1983). Connections beyond the termination of the two streams are based on common activation (see sect. 3).

ference copy to monitor and, if need be, adjust the movement in flight. Monitoring of the body likely involves the SPL more heavily than the cerebellum. Comparing the movement with the motor plan likely involves the cerebellum more heavily than the SPL.

1.3. Comparing the planning–control model to other models of action

Although the distinction between planning and control stages of action has a long history (cf. Fitts 1957; Keele & Posner 1968; Meyer et al. 1988; Woodworth 1899), the planning–control model has several features that make it unique among these and other models of motor control (e.g., Arbib 1981; Desmurget & Grafton 2000; Jeannerod 1988; Milner & Goodale 1995; Wolpert & Gharamani 2000). First and foremost, *only* the planning–control model postulates separate visual representations underlying the two stages of action. Even other models that include planning and control stages make no such distinction (e.g., Desmurget & Grafton 2000; Jeannerod 1988; Wolpert & Gharamani 2000; Woodworth 1899). In pursuance of this, only the planning–control model assigns the inferior and superior aspects of the parietal lobes to their specific roles in computing these visual representations. Second, the planning–control model makes no specific distinction between the information used during reaching versus grasping (as was central to Jeannerod 1988). Third, in assuming a gradual rather than discrete crossover between the two stages of action, the planning–control model differs from at least some (e.g., Crossman & Goodeve 1983; Keele & Posner 1968; Woodworth 1899) models of motor control that assume that control can only begin when feedback loops have had time to close. Similarly to Wolpert et al. (1995; see also Desmurget & Grafton, 2000; Wolpert & Gharamani 2000), the planning–control model suggests that efference copy may be used to adjust movements from any time after initiation.

Throughout the remainder of this article, the planning–control model is contrasted mainly with the perception–action model (Goodale & Milner 1992; Milner & Goodale 1995). This is done partly for the sake of brevity, and partly because the two models are the most readily comparable. The three main differences between these models can be summarized as follows. First, in the planning–control model, the two stages of action utilize distinct visual representations in the IPL and SPL, respectively. Conversely, in the perception–action model, both planning and control mainly utilize representations in the SPL, although certain classes of stored perceptual information may be imported from the "ventral" stream (see e.g., Haffenden & Goodale 2000; Milner & Goodale 1995), and the IPL "third" stream is said to play an important role in spatio-cognitive operations (Milner & Goodale 1995).

Second, the distinct representations in the planning–control model result in interactions between cognitive and visual information in planning but not control, whereas the perception–action model suggests that vision for action should generally be immune to cognitive influences. In particular, the perception–action model suggests that parameters of movement dependent on the spatial characteristics of the target will be both planned and controlled independently of cognitive and perceptual influences.

Third, whereas both models assume a role of nondorsal stream visual areas in target selection, and whereas the perception–action model also holds that some action planning processes require an "interaction" between streams, only the planning–control model assumes that the IPL is involved in the kinematic parametrization of *all* movements, not just those that require information regarding nonspatial target characteristics.

It will be seen in the ensuing review that the explanations of the planning–control and perception–action models often conflict for findings from both experimental psychology and neuroscience. For one thing, each predicts different effects of visual illusions and semantics on behavior. For another, each predicts different patterns of brain activations in imaging experiments. Finally, each predicts different patterns of behavior following brain damage to specific regions. It will be seen that where these conflicts exist, the planning–control model provides an account of the evidence superior to that of the perception–action model.

2. Evidence for planning and control in healthy subjects

There is much to support the planning–control distinction in healthy subjects. Specifically, available evidence agrees

with the notion that planning is a relatively slow process that is sensitive to both spatial (e.g., size, shape, orientation) and nonspatial (e.g., function, weight, fragility) visual information, as well as cognitive (e.g., goals, semantics) and perceptual (e.g., visual illusions) factors. The data also support the idea that control is a relatively fast process focused on the spatial characteristics of the target and actor, relying on visual and proprioceptive feedback, along with efference copy. Critically, the data from visual illusion and semantic interference effects on planning, but not control, are much more consistent with the planning–control model than with the perception–action model.

2.1. Planning considers overarching action goals

Marteniuk et al. (1987) provided the classic example of how planning incorporates overarching action goals into an action plan. In this study, participants had to reach for and grasp a chip in one of two conditions. In one condition, participants were instructed to place the chip into a small hole, whereas in another condition, participants were instructed to toss the chip into a large cup. Marteniuk et al. found that, when the goal was to "place" the chip, the requirement for a much more precise movement was reflected in longer movement times with extended decelerations, compared to when the goal was to "toss" the chip. This result supports the idea that planning incorporates overarching goals into immediate movements. Similar results have been obtained in other studies involving different types of goal specifications (e.g., Gentilucci et al. 1997b; Haggard 1998), and have also occurred when the overarching goal was two or more steps away (Rosenbaum et al. 1992).

2.2. Movement times are largely determined by the planning system

Fitts (1957) observed that speeded pointing movements directed towards targets that were difficult to hit took longer than movements directed towards targets that were easy to hit. In the planning–control framework, this speed–accuracy trade-off ("Fitts' Law" as it is commonly known) exemplifies how the planning system strategically accommodates the limitations of the motor system by adjusting the timing parameters of a movement. When the target is small and/or distant, planning processes are more apt to result in a large error, and control processes will benefit from having more time to correct the error. In the planning–control framework, planning is hypothesized to slow down movements made towards "hard" targets to allow the control system more time to operate.

Fitts' aiming task has since been extensively investigated and evaluated (e.g., Beggs & Howarth 1972; Carlton 1981; Crossman & Goodeve 1983; Hay & Beaubaton 1986; Wallace & Newell 1983). Many of these studies have found that the availability of visual feedback has a positive influence on movement accuracy, leading to a corresponding reduction in movement times, compared to when visual feedback is unavailable. The slowing of movements under conditions of reduced or absent visual feedback seems to reflect advanced planning related to the need to account for the difficulty of an upcoming movement (cf. Jeannerod 1988).

The idea that planning is responsible for movement times is controversial. A competing explanation of Fitts' Law is that increased movement times reflect control more than planning (e.g., Crossman & Goodeve 1983; Meyer et al. 1988; see also Plamondon & Alimi 1997). This explanation is based on the fact that longer movements tend to result almost entirely from an increase in the amount of time spent in deceleration. Indeed, it is clear that the lengthening of movement deceleration can either be preplanned or reflect the need for on-line adjustments that add to the time required to execute the movement (e.g., Paulignan et al. 1991a). It is important to reiterate here that in the planning-control framework, effects observed at or near the end of the movement do not necessarily reflect control processes alone, or at all. Just as grip force and other weight-related parameters reflect planning but not control, I suggest that whereas movement time can be extended during control under conditions such as target perturbations, in those cases such extensions may occur as a by-product of the adjustments themselves. Conversely, under most "natural" circumstances (e.g., when the target remains stationary), movement times mainly reflect processes that go on before movement initiation (i.e., during planning).

2.3. Planning considers both spatial and nonspatial target characteristics

It has often been shown that parametrization related to the spatial characteristics of the target is evident well before the movement is complete. For example, the opening and closing of the thumb-finger grip aperture in grasping an object correlates with the size of the target well before the target is contacted (Jakobson & Goodale 1991; Jeannerod 1984). This early scaling has been observed for many other spatial parameters as well, including velocity/acceleration (Gentilucci et al. 1997b; Klatzky et al. 1995), hand shaping (Klatzky et al. 1995), and hand orientation (Desmurget et al. 1995; 1996; Jeannerod 1981).

It has also been shown that planning considers the nonspatial characteristics of the target. For example, the weight of an object affects the amount of force used to grasp and lift it (Gordon et al. 1991). The coefficient of friction of an object's surface affects the velocity of the reach (Fikes et al. 1994; Fleming et al. 2002). Other examples of planning utilizing nonspatial target characteristics are available from everyday observation. For example, people normally acknowledge the function of tools by grasping them by the handle, as they generally avoid contacting hot or sharp surfaces, and so forth.

2.4. Control considers only the spatial characteristics of the target

In contrast to the large number of variables that are hypothesized to affect planning, the planning–control model predicts that the visual information used during control will be focused on only the spatial characteristics of the target. Specifically, control will rely on both feedback (visual and proprioceptive) and feedforward (i.e., efference copy) mechanisms to monitor and adjust movements on-line. There is abundant evidence that these mechanisms contribute to on-line control.

2.4.1. Fast visual feedback loops in control. Woodworth (1899) was the first to study the use of visual feedback in on-line control. Woodworth reported that when participants drew lines at a rate of 400 msec per line or faster, the

accuracy of the drawings was worse than if the lines were drawn at slower rates. Further, if the same task was done with eyes closed, participants' performance at all speeds was just as poor as when the task was done quickly with eyes open.

More recent studies have shown that visual feedback can operate much faster than the 400 msec estimate offered by Woodworth. For example, Elliott & Allard (1985) observed a time frame of 170 msec in which visual feedback mechanisms could operate in a study of visuomotor adaptation to distortion caused by wearing prism goggles. Zelaznik et al. (1983) showed that when subjects were aware of whether or not visual feedback would be available, visual feedback aided in the accuracy of pointing movements in as little as 120 msec (see also Carlton 1981).

2.4.2. Fast proprioceptive feedback loops in control. The importance of proprioception in action is well documented. When proprioception is lacking as a result of pathology of the brain or peripheral nerves, accuracy is reduced (Gentilucci et al. 1994; Jackson et al. 2000; Jeannerod et al. 1984; Lee & Tatton 1975; Sainburg et al. 1993). On-line corrections of actions based on proprioceptive feedback have been observed to take place in as little as 50–100 msec (Craggo et al. 1976; Evarts & Vaughn 1978; Lee & Tatton 1975; Smeets et al. 1990).

Time frames of less than 150 msec in which feedback mechanisms can operate are markedly less than reaction times to initiate a movement, which Stark (1968) estimated to be at least 250 msec (cf. Jeannerod 1988). These findings suggest that the planning and control of movements are separate processes. Planning appears to be a slower, more deliberate process in which a motor program is selected and initiated, whereas on-line control is much faster and more adaptable.

2.4.3. Use of efference copy in control. Von Helmholtz (1866) was the first to postulate the existence of efference copies ("blueprints" of the motor plan forwarded to control mechanisms). Although von Helmholtz was concerned with the dissemination of information regarding upcoming eye movements, it appears that the brain also uses efference copies to control body movements.

The use of efference copy in control is evident in studies in which participants' ability to localize unseen body parts was tested. When the participant actively moved the arm prior to localization, the ability to localize the arm with the other hand was relatively intact. In contrast, when the experimenter moved the arm, localization was relatively poor (Eklund 1972; Jones 1974; Paillard & Brouchon 1968). Neurological support for the existence of an efference copy in reaching was found by Bard et al. (1999; see also Duhamel et al. 1992). Bard et al. observed that a deafferented patient was able to partly accommodate changes in a target's position without the benefit of visual or proprioceptive feedback. As visual and proprioceptive feedback were denied this patient, any on-line adjustments must of necessity have relied on efference copy.

2.4.4. The perturbation paradigm. The perturbation paradigm involves suddenly changing a characteristic of the target, typically coincident with the onset of the movement (e.g., Georgopoulos et al. 1981; Soechting & Lacquaniti 1983; for a complete review see Desmurget et al. 1998). According to the planning–control model, on-line adjustments to perturbations of the spatial characteristics of the target should occur relatively quickly, whereas on-line adjustments to nonspatial perturbations should take much longer, if they occur at all. For example, the motor system should adjust the grip aperture quickly to any change in the size of the target that occurs after movement initiation, as grip aperture relies on size (a spatial characteristic). However, 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).

Many studies have demonstrated the ability of the control system to adjust to changes in the spatial characteristics of the target. For example, Paulignan et al. (1991b) studied the ability of the motor system to accommodate a change in object location that coincided with movement initiation. Paulignan et al. (1991b) placed three dowels on a table. By manipulating the lighting of the dowels, they were able to create the impression that the target had changed location on some trials. Paulignan et al. (1991b) found that the acceleration profiles of the participants changed only 100 msec after the appearance of the new target. Similar short time-frames have been found for reactions to perturbations of the target's orientation (Desmurget & Prablanc 1997; Desmurget et al. 1995; 1996), another spatial characteristic.

Paulignan et al. (1991a) studied the effects of a size perturbation on hand shaping in a thumb and finger grasp of a dowel. They observed that it took upwards of 300 msec for the finger movements used in grasping to be affected by a change in target size. However, a similar study by Castiello et al. (1993) showed that hand shaping could respond to a size perturbation in as little as 170 msec. The Castiello et al. study differed from Paulignan et al. (1991a) in that the participants were free to use as many fingers as desired to grasp the object; in the latter study participants were required to use the thumb and index finger only, an unnatural grasping pattern for a large object.

Castiello et al. (1998) modified the perturbation paradigm to introduce a simultaneous perturbation of size and location. Such a double-perturbation paradigm would also allow one to change the identity of the target (e.g., substituting a fragile target for a hard one). According to the planning–control model, it ought to take longer to accommodate the change in fragility by adjusting the force applied in grasping the object than to accommodate a change in location or size by adjusting the trajectory of the reach or the opening of the hand. It is notable, however, that Castiello et al. (1998) found relatively long adjustment times of grip aperture to the perturbation, suggesting that control processes can be slowed if more than one spatial characteristic is changed simultaneously.

2.5. Consciousness in planning and control

According to the planning–control model, only planning should be susceptible to conscious influence. Indeed, it is intuitively obvious that at least some degree of conscious control can be exerted on many aspects of planning. For example, one will typically choose one's targets consciously; on a lower level, one may speed up one's movements if in a hurry, or change posture consciously, and so forth. Behavioral evidence that conscious systems can influence plan-

ning comes from studies showing that participants are consciously aware of the kinds of interactions that can sensibly be had with objects (Klatzky et al. 1987; 1989). In contrast to this, several studies have suggested that mechanisms responsible for on-line control operate outside of conscious awareness and influence (e.g., Castiello & Jeannerod 1991; Gentilucci et al. 1995; Goodale et al. 1986; Pisella et al. 2000; Prablanc & Martin 1992; Savelsbergh et al. 1991).

2.5.1. Control is immune to saccadic suppression. The ability of our perceptual system to disregard motion of images on the retina during eye movements has the side effect of making it very difficult for us to notice small displacements that occur in the visual world during a saccade. Often objects can be moved several degrees of visual angle without the displacement being noticed consciously. This phenomenon is known as saccadic suppression (see Chekaluk & Llewelynn 1992, for a review). Despite the inaccessibility of these changes to conscious awareness, the motor system is able to accommodate them without difficulty (Goodale et al. 1986; Hallett & Lightstone 1976;

Goodale et al. (1986) had participants point to a target that, in some conditions, moved during an initial saccade to its location. Although participants were unable to say whether or not the target had moved during the saccade, they nonetheless accurately adjusted their saccades and pointing movements towards the target without vision of the moving hand. It appeared that the control mechanisms had adjusted to a change in the target's location that had remained consciously inaccessible. The fact that the adjustment occurred during the movement suggests that on-line control mechanisms were almost, if not entirely, responsible for the adjustment. In contrast, there is no evidence that planning processes play any role in the accommodation of the motor system to saccadic suppression.

2.5.2. Control is involuntary and unconscious. A study by Pisella et al. (2000) examined whether on-line adjustments could be subject to voluntary, conscious intervention. In their study, participants were required to make fast movements to targets that either remained stationary or jumped to a new location. In one condition, participants were instructed to correct their movements on-line when the target jumped. In another condition, participants were instructed to stop their movement when they noticed the target jump.

Pisella et al. found that when movements were fast (i.e., movement times of less than 250 msec), participants were often unable to avoid correcting their movements when the target jumped, even when they were explicitly instructed to stop the movement rather than correct it. This result suggested that fast control mechanisms operate outside of conscious control. Notably, Pisella et al. also found that an optic ataxic was impaired at making fast corrections even when instructed to do so, an important piece of evidence that I will return to in section 4.

2.6. Context-induced optical illusions and action

Studies of context-induced visual illusions and action offer an excellent opportunity to test the predictions of the planning–control model, because they involve the impact of a factor predicted to influence planning (the visual context) on the classes of visual information used by planning (spatial and nonspatial characteristics) as well as control (spatial characteristics). As illusions can affect both of these classes of visual information, the planning–control model can be used to make clear predictions as to how and when visual illusions should affect actions. Further, these predictions often conflict with those of the perception–action model, allowing for direct empirical tests of the two models.

2.6.1. Predictions of the planning–control and perception–action models. According to the planning–control model, planning (which incorporates the context) should be affected by illusions induced by the surrounding visual context, whereas control (which ignores the context) should be unaffected (for other reviews and viewpoints, see Bruno 2001; Carey 2001; Franz 2001). This means that illusion effects on all aspects of actions should be large early in the movements, but effects on parameters of actions based on the spatial characteristics of the target (e.g., size, distance, orientation) should progressively decrease as the movements unfold. Because the control representation is limited to the spatial characteristics of the target over a time-frame of two seconds, the on-line correction of illusion effects on action should only occur when visual information is currently or recently available. In contrast, illusion effects on nonspatial target characteristics should not be corrected on-line, nor should illusion effects on spatial characteristics when a delay of two seconds or more is imposed. Finally, because control relies on both visual and proprioceptive feedback as well as efference copy, removal of any one of these sources of information ought to result in larger illusion effects in the control stage of movements than when all of these sources of information are available to the control system.

The predictions of the planning–control model can be contrasted with those of the perception–action model (Goodale & Milner 1992; Milner & Goodale 1995). In the latter model, a single visual representation is said to subserve actions, whereas a separate representation subserves perceptions. According to the perception–action model, actions should generally be less susceptible to illusions than are perceptions (with some notable exceptions, such as movements made under delayed conditions – see Milner & Goodale 1995).

Critical to the ensuing review is the contrast between the planning–control model, which predicts dissociations in the effects of illusions on planning versus control, and the perception–action model, which predicts no such dissociations. In contrast, in the perception–action model, the effects of visual illusions should be consistent (either small or large) throughout the movement. Further, the perception–action model predicts that the effects of illusions should not depend on the availability of visual feedback during control.

Table 2 summarizes the literature on visual illusions and body movements. (For studies examining the effects of illusions on eye movements, see, e.g., Binsted & Elliott 1999; Binsted et al. 2001; Mack et al. 1985; Wong & Mack 1981.) It is clear from Table 2 that parameters determined by planning (e.g., lifting force, posture choice, movement time, grip acceleration) tend to exhibit large illusion effects, whereas those heavily influenced by control (e.g., maximum grip aperture, pointing accuracy, final hand orientation) tend to exhibit small or nonsignificant illusion effects.

For example, when a delay of two seconds or more is imposed between the offset of the visual stimulus and the initiation of the movement, illusion effects are larger than when no delay is imposed, which is consistent with the idea that the control representation has decayed during the delay, and the index of action is measuring planning processes only (this result is also consistent with the perception–action model). More critically, when illusion effects on a spatial parameter are compared at different times in the movements, the effects tend to be larger early in the movements than later.

2.6.2. Illusions affect planning. Many findings have been consistent with the idea that illusions affect planning. For example, van Donkelaar (1999) reported that the Titchener (or Ebbinghaus) size-contrast illusion affected movement times, but not the accuracy of pointing movements. Van Donkelaar (1999) had participants point to the center of a target circle subject to the Titchener illusion as quickly and accurately as possible. Whereas the accuracy and variable error of the pointing movements were not affected by the illusion, the movement times were affected. Consistent with Fitts (1957), pointing to targets that appeared smaller took longer than pointing to targets that appeared larger. This occurred even though the targets were in fact identical in size. Assuming that movement times reflect the timing of actions and thus planning processes (as I suggested in sect. 2.2), this study supported the idea that illusions affect action planning. Further, others have also found effects of illusions on movement times (Franz et al. 2001; Gentilucci et al. 1996; Smeets & Brenner 1995a; but see Fischer 2001). These results are generally consistent with the notion that illusions affect planning.

Brenner and Smeets (1996) and Jackson and Shaw (2000) studied the effects of the Ponzo size illusion on visuomotor estimates of weight. The Ponzo illusion results when an object is placed on a background of radiating lines. If the object is placed near the end of the background where the lines originate, it appears larger than if it is placed near the end where the lines are maximally spread. Brenner and Smeets (1996) found a significant effect of the Ponzo size illusion on lifting force (measured as the velocity with which the object was raised). Similarly, Jackson and Shaw (2000) found that the Ponzo illusion affected grasping force (the force applied to the sides of the object in lifting), another index of perceived weight. From these two studies, it appears that illusions affect motor parameters related to object weight (a nonspatial target characteristic), and that illusion effects on these parameters were not corrected on-line.

2.6.3. Illusions do not affect on-line control. Aglioti et al. (1995) measured the maximum grip aperture (distance between thumb and forefinger) as participants reached out to pick up a thin disk surrounded by a Titchener illusion display. They found that the maximum grip aperture was less affected by the Titchener illusion than were perceptual estimates of target size, the latter being measured using the method of comparison. (For difficulties associated with Aglioti et al.'s means of comparing perception and action, see Franz et al. 2000; 2001; Pavani et al. 1999.) However, maximum grip aperture was still affected by the illusion to some extent, suggesting that the context had played some role in the shaping of the hand. Haffenden and Goodale (1998; Haffenden et al. 2001) also showed that maximum grip aperture was less affected by the Titchener illusion than perceptions when participants were denied visual feedback of the moving hand. Although these authors argued that maximum grip aperture represented an index of action planning, this parameter occurs well into the control phase of the movement and allows ample time in which on-line corrections could take place. As such, this result is consistent with both the planning–control and perception–action models.

2.6.4. Availability of visual feedback reduces illusion effects. One important test of the planning–control and perception–action models is that only the planning–control model predicts a reduction of illusion effects when visual feedback is available. In contrast, the perception–action model argues that illusion effects should be just as small during planning as they are during control, and thus the size of the effect should not depend on whether visual feedback is available during on-line control.

Gentilucci et al. (1996) demonstrated the influence of visual feedback on pointing movements subject to the Muller-Lyer illusion. Participants were asked to start with their finger at one end of a Muller-Lyer shaft and move it to the other end. Gentilucci et al. (1996) manipulated the amount of visual feedback available to participants, ranging from full feedback of the moving hand and target, to a no-feedback condition with a five-second delay between lights out and movement initiation. Whereas only small effects of the illusion on accuracy were found in the full visual feedback condition, the effects of the illusion increased continuously over each condition in which less (or less recent) visual feedback was available. Similar interactions between illusion effects and the availability of visual feedback have been observed in other studies as well (Glover & Dixon 2001c; 2002a; Westwood et al. 2000a; 2000b).

These results suggested that visual feedback could play a significant role in reducing illusion effects on action. This is consistent with the planning–control model, in which visual feedback contributes to the on-line correction of illusion effects. It is not consistent, however, with the perception–action model, in which illusion effects should be small on both planning and control, whether or not visual feedback is available during the movement itself.

2.6.5. Delays increase illusion effects. It is clear from several studies (Bridgeman et al. 1997; Gentilucci et al. 1996; Westwood et al. 2001b) that illusion effects on action increase when a delay of two seconds or more is imposed between offset of the visual stimulus and initiation of the movement. This is consistent with the notion that the control representation has decayed in the interval, and that on-line corrections are absent under these conditions. According to the planning–control model, illusion effects after delays of two seconds or more reflect the influence of planning only, as control is unable to operate after delays. Note however that these results are also consistent with the perception–action model, as delays are said to result in a decay of the action representation and the use of a perceptual representation.

Another explanation may also be considered here. Franz et al. (2000; 2001; Franz 2001) have argued that both perception and action utilize a single visual representation, and that both are equally affected by illusions. On this account,

Table 2. Summary of the effects of context-induced optical illusions on actions

Illusion	Measure	Visual feedback	Planning or control?	*n*	Effect perception	Effect on action	Reference
Roelef's (motion)	Pointing Acc.	delay (4 sec)	P	10	2 deg. *	* (7/9 subjects)	Bridgeman et al. (1997) Exp. 1
″	Pointing Acc.	no vision	MC	10	2 deg. *	* (5/10 subjects)	Bridgeman et al. (1997) Exp. 1
Titchener (size)	MT	full vision	MP	6	—	20 msec (5.7) *	van Donkelaar (1999)
″	MT	full vision	MP	11	0.3 mm *	minus 5 msec (18) ns	Fischer (2001)
″	Grip Ap. @ 40% MT	no vision	MP	15	2.1 mm (0.5) *	1.9 mm (0.4) *	Glover & Dixon (2002a) Exp. 2
″	Grip Ap. @ 40% MT	full vision	MP	11	—	1.5 mm (0.5) *	Glover & Dixon (2002a) Exp. 1
″	Max. Grip Ap.	no vision	MC	18	2.4 mm (0.1) *	1.4 mm (2.3) ns	Haffenden & Goodale (1998)
″	Max. Grip Ap.	no vision	MC	18	2.6 mm (0.3) *	0.2 mm (0.4) ns	Haffenden et al. (2001)
″	Max. Grip Ap.	no vision	MC	26	1.5 mm (0.1) *	1.5 mm (0.4) *	Franz et al. (2000)
″	Max. Grip Ap.	full vision	MC	14	2.5 mm (0.2) *	2.1 mm (0.5) *	Aglioti et al. (1995)
″	Grip Ap. @ 100% MT	no vision	MC	15	2.1 mm (0.5) *	0.0 mm (0.4) ns	Glover & Dixon (2002a) Exp. 2
″	Grip Ap. @ 100% MT	full vision	C	11	—	0.6 mm (0.3) ns	Glover & Dixon (2002a) Exp. 1
Single contrast (size)	Max. Grip Ap.	delay (5 sec)	P		2.5 mm (0.5)	2.3 mm (0.7) *	Hu & Goodale (2000) Exp. 1
″	Max. Grip Ap.	no vision	MC		2.1 mm (0.4) *	1 mm (0.7) ns	Hu & Goodale (2000) Exp. 1
Ponzo (size)	Lifting force	full vision	P	8	—	*	Brenner & Smeets (1996)
″	Grip force	full vision	P	10	—	0.3 N ns	Westwood et al. (2000b)
″	Grasping force	full vision	P	8	—	0.19 N *	Jackson & Shaw (2000)
″	Max. Grip Ap.	full vision	MC	8	—	0.4 mm ns	Brenner & Smeets (1996)
″	Max. Grip Ap.	full vision	MC	10	—	0.7 mm ns	Westwood et al. (2000b)
″	Max. Grip Ap.	full vision	MC	8	—	0.1 mm ns	Jackson & Shaw (2000)
Parallel lines (size)	Max. Grip Ap.	no vision	MC	26	2.3 mm (0.3) *	1.2 mm (0.3) *	Franz et al. (2001) Exp. 4
Muller-Lyer (extent)	Pointing Acc.	delay (5 sec)	P	8	—	11.2 mm *	Gentilucci et al. (1996)
″	Max. Grip Ap.	delay (3 sec)	P	9	—	5.3 mm *	Westwood et al. (2000c)
″	Max. Grip Ap.	delay (2 sec)	P	10	6.5 mm (0.7) *	5.0 mm *	Westwood et al. (2001b)
″	MT	delay (5 sec)	P	8	—	47.3 msec	Gentilucci et al. (1996)
″	MT	no vision	P	8	—	10.2 msec	Gentilucci et al. (1996)
″	MT	full vision	P	8	—	16.4 msec	Gentilucci et al. (1996)
″	Max. Grip Ap. Pantomime	no vision	P	6	6.7 mm *	8.4 mm *	Westwood et al. (2000a)

Table 2. (continued)

Illusion	Measure	Visual feedback	Planning or control?	*n*	Effect perception	Effect on action	Reference
″	Peak Grip Vel.	delay (3 sec)	P	9	—	28 mm/s *	Westwood et al. (2001b)
″	Peak Grip Vel.	no vision	P	9	—	25 mm/s *	Westwood et al. (2001b)
″	Peak Grip Vel.	full vision	P	9	—	12 mm/s *	Westwood et al. (2001b)
″	Max. Grip Ap.	monocular vision	MP	14	12.8 mm *	2.6 mm *	Otto-de Haart et al. (1999)
″	Max. Grip Ap.	no vision	MC	9	3.1 mm *	4.8 mm *	Westwood et al. (2000c)
″	Pointing Acc.	no vision	MC	8	—	4.8 mm	Gentilucci et al. (1996)
″	Max. Grip Ap.	full vision	MC	9	—	2.1 mm ns	Westwood et al. (2000c)
″	Max. Grip Ap.	full vision	MC	8	—	1.2 mm *	Daprati & Gentilucci (1997)
″	Max. Grip Ap.	full vision	MC	16	2.0 mm (0.2) *	3.4 mm (0.4) *	Franz et al. (2001) Exp. 1
″	Max. Grip Ap.	full vision	MC	10	6.6 mm *	2.6 mm (1.0) *	Westwood et al. (2001b)
″	Max. Grip Ap.	full vision	MC	6	—	0.6 mm ns	Westwood et al. (2000a)
″	Pointing Acc.	full vision	C	8	—	2.4 mm	Gentilucci et al. (1996)
Velocity contrast (velocity)	RT	full vision	P	12	65 mm/s *	~ 20 msec *	Smeets & Brenner (1995a) Exp. 3
″	MT	full vision	P	12	65 mm/s *	~ 20 msec *	Smeets & Brenner (1995a) Exp. 3
″	Striking Acc.	full vision	C	12	65 mm/s *	9 mm ns	Smeets & Brenner (1995a) Exp. 3
Tilt (orn.)	Posture choice	full vision	P	10	2.0 deg (0.3) *	1.9 deg. (0.7) *	Glover & Dixon (2001a) Exp. 1
″	Hand Orn. @ MT 25%	full vision	MP	8	2.1 deg. (0.2) *	7.8 deg. (3.1) *	Glover & Dixon (2001a) Exp. 2
″	Hand Orn. @ 50% MT	no vision	MP	10	—	2.7 deg. (0.3) *	Glover & Dixon (2001c)
″	Hand Orn. @ 100% MT	no vision	MC	10	—	1.4 deg. (0.2) *	Glover & Dixon (2001c)
″	Hand Orn. @ 100% MT	full vision	C	8	2.1 deg. (0.2) *	0.8 deg. (1.2) ns	Glover & Dixon (2001a) Exp. 2
Simul. tilt (orn.)	Posting Orn. @ 100% MT	no vision	MC	12	8 deg. (1.7) *	6.8 deg. (0.8) *	Dyde & Milner (2002) Exp. 1
Rod in frame (orn.)	Hand Orn. @ 100% MT	no vision	MC	12	5 deg. (1.8) *	0.2 mm (0.4) ns	Dyde & Milner (2002) Exp. 2
Horizontal-vertical	Grip Ap. @ 100% MT pantomime	no vision	P	23	8% (1%) *	12% (6%) *	Vishton et al. (1999) Exp. 4
″	Max. Grip Ap.	no vision	MC		*	ns	Servos (2000)

Columns from left to right: the type of illusion; the measurement of action taken; the availability of visual feedback; whether the measure of action should reflect planning or on-line control; sample size; effect on perception (standard error), effect on action (standard error), and reference. Acc. = accuracy; Max. Grip Ap. = maximum grip aperture; Peak Grip Vel. = peak grip velocity; Orn. = orientation; P = planning only; MP = mainly planning; MC = mainly control; C = control only; - = perceptual effect not tested; N = Newton's force; * = statistically significant at the $p < 0.05$ level; ns = statistically nonsignificant. Notes: (1) In some cases standard errors and/or significant tests were not reported or deducible. (2) Effects on Max. Grip Aperture are scaled to reflect the typical grip aperture-target size correlation of 0.8 (Jeannerod 1988) at the time of MGA (cf. Franz et al. 2001; Glover & Dixon 2001a). All other data are as reported in the studies or estimated from reported statistics or figures. (3) Max. Grip Aperture typically occurs at 60–75% of movement duration (Jeannerod 1988).

apparently small illusion effects on action have arisen because of a failure to adequately match the attentional requirements of the task. For example, Franz et al. (2000) argued that small effects of the Titchener illusion on maximum grip aperture relative to perceptual judgments in the Aglioti et al. (1995) study were a consequence of the need to attend to only one of the Titchener displays in the action task, but to both in the perception task. This hypothesis is intriguing, but would not seem able to account for differential effects on action and perception tasks when the two are adequately matched, as they are in most studies of illusions and action reported in Table 2. Further, this model would have to predict that illusion effects on perception would increase when delays are imposed, just as they do for actions. Evidence to contradict this hypothesis has been found in a study comparing delay effects on pointing and perceptual judgments (Bradshaw & Watt 2002).

2.6.6. Dynamic illusion effects in reaching. Although the planning–control model provides a ready account of the findings described above, we aimed to investigate illusion effects on planning and control more directly (Glover & Dixon 2001a). This was done using a task in which participants grasped a small bar placed at various orientations. We manipulated the perceived orientation of the bar by placing the bar on a background grating that was misoriented with respect to the participants' sagittal plane. When the grating was rotated ten degrees clockwise or counterclockwise from sagittal, participants' perceptions of the bar's orientation were overestimated in the opposite direction. This orientation illusion effect was found to be roughly two degrees in a perceptual task in which participants were required to align the bar with their sagittal planes.

In one experiment, we gave participants a choice between abducting or adducting their hand in picking up the bar. Abducting the hand results in the thumb being placed on the rightward edge of the bar (from the participant's perspective), whereas adducting the hand results in the thumb being placed on the leftward edge of the bar. It has been shown that when an object is moved through a range of positions or orientations, participants' choice of postures will typically switch from one posture to another within a fairly narrow portion of that range (Kelso et al. 1994; Rosenbaum et al. 1990; 1992; Short & Cauraugh 1997; Stelmach et al. 1994). The question in this experiment was whether the orientation illusion would affect the threshold at which participants switched from one posture to another. Our assumption was that the choice of postures would be made during pre-movement planning, and although it would still be possible to change the choice made once the reach was underway, the costs would usually outweigh the benefits. Thus, we reasoned that posture choice would provide a relatively uncontaminated measure of the illusion's effect on planning.

We found that the choice of postures was affected by the orientation illusion. The threshold for switching from a hand-abducted to a hand-adducted posture was adjusted approximately two degrees by the orientation illusion, an effect roughly equivalent to the effect on perceptual judgments. This finding supported the idea that macroscopic aspects of planning are affected by illusions.

In another experiment, we set out to test the planning–control model more directly. Here, we had participants again pick up the bar, but had them use a hand-abducted (thumb-right) posture on every trial. The orientation of the hand was measured throughout the movement using optical recording equipment. We observed that the orientation of the hand was linked to the orientation of the bar, and this was evident early in the reach, as has been found elsewhere (Desmurget et al. 1995; 1996; Desmurget & Prablanc 1997; Glover & Dixon 2001b; 2001c). More interesting was the fact that the orientation illusion affected the orientation of the hand. The effect of the illusion on the orientation of the hand was large early in the reach, but decreased to near zero as the hand approached the bar. This "dynamic illusion effect" supported our prediction that participants would correct for illusion effects in flight. Large effects early in the movement presumably reflected the illusion's influence on planning, whereas continuously decreasing effects thereafter reflected the relative immunity of control.

It is difficult to accommodate the results of this study within the perception–action framework, however. For one reason, posture choice would seem to have to rely on an illusory "perceptual" representation, even though the bar and display were visible throughout each trial, and presumably enough information was present to select an appropriate posture. For another, it would appear that in reaching, the perceptual representation would have had to subserve the initial planning of the reaches towards the bar, whereas the action representation would have been responsible for the balance of the movements.

One study by Dyde and Milner (2002) looked at the effects of a simultaneous tilt illusion on "posting" behavior. In this study, participants aimed a card towards a rectangular figure drawn vertically on a background grating. Although Dyde and Milner (2002) did not specifically analyze illusion effects over time in this study, they did find a large effect of the illusion on posting behavior at the end of the movement. This result seems to contradict our own results using a very similar illusion (Glover & Dixon 2001a; 2001b; 2001c), and Dyde and Milner interpreted their results as suggesting that the orientation illusion arises at V1, thus affecting both perception and action. Although this hypothesis does not explain why we did not find similar effects at the end of the movement in any of our experiments, an explanation of the discrepancy between studies may be given. It is possible that the discrepancies resulted from the use of vertically-oriented targets by Dyde and Milner, whereas ours ranged in orientation from 5 to 35 degrees. In their study, the posting task may have included a strong demand to "match" the tilted appearance of the target with the card; in our study the orientation illusion was much less noticeable and so this demand was not present.

2.6.7. Dynamic illusion effects in grasping. We have also applied a similar kinematic analysis to the grip aperture in a reach to a disk subject to the Titchener size illusion (Glover & Dixon 2002a). The data in this study also supported the planning–control model. Illusion effects on grip aperture were largest early in the reach and decreased as the hand approached the target. Dynamic illusion effects have also occurred when vision of the hand and target were blocked during the reach (Glover & Dixon 2001c; 2002a), suggesting that proprioceptive and efference mechanisms can play a significant role in the on-line correction of illusion effects.

The results of this study involving the Ebbinghaus illu-

sion have been contentious, however. Danckert et al. (2002) reanalyzed two of the experiments previously carried out in the Goodale lab. Based on the reanalysis, they suggested that there was no evidence for an illusion effect at any time up to the point where maximum grip aperture was reached (i.e., at roughly two-thirds of movement duration), except for an effect in one experiment at the time of maximum grip aperture. I have questioned this conclusion, however, because there was no scaling of grip aperture effects to the changing dependence of the grip aperture on object size at different times during the reach (Glover 2002). Such scaling is vital in any analysis of the effects of cognitive or perceptual variables effects on action (for explanations, see, e.g., Franz et al. 2000; 2001; Glover & Dixon 2001a; 2002b).

2.7. Semantics interfere with planning but not control

Gentilucci and his colleagues (Gentilucci & Gangitano 1998; Gentilucci et al. 2000a) recently demonstrated interesting effects of semantics on actions. In these studies, words were printed on objects and participants reached to and grasped them. It was observed that the meanings of the words printed on the objects affected the kinematics of the participants' movements directed towards those same objects. For example, Gentilucci et al. (2000a) observed that the maximum grip aperture was larger for objects on which the word "GRANDE" ("large") had been printed than for words on which had been printed "PICCOLO" ("small"). This suggested that the motor system had been influenced by the meanings of the words when a motor program was selected. Effects were also observed for several other word pairs, including (the Italian equivalents of) "long" and "short," "near" and "far," and "high" and "low." Gentilucci and his colleagues interpreted these results within the framework of models that argue for a close relationship between language and motor processes (e.g., Kimura 1979; Rizzolatti & Arbib 1998).

We have recently extended the work of Gentilucci and his colleagues to measure the effects of words on action throughout the course of the movement (Glover & Dixon 2002b; Glover et al. 2004). In particular, we aimed to test the predictions of the planning–control model with respect to semantic effects. In the planning–control model, a cognitive process such as semantics should affect the planning of the movements, but not how they are controlled on-line. Thus, a similar result should occur as occurred with visual illusions: That is, there ought to be large effects of the words early in the movements but continuously decreasing effects as the hand approached the targets. And, in fact, these were the exact results we obtained. In one study, we found that participants had larger grip aperture early in the reach for objects on which was printed the word "LARGE" than for objects labeled "SMALL." However, as with illusion effects on action, these word effects faded as the hand approached the targets (Glover & Dixon 2002b).

A similar result was obtained when we had subjects first read a word, then grasp an object (Glover et al. 2004). In this study, the words could represent either relatively large objects (e.g., "APPLE," "BASEBALL") or relatively small objects (e.g., "PEA," "GRAPE"). Here, we observed that the size of the object represented by the word had a large effect on the grip apertures early in the reach. For example, reading words such as "APPLE" led to larger grip apertures than reading words such as "GRAPE." Again, however, this effect faded as the hand approached the targets, and participants were able to execute the grasps without difficulty.

These "dynamic word effects" provide further support for the planning–control model, but would be difficult to incorporate within a perception–action model. In the latter model, the motor system could presumably plan and execute the movement based simply on the relevant spatial characteristics of the target alone, independent of semantic processes. Conversely, if the perception–action model were extended to include the supposition that semantics could influence action by an interaction between perception and action systems, it would still have difficulty explaining why the words affected planning only and not control. In short, the effects of semantics on action seem to be much more consistent with the planning–control model than with the perception–action model.

2.8. Summary of studies on healthy participants

Studies of healthy participants have demonstrated the distinction between planning and control. Whereas planning represents a process that is relatively slow and complex, control mechanisms appear to be much more flexible and faster, yet limited in scope. Planning selects an action based on an integration of a broad range of visual and cognitive information. In contrast, control operates using a fast visual representation limited to the spatial characteristics of the target, coupled with visual and proprioceptive feedback, as well as efference copy, in monitoring and adjusting movements in flight.

Because planning incorporates the context surrounding the target, it is affected by context-induced visual illusions. Conversely, because the control representation excludes the context, it is relatively immune to these same illusions. This distinction is reflected in the pattern of illusion effects on action. Whereas indices of planning are affected by illusions, indices of control are much less affected, if at all. Critically, when measures of illusion effects on spatial parameters are taken throughout the movement, the effects of the illusion are large early in the reach, but decrease as the hand approaches the target (Glover & Dixon 2001a; 2001b; 2001c; 2002a). Similar results have occurred for the effects of semantics on action (Glover & Dixon 2002b; Glover et al. 2004), also consistent with the notion that cognitive influences on planning are corrected on-line during control. The results of these studies were much less consistent with the perception–action model, however.

Future studies may be aimed at expanding and clarifying the nature of the dissociations between planning and control. According to the planning–control model, these dissociations should generally take the form of influences of many visual and/or cognitive variables on planning, but a lack of an influence of these same variables on control. For example, the planning–control model predicts that the pattern of effects of semantics on action ought to be identical to the pattern of illusion effects (i.e., large effects on indices of planning, small or nonexistent effects on indices of control). More generally, nonspatial characteristics of the target, conscious awareness, visual context, memory processes, and overarching goals should all interact to affect planning, but only the spatial characteristics of the target should affect control.

3. Brain imaging of planning and control

Here, I briefly describe the anatomy and connectivity of the brain before discussing the neural bases of action. Figure 3 shows the main visual cortical pathways in the human and monkey brains. In the monkey, the visual pathways fall into two main "streams," a dorsal stream terminating in the inferior parietal lobule and a ventral stream terminating in the inferior temporal lobe (Mishkin et al. 1983). Boussaoud et al. (1990) also proposed the existence of a "third" visual stream, terminating in the superior temporal sulcus.

3.1. Functions of the two streams in monkeys

Originally, the two main visual streams were hypothesized to serve functions related to object identity and spatial localization (the "what versus where" distinction; Mishkin et al. 1983). However, numerous researchers have suggested a role of the primate parietal lobe in sensorimotor transformations (e.g., Mountcastle et al. 1975; Stein 1991; 1992). Some researchers have contended that the roles of the two streams may best be described not as "what versus where," but rather as "what versus how" (Goodale & Milner 1992; Milner & Goodale 1995), or similarly, as "semantic versus pragmatic" (Jeannerod 1994; 1997; Jeannerod et al. 1994; 1995).

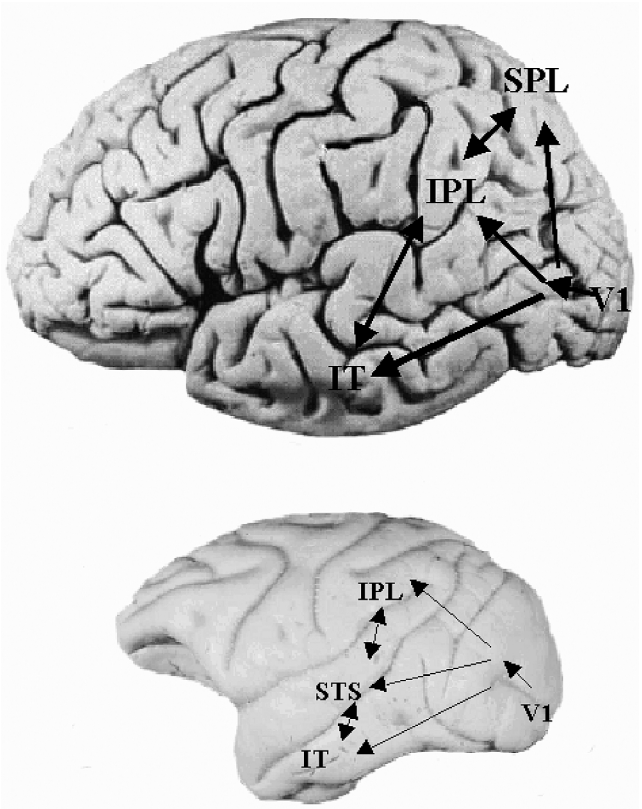

Figure 3. Illustration of putative visual pathways in the posterior regions of the human brain (top), and macaque brain (bottom – based on Boussaoud et al. 1990; Mishkin et al. 1983). Note that whereas the dorsal stream in the macaque brain terminates in the inferior parietal lobule, in the human brain it is hypothesized to terminate in the superior parietal lobule. The medial or "third" stream is hypothesized to terminate in the superior temporal sulcus in monkeys, but in the inferior parietal lobule in humans. Not to scale.

Such a reformulation of the functions of the two streams has drawn evidence largely from neurophysiological studies of monkeys. Numerous authors have argued that the dorsal stream pathway encodes the sensorimotor transformations necessary for goal-directed actions (Goodale & Milner 1992; Kalaska & Crammond 1992; Milner & Goodale 1995; Sakata et al. 1997; Wise & Desimone 1988). Support for this notion comes from studies showing activity of cells in the dorsal stream of monkeys related to the visual guidance of reaching (Taira et al. 1990) and grasping (Murata et al. 1996). Cells in the posterior parietal lobe of monkeys have also been shown to be sensitive to changes in motor plans independent of changes in visual attention (Gnadt & Andersen 1988; Snyder et al. 1997; 1998).

3.1.1. Functions of the two streams in monkeys may not map onto the human brain. A reasonable assumption to make is that human brain organization and function will closely parallel that found in monkeys. However, it will be seen that the data from both brain imaging and neuropsychology raise serious doubts about drawing such parallels in high-level vision (see also, e.g., Eidelberg & Galubardi 1984; Vandufell et al. 2002). In particular, I will show that the "what/how" distinction found in monkeys cannot be easily translated into an explanation of human brain organization. Rather, I suggest that the evolution of the human brain has resulted in the localization of planning processes in the phylogenetically newer cortex of the inferior parietal lobule. Tool and object use in particular has required that human motor planning processes integrate ventral stream functions related to object identification and context. I hypothesize that this integration occurs in the IPL. The role of the IPL suggested here is thus dramatically different from that proposed by Milner and Goodale (1995), who emphasized the role of the IPL in spatio-cognitive operations and praxis. These authors suggested that the dorsal stream generally possessed sufficient visual information for both the planning and control of actions, although on occasion it may be necessary for the streams to "interact," such as in movements to remembered targets, or movements made after a delay (Milner & Goodale 1995). In contrast to the perception–action model's predicted interactions between dorsal and ventral and/or IPL visual systems in some actions, only the planning–control model maps planning and control specifically onto the IPL and SPL, respectively.

The planning–control distinction can also be plausibly extended to other brain structures. Specifically, I hypothesize that the planning system includes regions in the frontal lobes, basal ganglia, and cerebellum. Similarly, although the visual representation in the SPL is said to be the crucial factor underlying on-line monitoring and control, I hypothesize that it operates in concert with other control centers in the cerebellum.

3.2. Brain images of action: Predictions of the planning–control and perception–action models

The planning–control and perception–action models can be used to make specific predictions regarding the brain regions active during motor behaviors. In the planning–control model, activation of the two systems should depend on the task at hand. Specifically, tasks that require heavy involvement of planning systems, such as selecting an appropriate posture, should preferentially activate planning re-

gions. Conversely, tasks that require major involvement of on-line control systems, such as manual tracking or adjustments to target perturbations, should preferentially activate control regions.

These predictions are in contrast to the predictions of the perception–action model (Goodale & Milner 1992; Milner & Goodale 1995). In this model, visual "action" representations are said to reside in the SPL. As such, the perception–action model predicts that motor behavior should generally lead to activation of the SPL but not the IPL, and that this should be true during both planning and control.

Three types of brain imaging paradigms have been used to study the neural underpinnings of planning and control. One paradigm involves motor tasks that encompass both planning and control, and thus reveals structures active during one or the other, or both stages. A second paradigm focuses on the neural structures involved in either planning or control, respectively. A third paradigm employs the use of "motor imagery," imagining the production of a movement without actually carrying it out. As predicted by the planning–control model, increased activity in regions of the planning system is strongly associated with the planning phase of action, whereas increased activity in regions of the control system is strongly associated with the on-line control phase of action.

3.2.1. PET and the motor brain. Several PET studies have shown increased activation of both planning and control regions during motor tasks. Kertzmann et al. (1997) studied the changes in brain activation during visually guided pointing. They found that activity increased in both the inferior and superior regions of the parietal lobe, the premotor cortex, and the basal ganglia (the cerebellum was not scanned) when pointing movements were made. Inoue et al. (1998) studied how pointing with or without visual feedback affected brain activation. Whether or not feedback was allowed, significant increases in activity occurred in both the inferior and superior regions of the parietal lobe during movement compared to rest trials, suggesting that the involvement of neither region was contingent on the availability of visual feedback. Activity was also observed in the frontal lobes, temporal lobes, basal ganglia, and cerebellum. Rizzolatti et al. (1996) studied the neural underpinnings of grasping movements using PET. Grasping an object resulted in increased activity in both the IPL and posterior regions of the SPL, as well as the basal ganglia and cerebellum.

The studies reviewed above show that motor behavior results in increases in activity in both the inferior and superior regions of the parietal lobe, as well as the frontal lobes, basal ganglia, cerebellum, and in one case, the temporal lobes. Whereas these studies are consistent with activation of both of the networks I have proposed in this article, they do not allow one to dissociate activity related to planning from that related to control. For that purpose, it is necessary to turn to more direct investigations of planning versus control.

3.2.2. PET and planning versus control. Figure 4 summarizes the results of studies comparing brain activity during the planning and control of actions, respectively. Grafton et al. (1998) measured changes in brain activity when participants made a choice between a power and precision grasp, the former involving the entire hand and the latter involving the thumb and forefinger only. In two conditions, grasp choice was mandatory. In another condition, a cue occurred

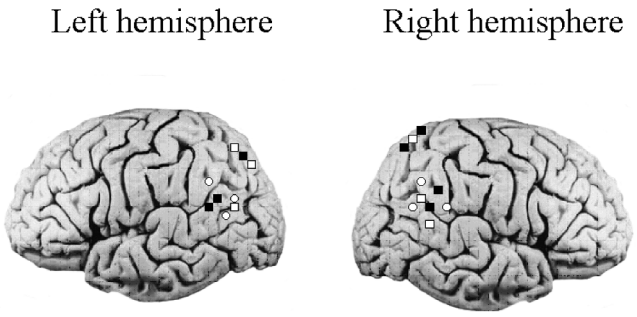

Figure 4. Summary illustration of increases in brain activity in the posterior parietal lobe related to motor planning, on-line control, and motor imagery. Filled squares: increased activity related to planning; empty squares: increased activity related to on-line control; filled circles: increased activity related to motor imagery. See text for details.

prior to each trial that informed the participants of which grasp to use.

Significant increases in activation occurred in the IPL and basal ganglia in all movement conditions, whereas increased activation in the SPL only occurred in the cued versus mandatory comparison. That is, only when participants had to focus attention on an upcoming cue was activity in the SPL elevated. This finding concurs with other PET studies that suggest that the SPL is involved in visuospatial attention (Corbetta et al. 1993; 1996; Haxby et al. 1994; Jovicich et al. 2001; Nobre et al. 1997). Increased activity also occurred in the premotor cortex in the cued versus mandatory comparison.

Deiber et al. (1996) also studied brain activation during movement selection. This study had the added control of having delays imposed between cue and response. This allowed for a greater proportion of scanning time being devoted to measuring regions involved in planning. Flexion or extension of either the forefinger or little finger was required, and cues could inform participants of the finger to be used, the movement required, both the finger and movement required, or neither. Another condition allowed participants to freely decide which movement to make with which finger.

Deiber et al. (1996) showed that increased activation of the IPL, premotor cortex, and cerebellum occurred in all of the selection conditions relative to a rest condition, whereas increased activation of the SPL was present only when the cue was uninformative or only partly informative. Similar to Grafton et al. (1998), the results of Deiber et al. (1996) suggest that the IPL was activated during planning whether the cue was informative or not, whereas the SPL was only activated during the planning phase when attentional demands were high.

Krams et al. (1998) utilized a task in which participants were required to copy a hand posture shown to them on a screen. Three conditions manipulated the relative import of planning and control. In one ("execute only") condition, participants simply copied the movement immediately after its presentation. In another ("plan and execute") condition, a pause was given between the presentation of the movement and a subsequent cue to imitate. Participants were instructed to use this delay to prepare the movement. A third ("plan only") condition had participants prepare the movement, but withhold its execution.

The design of Krams et al. (1998) allowed them to dissociate the changes in activity during planning from the changes during on-line control. When the "plan only" condition was compared to the rest condition, increased activity was found in the supramarginal gyrus of the IPL, premotor cortex, basal ganglia, and cerebellum. No increase in activity was observed in the SPL. Increased activation of the IPL and premotor cortex was also observed in the "plan and execute" condition compared to the "execute only" condition, another measure of planning. However, there was no increase in activity in the SPL, cerebellum, or basal ganglia in this comparison.

The reverse comparisons (i.e., "execute only" versus rest, "plan and execute," versus "plan only") showed what happened during the execution phase of a movement. In the former of these comparisons ("execute only" versus rest) increased activity occurred in the intraparietal sulcus bordering the IPL and SPL, the frontal lobes (including premotor and primary motor cortex), and the cerebellum, suggesting that these regions were involved in executing the actions. The latter comparison ("plan and execute" versus "plan only") showed increased activity in the basal ganglia and cerebellum. Some increase was also observed in the IPL in the "execute only" condition; this may have reflected the necessity of at least some planning preceding the movement's initiation. These results suggest that, for copied movements at least, the planning system, including the IPL, premotor cortex, and basal ganglia, is more heavily involved in the planning of actions, whereas the control system, including the SPL and cerebellum, is more heavily involved in their execution.

Desmurget et al. (2001) examined brain activation associated with target perturbations during pointing movements while visual feedback of the hand was unavailable. In this study, participants had to look at and point to targets. The target itself either remained stationary or was perturbed during the saccade. This allowed Desmurget et al. to dissociate activity related to large corrections required for perturbed targets from activity related to much smaller or nonexistent corrections required for stationary targets. Desmurget et al. found that perturbing the target (thus requiring a large on-line correction) led to increased activity centered in the left intraparietal region bordering the IPL and SPL, as well as right cerebellum. This suggested that nonvisual feedback loops at least were reliant on the control regions as indicated by the planning–control model.

Grafton et al. (1992) investigated the brain regions active during manual tracking. Because manual tracking of a moving target is a long-lasting movement requiring a continual updating of the relationship between the hand and target, I have suggested that it can be considered to be largely under the influence of control. If on-line control relies primarily on the regions I have hypothesized, one might expect these "control regions" to be active during the task, but not necessarily the "planning regions," as planning requirements would be negligible. This is generally what occurred. Increased activity in the SPL, supplementary motor area, and cerebellum was found by Grafton et al. during manual tracking, whereas activity in the IPL and basal ganglia was unaffected by performance of the task.

3.2.3. PET and motor imagery. A third set of evidence in favor of ascribing planning and control to different brain regions comes from studies of motor imagery. In these studies, participants are asked to imagine they are making the requested movements, but to not actually make the movements themselves. There is considerable evidence that brain regions that are more active during motor imagery are very similar to those that are more active during motor preparation (Jeannerod 1994; 1997), but less similar to those involved during execution. According to the planning–control model, studies of motor imagery ought to reveal increased activity in the planning but not the control regions.

Decety et al. (1994) studied brain activation while participants performed one of two tasks. In one condition, participants viewed pictures of a hand grasping an object, whereas in the other condition, participants imagined grasping objects with their own hand. In neither condition did participants themselves move. Imagined grasping increased activity in the IPL, prefrontal, premotor, basal ganglia, and cerebellar regions, but not the SPL, as compared to a rest condition. Increased activation was also found in the IPL, prefrontal, premotor, and basal ganglia regions in the imagined grasping condition compared to the observed grasping condition, but not in the SPL or cerebellar regions. This showed that the increase in the planning regions was a result of motor imagery and not visual imagery. The fact that participants did not move at all during the experiment supports the idea that activity in the planning network was related to the planning of such movements and not their execution.

Similar studies by Grafton et al. (1996) and Deiber et al. (1998) found results consistent with Decety et al., although the Grafton et al. study also showed some increased activity along the border between superior parietal and occipital regions. From these four studies combined, it would appear that motor imagery activates the IPL and related planning regions more than it does the SPL and control regions.

3.3. Summary of brain imaging studies

Brain imaging studies of action can be divided into three main categories. One type of study is concerned with motor-related activity only and does not attempt to distinguish between planning and control. These studies typically find increased activation in both the planning (IPL, frontal lobes, basal ganglia) and control (SPL, cerebellum) regions of the brain (Inoue et al. 1998; Kertzmann et al. 1997; Rizzolatti et al. 1996).

Another type of study aims to dissociate the effects of planning from those of control by focusing the scanning time on one or the other process. These studies typically find increased activation of the planning regions during motor planning, with increased activation of the control regions restricted to the execution phase (Deiber et al. 1996; Desmurget et al. 2001; Grafton et al. 1992; 1998; Krams et al. 1998). When increased activation of the SPL does occur during the planning stages (Deiber et al. 1996; Grafton et al. 1998), it can readily be explained by the attentional demands of the task. In some cases, the cerebellum is also active during planning. Such activation was not predicted by the planning–control model, and leaves open a controversy over the exact role of the cerebellum in motor learning, planning, and/or control (see e.g., Kitazawa et al. 1998; Stein 1986).

A third type of study investigates the neural underpinnings of motor imagery; these provide interesting parallels with studies of planning. In accord with the hypothesis that motor imagery is a form of planning in which the move-

ments are never carried out (Jeannerod 1994; 1997), planning regions are more active during motor imaging than control regions (Decety et al. 1994; Deiber et al. 1998; Grafton et al. 1996;).

These results were generally not consistent with the perception–action model, however, which predicts motor-related activity in the SPL but not in the IPL. The fact that activity occurred in both regions, coupled with the distinction between planning and control shown for the IPL and SPL, strongly favors the planning–control model over the perception–action model with regard to the brain imaging data.

The planning–control model predicts that future brain imaging studies should be able to correlate activity in the IPL, frontal lobes, and basal ganglia with the behaviors I have associated with planning. These include target selection, macroscopic selection of postures, and movements requiring the integration of nonspatial target characteristics. One example of a task involving the heavy involvement of the planning system would be grasping a tool appropriately when such a grasp is not the most convenient. Conversely, activity in the SPL ought to continue to be correlated with control behaviors, emphasized in such behaviors as manual tracking and reactions to perturbations. Paradigms that specifically isolate the planning and control stages of actions (e.g., Desmurget et al. 1999; Grafton et al. 1992; Krams et al. 1998) should be among the most useful in this respect. Finally, the role of the cerebellum in either planning and/or control has been ambiguous in PET studies, and needs to be clarified.

4. Disruptions in planning and control following brain damage

Whereas PET imaging studies provide a clear indication that planning and control rely on relatively independent networks within the brain, human neuropsychology presents a somewhat more complex story. The inherent difficulties in using human neuropsychology to understand brain function can be traced to several factors (see Kolb & Whishaw 1995), the three most important of which I will describe here. First, lesions rarely restrict themselves to neat anatomical divisions that researchers can isolate. Second, damage can often result in the disturbances of function in cells far removed from the lesion. Third, the plasticity of the brain often allows for significant recovery of function, or at the very least, the acquisition of compensatory strategies. Therefore, it may not be too surprising that human neuropsychology does not offer quite as clear a distinction between planning and control as that offered by PET. Nevertheless, it will be seen that parallels do exist between the results of brain imaging and neuropsychology.

The planning–control model predicts that damage to brain regions responsible for either planning or control will result in distinctly different deficits. Damage to planning centers in the IPL, frontal lobes, or basal ganglia, for example, should disrupt the integration of visual and cognitive processing into a coherent action plan. Because of the complexity of planning processes, deficits can be manifest in several ways, not all of which will follow from damage to a specific region. These deficits might be manifest in the impaired performance of overlearned movements based on visual input, or in the ability to incorporate future goals into current actions. Damage to a planning region ought to also result in impairments in the parametrization of movements. For example, the early portions of the grip aperture or hand orientation profiles might be disrupted when damage to planning regions occurs. Given the role of the IPL in integrating visual sources of information, damage to this region would be expected to lead to deficits in the "visual" component of planning, for such things as the coding of object characteristics and/or contextual elements. For example, the scaling of grip force to an object when grasping it might be disrupted following damage to the IPL. Difficulties in accommodating the visual context surrounding the target might also occur, either in target selection or obstacle avoidance. Finally, because planning is responsible for movement timing and initiation, damage to at least some regions ought to result in deficits to these aspects of action.

Damage to the SPL or cerebellum, on the other hand, ought to lead to impairments in on-line control. These deficits should be most evident in actions requiring a large degree of on-line control, such as adjusting to a perturbed target, or tracking a moving target. Deficits ought to be limited to those movement parameters dependent on the spatial characteristics of the target, such as grip formation or hand trajectory. Deficits ought to be larger when the planning system is handicapped in some way. For example, when the situation is unfamiliar, or when the target is not foveated. Further, when delays of two seconds or longer are imposed between offset of vision of the stimulus and movement initiation, the movement should come entirely under the influence of planning – performance should actually improve. Finally, deficits resulting from damage to the control system should be most evident in the latter stages of the actions when control processes are most influential.

The predictions of the planning–control model again contrast with those of the perception–action model (Goodale & Milner 1992; Milner & Goodale 1995), in which a single visual representation underlying action is said to exist in the SPL. Accordingly, damage to this representation or its frontal projection regions should disrupt action. Although proponents of the perception–action model acknowledge the role of the IPL in praxis (Milner & Goodale 1995), they do not specifically characterize the IPL/SPL distinction as being between planning and control. As such, the perception–action model would predict that damage to the SPL should lead to the greatest deficits in actions, and that these deficits should be equally prevalent during both planning and control.

It will be seen that the evidence from human neuropsychology is generally more consistent with the planning–control model than with the perception–action model. In particular, the critical evidence suggests that damage to the IPL disrupts planning, that damage to the SPL leads to deficits in on-line control, and that damage to the allied brain regions of planning and control result in deficits related to their role in one or the other stage.

4.1. The left IPL and the "visuokinesthetic engram"

Damage to the left IPL (or its visual inputs) often results in ideomotor apraxia, a deficit in executing learned movements (although, note that ideomotor apraxia can occur with damage outside of these regions as well). Heilman, Poizner, and their colleagues (e.g., Clark et al. 1994; Heilman et al. 1985; Poizner et al. 1990; 1995), following an idea originally suggested by Liepmann (1920), have argued that

the left IPL in right-handers contains "visuokinesthetic motor engrams," stored representations of learned acts. When the left IPL is damaged, or when it is disconnected from frontal premotor areas, apraxia is said to result from the inability to access these stored representations of actions.

4.1.1. Studies of performance in ideomotor apraxics. One of the interesting sequelae of ideomotor apraxia occurs when a patient is presented with an overlearned, commonplace task they are quite familiar with, yet they are unable to perform the task appropriately. In one study, Clark et al. (1994) studied the kinematics of three apraxic patients as they carried out the act of slicing bread. The patients had varying degrees of brain damage, with the common locus being the IPL, its connections, or its underlying white matter. In four conditions, patients were asked to carry out the act with varying numbers of cues: (1) no cue available (pure pantomime); (2) bread but no knife; (3) knife but no bread; and (4) actual execution of the act of slicing bread, with both bread and knife.

Clark et al. (1994) reported that although the patients clearly understood what they were to do and made every effort to complete the task, their performance was severely impaired. Several kinematic indices of the action were disturbed in the apraxic patients relative to controls. Movements as a whole were of lower amplitude, with a lower peak velocity, and had longer movement times in each slicing cycle relative to controls. Moreover, the planes of the slicing motions were incorrectly oriented, being nearer to the patients' sagittal than frontal planes. The planes of motion were less consistent in the ideomotor apraxics than controls, and tended to be more curved than linear. In short, the patients were unable to execute movements with anywhere near the same fluidity and competence as the controls. These deficits were greatest when no visual cues were available (i.e., in the pure pantomime condition), but were only slightly ameliorated by the presence of the bread and/or knife.

A follow-up study done by Poizner et al. (1995) on the same three patients tested by Clark et al. (1994) showed that the patients also had other kinematic deficits in the act of slicing bread. There were distorted relationships between the relative angles and velocities of joints in the arm, as well as a lack of synchrony between the elbow and shoulder joints in the apraxics relative to controls.

These studies demonstrate that damage to the left IPL or its connections can result in the disruption of the stored memories of how to execute a learned task. These memories, or "visuokinesthetic engrams," clearly relate to the planning of action. This type of finding is consistent with what I have proposed as an important role for the left IPL in planning.

In contrast to the deficits ideomotor apraxics show for learned movements, they may often appear to be relatively normal in the execution of simple pointing and grasping movements (i.e., they are not spatially inaccurate the way optic ataxics are). I contend that this difference depends on the requirements of the task itself. For one thing, learned movements based on stored memories emphasize the planning phase of the action. In contrast, it will be seen that pointing and grasping movements to unfamiliar targets emphasizes the on-line control phase. For another, errors in the accuracy of movements early in a trajectory can be corrected on-line as long as the control system remains intact (just as happens with visual illusions and semantic interference). Because damage to the IPL does not lead to errors in accuracy at the end of a simple reaching and grasping movement, does not mean these errors were not present earlier in the movement. The planning–control model predicts that such errors would be found should careful kinematic analyses of reaching and grasping movements in patients with damage to the IPL be undertaken.

Only a few studies have examined the relationship between ideomotor apraxia and kinematic abnormalities. Although one study has found correlations between incidence of ideomotor apraxia and deficits in premovement planning (Haaland et al. 1999), others have found less of a relationship (e.g., Hermsdorfer et al. 1996; 1999; Ietswaart et al. 2001). Notably, the areas of damage in these patients were quite diverse, and so these studies cannot be used to draw strong conclusions regarding the function of specific brain regions. One of the reasons for the dearth of studies may be that subtle deficits in kinematic parametrization in apraxics in reaching and grasping tasks are unnoticeable or overshadowed by larger deficits in action selection. Clearly, more numerous and stringent tests of the planning–control hypothesis are needed for patients with damage centered on the left IPL or its visual inputs.

4.2. The right IPL and action planning

The right IPL has also been shown to play a role in motor planning processes. Damage to the right IPL is most closely associated with the syndrome of unilateral neglect, commonly characterized as a disorder in orienting attention to contralateral space (Kinsbourne 1987) or in the representation of the contralateral half of space (Bisiach & Vallar 1988; Bisiach et al. 1985). It is often difficult to show a relationship between the right IPL and motor deficits in these patients, because the damage often includes many other brain regions. However, studies have also demonstrated that neglect can include a motor component (Goodale et al. 1990; Heilman et al. 1985; Mattingley et al. 1994; 1998; Reuter-Lorenz & Posner 1990). In some cases, large errors early in the trajectory are corrected on-line using visual feedback (Edwards & Humphreys 1999). When visual feedback was made unavailable to the neglect patient, large errors remained, suggesting that feedback-based control was being used to correct errors in planning.

4.3. The frontal lobes and basal ganglia in planning

Just as damage to the left IPL often results in ideomotor apraxia, with its attendant errors in the spatio-temporal characteristics of movement, damage to the frontal lobes can lead to ideational apraxia. In this variant of apraxia, it is the representation of the incorporation of the *goal* of the movement that appears to be disrupted rather than the execution of the movement itself (Heilman & Gonzalez Rothi 1993). This can often be manifested in deficits in sequencing movements. The presence of ideational apraxia following damage to the frontal lobes is consistent with a role of the frontal lobes in motor planning.

The basal ganglia is also important for action planning. This region has been implicated in Parkinson's disease, a complex syndrome that includes such things as tremor, rigidity, speech disturbances, and so forth. Perhaps the most relevant symptom to the role of the basal ganglia in planning is akinesia, a difficulty in initiating movements. Damage to other regions of the basal ganglia can also cause

various symptoms, such as involuntary movements and hypokinesia (Zigmond et al. 1999).

4.4. The SPL: Optic ataxia as a deficit in on-line control

A common consequence of damage to the SPL is optic ataxia, characterized by inaccuracy in movement. According to the planning–control model, optic ataxia reflects a deficit limited to the on-line control of movements (cf. Gréa et al. 2002; Pisella et al. 2000). As such, errors in optic ataxics should be most evident in circumstances in which large corrections are required. These include movements made to perturbed targets or manual tracking movements, as well as movements made without the benefit of having foveated the target, or those made to unfamiliar targets (resulting in less accurate planning). Deficits in optic ataxics should be concentrated in the later stages of movement, and should be limited to the spatial parameters of movement, such as accuracy, grip aperture, and so forth.

The perception–action model gives quite a different account of optic ataxia, however. According to this model, the SPL is equally important during both planning and control. As such, none of the predictions of the planning–control model given above should hold true. Specifically, movements should be equally inaccurate whether or not the target is foveated, whether or not the position of the target is perturbed during reaching, or whether the task is manual tracking versus simple aiming. It will be seen that the data from SPL patients clearly favors the interpretation of optic ataxia as being a deficit concentrated in the control stage of action, consistent with the planning–control model but not the perception–action model.

4.4.1. The Perenin and Vighetto studies of optic ataxia. Although Balint (1909) and Holmes (1918) were among the first to describe the condition of optic ataxia, two of the most detailed studies carried out on optic ataxics were those of Perenin and Vighetto (1983; 1988). Perenin and Vighetto (1983) studied six patients with optic ataxia. In one task, patients reached to and grasped objects placed in various parts of their visual fields while maintaining central fixation. In a second task, patients were asked to "post" their hand into a rectangular slot oriented at different degrees in the frontal plane. A third task had patients point to targets in the periphery while manipulating the use of central versus peripheral vision and the availability of visual feedback.

In the reaching and grasping task, patients either missed the target altogether, or had to deliberately correct their movements to acquire the target. Reaching and grasping in these patients was vastly improved when they were allowed to fixate the targets. Patients were able to orient their hand correctly in the posting task, although deliberate corrections were often required.

In the pointing task, patients were accurate when they were allowed to foveate the target and to see their hands while they reached. Errors occurred when patients had to maintain central fixation, or when patients were not allowed visual feedback of the moving hand. Performance improved if patients were allowed to see their hand just before initiating the pointing movement.

Perenin and Vighetto (1988) used two of the tasks used by Perenin and Vighetto (1983), the reaching and the posting tasks. The patients in this study were similar to Perenin and Vighetto's (1983) patients, in that the common locus of damage was in the SPL, and also in that elementary motor, perceptual, and somasthetic capacities were largely intact. This study had similar results to the original, in that errors were prevalent in all tasks, and were greatest when patients were not allowed to foveate the targets (see also Carey et al. 1997).

4.4.2. Disruption of control in optic ataxic prehension. Deficits in the on-line control of grasping after damage to the SPL have also been reported. Jakobson et al. (1991) observed a patient who exhibited a gross deficit in grasping. Although their patient, V.K., showed an apparently normal early phase of hand opening during attempts to grasp an object, her on-line control of grip aperture quickly degenerated, resulting in numerous secondary peaks in the grip aperture profile (a normal profile consists of a single peak). A similar result was found in a patient studied by Jeannerod (1986; see also Binkofski et al. 1998).

Analysis of the trajectory of a reaching and grasping movement made by optic ataxics revealed velocity and grip aperture profiles that were relatively intact in the first stages of the movement (Binkofski et al. 1998; Jakobson et al. 1991; Jeannerod 1986), although the initial heading was not studied. Disturbances in the velocity or grip aperture profiles were greatest after the first "peak" has been reached (i.e., maximum velocity or maximum grip aperture).

Jeannerod et al. (1994) observed a patient with extensive damage to the SPL, secondary visual areas, and some damage to the IPL. The patient, A.T., showed marked deficits in hand shaping when grasping a plain white cylinder. These deficits existed independent of any deficit in the transport phase of reaching. However, A.T. showed a relatively normal ability to grasp familiar objects.

4.4.3. Optic ataxia disrupts adjustments to target perturbations. By adapting the perturbation paradigm to the study of an optic ataxic (I.G.), Pisella et al. (2000) provided a critical test of the importance of the SPL in control. Pisella et al. had healthy participants and I.G. point to targets that sometimes changed location coincident with movement initiation. Pisella et al. found that I.G. showed accuracy comparable to the healthy subjects in her movements to stationary targets. However, whereas normal controls were usually able to adjust to perturbed targets, I.G. was unable to make such corrections in flight. It was only when the patient was allowed to slow her movements down considerably that she was able to correct her movements.

A follow-up study of on-line adjustments in optic ataxia was carried out by Gréa et al. (2002). In this study, I.G. was instructed to reach out to and grasp an object. On some trials, the object could suddenly jump to a new position coincident with the onset of the movement. In trials in which the target remained stationary throughout the reach, I.G.'s performance was indistinguishable from the healthy controls. However, in trials in which the target changed location, I.G.'s performance was quite impaired. Whereas healthy control subjects quickly and easily adapted their movements to the new location of the target, I.G. appeared unable to adjust her movement in flight. Rather, I.G. executed two reaching and grasping movements: a movement to the original location of the target, followed by a second movement to the new location of the target. This effect was not a result of any deficit in noticing the change in target position by I.G.; she was just as quick to respond to such a change as were the healthy controls.

4.4.4. Effects of previews on an optic ataxic. Milner et al. (2001) studied the effects of previews on prehension in I.G.. Whereas I.G. showed considerable deficits in the scaling of her maximum grip aperture to the size of an object, her grip scaling was much better when the target was taken out of her sight for five seconds after its initial presentation (vision of the target was restored coincident with the signal to move). A second experiment by Milner et al. (2001) examined what happened when the target was replaced by a differently sized object during the delay period. In these cases, the optic ataxic I.G. showed a surprising amount of grip scaling to the object that had previously been shown, as opposed to the object that was currently present.

Milner et al. (2001) argued that the delay resulted in the use of the ventral stream in action production, which presumably resulted in movements after delays that were accurately based on the previously seen object (whether the same as or different from the one acted upon). In the planning–control framework, the ventral stream projections to the IPL would always be used for planning, and delays serve to "cancel" the control phase of the movement. As such, both models appear to give plausible explanations for these results.

4.5. Cerebellar ataxia

Whereas damage to the SPL can result in a deficit in the accuracy of movements under visual control, damage to the cerebellum may result in a more general form of ataxia. Cerebellar ataxics differ from optic ataxics in that their disorder does not seem to be related to vision, but rather seems to manifest itself as an overall spatial inaccuracy in movement, which, unlike optic ataxia, may include deficits in localizing points on the body (Kolb & Whishaw 1995). This deficit implicates a role for the cerebellum in the control system.

4.6. D.F.: Disrupted planning processes with intact control

In this section I describe the patient D.F., a woman who suffered severe damage to the ventral visual stream following carbon monoxide poisoning. The brain damage severely undermined D.F.'s ability to perceive form, yet left her ability to interact with objects manually relatively intact. In the planning–control framework, damage to D.F.'s ventral stream should impair many aspects of how she plans movements, but should leave her control processes essentially intact. In contrast to this, proponents of the perception–action model have argued that D.F. represents a single dissociation: damage to the ventral stream that affects perception but not action. This they have contrasted with the studies of optic ataxics described above.

4.6.1. Impaired motor abilities in D.F. Many deficits in action have been reported in D.F., consistent with an impaired planning system. For example, D.F. exhibited hypokinesia (Milner et al. 1991), similar to many patients with damage in planning regions. She was unable to reach appropriately to a target after a delay (Goodale et al. 1994a). When trying to post a T-shaped target, she was correct on half the trials, but misoriented her hand to the target by 90 degrees on the other half of the trials. Her ability to reflect knowledge of the functions of objects by choosing an appropriate reach and grasp was also impaired. Similar to many apraxics, D.F. grasped everyday objects in a manner inappropriate to their use when they were presented in noncanonical orientations (Carey et al. 1996).

4.6.2. Spared motor abilities in D.F. Despite numerous deficits in action planning, D.F. appears to possess relatively intact on-line control. For example, she was able to orient her hand correctly in a posting task similar to the one used by Perenin and Vighetto (1983; 1988) (Goodale et al. 1991; Milner et al. 1991); she could choose relatively adaptive points of contact in grasping odd-shaped objects (Goodale et al. 1994c); and showed near-normal on-line scaling of both reach and grasp parameters (Carey et al. 1996; Goodale et al. 1991; Milner et al. 1991).

Taken in sum, the constellation of impaired and spared behaviors in D.F. are just as consistent with the planning–control model as with the perception–action model. In particular, her many deficits in motor behavior can be likened to those suffered by many apraxics, whereas her spared abilities can be likened to those impaired in many optic ataxics.

4.7. TMS studies of motor control

Transcranial magnetic stimulation (TMS) appears to allow for the temporary disabling of localized brain regions (Walsh & Rushworth 1999). TMS applied over the visual motion area V5, for example, temporarily disrupts the perception of motion (Beckers & Zeki 1995). It seems logical then to assume that TMS "lesions" of motor areas underlying planning and control should lead to corresponding deficits in these behaviors, just as real lesions do. Assuming this is true, the data from studies employing TMS have been generally consistent with the predictions of the planning–control model.

Rushworth et al. (2001a) examined the importance of the IPL in premovement planning (what Rushworth et al. called "motor attention"; see also Rushworth et al. 1997b; 2001b). When TMS was applied over the angular gyrus in the left IPL, reaction times to initiate button presses in a choice response task were lengthened relative to when TMS was applied over other regions of the parietal lobes. This suggested that the left IPL was involved in the planning functions of response selection and/or initiation.

A complementary study used TMS to examine control (Desmurget et al. 1999). These authors found that TMS applied over the intraparietal region bordering the IPL and SPL disrupted the ability of participants to make on-line corrections to perturbations of a target's location. Notably, however, the application did not affect the accuracy of movements to stationary targets, in which case it might be assumed that on-line adjustments were much less necessary. This suggested that the intraparietal region was specifically involved in on-line control. Desmurget et al. were unable to localize the region of disruption to either the IPL or SPL, and the application site seems to imply the inclusion of the intraparietal region in the control system.

4.8. Summary of studies of brain-damaged populations

The evidence from human neuropsychology generally supports the distinction between action planning and control. Ideomotor apraxia, a common consequence of damage to the left IPL, can seriously impair the ability of the motor

system to plan familiar, overlearned actions (Clark et al. 1994; Poizner et al. 1995). This occurs despite the fact that these patients do not show many of the deficits in on-line control observed in optic ataxics (Heilman & Gonzalez Rothi 1993). Damage to the right IPL has been linked with hypokinesia (Mattingley et al. 1998), and hemineglect that can include errors in the initial heading of the movement (Edwards & Humphreys 1999). Damage to the frontal lobes can result in deficits in the selection of movements (Heilman & Gonzalez Rothi 1993), whereas damage to the basal ganglia can lead to Parkinson's disease, one symptom of which is akinesia (Zigmond et al. 1999).

In contrast, damage to the control regions of the brain results in a much different constellation of deficits. Three particular pieces of evidence highlight the role of the SPL in particular in control. First, optic ataxics have greater difficulty with movements to nonfoveated than foveated targets (Perenin & Vighetto 1983; 1988), the former presumably allowing for less accurate planning. Second, the kinematic profiles of optic ataxics can be relatively intact early in the reach, but become disrupted in the later stages (Jakobson et al. 1991; Jeannerod 1986). Third, an optic ataxic has been shown to be severely impaired in making on-line corrections to perturbed targets, although she can accurately direct movements to stationary targets (Gréa et al. 2002; Pisella et al. 2000). Taken in sum, these results suggest a specific role of the SPL in control.

D.F. presents a unique opportunity to study the effects of visual agnosia on planning and control. D.F.'s motor system has difficulty in tasks that emphasize planning, such as in pantomiming delayed actions to remembered targets (Goodale et al. 1994a), or when the nonspatial properties of objects, such as function, must be encoded (Carey et al. 1996). In cases of relatively straightforward manual interaction with objects, D.F.'s control processes seem to intervene and ensure accurate execution of the action (Carey et al. 1996; Goodale et al. 1991; 1994c; Milner et al. 1991).

A new area of study uses transcranial magnetic stimulation (TMS) to temporarily disable small regions of the brain. The results of these studies have generally been consistent with the planning–control model. Whereas planning is disrupted by stimulation over the IPL (Rushworth et al. 2001a), control is disrupted by stimulation to the intraparietal sulcus (IPS), bordering the SPL (Desmurget et al. 1999).

More studies will be needed to test each type of patient group (or its TMS equivalent) with the paradigms used to examine planning and control in healthy participants. For example, one could investigate the ability of ideomotor apraxics and optic ataxics to accommodate optical illusions, or to extend the work of Gréa et al. (2002) and Pisella et al. (2000) using perturbations of other spatial and nonspatial target characteristics. Apraxics and patients with Parkinson's disease might be examined using other kinds of tasks that emphasize planning, such as when affordances must be computed and postures selected (e.g., Rosenbaum et al. 1992; Short & Cauraugh 1997). D.F. might be tested on her ability to accommodate various optical illusions or perturbations. Investigations along these lines could be quite useful in expanding our understanding.

The planning–control model makes specific predictions regarding studies involving each of these classes of brain-damaged patients. For example, damage in the SPL and/or cerebellum should result in an inability to correct illusion effects on-line, owing to the disruption of the control system. These patients should also be impaired at adjusting to target perturbations on-line, as has already been found in the optic ataxic I.G. (Gréa et al. 2002; Pisella et al. 2000). Similarly, semantic interference effects on these patients ought to remain large throughout the movement. Conversely, damage to planning regions ought to result in the lack of appropriate posture selection in tasks, such as was used by Rosenbaum et al. (1992), as well as in deficits in other movements dependent on planning, such as movements to remembered targets after a delay of two seconds or longer. Finally, the patient D.F. ought to be normal in her ability to accommodate perturbations, and show similar patterns of effects of visual illusions as healthy participants.

5. Conclusions

The studies reviewed here are consistent with the characterization of the planning and control of actions hypothesized in the planning–control model. This evidence suggests that a rich and detailed visual representation exists in the IPL, which operates in concert with frontal and basal ganglia regions in movement planning. During execution, movements come increasingly under the influence of a control representation in the SPL, operating in concert with the cerebellum. The studies reviewed here are less consistent, however, with a perception–action model in which actions are thought to be both planned and controlled using a single visual representation in the SPL.

Studies of healthy participants indicate that planning and control are distinct processes that rely on distinct types of information. Perhaps the most dramatic evidence of this occurs in cases where on-line control operates outside of conscious awareness, such as during saccadic suppression (Goodale et al. 1986; Prablanc & Martin 1992), or in the on-line correction of movements made to targets subject to visual illusions (Glover & Dixon 2001a; 2001b; 2001c; 2002a) or semantic interference effects (Glover & Dixon 2002b; Glover et al. 2004).

Brain imaging studies suggest the existence of an inferior parietal/superior parietal distinction between planning and on-line control. When planning occurs without execution (Deiber et al. 1996; Grafton et al. 1998; Krams et al. 1998), the IPL tends to be much more active. During execution, activity in the SPL increases (Desmurget et al. 2001; Grafton et al. 1992; Krams et al. 1998). The planning–control distinction generally extends to other regions of the brain as well, in that planning is associated with activity in the frontal lobes and basal ganglia, whereas control is often (though not always) associated with activity in the cerebellum.

Human neuropsychology provides a useful complement to other studies of brain organization. In humans, damage to the left IPL is linked with ideomotor apraxia, which includes the loss of the ability to carry out learned actions effectively (Clark et al. 1994; Poizner et al. 1995). Damage to the right IPL often results in unilateral neglect, although this gross deficit has been shown to mask subtle defects in action planning (Edwards & Humphreys 1999; Mattingley et al. 1998). Damage to the SPL typically results in deficits in on-line control, reflected in spatial inaccuracies in reaching and grasping and kinematic profiles that appear to be disrupted mainly in the second half of the movement (Jean-

nerod 1986; Jeannerod et al. 1994; Perenin & Vighetto 1983; 1988). Damage to the SPL can also result in an absence of on-line corrections to perturbed targets (Pisella et al. 2000). The patient D.F., with damage in the ventral stream, exhibits some planning deficits, but relatively intact on-line control (Carey et al. 1996; Goodale et al. 1994b; Milner et al. 1991; Milner & Goodale 1995).

Although I have outlined a collection of regions associated with both the IPL and planning, on the one hand, and the SPL and control, on the other, future studies will be needed to clarify and elucidate the roles of these allied regions in their respective stages. Methods such as fMRI and TMS, coupled with innovative behavioral and neuropsychological studies, should offer excellent chances for isolating and examining the respective neural and behavioral bases of the planning and control of actions.

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fMRI evidence for and behavioral evidence against the planning–control model

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Abstract: Consistent with the planning–control model, recent fMRI data reveal that the inferior parietal lobe, the frontal lobes, and the basal ganglia are involved in motor planning. Inconsistent with the planning–control model, however, recent behavioral data reveal a spatial repulsion effect, indicating that the visual context surrounding the target can sometimes influence the on-line control of goal-directed action.

Glover's planning–control model postulates distinct brain areas mediating planning and on-line control of action. In this view, planning involves the inferior parietal lobe, the frontal lobes, and basal ganglia, whereas control involves the superior parietal lobe and the cerebellum. In support of this distinction, Glover cites several neuroimaging studies that used PET. Recently, we completed an fMRI study that was specifically designed to study the neural mechanisms of motor planning (Adam et al. 2003). Importantly, this study used the finger-precuing task (Miller 1982) to measure motor planning. The finger-precuing task requires subjects to respond to spatial-location stimuli with discrete responses from index and middle fingers of both hands. Preceding the target stimulus, a spatial precue indicates a subset of possible finger responses; this allows the selection and preparation of two finger responses. The fMRI data revealed that the preparation of discrete finger responses was associated with increased activation levels in the parietal cortex (inferior and superior regions, intraparietal sulcus), the frontal cortex (middle frontal gyrus, premotor and supplementary motor cortex), and the basal ganglia (caudate nucleus and putamen). This outcome generally corroborates the planning network as proposed by Glover, except for the involvement of superior parietal lobe (and possibly the intraparietal sulcus bordering the inferior and superior parietal lobe). However, as Glover has pointed out, and consistent with other neuroimaging studies, the increased activity in the superior parietal lobe probably reflects the attentional effects of the spatial cues.

Furthermore, the planning–control framework introduced by Glover postulates a distinction between planning and on-line control of actions. Whereas planning is assumed to take into account various sources of visual and cognitive information, control is limited to the spatial characteristics of the target and the actor. Importantly, according to the planning–control model, the visual context (e.g., objects surrounding the target) is ignored during on-line control. However, recent data suggest that the visual context also can influence control. In two studies (Keulen et al. 2002; 2003), we investigated distractor interference in selective reaching. Participants pointed to a target appearing in isolation or concurrently with a distractor. The distractor could appear either in front of or beyond the target. With a small (i.e., 5 mm) separation between target and distractor we observed a spatial repulsion effect; that is, the movement endpoints were biased away from the location of the distractor. In other words, participants ended their movements within the prescribed target area so as to maximize the distance to the adjacent distractor (for a first demonstration of this effect, see Fischer & Adam 2001). The fact that the repulsion effect was small but consistent (i.e., 0.6 mm on average), and occurred only when target and distractor were close to each other, suggests that the spatial repulsion effect reflects on-line control rather than planning. Thus, the spatial repulsion effect indicates that the immediate visual context surrounding the target can influence the on-line control of actions. Certainly, this observation is not fatal for Glover's model, but it represents a minor qualification to one of its premises.

At least some electrophysiological and behavioural data cannot be reconciled with the planning–control model

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Abstract: The planning/control distinction is an important tool in the study of sensorimotor transformations. However, published data from our laboratories suggest that, contrary to what is predicted by the proposed model, (1) structures in the superior parietal lobe of both monkeys and humans can be involved in movement planning; and (2) fast pointing actions can be immune to visual illusions even if they are performed without visual feedback. The planning–control model as proposed by Glover is almost certainly too schematic.

Can we make a sharp distinction between planning and control in human action production? There is little doubt that planning must precede the onset of movement, whereas on-line control must become increasingly important as the action progresses. It remains to be seen, however, whether this obvious temporal ordering is

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 endopoint, 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; Plamandon 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 midline 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

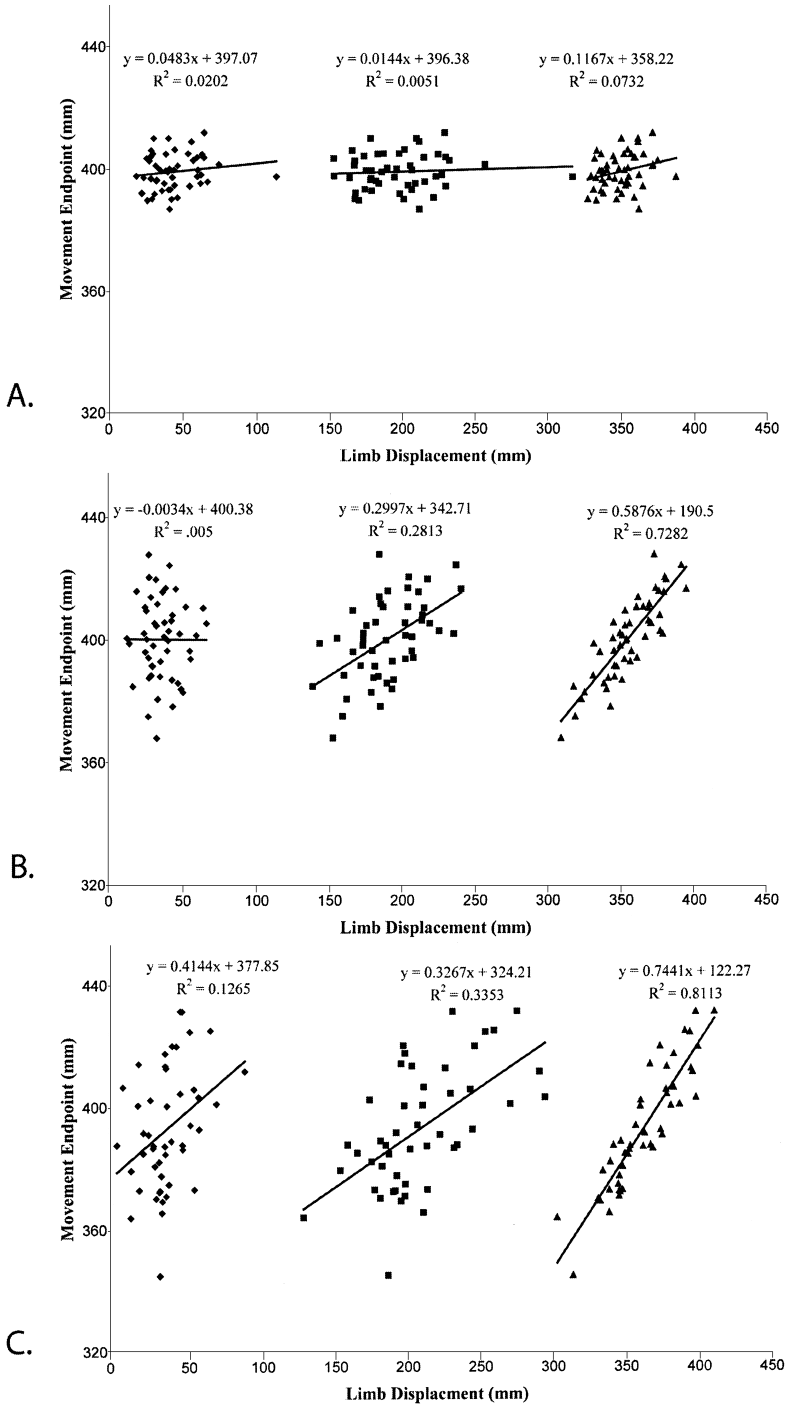

Figure 1 (Binsted & Heath). Predictability of movement endpoint from mid-trajectory limb positions. The proportion of endpoint variance (R^2) in movement endpoints (primary movement axis) explained by the limb position at three positions (25% ◇, 50% ■, and 75% ▲ of movement time) is presented for an 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).

ACKNOWLEDGMENTS

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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 together 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).

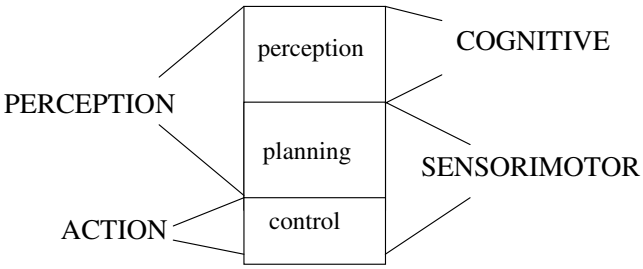

Figure 1 (Bridgeman). Three ways of parsing perception, planning, and control functions.

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

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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

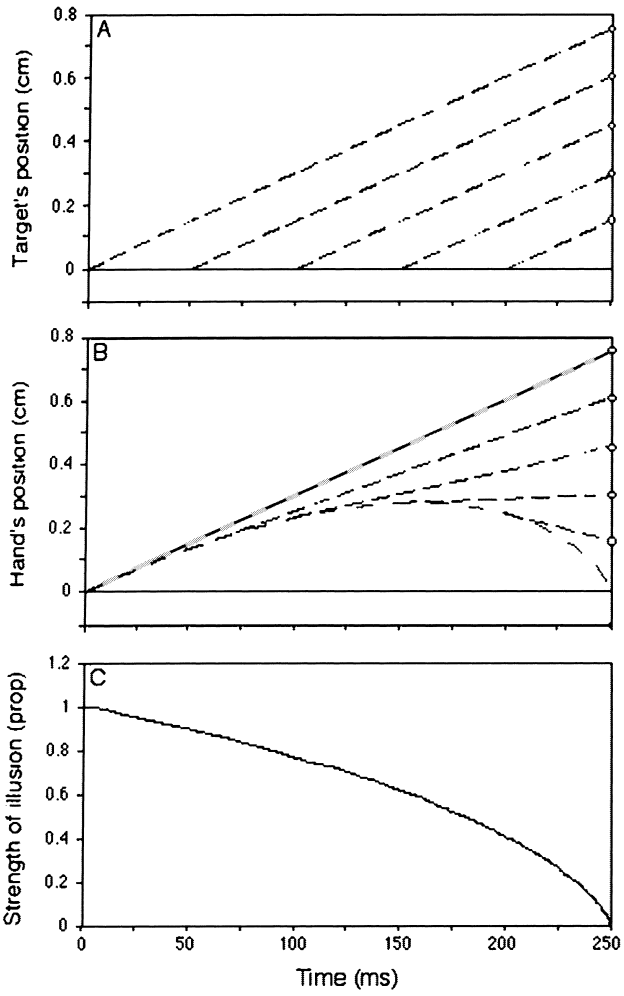

Figure 1 (Brouwer et al.). Hitting a moving disc when the direction of motion is misperceived. Schematic illustration of the disc's predicted final positions (A), the direction of hand movement (B), and the scaled magnitude of the effect of the illusion (C). The hand was simulated to move for 250 msec (which was about the average movement time in our experiment). **A:** The solid line indicates the lateral position over time of a disc that moves straight down but is perceived to move at an angle of 9.5 degrees from the vertical. The dashed lines indicate the disc's extrapolated movement at time samples of 0, 50, 100, 150, and 200 msec after the hand started to move. The disc's correctly perceived position and its misperceived direction of motion are used for the extrapolation. The white dots represent the disc's predicted final positions. **B:** The lateral position of the hand over time when hitting (a) a disc that moves straight down (vertical velocity of 18 cm/sec, horizontal velocity of 0 cm/sec) with a correctly perceived direction of motion, indicated by the black solid line, (b) a disc that moves at an angle of 9.5 degrees (vertical velocity of 18 cm/sec, horizontal velocity of 3 cm/sec) with a correctly perceived direction of motion, indicated by the grey solid line, and (c) a disc that moves straight down, but is perceived to move at an angle of 9.5 degrees (an illusory horizontal velocity of 3 cm/sec), indicated by the curved dashed line. For this disc, the straight dashed lines indicate that at each time sample, the hand moves straight towards the disc's final position as predicted at that time sample. The dashed line for the first time sample overlaps the solid grey line. **C:** The effect of the illusion over time. This is the lateral hand position for hitting a disc with an illusory direction of motion of 9.5 degrees divided by the lateral hand position for hitting a disc with an actual direction of motion of 9.5 degrees. The effect of the illusion decreases during the movement.

effect of the illusion arises because of a timing difference between the increase in grip aperture caused by a larger approach parameter and that caused by a larger target. Additionally, the illusion necessarily decreases to zero because the digits continue to move to the intended contact positions. In a similar vein, the model can account for the dynamic effect of the Müller-Lyer illusion (a larger approach parameter for the line with the inward directed arrows, to avoid the protrusions). The model is also consistent with the observed decrease in the effect of an orientation illusion on the hand's orientation during grasping (Smeets et al. 2002).

In conclusion, we believe that the dynamic illusion effect in action does not justify the assumption of different visual representations for planning and control, or even the use of different sources of information before and during a movement. We have shown that the dynamic illusion in both interception and grasping can be explained without assuming a change in the information used.

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Planning and controlling action in a structured environment: Visual illusion without dorsal stream

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Abstract: Some data concerning visual illusions are hardly compatible with the perception–action model, assuming that only the perception system is influenced by visual context. The planning–control dichotomy offers an alternative that better accounts for some controversy in experimental data. We tested the two models by submitting the patient I. G. to the induced Roelofs effect. The similitude of the results of I. G. and control subjects favoured Glover's model, which, however, presents a paradox that needs to be clarified.

Since the pioneering work carried out by Woodworth (1899), a recurrent issue in the studies relating to visuomotor control concerns the way visual inputs are used to locate a target in the reaching space. A large body of data in the recent scientific literature has underlined the fact that planning a movement requires that many spatial aspects of not only the target but also of the surrounding contextual elements have been previously considered together. As an illustration, a luminous target in a dark context is perceived as being closer than its actual position and is undershot when reached manually with no visual feedback about the hand trajectory (Conti & Beaubaton 1980; Foley 1980). By contrast, spatial performance improves when the visual environment is structured; merely adding a textured background in the workspace improves movement terminal accuracy (Coello et al. 2000).

Another line of evidence is the fact that having the hand and the target in the visual field simultaneously improves the visuomotor performance, which indicates that an accurate assessment of the gap separating the hand and the target is one of the main determinants of spatial performance (Rossetti et al. 1994). In agreement with the latter point, the location of contextual information in relation to the self and the target plays a crucial role in determining reaching accuracy, with elements placed in the space through which the reach occurs conferring the most benefit (Coello 2002; Grealy et al. 2003). Interestingly, structuring the visual field has a broad effect on the control of movement amplitude but leaves the control of movement direction unaffected (Coello & Magne 2000). We recently reported that unexpectedly append-

ing a textured background in the action space had an instantaneous concomitant effect on movement amplitude and peak velocity (Magne & Coello 2002), indicating that the improvement in the motor performance was mainly the consequence of a more accurate visual system.

These observations are partly in agreement with Glover's contention that motor planning process depends on a number of factors including the object of the action (spatial and nonspatial characteristics), the surrounding environment, and the internal state of the actor, while control process focuses mainly on the on-line minimisation of the spatial error of the movement (sects. 1.1.1, 1.1.2). Adjusting the planning process in flight, the control system is restricted to the spatial characteristics of the target and is thus immune to the interference of visual context (sect. 1.1.3). The idea of a certain independence of planning and control processes is supported by numerous data and has been already suggested in the past (e.g. Pisella et al. 2000). However, assuming together that (1) context information plays a crucial role in target coding (as shown above), and that (2) the function of the control system is to amend the planning process in flight on the basis of only the spatial characteristics of the target, leads to a neglected paradox. Disregarding the situation where direct visual control is available, one may wonder what would be the benefit of a control system adjusting the displacement of the hand (estimated through proprioceptive signal and efferent copy) towards a visual target that is perceived at an erroneous distance (which is the case when contextual information is not included in target coding). Furthermore, providing contextual information in the form of a textured background was found to improve the planning process – but also the on-line control process. Indeed, the benefit of providing contextual information during both movement planning and movement execution (in the form of a textured background) was exactly equal to the sum of the benefit of providing contextual information during only movement planning or only movement execution (see Fig.1). This additive effect cannot be accounted for by the fact that the planning system overlaps the control system during movement execution (sect. 1.1.4).

Furthermore, the magnitude of the effect was higher in the execution than in the planning stage. This outcome supports the idea of an independent use of visual information during planning and control processes, in agreement with Glover's model, but demonstrates that the control process cannot be considered to be immune to the interference of visual context (sect. 1.1.3), at least not when distance coding is taken into account.

This parametric framework is of paramount importance to understand the dissociation between perception and action. As indicated by Glover, the dominant theory during the past decade has been the one propounded by Milner and Goodale (1995). According to this theory, a single visual representation is considered to subserve actions, whereas a separate representation subserves perceptions (sect. 2.6.1). The core idea of the theory is that the processing of visual information is thought to involve independent streams from the primary visual cortex. Visual processing for goal-directed behaviour is predominantly supported by the occipito-parietal pathway (dorsal stream), while visual processing for conscious perception is performed through the occipito-temporal pathway (ventral stream). These two types of processing have been assumed to give rise to the independent "sensorimotor" and "cognitive" representations of visual space (Paillard 1987; Rossetti 1998).

Many findings are consistent with the idea that visual illusions influence perception more than action. The first evidence came from the Induced Roelofs Effect (IRE; Bridgeman 1991b). Observers were asked to estimate the egocentric position of a luminous target appearing inside a surrounding frame at various locations along the fronto-parallel axis. When the frame had a lateral offset, the target was misperceived to be in the controlateral direction when estimated verbally but not when located with a manual reaching response. The interpretation of such dissociation was that the cognitive system dealing with relative positions elaborates an explicit qualitative representation, which includes information

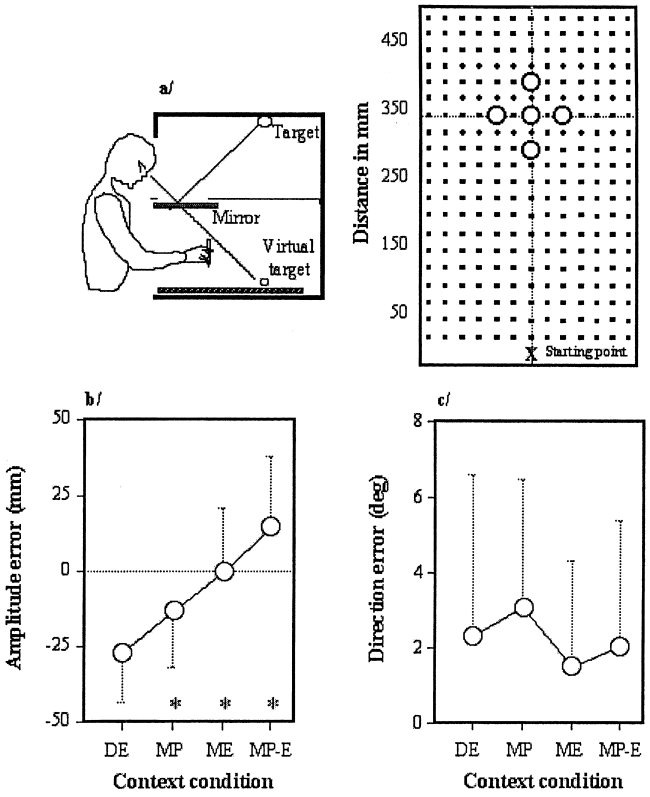

Figure 1 (Coello & Rossetti). (**a**) Apparatus and visual scene seen by the participant in presence of a textured background. (**b**) Mean amplitude error and (**c**) mean direction error of pointing movements as a function of the context condition: dark environment (DE), background during movement planning (MP), background during movement execution (ME), background during movement planning and movement execution (MP-E). (*) Indicates when performances were significantly influenced by the presence of a textured background, with respect to the dark condition. (Adapted from Coello & Magne 2000.)

relating to the whole visual scene even when the processing of contextual elements leads to localisation errors. Conversely, dealing with absolute positions, the sensorimotor system elaborates an implicit quantitative (metric) representation of visual space that is insensitive to contextual information (Bridgeman 1991b; 2000). According to Glover, the lack of effect of the contextual frame on the manual response might be due to the fact that the control system adjusts the motor performance in flight on the basis of a spatial analysis that remains immune to the interference of visual context (sects. 1.1.3 and 2.6.2). However, we recently reported data that support none of these interpretations (Coello et al. 2003). Using the IRE, but in slightly different experimental conditions, we found a dissociation in the influence of the off-centre frame on the motor response that was dependent on the spatial dimension tested. When the frame was displaced along the fronto-parallel axis, the target was misperceived along the same axis but in the opposite direction, while the manual capture of the target remained unaffected in keeping with the original study. However, the IRE interfered with perceptual and pointing responses in identical ways when the frame was displaced along the sagittal axis. Hence, the processing of visual information for action is not always immune to contextual influence, which appears to be dependent on the spatial dimension (direction or distance) that the task emphasises.

The crucial issue that remains to be addressed concerns the neurophysiological substrate which can subserve the distinct influence of visual context on distance and direction parameters. Based on a case study of optic ataxia, Mon-Williams et al. (2001)

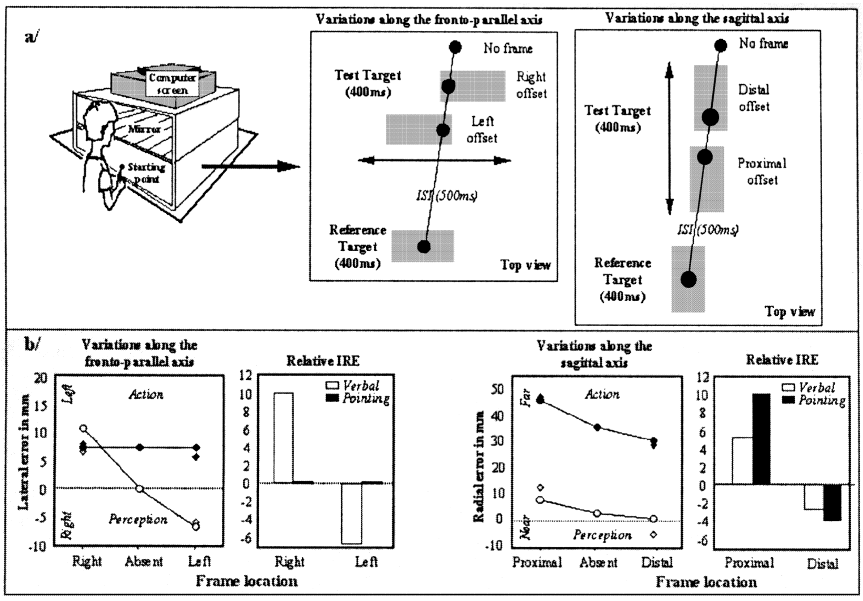

Figure 2 (Coello & Rossetti). (**a**) Apparatus and sequence of stimuli presented to the patient I.G. The Reference Target was presented simultaneously with a centred frame for 400 msec at two possible locations. Following a blank period of 500 msec, a Test Target was presented at a position similar to that of the Reference Target, at ±8mm, or at ±16mm along the fronto-parallel axis, or along the sagittal axis. It was accompanied with an off-centre frame or was presented alone. The task was to determine whether the Test Target was at the same position or not, compared to the Reference Target position, or to point towards the Test Target (for a detailed presentation of the method, see Coello et al. 2003). (**b**) Induced Roelofs effect along the fronto-parallel axis (left) and sagittal axis (right) for the patient I.G. Considering the fronto-parallel dimension, the induced Roelofs effect influenced the verbal response (open circle) but not the pointing response (filled circle) though the patients showed a constant bias to the left. Considering the sagittal dimension, the induced Roelofs effect influenced both the verbal response (open circle) and the pointing response (filled circle), the latter showing a constant overshoot of the target. Control performances (adapted from Coello et al. 2003) are indicated by the diamond, but normalised with respect to the no frame condition in order to allow a direct relative comparison of effect size in IG and controls.

suggested that the ventral stream is responsible for extracting distance information from monocular retinal cues, such as shading, texture, and perspective, while the dorsal stream has access to binocular information from disparities and vergence. This makes our results compatible with the Milner and Goodale model. Thus, the lack of dissociation between perception and action along the sagittal axis with the IRE could be interpreted as a greater participation of the ventral stream in distance processing, independent of the type of response or the viewing condition. However, according to Glover's model, the ventral system is involved in any aspect of motor planning. In this model, simple movements, such as reaching and grasping, tend to rely on the IPL for movement planning. Visual information can be projected to the IPL via the temporal lobe (which carries out information about spatial and nonspatial characteristics of a target and the surrounding context) and the "third" visual stream (sect. 1.2.2; but see review: Rossetti et al. 2000; Rossetti & Pisella 2002).

One way to contrast these two models would be to evaluate the performance of a patient with an impaired dorsal stream when confronted with the IRE. According to the ventral-dorsal dichotomy, an impaired dorsal stream would lead the patient to be unable to perform accurate motor acts considering the strong implication of the dorsal stream in motor control. Previous observations have shown, however, that this is not the case (Rossetti et al. 2003). Another possibility would be that the participation of the ventral stream is strengthened in the organisation and control of the motor acts in order to compensate for the impaired dorsal stream (Milner & Dijkerman 2001; Rossetti & Pisella 2002). One would therefore expect an effect of the IRE in both the fronto-parallel and the sagittal axes. By contrast, according to the planning-control dichotomy, the ventral stream participates in movement planning in all aspects and therefore, no discrepancy between the patient and the control participants is expected. We recently tested patient I.G., a 31-year-old woman who had suffered bilateral parieto-occipital infarction one and a half years ago, resulting in a severe bilateral ataxia (see Pisella et al. [2000] for a detailed description). As shown in Figure 2, when submitted to the IRE, I.G. showed a pattern of results very similar to that of the control subjects, which stands in support for Glover's model.

In conclusion, many of the recent data concerning visual illusions are hardly compatible with the simple perception–action model, assuming in particular that only the perception system is subjected to context influence. The planning–control dichotomy offers an alternative that better accounts for the apparent controversy in experimental data related to visual illusions. However, to provide a general framework, it seems imperative to solve the paradox in the model, which originates from the fact that the role of the control system is thought to reduce spatial errors denying context information, while it nonetheless has been demonstrated that visual context broadly contributes to the accurate coding of target location.

The planning–control model and spatio-motor deficits following brain damage

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Abstract: Glover's planning–control model accommodates a substantial number of findings from subjects who have motor deficits as a consequence of brain lesions. A number of consistently observed and robust findings are not, however, explained by Glover's theory; additionally, the claim that the IPL supports planning whereas the SPL supports control is not consistently supported in the literature.

Although we agree that the distinction between planning and control of action provides a useful framework for analyzing motor performance, the claim that motor planning is mediated by the inferior parietal lobe (IPL) and control by the superior parietal lobe (SPL) appears to be too strong. Whereas the planning–control hypothesis offers an adequate account of the basic features of ideomotor apraxia and optic ataxia, there are several important aspects of these clinical syndromes that are not accommodated by the planning–control model as articulated by Glover.

1. Planning and praxis. The planning–control model bears a number of similarities to a model of apraxia we recently proposed (Buxbaum 2001). We suggested that skilled action retrieval and production is a constructive process, requiring that stored representations of object-related actions mediated by the left IPL be tempered on-line by the dorsal stream in response to current environmental contingencies. We argued that the most common type of ideomotor apraxia is attributable to damage to what we called the "representational" IPL system and relative preservation of the "dynamic" dorsal system. The planning–control model goes beyond this proposal to explicitly align the representational system with planning stages of action, and we believe that this nuance has the potential to offer additional insights about the behavior of apraxic patients.

One observation consistent with the planning–control model is that IPL-lesioned apraxics are deficient in their ability to generate or recognize hand postures associated with using familiar objects in a skilled manner, but intact in their ability to generate and recognize postures for grasping the same objects. In fact, in the former situation, they often "default" to a generic grasping posture. This suggests that their deficits in the IPL-mediated skilled knowledge system force reliance on dorsally mediated on-line motor control (Buxbaum et al. 2002). Even more directly relevant to the planning/control distinction is the observation that apraxics are deficient in motor imagery (Sirigu et al. 1996). Apraxics are impaired in planning grasp of objects based on their orientation in space, as judged by their deficient motor imagery of the grasp posture they would use if they were to grasp the object. In contrast, their actual grasping of the same objects is intact. Presumably, once movement is launched, reliance upon intact feedback loops from proprioception and sensation enables correction of error arising in the earlier planning component (Buxbaum et al., submitted).

Another observation consistent with the proposed model is that object manipulation knowledge (arguably a form of semantic knowledge) appears to be mediated by the IPL. Knowledge of the manner in which an object is manipulated (but not knowledge of an object's function) is disrupted in apraxics with IPL damage (Buxbaum & Saffran 2002). In parallel, several recent fMRI studies have shown that questions about how objects are manipulated activate regions of the IPL and intraparietal sulcus (Boronat et al., submitted; Kellenbach et al. 2003). These data are suggestive of a relationship between action planning and semantic information similar to that proposed by Glover.

On the other hand, there are at least two observations from apraxia suggesting that the model requires refinement. One observation is that apraxics have difficulty learning new gestures (Gonzalez Rothi & Heilman 1984). The model doesn't account for the links between motor planning, new learning, and retention of previously learned motor skills. One possible explanation for this relationship is that all three require the ability to generate and maintain internal (forward and inverse) models of action. The second observation is that there is a large and frequently cited disparity between transitive (object-related) and intransitive (non-object-related) gesture. Critically, left IPL-lesioned apraxics often perform normally on tasks requiring retrieval of intransitive gestures from memory. This suggests that the left IPL is specialized not just for action planning, but for skilled object-oriented action planning as well. This proposal is consistent with the putative importance of this structure in mapping between ventral stream representations of objects, on the one hand, and dorsal action systems, on the other (Buxbaum 2001).

2. The planning–control model and reaching. The hypothesis that the IPL is specialized for planning skilled object-oriented action (and not just action in general) would explain the apparent preservation of planning of non-object-related movements (e.g., reach) in several patients we recently reported. One such patient (J.D.; cf. Schwoebel et al. 2001) had a predominantly left IPL lesion in the context of generalized atrophy. She exhibited a striking deficit in "motor control," in that she was unable to reach to a target after passive movement of her arm. For example, when J.D. reached toward a visually presented target after closing her eyes, terminal error was relatively small. If, on the other hand, her arm was passively moved to a new position after visualizing the target and closing her eyes, reaching was grossly inaccurate. In a different experiment, J.D. visualized a target, touched her nose, closed her eyes, and reached. Performance did not differ substantially from the condition in which she did not move her arm prior to reaching. In contrast, if J.D.'s hand was passively moved to her nose after visualizing the target and closing her eyes, reaching accuracy deteriorated markedly. We suggest that J.D. is unable to use proprioceptive feedback to guide reaching behavior, and despite her IPL lesion, relies on a "forward," or predictive, model for motor control. These and other data from patients with predominantly IPL lesions (e.g, Schwoebel & Coslett 2002) suggest that the claim that planning and control are mediated by the IPL and SPL respectively is too strong.

Finally, the account of optic ataxia offered by the planning–control account fails to address the often robust effects of factors such as the hemispace in which the action is performed. The fact that optic ataxia may be manifested by the contralesional hand in only one hemispace or exhibited in the contralesional hemispace by either hand suggests that both the "control" and the "planning" components of the model – and the boundaries between them and related perceptual and motor representations – need substantial elaboration (see Buxbaum & Coslett 1997, 1998; DeRenzi 1982).

In summary, we believe that Glover's assertion regarding the anatomic underpinnings of motor planning and control is overly simplistic, and we note a number of respects in which the account is underspecified. Nevertheless, as the hypothesis accommodates a substantial amount of evidence from diverse sources and generates specific, testable predictions, the planning–control model as articulated by Glover represents a welcome contribution to the rapidly evolving field of motor cognition.

Scale errors by very young children: A dissociation between action planning and control

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Abstract: Very young children occasionally commit *scale errors,* which involve a dramatic dissociation between planning and control: A child's visual representation of the size of a miniature object is not used in planning an action on it, but is used in the control of the action. Glover's planning–control model offers a very useful framework for analyzing this newly documented phenomenon.

The target article by Glover focuses exclusively on research with adults, but the planning–control model also has useful applications in the developmental domain. In particular, it is very helpful for thinking about a new developmental phenomenon – *scale errors* – that my colleagues and I have recently described (DeLoache et al. 2003).

Scale errors involve a dramatic dissociation between planning and control that occurs occasionally in the behavior of very young children: A child's visual representation of the size of an object is basically ignored in the process of planning an action on it, though

it is brought to bear in the motor control of the action. A prototypical example of a scale error, and one of the original observations that sparked our interest in this topic, is a toddler attempting to sit on a miniature (dollhouse-size) chair. Other examples we have informally observed include young children trying to lie down in a doll's bed and attempting to get into a small toy car.

A scale error is defined as an attempt to perform an action that is totally impossible because of extreme differences in size – in this case, between a child's own body and a target object. When committing scale errors, children appear to be completely serious, with no indication of pretense or joking.

In our initial study designed to document the phenomenon of scale errors, children between 18 and 30 months of age were induced to play with three large toys in a laboratory playroom. They climbed up and slid down an indoor slide, sat in a child-sized chair, and got into and propelled a car around the room. Then, while the child was out of the room, each of the three large items was replaced by a miniature replica.

When they returned to the room, almost half of the children committed scale errors that were captured on camera. Some of them tried to climb up the stairs of the little slide, typically causing it to tip over. Others sat on top of the slide and attempted to go down it, often falling off in the process. Some of the children sat firmly down on the tiny chair, whereas others perched gingerly on top. Most remarkable of all, some children earnestly tried to get into the miniature car. After opening the car door, they attempted – sometimes quite persistently – to shove their foot in the small opening. The best way to appreciate the nature of these scale errors is to see them in action (which can be done by going to the following website: http://faculty.virginia.edu/childstudycenter/projects.html).

A particularly intriguing aspect of scale errors is that although the child's general plan is impossible because of the size of the target object, some of the movements that the child makes toward the object are accurately scaled. When trying to sit in a tiny chair, children typically check visually to see where the chair is, sometime even bending over and looking between their legs to locate it precisely. They then squat over it, lowering themselves to the point of contact. When trying to get into the miniature car, children first use fine motor control to open the car door. In addition, they sometimes hold on to the top of the car while trying to force their foot through the door, especially if their initial effort to get in has caused the car to skitter away.

It is this remarkable combination of wildly inaccurate and highly accurate behavior for which we find Glover's planning–control model to be particularly helpful. Interpreting scale errors in terms of his theory places their origin in the planning system. When a very young child encounters a miniature replica of a highly familiar type of object, visual processing of the replica activates the child's semantic representation of the larger object, or the class of objects, it stands for. Included in the activated memory representation of the full-sized object is the motor program or routine for interacting with it. Normally, visual processing of the size of the replica inhibits execution of the activated motor routine, and the child either does not attempt to act on the replica at all or carries out a very different action, such as pretense (for example, setting a doll in the miniature chair or pushing the car around on the floor making "vroom" sounds). Occasionally, however, for some reason an action plan is formed that does not take the available size information into account. Once the plan is initiated, the control system draws on the visual representation of size and adapts the child's movements to the actual size of the object. Thus, in the commission of a scale error, a child formulates an impossible plan but then employs finely controlled motor actions in the futile pursuit of it.

The application of Glover's theory to the scale error phenomenon extends it in three ways. First, in contrast to most of the research on which the model was originally formulated, here it is applied to full-body movements performed in large-scale space on real objects. Second, the planning–control dissociation is shown in the behavior of individuals, rather than by comparisons across participants. The same child fails to use size information in the process of formulating a fundamentally faulty plan, but does incorporate perceived size in the attempted execution of the plan. Third, applying Glover's planning–control model to the scale errors of very young children extends it to the developmental domain. Some developmental researchers have profitably applied the dual visual systems theory of Milner and Goodale (1995) to research on visually directed reaching in infants (e.g., Bertenthal 1996; Newman et al. 2001; Vishton 2003; Von Hofsten et al. 1998), and further valuable insights are likely to result from the consideration of early behavior in the light of the planning–control model.

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Visual context can influence on-line control

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Abstract: Several lines of evidence indicate that the on-line control of rapid target-aiming movements can be influenced by the visual context in which the movements are performed. Although this may result in movement error when an illusory context is introduced, there are many situations in which the control system must know about context in order to get the limb to the target rapidly and safely.

Beginning with the seminal work of Woodworth (1899), there is a long history of theorizing about the separate contribution of movement planning and on-line control processes to the regulation of goal-directed movement (see Elliott et al. [2001] for a recent review). However, Glover's planning and control formulation does have several features that make it a unique dual-process model of motor control. The most important of these features is the postulate that separate visual representations subserve movement preparation and on-line control. Although it is clear that different types of visual information are important for response selection, movement parameterization, and the rapid on-line modulation of movement, we are not convinced that the dichotomy described by Glover captures the flexible nature of on-line control. In this commentary, we review evidence from several aiming studies that indicates control processes can be sensitive to the visual context in which the aiming movement is performed.

In two of our recent experiments (cf. Meegan et al., in press), participants were required to aim a stylus from one vertex of Müller-Lyer figures to the other. In the first experiment, vision of both the limb and the figure was eliminated upon movement initiation, and in the second experiment participants were able to see their limb but not the figure during the movement. Regardless of whether there was a delay between elimination of the target figure and movement initiation, participants' aiming accuracy was biased by the Müller-Lyer configurations. Measures of displacement taken at peak velocity, at peak deceleration, and at the end of the movement indicated that the absolute magnitude of illusion-induced biases actually increased as the movement progressed. This was in spite of a dramatic trial-to-trial spatial variability decrease between peak deceleration and the end of the movement, indicating that participants were engaged in on-line control. These results are incompatible with both Glover's planning–control model, and Goodale and Milner's (1992) ventral-dorsal model.

In this same theoretical context, Proteau and Masson (1997) reported work that creates difficulty for the notion that the control system is uninfluenced by the visual environment surrounding the target. Their research involved participants making aiming move-

ments to a stationary target embedded in a background that moved in either the same direction as the effector or in the opposite direction. These background perturbations, which were introduced at movement initiation, produced systematic overshooting and undershooting of the target respectively. Proteau and Masson postulated that when the background was moving in the same direction, the effector was judged to be moving more slowly than it really was and the movement was not terminated as soon as it should have been (i.e., a target overshoot). When the background was moving opposite to the direction of the movement, movement velocities were judged to be greater than they really were and the movement was terminated too early (i.e., target undershoot). Once again limb control appears to be susceptible to an illusory visual context. In a related study, Brenner and Smeets (1997) demonstrated that background motion introduced after planning affected the trajectory of manual aiming movements directed at foreground targets.

The notion that the control phase of an aiming movement is affected by visual context is consistent with aiming experiments in which the size-contrast illusion has been shown to influence movement time (e.g., van Donkelaar 1999). Although we agree with Glover that movement planning is partially responsible for the movement time-target size relation (e.g., peak velocity and the time to peak velocity), experiments in which target size changes on movement initiation (e.g., Heath et al. 1998) indicate that the time after peak velocity depends more on the target size after movement onset than the size of the target prior to the initiation of the movement. Moreover, the control system is able to adjust the temporal characteristics of the movement very rapidly in order to deal with target size perturbations.

While in some of the experiments described above, the visual surround contributed to either spatial error or temporal miscalculation, under many normal circumstances, visual context may prove to be important for efficient and safe on-line control. For example, when picking a berry from a thorny bush, or removing a steak from the grill, "good planning" may not always be enough to avoid an injury. The control system needs to take into consideration objects that surround the target or unexpectedly obstruct the path to the object once the movement is already underway. Certainly our ability to intercept a moving target depends partly on the expansion-contraction of the target's image on the retina relative to other objects. Similarly, the velocity of the effector used to intercept the target object will be judged relative to the visual environment in which it moves.

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Is there a dynamic illusion effect in the motor system?

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Abstract: Glover's planning–control model is based on his finding that visual illusions exert a larger effect in early phases than in late phases of a movement. But evidence for this dynamic illusion effect is weak, because: (a) it appears difficult to replicate; (b) Glover overestimates the accuracy of his results; and (c) he seems to underestimate the illusion effect at late phases.

Scott Glover draws a plausible picture of the visuo-motor system, such that we might be tempted to follow his arguments and believe in a planning–control model of action. However, Milner and Goodale (1995) also provided a plausible account of the visuo-motor system, as have other researchers (e.g., Livingstone & Hubel 1988; Schneider 1969; Trevarthen 1968; Ungerleider & Mishkin 1982). Logically, it seems unlikely that all these theories are correct. This necessitates a careful examination of the evidence used by the researchers. Here, I argue that Glover's most important evidence, the dynamic illusion effect, is weak. In fact, the dynamic illusion effect might not exist.

Glover and Dixon (2001a; 2001b; 2002a; 2002b) found that visual illusions exert a larger effect on early phases of a movement than on late phases. However, a careful examination of the studies shows that there are a number of problems related to this finding of a dynamic illusion effect. I will explain these problems using data from one of our studies (Franz et al. 2000), which I reanalyzed to test Glover's account (Franz 2003; submitted). In this study, participants repeatedly grasped objects of different sizes while perception of size was distorted by two different levels of the Ebbinghaus illusion. The aperture between the fingers was measured at different time points in the reach-to-grasp movements. The illusion effects are shown in Figure 1a. At first sight, the illusion seems to increase over time (instead of decrease, as suggested by Glover).

However, at early time points, the grasp aperture hardly responded to *any* variation in size, even if the physical size was varied (Fig. 1b). For an evaluation of the illusion effects, we have to take into account this smaller degree of responsiveness: We have to "correct" the illusion effects for the physical size effects. Only after this correction, can we detect a dynamic decrease of the illusion effect (if it exists).

In principle, the correction could be fairly easy: At each time point, we simply divide the illusion effect by the physical size effect (cf. Franz et al. 2001; Glover & Dixon 2001a). However, we also need to estimate confidence limits for the corrected illusion effects. This is not trivial, because we have to take into account the variability of the numerator and of the denominator. Consider the case where the confidence interval of the denominator contains a zero value. In this case, the corrected illusion effect can become arbitrarily large (or small), with arbitrarily large variability.

The method Glover and Dixon used to calculate confidence limits (or standard errors) for the corrected illusion effects ignores the variability of the denominator. This underestimates the variability of the corrected illusion effects. As I have discussed in detail (Franz, submitted), this problem can be most pronounced in early phases of the movement because here the physical size effect (i.e., the denominator) is close to zero.

Figure 1c demonstrates this problem for our data: Using Glover's method, one might be tempted to interpret the large corrected effect at $t = 0\%$ as evidence for a dynamic decrease of the illusion effect. The mathematically exact method (Fieller 1954; Franz, submitted), however, clearly shows that this value is a statistical outlier (Figure 1d): The confidence limits are *infinite*, because the physical size effect is too close to zero.

Figure 1d shows that (except for the outlier at $t = 0\%$), the corrected illusion effect is surprisingly constant, contrary to Glover's proposal. Now, it may be argued that these data have a drawback: Time points occurring after the maximum grip aperture (MGA) were not included in the analysis ($t = 100\%$ corresponds to the time of the MGA). However, the reason time points beyond the MGA were not included is because the fingers are already very close to the target after the MGA, and quite often will touch the target object, which would contaminate the data. But what if the dynamic illusion effect shows up only at time points after the MGA? To test for this, we reanalyzed the data of another study (Franz et al. 2003) and made sure that the trajectories were included as long as possible, but without the fingers touching the target object. Again, we found constant illusion effects over time, without any indication of a decrease. If at all, the corrected illusion effects slightly increased over time (Franz & Scharnowski 2003).

Why, then, did Glover and Dixon find a dynamic illusion effect? A close inspection of their results shows that the decrease of the corrected illusion effect occurs mainly at very late time points,

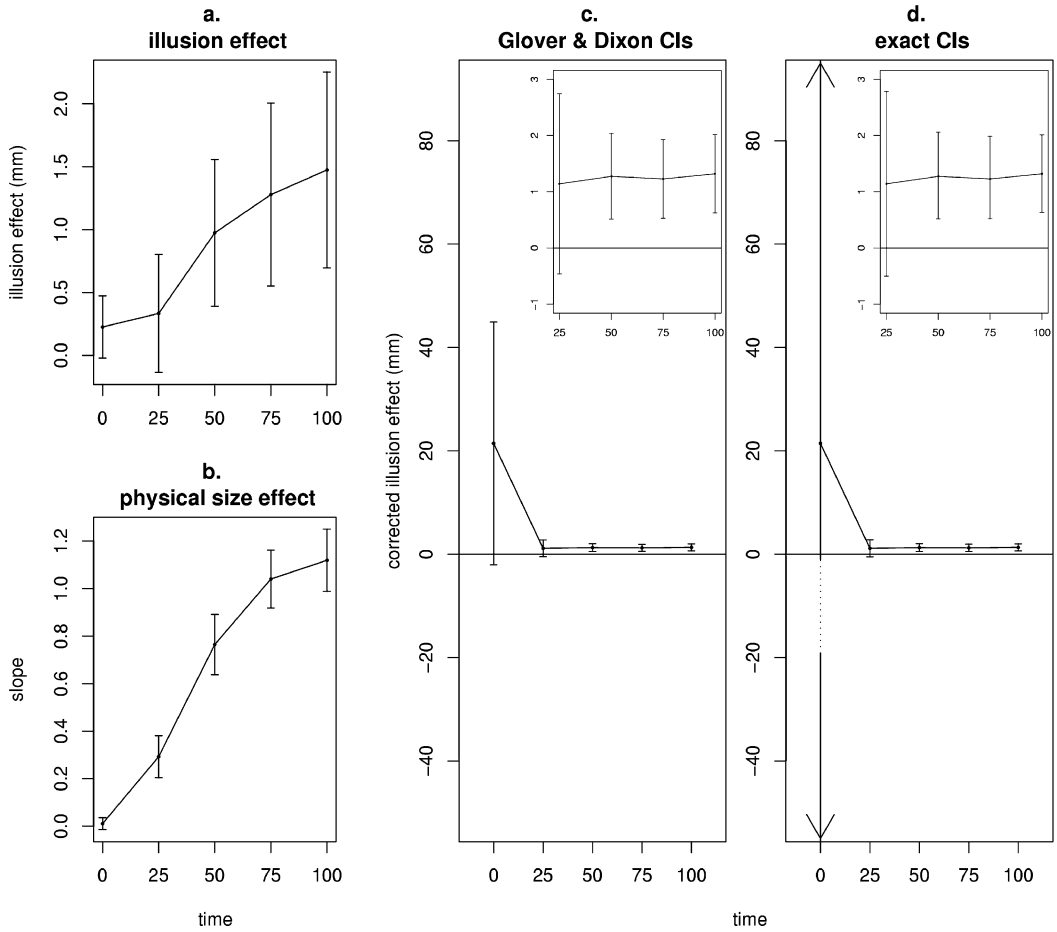

Figure 1 (Franz). Testing whether the dynamic illusion effect exists. (**1a**) Effects of the Ebbinghaus illusion on grasping as a function of time: The illusion effect is the mean difference in aperture when grasping one or the other version of the illusion. (**1b**) Effects of a physical variation of size on grasping: The physical size effect is the mean slope of the functions which relate grip aperture to physical size. (**1c**) Corrected illusion effects (i.e., illusion effects divided by physical size effects) and 95% confidence limits as calculated by Glover and Dixon's method, which ignores the variability of the physical size effects. (**1d**) Confidence limits, as calculated by the mathematically exact method (Fieller 1954; Franz, submitted): The exact method gives infinite confidence limits at $t = 0\%$; only the points on the dotted line are excluded from the confidence set, all other values are included! Data are from Franz (2003). Time is normalized, such that $t = 0\%$ corresponds to the start of the movement and $t = 100\%$ to the time of the maximum grip aperture (MGA). The insets magnify the data between t = 25% and $t = 100\%$. Error bars depict 95% confidence limits.

well beyond the time of the MGA. Most likely the fingers touched the target object at these late time points, because the trajectories were analyzed until the thumb ceased to move in a forward direction. Try it yourself: Place an object in front of you, grasp it, and move it back toward yourself (as participants did in the Glover & Dixon [2002a] study). Usually, you will have touched the object when your thumb no longer moves forward. Including time points in the analysis when participants have already touched the target object leads to a decrease of the illusion effects which is simply due to the mechanical interaction with the object and not to neuronal control processes.

In my opinion, the case of the dynamic illusion effect is not yet resolved. One possibility is that a dynamic illusion effect only shows up if participants can see their fingers during grasping. In contrast, in our studies participants could not see their fingers during grasping (note, however, that Glover and Dixon found the largest decrease in such an open loop condition). Future research should clarify this issue.

Finally, it would be interesting to know what the results of the Glover and Dixon studies would look like, if they used the mathematically exact method to calculate confidence limits and if they excluded parts of the trajectories at which participants touched the target object. Will the dynamic illusion effect survive these tests?

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Do movement planning and control represent independent modules?

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Abstract: We address three issues that might be important in evaluating the validity of the planning–control model: (1) It could be artificial to distinguish between control and planning when control involves the re-planning of a new corrective submovement that overlaps with the initial response; (2) experiments involving illusions are not totally compelling; (3) selectively implicating the superior parietal lobe in movement control and the basal ganglia in movement planning, appears questionable.

In this interesting article, Glover reviews evidence for a dichotomy between the planning and on-line control of actions. Although we

are friendly to this hypothesis (Desmurget & Grafton 2000; Desmurget et al. 1999), we believe that several key arguments put forward in the target article are debatable.

The first issue we would like to address is the ambiguity of the apparently obvious term *on-line control.* The "perturbation" paradigm illustrates this point: According to Glover, the pioneering experiment by Paulignan et al. (1991a) demonstrates the ability of the control system to accommodate a change in object location. When the kinematic characteristics of these changes are analyzed, however, it appears that the corrections are made, not by amending the current movement per se, but by aborting it and by replacing it by a new movement – that is, by re-planning a new response. In Paulignan et al.'s terms, the response to the perturbation "appeared to be composed of two submovements, the first one directed at the location of the initial target and the second one at the location of the new target." This type of "iterative correction" has also often been reported for movements directed at stationary targets (Meyer et al. 1988; Milner 1992). These corrections have been modeled using three different approaches, designated: (1) *Sequential,* in which the secondary movements are initiated at the end of the primary movement (Meyer et al. 1988). (2) *Overlapping,* in which the secondary movements are initiated before the end of the primary movement; the global motor response can then be characterized as a composite of several submovements overlapping with each others (Flash & Henis 1991; Milner 1992; Novak et al. 2002); (3) *Abort and replan,* in which the primary movement is aborted and replaced by a new movement when the error is detected (Massey et al. 1986; Paulignan et al. 1991a).

What is important here is that all these approaches rely on a similar observation, namely, that corrections are achieved by planning a secondary movement and adding it to the current one. This usage of the planning system to achieve movement corrections emphasizes the lack of clear distinction between control and planning, which raises questions about the validity of the strict division proposed by Glover in his model.

A second issue is the interpretation of several illusion experiments. In his article Glover refers, for example, to the study of Aglioti et al. (1995) to argue that illusions do not affect on-line control. A significant effect of the illusion on grip aperture was, however, observed in this study. The fact that this effect was less important than the perceptual estimate of the target size does not mean that it was not present and that it could be disregarded. In the same vein, Glover argues that visual feedback reduces illusion effects. It may be that the lack of effect under visual feedback lies in the fact that control is carried out, in this case, in allocentric coordinates. In other words, when vision is available toward the end of the movement, the correction is based on a retinal error signal that compares the state of the target directly with the state of the effector. This is what happens, for instance, when a subject wears small prisms and moves slow enough to allow feedback loops to operate: He reaches the target accurately without even being aware that he is wearing prisms (Guillaume et al. 2000). This point may explain the difference, emphasized by Glover, between the results published by Glover and Dixon (2001c) and those reported by Dyde and Milner (2002) in two similar studies involving the "tilt illusion": In the first study, the hand was visible during the last part of the movement and no effect of the illusion was reported; in the second study, vision of the hand was never available and an effect of the illusion was observed.

A third issue we want to stress is the existence of a specific contribution of the superior parietal lobe (SPL) to movement control and of the basal ganglia (BG) to movement planning. Regarding the SPL, imaging and patient data do not seem as clear as implied in the target article. In particular, two PET studies investigating the functional anatomy movement guidance have failed to reveal any specific contribution of the SPL. For visual feedback loops Inoue et al. (1998) reported a contribution of the inferior parietal lobe (supramarginal gyrus; Table 3). For nonvisual feedback loops, an activation was found over the intraparietal sulcus, but not within the SPL (Desmurget et al. 2001). In addition, it seems perilous to regard optic ataxia (OA) as a pure feedback-deficit on the basis of a single case study (Pisella et al. 2000). Clinicians often report that the hand goes "in the wrong direction from the beginning" in OA patients. In agreement with this claim we have shown, in a recent study, that the initial movement direction (a planning-related parameter) is affected in patients with OA (Desmurget et al., in preparation). Regarding BG, a direct link has recently been proposed between a deficit in on-line movement guidance and a dysfunction within the BG network (Lawrence 2000). The most convincing argument supporting this view was reported by Smith et al. (2000), who showed that patients with Huntington's Disease (in which early cell loss is restricted largely to the striatum) fail to correct for self-generated or externally imposed errors in movement trajectory. To explain this result, it was proposed that the sensory signal is biased when the BG are damaged, leading to an erroneous forward estimation of the motor state. Electrophysiological observations support this view by showing that passive limb movements activate the BG neurons (DeLong et al. 1985; Hamada et al. 1990) and generate abnormal (exaggerated) sensory responses in the pallidal neurons of Parkinsonian monkeys (Filion et al. 1988). This impaired responsiveness of the BG neurons to peripheral input could lead to an overestimation of the distance covered by the hand, and thus, hypometria (Klockgether et al. 1995).

How are cognition and movement control related to each other?

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Abstract: Our commentary focuses, first, on Glover's proposal that only motor planning is sensitive to cognitive aspects of the target object, whereas the on-line control is completely immune to them. We present behavioural data showing that movement phases traditionally (and by Glover) thought to be under on-line control, are also modulated by object cognitive aspects. Next, we present data showing that some aspects of cognition can be coded by means of movement planning. We propose a reformulation of Glover's theory to include both an influence of cognition on on-line movement control, and a mutual influence between motor planning and some aspects of cognition.

Glover proposes that motor planning and on-line motor control are two separate processes which follow two separate and independent visuo-motor pathways. In our opinion this seems too schematic, especially when behavioural and anatomic-functional data are taken into account.

Glover's first proposal is that motor planning is under the influence of a wide variety of visual (including spatial and nonspatial) and cognitive information, whereas on-line control is under the control of solely spatial characteristics of the target. This arises from both the assumption that the initial arm kinematics reflect movement planning and the findings that only the initial arm kinematics are affected by cognitive information. However, let us consider previous visual perturbation experiments (see, e.g., Gentilucci et al. 1992; Paulignan et al. 1991b). Corrections to visual perturbations occurred during the acceleration phase of arm movements (80–120 msec after perturbation). Because perceptual and/or cognitive information can lead planning into errors on target localization (see, for example, the illusion and the automatic-word-reading effects on arm movements), these should be quickly corrected (during the acceleration phase), if the on-line control is solely under the influence of the spatial characteristics of the target. Since this did not occur, it is possible that – at least in the initial movement phases – the on-line control is penetrable to cognitive aspects of the target object. Moreover, cognitive information affects the arm homing (deceleration) phase as well.

Marteniuk et al. (1987) showed that an effect of object fragility was also present in the last phase of arm movements (deceleration). We can therefore suppose that the final movement phase is planned as well, and that the on-line control is not immune from effects of cognitive aspects of the target. If this were not true, lengthening of the deceleration phase as a result of greater object fragility (i.e., object familiarity) should be quickly corrected. Recently, Gentilucci (2002; 2003b) observed that the familiarity of target objects (in this case, fruits) affects grasp parameters (maximal finger aperture), which, according to Glover, should be under on-line control. Summing up, behavioural studies suggest that on-line control is partially affected by cognitive aspects of the target. We can explain the final corrections of errors in target location, attributable to perceptual/cognitive information, by proposing that the strength of egocentric cues increases with movement progression. To this purpose, we found that fixation of the vertex of the Müller-Lyer illusion, target of a pointing movement, reduced the localization error when compared with the condition in which the other vertex was fixated (Gentilucci et al. 1997a). In other words, when the flow of information in egocentric coordinates exceeds other information, movement control is only egocentrically driven.

According to Glover, the clear-cut distinction between motor planning and on-line control finds an anatomical counterpart in two sensorimotor pathways located in the ventral and dorsal parietal-premotor cortices, respectively. An argument in favour of the hypothesis that the dorsal parietal-premotor pathway is exclusively involved in the control of movement execution is provided by motor deficits observed in patients with optical ataxia due to lesions of the posterior dorsal parietal cortex. Recently, Roy et al. (in press) studied the reaching-grasping kinematics of a patient with a unilateral lesion restricted to the posterior part of the dorsal parietal cortex. Although this patient showed an apparent recovery from optic ataxia, the early kinematic aspects of the patient's reaching-grasping movements were not normally modulated by either intrinsic or extrinsic visual properties of objects. These results constitute evidence that the posterior region of the dorsal parietal cortex, besides playing a role in the on-line control of movement execution, may also be involved in aspects of planning such as implementing and coordination of the various phases of arm movements (Gentilucci et al. 2000b; Roy et al., in press).

The ventral parietal-premotor circuit can also be involved in aspects related to perception and semantics other than those specifically related to planning an action. Indeed, neuroimaging studies have shown that the naming of tools or tool actions (Grabowski et al. 1998; Grafton et al. 1997; Martin et al. 1995), as well as viewing pictures of tools (Chao & Martin 2000), activates the human lateral premotor cortex. These findings suggest that the representations of an object (i.e., the actions associated with the object) can be automatically activated or retrieved by simply naming or viewing the object, without executing (and probably preparing) an object-related action. These results have their counterpart in behavioural data (Gentilucci 2003c) showing that class of word can be a factor selectively influencing motor control. Indeed, automatic reading of verbs more strongly influenced arm kinematics than adjectives.

Finally, action preparation and observation can be used to understand the meaning of an action (Rizzolatti et al. 2001) and to communicate with other individuals (Gentilucci 2003a; Gentilucci et al. 2001). The fact that the semantic face of speech and the arm gestures are reciprocally related, is supported by a new observation (Chieffi et al., in preparation) showing a reciprocal influence between the direction of deictic gestures (pointing towards a remote position or one's own body) and deictic terms (*QUA*, here, or *LA*', there) simultaneously pronounced. Indeed, the results showed that arm kinematics and voice spectra were reciprocally interfered with when the arm gesture was incongruent with the meaning of the deictic term.

Summing up: In our opinion, the distinction and definition of programming and on-line control of actions proposed by Glover can be partially reformulated. First, definition of on-line movement control should take into account that cognitive aspects of the object can at least partially penetrate into the feedback control of a movement. Second, definition of movement planning should take into account that some aspects of cognition (in particular semantics and speech) can be coded by action preparation.

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Plans for action

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Abstract: It is our contention that the concept of *planning* in Glover's model is too broadly defined, encompassing both action/goal selection and the programming of the constituent movements required to acquire the goal. We argue that this monolithic view of planning is untenable on neuropsychological, neurophysiological, and behavioural grounds. The evidence demands instead that a distinction be made between action planning and the specification of the initial kinematic parameters, with the former depending on processing in the ventral stream and the latter on processing in the dorsal stream.

Introduction. For the most part, Scott Glover's proposed "planning–control" model (PCM) bears a strong family resemblance to our "perception–action" model (PAM: Goodale & Milner 1992; Milner & Goodale 1995), and indeed it makes many similar predictions. But there are differences, and it is important to isolate precisely what they are, as well as to give a fair and correct account of the PAM. Take for example, this seemingly innocuous sentence taken from Glover's "Conclusions" section:

> The studies reviewed here are less consistent . . . with a perception–action model in which actions are thought to be both planned and controlled using a single visual representation in the SPL. (target article, sect. 5, para. 1)

Is this statement correct? Well, although it might be convenient for Glover if it were, the stubborn fact is that we never proposed that actions are "planned and controlled by a single visual representation in the SPL." It may suit the confrontational style of *BBS* to set up a straw man of this kind, but a closer look at what we have argued will show that the PAM makes no such simple-minded proposal. But first let us examine Glover's last clause in this sentence more closely since it does carry the germ of the real disagreement between us.

We can set to one side two relatively minor errors that are implicit in the sentence. The first error is to locate the human dorsal stream entirely within the SPL (superior parietal lobule). There is now ample fMRI evidence that the dorsal stream, particularly those regions involved in voluntary saccades and object-directed grasping, is centered on the human IPS (intraparietal sulcus), on the border between IPL and SPL (Binkofski et al. 1998; Connolly et al. 2002; Culham 2004; Culham & Kanwisher 2001; Culham et al. 2003). Only the region associated with visually guided reaching (as opposed to looking or grasping) appears to be located entirely within the SPL (Connolly et al. 2003). These neuroimaging results broadly back up the lesion localization evidence of Perenin and Vighetto (1988, Table 1), who found that a group of eight patients with optic ataxia all had brain damage that included the IPS, whereas only five of them had SPL damage. Indeed, the overlapping region in their patients was largely centered on the IPS. The

second error in the sentence is the implication that we envisage that there are "visual representations" existing within the dorsal stream to control action. In fact, we have always been careful to emphasize our belief that visual information has *direct* control over action in the dorsal stream, without any intervening "representations." As Frith et al. (1999) have argued, not all neural activity is correlated with mental representations – at least in the sense of enduring representations of objects in the world. In our view, the neural activity in the dorsal stream does not reflect the representation of objects or events but rather the direct transformation of visual information into the required coordinates for action.

Much more central to our disagreement with Glover is that his summary sentence imputes to PAM the view that the dorsal stream plays a "master" role in the planning as well as the control of actions. This we find a surprising suggestion. In the first chapter of Milner and Goodale (1995) we wrote:

> As we shall see, despite the complexity of their interconnections, primate cortical visual areas can be divided into two functional groupings: one with rather direct links to motor control systems, and the other with connections to systems associated with memory, *planning,* and other more "cognitive" processes. (p. 19, emphasis added)

We have never associated planning with the dorsal stream, in any of our publications, before or since. Indeed, like Glover, we have argued for some time that the perceptual system, vested in the ventral stream and elaborated in the right IPL, provides a perceptual representation of the surrounding visual world that is used in the planning of actions.

So how has this apparent misinterpretation come about? The answer comes in section 1.1.2, paragraph 1 of the target article:

> At a high level, planning is responsible for such things as selecting an appropriate target, or choosing to grasp an object in a certain manner. Beyond these selection processes, however, planning also determines the initial kinematic parametrization of the movements, including their timing and velocity.

In other words, for Glover, "planning" is given a very broad meaning quite different from most usages of the term in the literature, in that it includes what he calls the "initial kinematic parametrization of the movements." According to Glover, planning includes processes that extend from goal selection right through to the initial programming of the constituent elements of the goal-directed action. To put it starkly, then, for Glover, the movements constituting the act of reaching out and grasping even a simple block are initially calibrated by a rich visual representational system (in the IPL) that is subject to the full panoply of contextual and cognitive influences. This, as far as we can see, is the crux of the disagreement between the PAM and the PCM.

According to our view, action planning and selection need to be separated, both conceptually and empirically, from the specification of initial movement parameters; and we have proposed that these two sets of processes each use a different visual information stream. We believe that action planning depends on visual processing in the ventral stream and right IPL, but that the initial movement parameters of the selected action are determined by processing in the dorsal stream (i.e., IPS/SPL). Our chief disagreement thus comes down to one crucial question:

> Is the initial kinematic specification of an action performed using "bottom-up" visual information within the dorsal stream, as we propose, or is it a part and parcel of the "planning" process, along with target selection and hand posture selection, and thus driven by the ventral stream, as Glover proposes?

Evidence from neurophysiology and neuroimaging. Our belief that movement parameter specification occurs within the dorsal stream rests on a consideration of a broad range of physiological, neuropsychological, and behavioural data. A large amount of single-neuron recording evidence reveals the existence of neurons within the monkey's posterior parietal cortex that have both visual receptive fields and time-locked responses to the eye and arm movements directed at targets located in different regions of the visual field. A saccade-related area has been found in the lateral bank of the IPS, in a region now known as lateral intraparietal area (LIP) (Andersen et al. 1992). More recent neurophysiological studies have also revealed a "parietal reach region" (PRR) located in the posterior and medial part of the intraparietal sulcus extending into neighbouring area V6A (Galletti et al. 1997b; Snyder et al. 1997). Damage to this region is reported to cause misreaching with initial heading errors that are misdirected to the medial side of the target as well as deficits in wrist orientation (Battaglini et al. 2002a; Faugier-Grimaud et al. 1978). More anterior to LIP lies an area (anterior parietal area [AIP]) where neurons respond to the geometric appearance of objects and have motor responses linked to grasping movements directed to these objects (Taira et al. 1990). Therefore, contrary to previous belief – echoed here by Glover – that "the dorsal stream in the macaque brain terminates in the inferior parietal lobule" (see target article, sect. 3, and Fig. 3 caption), current evidence now locates it in and around the IPS. Also, as we mentioned earlier, direct homologues of LIP, PRR, and AIP have now been identified using functional MRI in humans (Binkofski et al. 1998; Connolly et al. 2000; 2002; 2003; Culham 2004; Culham et al. 2003). It would therefore appear that the areas in and around the IPS make up the dorsal stream in both the human and the monkey posterior parietal cortex.

The evidence from fMRI in humans, like the neurophysiological studies in monkeys, suggests that the transformation of visual information into the appropriate motor coordinates for action takes place within the dorsal stream. Thus, in a recent event-related fMRI experiment, Connolly et al. (2002) showed that there is no activation in the human homologue of LIP as subjects prepare to make a saccade to a target that had not yet been presented. Activity increased in this region only when the target appeared. This suggests that LIP (unlike the frontal eye fields and other premotor areas) does not play a significant role in preparing for action – unless the location of the target has already been specified. In other words, the activity in LIP is related to the programming of eye movements to particular spatial locations but not to action planning in general. These findings are entirely consistent with results from similar studies in the monkey (Andersen et al. 1992; Snyder et al. 1997). In another event-related fMRI study, Culham et al. (2003) demonstrated that the lateral occipital complex (LOC), a ventral stream area implicated in object perception and recognition, shows no differential activation during visually guided grasping as compared to visually guided reaching – suggesting that the visually driven specification of the required movements for grasping is mediated entirely in AIP, which shows greater activation during grasping as compared to reaching. In short, the weight of physiological (and human neuroimaging) evidence indicates that the visually defined movement parameters are set within the dorsal stream in both monkeys and humans.

It is perhaps worth pointing out that not only is Glover's review of neuroimaging literature confined almost entirely to PET studies, but the evidence he presents on planning and control does not differentiate between the predictions and theoretical assumptions of the PCM and the PAM. None of the studies he discusses had sufficient temporal resolution to establish whether the activation that was observed corresponds only to the on-line control of movement, and not also to the programming ("planning," in the PCM sense) of a visually guided movement. We surmise that both would have contributed to the observed activations. Yet Glover goes on to argue that the "results were generally not consistent with the perception–action model . . . which predicts motor-related activity in the SPL but not in the IPL" (sect. 3.3, para. 4). But as we have already discussed, this argument is based on a misunderstanding of the location of the dorsal-stream areas within the parietal cortex, many of which are located within the IPS. This is compounded by the fact that the spatial resolution of PET is not nearly as good as that seen in fMRI, particularly in the high-field fMRI used today. As a consequence, motor control activations that were apparently localized to the IPL could sometimes have been located in

the IPS. (The same arguments a fortiori apply to the TMS studies cited by Glover.)

Evidence from neuropsychology. Our PAM is also, we believe, supported strongly by neuropsychological evidence. This is principally derived from patient D.F., whose profound visual form agnosia we now know results from bilateral damage to the ventral-stream area LOC (James et al. 2003), and patients I.G. and A.T., who both have bilateral optic ataxia from bilateral damage to the dorsal stream (including IPS and SPL, though also more inferior parietal regions in A.T.'s case). Glover's PCM makes two strong predictions about these patients, which he states as follows:

1. "Deficits in optic ataxics should be concentrated in the later stages of movement" (sect. 4.4, para. 1).

2. "In the planning–control framework, damage to D.F.'s ventral stream should impair many aspects of how she plans movements, but should leave her control processes essentially intact" (sect. 4.6).

Optic ataxia. In a recent study, we directly addressed the question of whether optic ataxia affects only the later stages of movement (Milner et al. 2003). We examined reach trajectories in both of our patients right from the outset of each movement to see whether there was any problem in their initial heading direction. Strong and consistent heading errors were present in both patients right from the start of each of their reaches: In fact, the heading error predicted the final error very accurately. In other words, although these patients certainly do have serious problems with the on-line control of their reaching (as demonstrated by use of perturbation paradigms, Gréa et al. [2002]), they also have problems with the initial specification of their movements. It is important to bear in mind here that although A.T. has brain damage that extends well into the IPL, I.G. has only slight damage there (Pisella et al. 2000). Her heading errors therefore most likely arise, as far as we can tell, from her IPS/SPL damage.

Consistent with these results is the well-established finding, as Glover notes in his article (sect. 4.4.1), that optic ataxic patients are impaired in open-loop reaching. In this case, no on-line visual corrections are possible, because there is no visual feedback from the hand. So in Glover's terms, this task should be one of "pure planning." Why, then, are optic ataxic patients so inaccurate? The reason seems likely to be the same as in our closed-loop reaching task: The patients head off in the wrong direction from the outset, something that is never observed in normal subjects. It is also worth remembering that human optic ataxia looks strikingly similar to the misreaching and misgrasping seen in monkeys with dorsal-stream lesions. In fact, a direct comparison between monkeys with ventral- or dorsal-stream lesions (Glickstein et al. 1998) yields the same double dissociation between perception and action that we have observed in our patients. Glover seems to accept this, but nonetheless insists that "the 'what/how' distinction found in monkeys cannot be easily translated into an explanation of human brain organization" (sect. 3.1.1). It seems premature to dismiss so cavalierly the striking similarities in visual processing at all levels between humans and our primate cousins. The parsimonious and indeed most plausible default assumption to make is always one of biological continuity, and one should demand extremely persuasive evidence to reject it.

Visual form agnosia. In direct counterpoint to our optic ataxia results, we have found that D.F. has no difficulty at all in the initial specification of her movement parameters. In our first study of her visually guided movements (Milner et al. 1991), we videotaped her reaches to post a card into an oriented slot. As documented in that study, she began to turn her hand toward the target orientation *right from the very start of her movements.* D.F.'s reaching to point targets is also indistinguishable from normal, with no sign that early aspects of the movements are not normally programmed. This finding cannot be reconciled with Glover's view that the ventral/perceptual system plays a leading role in the early stages of movement planning (e.g., programming the initial movements of the hand in a reaching or grasping movement).

Yet, it is true that D.F. does have problems with certain high-level aspects of action, such as her inappropriate (but highly adept) grasping of tools. When, for example, she reaches out to pick up a screwdriver that has been placed on the table with the handle pointed away from her, she picks it up quite deftly but grasps it by its shaft rather than its handle – and only then rotates it in her hand so that she can hold it properly. In other words, because her damaged ventral stream is unable to process the screwdriver's shape, D.F. has no idea what it is ahead of time and is therefore unable to generate the functionally appropriate grasping movement shown by normal subjects when faced with the same task. Nevertheless, the intact visuomotor systems in her dorsal stream can still compute the required metrics to ensure that her grasping movement, however inappropriate, is well formed and efficient. To reiterate, we have never found any sign of faulty specification of her movement parameters, strengthening our belief that the selection of the appropriate functional hand posture needs to be distinguished from the metrical scaling of the constituent movements. We agree with Glover that D.F.'s "deficits in motor behavior can be likened to those suffered by many apraxics, whereas her spared abilities can be likened to those impaired in many optic ataxics" (sect. 4.6.2), but for different reasons. According to the PCM, patients with ideomotor apraxia would be predicted to have faulty specification of the initial movement parameters (as indeed should D.F.). Yet in fact most of these patients (like D.F.) do not have any measurable visuomotor abnormalities (Ietswaart et al. 2001) – and those who do (Haaland et al. 1999), appear to have damage extending to more superior parietal regions, including the IPS.

Before leaving this issue, it is important to emphasize that D.F. does not have ideomotor apraxia. Her problem is one of identifying the goal object on the basis of its shape, not one of selecting an action appropriate to its function. If she knows what the object is, she has no problem selecting a hand posture that matches its function.

Evidence from visual illusions. The study of visual illusions in healthy subjects does not bear directly on issues of visual processing streams. But PAM theory has allowed us to make certain counterintuitive predictions about illusions. Essentially the story goes like this: The perceptual (ventral stream) system uses an obligatory relative or contextual coding system for size, distance, and orientation, while the visuomotor (dorsal stream) system is designed to use "real world" metrics. We therefore predicted that some simple movements might be made without the influence of visual context or top-down visual knowledge. The remarkable fact is that the prediction has frequently worked: In several suitably engineered situations (particularly with so-called *pictorial* illusions, such as the Ebbinghaus and Ponzo), context really does have no – or minimal – effect on action parameters. There are exceptions, of course, but often these exceptions are highly instructive in themselves.

The simultaneous tilt illusion (STI), extensively used by Glover, is a good case in point. This illusion affects perception and action in much the same way, and indeed the perceptual and action effects are highly correlated (Dyde & Milner 2002). This result can be easily explained if we assume that the STI is mediated by an early (e.g., area V1) mechanism, and would thus affect both visual streams. Of course, the effect of the illusion on action is most evident in tasks in which observers receive no visual feedback during their reaches. When feedback is available, unsurprisingly, subjects do correct their actions, so that the illusion has a reduced magnitude at the movement endpoint (e.g., Glover & Dixon 2001c). These results, obtained in several studies by Glover and colleagues, would seem merely to reflect the fact that on-line feedback causes on-line corrections, but Glover argues that his results are "much less consistent with the perception–action model" (sect. 2.8, para. 2). In our view, it is obvious that on-line corrections will negate illusory effects, by allowing the subject to compare quite directly the orientation of the hand with the orientation of the goal during the closing phases of the movement. After all, that's what (in part) the on-line correction system is there for.

Our perception–action model, of course, has the major virtue that it provides a theoretical rationale for those perception-action dissociations that can be demonstrated using pictorial illusions. It is true that the PAM and the PCM both agree that such illusions can affect the planning of actions – the question is, *why* do illusions affect such planning? Glover gives no reason, simply assuming that the "planning representations" are contextually dependent. It is unclear, furthermore, what he means by "planning representations." Are these just action plans or are they something else? We provide a more specific answer: Illusions affect the action planning because planning (a cognitive activity) requires *perceptual* representations, and it is these representations that are subject to illusory effects. This is a prediction, not an assumption. For example, if we plan to pick up the smaller of two objects in an Ebbinghaus display (in which the objects are in fact the same size), our choice can clearly be influenced by the illusion. Nevertheless, the programming of the actual movements to the selected object can escape such illusions, because the visuomotor system is not influenced by the top-down contextual information that drives perception. Parenthetically, if our theoretical position is correct, then losing crucial perceptual processing hardware should thereby also destroy the effects of pictorial illusions on action planning. Therefore, we would make a prediction directly opposite to one made by Glover, who argues that "the patient D.F. ought to . . . *show similar patterns of effects of visual illusions as healthy participants*" (sect. 4.8, last para., emphasis added).

Another strong prediction of the PCM is that *all* perceptual illusions should affect the initial phase of movements made toward the illusory target – after all, all movements require planning of some sort. Danckert et al. (2002), however, have provided rather unambiguous evidence showing that the Ebbinghaus illusion does *not* influence the finger-thumb aperture even at the very start of the reach – a result that is difficult to square with the PCM (although it is quite consistent with the PAM). In fact, even under certain conditions in which perception intrudes and the Ebbinghaus illusion affects grasping (Franz 2003), the size of that effect does not appear to change during the entire movement – a finding that is again inconsistent with Glover's view. Finally, the PCM predicts that there should never be a residual illusion at the end of the reach, because the action control system will always kick in during the final phase – even when visual feedback is not available. Yet this prediction is contradicted by Glover's own data: Glover and Dixon (2001c) found that a sizeable orientation illusion remained in their STI reach data when visual feedback was occluded (although they downplay this result). In contrast, when Dyde and Milner (2002) used an orientation illusion where the inducing background was changed from a contiguous grating (the STI) to a distant frame (the rod and frame illusion or RFI), they found no illusory effect on action at all, even though again no visual feedback was available. The PAM can explain this result by invoking the usual account of the RFI as a contextual illusion par excellence (Howard 1982), one that is presumably mediated by the scene-based frames of reference characteristic of the ventral stream. In contrast, the PCM can offer no explanation as to why there should be any dissociation between the STI and the RFI – both should affect hand orientation at the outset, and then the effects should disappear towards the end of the movement. The former prediction doesn't hold for the RFI (there is no illusion), and the latter prediction doesn't hold for the STI (it is still present at the end of the movement).

Summary. Our main criticism of Glover's PCM is that the concept of "planning" is used in a vague and overly broad fashion. It encompasses not only cognitive control (the selection of the goal object and, if necessary, an appropriate functional posture) but also the detailed programming of the constituent movements required to acquire the selected object. We believe that this monolithic view of planning is untenable on neuropsychological, neurophysiological, and behavioural grounds. The evidence demands instead that a distinction be made between action planning and the specification of the initial kinematic parameters. It is this distinction, along with Glover's failure to acknowledge it, that lies at the root of our disagreement.

The organization of action representations in posterior parietal cortex

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Abstract: Glover suggests that representational systems for planning versus control are mapped exclusively to the inferior (IPL) versus superior (SPL) parietal lobules respectively. Yet, there is ample evidence that the IPL and SPL both contribute to action planning and control. Alternatively, I distinguish between the parietal-frontal systems involved in the representation of acquired manual skills versus nonskilled actions.

Glover advances an interesting and provocative hypothesis concerning the organization of visual representations for action planning and control and their underlying neural substrates. Glover makes a strong case that action planning and control can be dissociated behaviorally, implying that these processes may depend on functionally dissociable representational systems. When the systems for planning versus control are respectively mapped to the inferior (IPL) versus the superior (SPL) parietal lobules, however, the theory goes awry. As I selectively review below, there is ample evidence that both the IPL and SPL contribute to action planning and control in primates. Based on this evidence, I offer an alternative model that distinguishes between parietal mechanisms involved in representing previously acquired skills versus those contributing to the planning and control of nonskilled actions.

Electrophysiological studies in macaques indicate that a variety of visually guided actions are planned in and controlled by functionally specialized parieto-frontal circuits involving both SPL and IPL regions. Accumulating evidence from functional neuroimaging suggests a similar organization in humans (see review by Culham & Kanwisher 2001). Counter to Glover's assertions, regions within the IPL are involved in movement control. For example, saccadic eye movements involve the lateral intraparietal area (LIP) in macaque IPL, and a putative homologue in humans has been identified (Sereno et al. 2001). Likewise, another IPL region – the anterior intraparietal area (AIP) – controls visually guided grasping in macaques. A probable homologue of AIP is also associated with grasping in humans (Binkofski et al. 1998). Furthermore, regions within the SPL participate in movement planning. The parietal reach region (PRR), located within the medial intraparietal sulcus (IPS) of macaque SPL, is involved in the control of visually guided reaching (Andersen et al. 1997). A homologous area has also been reported in humans (Kertzman et al. 1997). Importantly, cells in the PRR also engage in premovement planning; during multi-step actions, they represent forthcoming, intended movements (Batista & Andersen 2001). Consistent with this hypothesis, we have observed activation in human medial IPS (putative PRR), during mentally simulated reaching (Johnson et al. 2002).

Contrary to Glover's interpretation, the human lesion data also do not support the hypothesis that planning occurs exclusively in the IPL and control in the SPL. Patients with optic ataxia have difficulties controlling reaching toward and/or grasping objects located in peripheral vision. Optic ataxia is associated frequently, though not exclusively, with damage to the SPL (Perenin & Vighetto 1988). Given the substantial variation in naturally occurring brain injuries, this disorder is often likely to reflect damage to regions within IPL as well (Guard et al. 1984). For instance, one would expect IPL lesions in putative AIP to be an important factor in cases of optic ataxia where visually guided grasping is compromised (Goodale et al. 1994c; Jeannerod 1986). Indeed, Binkof-

ski et al. (1998) have shown that damage to putative AIP results in impairments of visually-guided grasping.

In contrast to optic ataxia, ideomotor apraxia is a disorder that primarily affects planning of skilled actions, while leaving on-line control relatively unaffected. For example, these patients often have considerable difficulty pantomiming tool-use actions, yet have little or no difficulty reaching and grasping visually presented objects (for a comprehensive review see Heilman, 1997). Since the turn of the previous century, it has been known that ideomotor apraxia results almost exclusively from damage to, or disconnection of, the left cerebral hemisphere (Leiguarda & Marsden 2000). Recent analyses implicate both the IPL and SPL in this disorder. Lesion overlap is most frequent in areas within and adjacent to the left IPS, including SPL (BA 7) and IPL (BA 39 and 40), as well as interconnected regions of the middle frontal gyrus (GFm: Haaland et al. 2000). Corroborating evidence comes from several functional neuroimaging studies of healthy adults showing activation of these regions during overt *or imagined* tool use actions involving either hand (Choi et al. 2001; Johnson-Frey 2003; Moll et al. 2000). Together, these findings indicate that representations necessary for planning skilled movements involve a left-lateralized parieto-frontal system. Further, this cerebral asymmetry appears to be true regardless of one's hand dominance (Johnson-Frey et al., submitted; Lausberg et al. 1999; Raymer et al. 1999). This contrasts sharply with the apparent contralateral organization of parietal mechanisms involved in on-line control that are damaged in optic ataxia. These differences should serve as an important constraint on theories concerning the organization of action representations.

Glover is correct in asserting that the contrasting deficits of optic ataxia and ideomotor apraxia patients suggest that actions do not depend on a unitary representational system. However, the distinction is not between planning and control but, rather, between actions that are planned and controlled entirely on the basis of immediate perceptual information versus skills that additionally involve accessing stored memories (Johnson-Frey 2003; Johnson-Frey & Grafton 2003). As reviewed above, on-line manual actions are controlled by functionally specialized parieto-frontal circuits that include contralaterally organized regions belonging either to the SPL or the IPL. By contrast, in the vast majority of individuals, manual skills (e.g., tool-use) are represented in a left lateralized parieto-frontal system. Of course, the actual implementation of a skilled action in the real world necessarily involves cooperation between these two systems.

In short, this position differs from Glover's in at least two respects. First, planning takes place in *both* representational systems, but for different types of actions; that is, skills versus non-skills. Second, depending on nature of the movement(s) involved (e.g., reaching, grasping, saccades), control can be accomplished in the SPL and/or IPL.

Is there an independent planning system? Suggestions from a developmental perspective

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Abstract: Glover argues that separate representations underlie the planning and the control phase of actions, and he contrasts his model with Goodale and Milner's perception/action model. Is this representation indeed an independent representation within a more general action system, or is it an epiphenomenon of the interaction between the perception/action systems of the Goodale–Milner model?

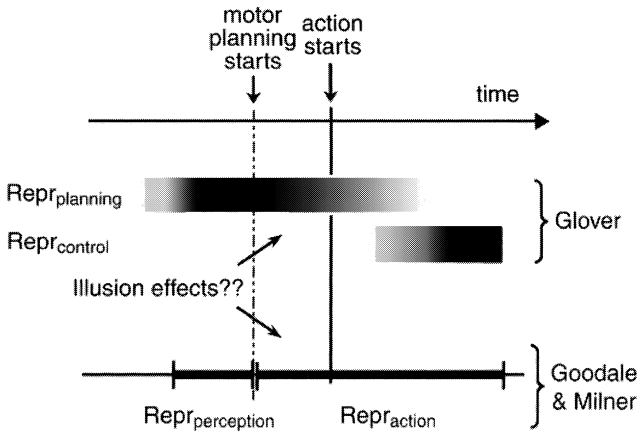

Figure 1 (Káldy & Kovács). Comparison of the Glover and the Goodale–Milner models. This schematic diagram represents the temporal relations between the two separate visual representations according to the Glover versus the Goodale–Milner model. In our view, the most significant difference is in how the two models conceptualize the acting representation between the beginning of motor planning and action.

We contrast the Glover and the Goodale–Milner models in Figure 1. According to our understanding, one of the main differences between them is the way they conceptualize the representation that the motor program is based on. In the Goodale–Milner model (Goodale & Milner 1992), it is the "action" representation of the dorsal stream ($Repr_{action}$); while in Glover's model, it is a representation underlying the planning phase ($Repr_{planning}$). The two models disagree about the potential effects of visual context on this representation. According to Glover's model, context has a potentially large effect on $Repr_{planning}$, while in the Goodale–Milner theory it does not (or the effect can only be small). Glover also claims that $Repr_{planning}$ determines certain parameters of the motor program, such as lifting force, posture choice, movement time and grip acceleration, and these parameters can be strongly influenced by illusion effects (see Glover, sect. 2.6.1. para. 4). Not all motor program parameters are under the control of $Repr_{planning}$; some – such as maximum grip aperture and pointing accuracy – are driven by $Repr_{control}$, and these are the parameters that context-induced illusions do not influence.

We propose an experiment motivated by our recent developmental studies that could significantly contribute to this issue. We have studied four-year-old children's and adults' performance in a 2AFC version of the Ebbinghaus illusion (Titchener circles) task (Káldy & Kovács 2003; see also Kovács 2000). Both children and adults were asked to decide which one of the target circles amidst the context circles appeared larger. The task was entirely perceptual, that is, no action was required toward the target circles. Our results have shown that the magnitude of the illusion effect was significantly smaller in children than in adults, and our interpretation is that visual context integration is not fully developed in four-year-olds. In terms of the Goodale–Milner model, we found an age-dependent effect of the magnitude of the context-induced illusion on $Repr_{perception}$. We proposed earlier that the ontogenetic development of the dorsal "action" system is faster than that of the ventral "perception" system in humans (Kovács 2000). Based on the age-dependent illusion effect on $Repr_{perception}$, and on the faster maturation of the "action" system, we suggest an experiment that could decide about the independent existence of the "planning" system in Glover's model. As Glover suggests, there are particular parameters of movement that seem to be affected by illusions because they are determined by $Repr_{planning}$. Movement time as measured in the Ebbinghaus illusion is one of those parameters (van Donkelaar 1999). Taking into account the faster

maturation of planning related areas, the Glover model would predict that children should demonstrate adult-like illusion effects in terms of movement time well before they do in the perceptual version of the Ebbinghaus illusion task. However, the Goodale–Milner model, in the strict sense, does not allow for illusion effects arising from the "action" system; therefore, the origin of the illusion should be in $Repr_{perception}$. In this case, young children should behave the same way as in the perceptual task: They should demonstrate much smaller illusions than adults. This test would be an interesting way to study the relationship between the two hypothetical concepts, $Repr_{planning}$ and $Repr_{perception}$, and the controversial period before the action starts.

Action planning in humans and chimpanzees but not in monkeys

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Abstract: Studies with primates in sequence production tasks reveal that chimpanzees make action plans before initiating responses and making on-line adjustments to spatially exchanged stimuli, whereas such planning isn't evident in monkeys. Although planning may rely on phylogenetically newer regions in the inferior parietal lobe – along with the frontal lobes and basal ganglia – it dates back to as far as five million years ago.

Glover argues that planning is largely the province of a phylogenetically newer cortex in the inferior parietal lobe (IPL), and he suggests that "the role in the human IPL in action planning may have arisen quite recently in evolution and may be manifest in the uniquely human population lateralization in hand preference" (target article, sect. 1.2.1). Although planning is limited in macaque monkeys, as he suggests, a series of studies have revealed that chimpanzees, which are hominoids, are greatly skilled in action planning, just as humans are.

Ohshiba (1997) compared the reaction time of macaque monkeys and a chimpanzee in a sequence production task. Both species of primates were taught to select differently sized circles in an arbitrarily defined order. An analysis of the reaction times suggested that the monkeys identified only the first target to be selected in the task; and only after (and/or during) the selection of that target – which resulted in its disappearance – would they search for the next target to be selected. This was because reaction times to subsequent targets decreased in a monotonic function. In contrast, a chimpanzee doing the same task spent the longest amount of time in selecting the first item of the sequence, followed by shorter reaction times for the remaining items. These reaction times did not differ from each other. These results suggest that monkeys employ a serial search strategy, whereas chimpanzees plan before selecting the first item in a sequential task.

Kawai and Matsuzawa (2000b) provide more decisive evidence for chimpanzees' ability to plan. The chimpanzee named Ai learned to count dots on a computer monitor as well as count real objects, and to select the corresponding Arabic numerals on a touch-sensitive monitor (Matsuzawa 1985). Ai also learned to order the numbers from zero to nine in sequence, regardless of the inter-integer distance. Utilizing her numerical skills, we set up a memory task. In our experiment, three to five random but different numerals picked from 0–9 were distributed on a touch-sensitive monitor (e.g., 1, 3, 4, 6, and 9). Ai was required to select the numerals in an ascending order. Immediately after selecting the lowest numeral (i.e., "1"), all the remaining numerals were masked by a white square (Fig. 1). Therefore, Ai had to memorize the numerals (now masked) accurately to select the correct sequence. Ai attained more than 90% accuracy with four numerals and 65% with five, significantly above chance in each case (17% and 4%, respectively). In this and other similar studies (Kawai 2001; Kawai & Matsuzawa 2000a; 2000b; 2001a; 2001b), only the reaction time for the first numeral was longer than those for the remaining numerals, which did not differ (Fig. 2). These results indicate that she could memorize the correct sequence of any five numerals (Kawai & Matsuzawa 2000b).

Figure 1 (Kawai). The chimpanzee Ai performing the numerical ordering task in the "masking" trial (Kawai & Matsuzawa 2000b). The numerals were presented on the touch-sensitive monitor. Immediately after Ai had correctly chosen the lowest numeral (1), the remaining numerals were automatically masked. Ai continued to identify the numerals one by one in ascending order.

The chimpanzee Ai also exhibits skillful on-line control of action. In the same numerical ordering task with three different numerals (e.g., 1, 3, 7), the on-screen positions of the remaining two

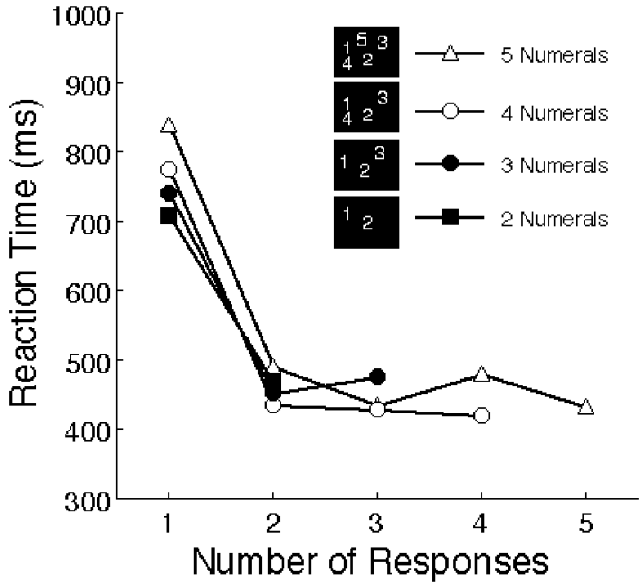

Figure 2 (Kawai). Reaction times selecting the first, second, third, fourth, and fifth items in the numerical ordering task with the chimpanzee Ai (Kawai 2001). Only the reaction time for the first numeral was longer than those for the remaining numerals, which did not differ.

numerals were occasionally exchanged by the computer, immediately after she correctly selected the lowest numeral in a given series (Biro & Matsuzawa 1999). Her accuracy dropped to 45% in these "switch" trials as compared to 95% correct in the normal background trials. These indicate that Ai planned a trajectory for a correct response; however, when the first and former "second" numerals were relatively distant from each other, she made on-line adjustments to the spatially exchanged stimuli.

Glover attributes the human planning system to the presence of an enlarged parietal lobe, hand preference, and tool-use. The latter two were once thought of as being unique to humans (sects. 1.2.1 and 3.1.1). We now know that a wide variety of tools is used by chimpanzees (Whiten et al. 1999). Recent studies revealed that chimpanzees exhibit preferential use of the right hand in gestural communication (Hopkins & Cantero 2003). These findings may not contradict Glover's speculation. However, future comparative studies will be needed to clarify the contributions of hand preference and tool-use to the evolution of a planning system. These should be conducted by comparing great apes that exhibit neither tool-use nor hand preference (e.g., gorillas), and those that use tools but have no hand preference (e.g., orangutans) (van Schaik et al. 2003).

In summary, whereas planning may rely on phylogenetically newer regions in the inferior parietal lobe along with the frontal lobes and basal ganglia, chimpanzees, but not monkeys, seem to share this advanced behavior.

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Form follows function in visual information processing

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Abstract: Understanding neural anatomy and physiology depends on first understanding the behaviour being mediated. Glover, in his review of earlier work suggesting various dichotomies in visual processing, shows how there is a tendency to oversimplification if this approach is ignored. His own new proposals demonstrate the advantages of allowing function to drive anatomical analysis. Nevertheless, the new planning–control dichotomy he proposes, though a valuable advance, is itself an oversimplification of what must be a multi-channel system.

A particular visual function can be present only if there is a physical mechanism present in the brain to mediate it. However, it is the visual function, or rather the behaviour dependent on that function, that is selected for by evolution. Put simplistically, a physical mutation in the structure of the brain will only be selected for if it facilitates a behavioural capacity that enhances survival. Glover provides a possible example of this in his suggestion that the phylogenetically newer cortex in the human inferior parietal lobule, not present in the monkey brain, has evolved to mediate a planning function in motor control (sect. 1.2.1 and 3.1.1).[1]

A similar argument applies to environmentally modulated developmental processes. A world full of vertical lines will, through the continual processing of those lines, lead to a different neural structure from a world full of horizontal lines (Blakemore & Cooper 1970). So in a real sense, in both evolution and development, the function of the brain determines its structure. Form follows function.

The significance of this is that an understanding of behaviour is essential, and arguably has to precede, an understanding of the structure of the brain mediating that behaviour. The term *behavioural neuroanatomy*[2] perhaps best encompasses this approach. Glover's article is an excellent illustration of the value of using behaviour to drive a neuroanatomical analysis. By beginning with a historical review of motor control, he focuses the subsequent anatomical analysis on meaningful possibilities. Having presented evidence for the existence of a separate planning function that is independent of on-line motor control, he then looks at the neuroanatomical evidence to find where it might be mediated.

This, as Glover's review demonstrates, is a very different approach from some of the earlier work, particularly lesion studies, looking at the link between anatomy and behaviour. The emphasis in this earlier work tended, probably necessarily because of our limited knowledge at the time of both anatomy and behaviour, to be on rather open-ended searches for a behavioural deficit, ideally achieving a double dissociation of lesion and deficit to control for nonspecific effects (Teuber 1955). The dichotomy in visual processing between the "what" of the cortical pathway and the "where" of the retino-collicular pathway proposed by Schneider (1969) was an influential example of this approach. This emphasis on the binary division of visual behaviour continued with the subsequent subdivision of primate cortical systems into their own "what" – ventral – and "where" – dorsal – pathways (Ungerleider & Mishkin 1982). This was subsequently refined into the "perception for recognition," ventral and "perception for action," dorsal pathways of Goodale and Milner (1992). Now, Glover, very convincingly, proposes a binary sub-division of the dorsal pathway into separate planning & control systems with distinct visual inputs. So we have a binary cascade model of scientific advance with a significant division roughly every ten years (Fig. 1).

Binary subdivisions are a powerful way of getting to specifics, as anyone who has played the party game of finding a secretly chosen word in a dictionary by this means will know, but does it create an accurate description of the behavioural neuroanatomy of the brain? It fits well with the experimental designs most commonly used, for example, double dissociations, and this may be one of the reasons it is so common. We like to compare things and divide them into two categories.[3] Many behavioural studies are deliberately designed to discriminate between just two alternatives. This can be fruitful, as in the present case, but it usually leads to oversimplifications of the actual picture. Particular problems arise when there are sets of overlapping binary divisions that do not integrate easily. One of many possible examples of this in the motor control area is line bisection in neglect patients. There is good evidence that visual information feeding this relatively simple task both varies according to whether the line is in peripersonal or extrapersonal space (Cowey et al. 1994; 1999) and also depending on whether the patient is using a stick or a laser to indicate the line centre (Pegna et al. 2001). Another example is the differential role of subcortical and cortical oculomotor systems in practised (predominantly superior colliculus) and unpractised (frontal eye-fields) visual search (Latto 1978a; 1978b). As far as I can see, these various binary subdivisions do not map in a simple way onto the control-planning model.

The alternative approach is much more complex. It involves producing a global model of motor control that can then be mapped on to the neuroanatomy. This kind of approach is beginning to be fruitful in visual perception with attempts to link the modularity of processing to anatomical modularity (Livingstone & Hubel 1988; Zeki 1978). However, it is probably a little way off in our attempts to explain visuomotor processes. Meanwhile, we have to move forward in a more piecemeal way through insightful articles like the present one, always bearing in mind that the ultimate explanation will be a multifactorial one, with the nature of the neural processing driven by the needs of the outcome. Form follows function and there will be as many different neural systems, and visual inputs to those systems, as there are different kinds of motor outputs.

NOTES

1. It is perhaps worth noting that it seems unlikely that nonhuman primates do not have some element of planning in their motor control and that neural mechanisms in the frontal lobes, particularly the frontal eye-fields, have been suggested in this context (Collin et al. 1982; Latto 1986).

2. The first usage of this useful term that I can find is Mesulam (1985; 1989).

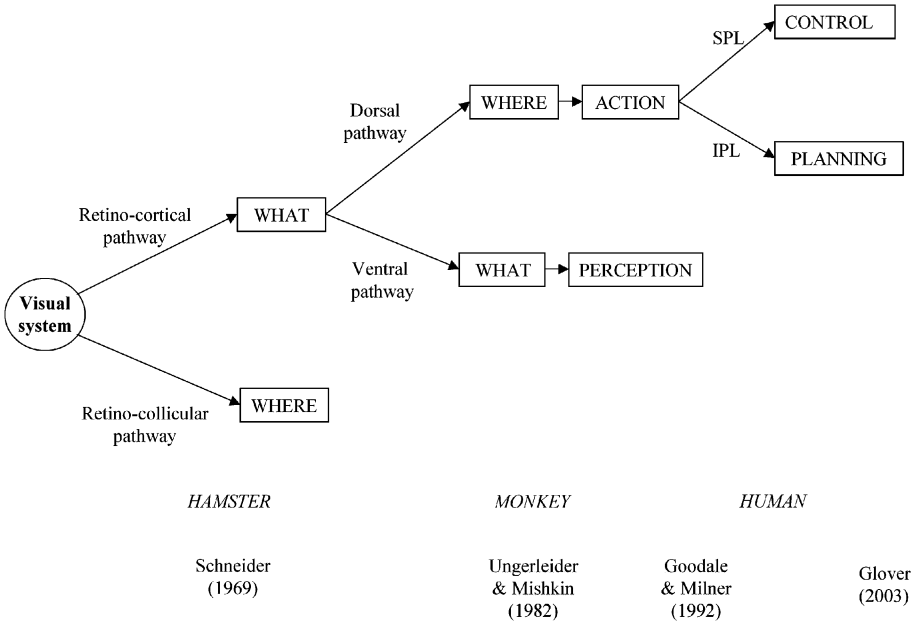

Figure 1 (Latto). The binary cascade model of the development of our understanding of the organisation of the visual system.

3. The fact that English has a specific part of speech, the comparative inflection of the adjective, to identify a binary category (higher, lower, etc.) raises the possibility that the tendency to form binary subdivisions is a fundamental process in human thought. Maybe, as with some primitive counting systems ("one, two, many"), two subdivisions are as many specific categories as we can easily cope with.

Automaticity and inhibition in action planning

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Abstract: We question the generalizability of Glover's model because it fails to distinguish between different forms of planning. The highly controlled experimental situations on which this model is based, do not reflect some important factors that contribute to planning. We discuss several classes of action that seem to imply distinct planning mechanisms, questioning Glover's postulation of a single "planning system."

Glover characterizes planning as a discrete and monolithic system operating, to a large extent, prior to the initiation of an action. While this model is a welcome addition to recent models distinguishing perception and action, we believe that the mechanisms underlying planning may be much more diverse than suggested by the target article. Humans are unquestionably adept at planning skillful action, yet this function need not be meditated by a single system any more than memory, say, need consist of a single mechanism. The mechanisms underlying planning in the highly controlled experimental situations cited in support of the planning–control model do not do justice to the full diversity and complexity of human action. It has been noted, for example, that apraxic patients demonstrate strikingly few difficulties interacting with objects in naturalistic situations even as they fail completely to demonstrate such ability in controlled laboratory situations (see Cubelli & Della Sala 1996). It is important to further differentiate the construct of planning if the planning–control model is to generalize beyond simple actions involving pointing, reaching, and grasping at isolated objects.

One important distinction made by researchers in diverse fields is that between direct and mediated actions. The former category assumes a direct mapping between perception and action, whereas the latter assumes that action is mediated by stored representations. Glover emphasizes the role of mediated actions, focusing on the relation of so-called visuokinesthetic engrams in the inferior parietal lobe (IPL) to planning (sect. 4.1.1, para. 4). In addition to the evidence he cites, such representational mediation is implied by patients with visuo-imitative apraxia who are able to imitate familiar but not unfamiliar gestures (Goldenberg & Hagmann 1997). Patients with so-called *pantomime agnosia,* on the other hand, are able to imitate gestures that they are unable to recognize (Rothi et al. 1986), implying a separate pathway from perception to action that bypasses stored representations used by patients with visuo-imitative apraxia. To account for such dissociations, recent models of deficits in apraxia (e.g., Cubelli et al. 2000; Rothi et al. 1991) have found it necessary to include multiple pathways from perception to action. There is no place for a single "planning system" in these models. Rather, planning is conceptualized as consisting of multiple and diverse neural circuits that differentially contribute as a function of task, context, experience, and the available control and coordination of the relevant actions.

Some researchers have also distinguished between actions that are externally versus internally motivated, the former made in response to some distal cue, the latter generated volitionally by the subject on the basis of stored representations. These two types of behavior are mediated largely by distinct lateral and medial premotor systems respectively (Goldberg 1985; 1987; Passingham 1993).

A related distinction is that between automatic and volitional actions. In some cases, perceptual stimuli seem to elicit corresponding action plans automatically. Rizzolatti and colleagues, for example, have identified neurons in the monkey's premotor cortex that code goal-directed actions and are also activated visually by objects affording that action ("canonical neurons"; Rizzolatti et al. 1988) or by the same action being performed by the experimenter ("mirror neurons"; di Pellegrino et al. 1992). Recent behavioral studies in humans have demonstrated similar effects. Gentilucci (2002), for example, has demonstrated that the affordances of task-irrelevant objects systematically influence reach

kinematics. Subjects' grip aperture is increased when reaching for a dowel sitting on a larger as opposed to a smaller sphere, even though the target dowel does not differ between conditions. Similarly, when attention is diverted, individuals have been observed to unwittingly engage in behavioral mimicry (Chartrand & Bargh 1999; Stengel 1947). Hommel (2000) reviews evidence of at least four distinct forms of automatic stimulus response translation which appear to arise from different processes.

Such automatic activation is most apparent when inhibitory control is lacking, either following brain insult or during early infancy. Denny-Brown (1958), for example, observed that following lesions of the medial frontal lobes, patients showed a compulsive drive to interact with objects in their environment, what he termed *magnetic apraxia.* Similar compulsivity was observed by Lhermitte (1983; Lhermitte et al. 1986) following frontal lobe damage. These patients demonstrated a total dependence on environmental stimuli to guide their actions, compulsively using objects (utilization behaviors) and mimicking the experimenter (imitation behavior). Similar behaviors can be observed in infancy. Baldwin (1892) described the young infant as "suggestible," in that environmental stimuli would automatically evoke congruent behavior. Such behaviors were observed by McGraw (1941), who found early reaching movements in response to objects notable for their "autonomous quality," in that these reactions seemed "in no way connected with a desire on the part of the child to possess or manipulate the object" (p. 130).

Our own work (Longo 2003) demonstrates that perseverative search can be elicited in nine-month-old infants to a location where they had seen the experimenter reach is but had not reached to themselves, suggesting that the perception of the experimenter's action had activated analogous motor responses in the infant. This is consonant, as well, with findings of imitation in very young infants (e.g., Meltzoff & Moore 1977), which can also be explained in terms of motor priming (Kinsbourne 2002), followed by a decline over the first few months of life (Fontaine 1984; Maratos 1982), presumably on account of increased inhibitory control.

Glover describes planning as having "the goal of selecting and initiating an adaptive motor program" (sect. 1.1.2, para. 1). In complex ecological situations, however, planning frequently has the goal not only of selecting adaptive motor programs, but also *inhibiting non-adaptive* motor programs which have been automatically activated by environmental stimuli. Consider, for example, the mostly automated actions of a skilled baseball player hitting a pitched ball, relative to the tentative and uncoordinated actions of a novice. The former player not only does a better job of anticipating and coordinating his or her movements, but also is more adept at inhibiting erroneous movements, such as swinging at balls out of the strike zone. Such inhibitory control does not fit easily into the planning–control framework articulated by Glover and, therefore, we question the sufficiency of the current model to account for much of naturalistic behavior.

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Evidence from optic ataxia does not support a distinction between planning and control mechanisms in human motor control

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Abstract: Evidence from optic ataxic patients with bilateral lesions to the superior parietal lobes does not support the view that there are separate planning and control mechanisms located in the IPL and SPL respectively. The aberrant reaches of patients with bilateral SPL damage towards extrafoveal targets seem to suggest a deficit in the selection of appropriate motor programmes rather than a deficit restricted to on-line control.

Glover is to be commended for his extensive review of this largely unresolved current issue in motor control. His planning–control model, however, is not as parsimonious as many existing models and is unconvincing for several reasons. Furthermore, the distinction between planning and control processes appears rather arbitrary and unnecessary when a single continuous mechanism for both would be far more practical and elegant. Glover's distinction between planning and control mechanisms is an expansion of traditional models based upon the observation that on-line adjustments are usually seen only towards the latter stages of fast aiming movements. The lateness of such adjustments, however, probably has as much to do with the inertial properties of the limb as they have with a putative switch between planning and control mechanisms. Although the model might successfully explain experimental data more accurately than the perception and action model (Milner & Goodale 1995), a more succinct and parsimonious model is the inverse-forward model (Wolpert & Ghahramani 2000). The latter not only allows for a single continuous recursive process active from before movement onset until movement endpoint but can also be applied to eye movements, whereas the planning–control model cannot. Overall, the planning–control model does not advance our understanding of motor control above and beyond existing models; although we believe the model has numerous flaws, this commentary will focus specifically on optic ataxia and deficits of on-line control.

According to the planning–control model, a patient suffering from optic ataxia has deficits that are limited to on-line control but has *unimpaired* movement planning. The "planning" stage has access to all of the necessary spatial characteristics relating to the actor, effector, and target in order to plan a goal-directed reach and specify the velocity and timing of the reach. The "control" phase of the movement determines the fine-tuning of certain elements of the reach, such as grip aperture, hand configuration, and target acquisition. We could therefore expect the reaches of optic ataxic patients to head generally in the right direction, under the influence of an efficient motor plan, but expect their final endpoint or grip formation to be inaccurate. This is not the typical observation with many optic ataxic patients, however, for whom the initial reach direction is also often grossly inaccurate. For example, nonfoveal patients (see Buxbaum & Coslett [1997] for this distinction) typically misreach towards fixation when reaching to extrafoveal targets. It is important to note that, contrary to what Glover's model suggests, it is *not* the case that (a) their initial reach direction is accurate, and (b) their subsequent aberrant on-line control makes the reach inaccurate.

This is particularly apparent in patients with bilateral damage to the superior parietal lobes. Patients Mrs. D. (Carey et al. 1997), D.P. (Buxbaum & Coslett 1997), J.J., and M.U. (Jackson et al. 2004) all present with bilateral superior parietal damage and all show a type of "magnetic misreaching" akin to nonfoveal optic ataxia. For example, Mrs. D., with asymmetric slowly progressive

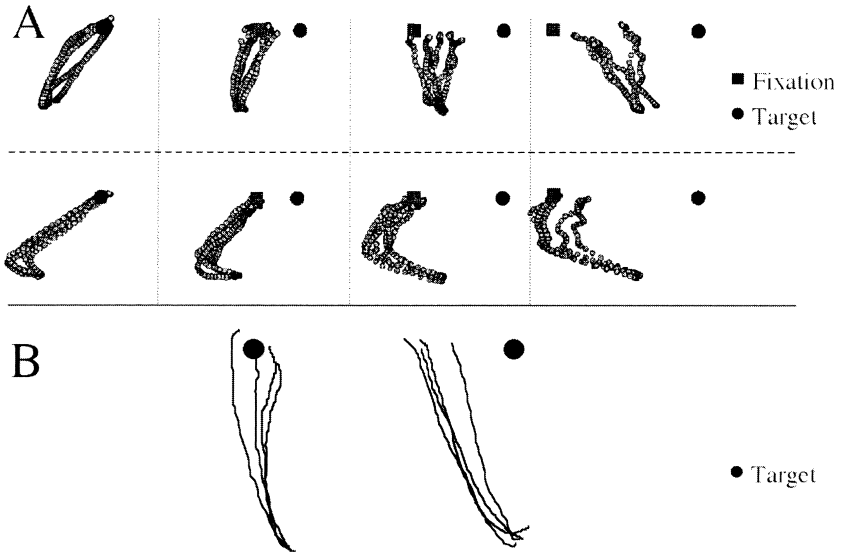

Figure 1 (Newport et al.). Evidence that optic ataxia involves a deficit of movement planning. **A.** Mrs. D., pointing with left (upper) and right (lower) hands towards foveal and extrafoveal (10°, 20°, and 30°) targets (from Carey et al. 1997). **B.** J. J. reaching bimanually while foveating left target.

bilateral lobe degeneration largely restricted to the SPL, could reach only towards the point of fixation with either hand. J.J., a right-handed male with asymmetrical bilateral posterior atrophy (damage to the left hemisphere involving the SPL and IPS, angular gyrus; damage to the right hemisphere involving the IPS and also over the posterior aspect of the angular gyrus), also tended to reach towards his point of fixation rather than towards the target. For example, when reaching bimanually for separate targets placed shoulder width apart while looking only at the left hand target, his right hand would err towards the fixated target for the left hand. As can be seen from Figure 1, reaching, for both patients, is inaccurate from the outset of the movement consistent with a deficit in both planning and on-line control, suggesting that a single mechanism might be responsible for both. It was *not* the case that the initial movement direction was correct and that aberrant on-line control then caused the hand to be directed towards the fixation; rather, the initial movement direction was incorrect and movement direction remained incorrect throughout the movement. This data is inconsistent with Glover's account of both optic ataxia and the role of the SPL. Glover also suggests that reaching errors in optic ataxia should be most evident in circumstances in which large corrections are required, including reaches towards extrafoveal targets. This implies the unlikely notion that the reaches of a neurologically intact individual towards an extrafoveal target would initially be as inaccurate as those of Mrs. D. and J.J. (because planning mechanisms are intact in both patients and controls), but that in normal subjects, unimpaired on-line control processes would correct for this error to make the final outcome accurate.

Furthermore, Glover cites the inability of patient I.G. to make in-flight adjustments to perturbed targets (Gréa et al. 2002) as evidence for the locus of on-line control within the SPL (I.G. presents with bilateral SPL damage). I.G., however, has preserved grip aperture formation, which according to Glover is also the preserve of on-line control. Patient J.J., on the other hand, does not adapt to prisms under terminal exposure conditions, which suggests a deficit of movement planning; terminal exposure does not allow time for on-line corrections. The erroneous hand position is seen only at the very end of the movement, and adaptation therefore requires that a reach be planned away from the direction of gaze (as gaze direction specifies the perceived rather than the actual target location). J.J. is unable to select the appropriate motor programme and as a consequence consistently reaches to the perceived target location (i.e., his point of gaze). According to Glover, however, such movement planning should be intact as J.J.'s IPL, the supposed locus of planning, is spared bilaterally. It is likely that the parietal lobes are responsible for comparing and maintaining current internal representations of the body, which are then communicated to the cerebellum, rather than having specific planning or control functions.

Planning and control of action as solutions to an independence of visual mechanisms

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Abstract: Glover proposes a planning–control model for the parietal lobe that contrasts with previous formulations that suggest independent mechanisms for perception and action. The planning–control model potentially solves practical functional problems with a proposed independence of perception and action, and offers some new directions for a study of human performance.

Glover proposes roles for the inferior and superior parietal lobes in the planning and control of action. He is somewhat at variance with the independent roles for the dorsal and ventral visual pathways previously hypothesized for the control of action and object identification (Goodale 2001; Milner & Goodale 1995). However, we agree that a reformulation of Milner and Goodale's position is required. Glover's planning–control model is laudable because it potentially solves a problem with a proposed independence of action and object identification, namely that of *independence* of mechanism within a context of functional and evolutionary *dependence.* By establishing the conditions under which these processing modes interact, Glover offers insights into coordinative

mechanisms, and potentially offers new directions for studies of stimulus-response compatibility.

Although action and perception are considered to involve separate mechanisms (Goodale 2001), a hypothesis of independence is equivalent to accepting a null hypothesis. This is a statistically weak position, and if there is good reason to suppose that the mechanisms for the identification of an object interact with action, then there is reason to suspect a Type I error. A hypothesis of independence is liable to generate challenges, because researchers can potentially identify weak interplay between the mechanisms responsible for object identification and action, or establish the limiting conditions under which the mechanisms interact. Effectively, Glover has commented upon the conditions under which the independence between object identification and action breaks down, and described the processes whereby this would occur.

Goodale's independence of perception from action offers a potential functional paradox, as object properties can be important for human movements. As tool users, humans can detect the affordances offered by an object and employ it as a tool. And from this viewpoint, the motor system has to be able to take into account object properties to allow tool-users to achieve desired endpoints. If separate mechanisms are involved for perception and action, this leads to questions about how the affordances of objects such as tools are mapped into ongoing behavior. By offering planning and control as separate visual streams, Glover offers some starting points for such considerations.

In particular, the functional interplay of perception and action seen in tool use is important for human evolution. For humans, tool use has been assigned a key ancestral role and it is associated with evolutionary changes in brain size or structure. From an evolutionary perspective it is thus surprising that there would be an independence of pathways responsible for object identification and control of movement (Goodale 2001), as it offers no insights as to how humans can use tools. At least in humans, this independence is liable to cause problems. There is therefore a need for a better understanding of how one of these systems operates in the context of the other to bring about the sorts of fine motor coordination humans are known for. Glover offers a redescription that assists in this regard. The inferior parietal lobe plays a part in planning, presumably identifying the affordances of objects, while the superior parietal lobe engages in on-line supervisory adjustments. According to Glover, an independence occurs at shorter time periods, but is resolved with the passage of time.

Glover reviews the circumstances under which object properties influence action. Glover's studies reveal that object properties influence the early part of movement trajectories. Others have demonstrated that object properties assume a greater role when there is a reduced availability of visual information for the control system. We have recently observed that precision (rather than time) can moderate these effects. Phillips et al. (2003) examined the potential conflict between object properties and action during cursor positioning within the graphical user interface. When precision requirements were low, the arrowhead cursor shape influenced cursor placement, with the effects in keeping with those effects of arrowheads seen in optical illusions. Namely, as for the Müller-Lyer illusion, extent was overestimated and overshooting occurred in the direction the arrowhead pointed. When precision requirements were low, the arrowhead cursor shape influenced movement durations instead, with the effects again as might be expected from illusory figures.

Such studies indicate that object properties can interfere with action. Indeed, one of us has delineated a number of forms of stimulus-response compatibility that involve a conflict between the cues offered by object properties and required action (cf. Kantowitz et al. 1990). For example, arrowhead cursors cue both location and direction (Kantowitz et al. 1990), and thus offer a potential source of conflict between the mechanisms responsible for processing objects, and those controlling action. Other confusions arise when users of tools have to decide whether the tool is figure or ground, that is whether to move the tool or move the background, and these have clear implications for subsequent coordination (Guiard 1988).

There is therefore a need for a better understanding of how one of these systems functions in the context of the other to bring about the sorts of fine motor coordination humans are known for. If separate mechanisms are involved for perception and action, this is particularly important for humans, as it leads to questions as to how the affordances of objects such as tools are mapped into ongoing behavior. A consideration of such matters is likely to address a phylogenetically important ancestral trait of humans. Unfortunately, research into motor coordination tends to focus upon simpler and less directly human phenomena (e.g., pointing or walking). There is therefore a need to address the *challenges to motor coordination posed by the use of tools*, considering the impact of object properties upon coordinative mechanisms. Indeed, the disturbances of coordination caused by incompatible tools potentially offer insights into the adaptive mechanisms that feature prominently in human evolution.

Two types of object representations in the brain, one nondescriptive process of reference fixing

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Abstract: I comment on two problems in Glover's account. First, semantic representations are not always available to awareness. Second, some functional properties, the affordances of objects, should be encoded in the dorsal system. Then I argue that the existence of Glover's two types of representations is supported by studies on "object-centered" attention. Furthermore, it foreshadows a nondescriptive causal reference fixing process.

Glover argues that the dorsal system controls the on-line execution of action, while planning for action is subserved by a third visual stream that leads from the occipital lobe to the frontal lobes. Along this pathway, in the inferior parietal lobe (IPL), representations of objects are stored (IPL-r) that integrate information from both the ventral and the dorsal system. The former delivers to the IPL information regarding nonspatial properties of objects. The latter delivers spatio-temporal, size, viewer-centered shape, and orientation information, which is stored in the superior parietal lobe (SPL-r). The information in the SPL is retrieved bottom-up (i.e., in a cognitively impenetrable way), evades awareness, and precedes the information encoded in the IPL-r. The information stored in the IPL-r has a semantic conceptual component, requires reference to stored memories, and enters the realm of consciousness (target article, sects. 1.2.2, 2.5, 2.7).

I comment, first, on two problems in Glover's account: (1) It is not clear that representations with semantic content are always available to awareness. (2) Some functional properties are not encoded in the IPL; the affordances of objects should be encoded in the SPL. Next, I argue that Glover's postulation of two types of object representations in the brain accords with evidence adduced from studies on "object-centered" attention. Furthermore, it allows recasting of the problem of grounding representations, by providing the tools to construct a viable version of a causal reference fixing process.

Glover claims that the IPL-r contains semantic information and that the viewer is aware of the content of this representation. However, there are studies (Kanwisher 2001; Merikle et al. 2001) suggesting that semantic information can be processed without the person being aware of that content. Lamne (2003) postulates a distinction between phenomenal awareness and access awareness related to different kinds of representations, which correspond roughly to the SPL and IPL representations, that are both located in the ventral system. Hence, there are additional compli-

cations with respect to the issues of awareness, and the types of representations and where they are stored.

Glover states that the functional properties of objects are stored in the IPL. The affordances of objects, though, are retrieved from a scene directly, and are perceived independently of object-specific knowledge and of the subject's will (Bickhard 1993; Norman 2002). Petitot (1995) discusses the early vision processes that retrieve bottom-up from a scene its aspectual properties, such as "transfer." The affordances of objects, therefore, cannot be among the contents of the IPL-r.

Let me move to Glover's postulation of two types of object representations. There is substantial evidence for an object-centered component to visual attention, in which attentional limitations are characterized in terms of the number of defined discrete objects which can be processed simultaneously (Pylyshyn & Storm 1988; Scholl 2001; Scholl & Leslie 1999). This attentional mechanism is designed to provide a representation of objects as discrete spatio-temporal entities. The representation encodes primarily spatio-temporal information. It functions as an indexing mechanism that focuses on and individuates objects. Object-centered attention may override featural information other than spatio-temporal information. Thus, there is evidence that there exists a level of visual processing in which objects in a scene are parsed and tracked as distinct entities without being recognized as particular objects. Object individuation precedes object identification.

It is at this point that Glover's dual representation comes into the scene. The SPL-r provides the content of the representation needed for object individuation, whereas the IPL-r is related to object identification and recognition. Recall also that the information stored in the SPL (i.e., spatio-temporal information, and information about size and viewer-centered shape) is retrieved bottom-up from the scene (see also Norman 2002; Raftopoulos 2001).

The descriptive theories of reference hold that a symbol is associated with a concept in the mind, which constitutes its meaning. This concept determines what the symbol refers to, since it allows one to pick out the objects that are "described" by it. By explaining references by descriptive means, these theories of reference appeal to descriptions of other words; they explain reference by appealing to the reference of other words. To escape from the infinite regress, there must be some words whose reference is founded directly in the world. If the fixing of reference of perceptual demonstratives could be achieved by means of a direct causal link with the environment without the mediation of descriptions, then the first move toward grounding representations in the world would be achieved, since the direct causal link would ground perceptual representational content in the world.

The content of the SPL-r that is retrieved bottom-up from a visual scene without any conceptual involvement provides the direct causal link that fixes the reference of perceptual demonstratives. A plausible neural mechanism that implements this is expounded in Ballard's theory of deictic codes. The shortest time at which actions and movements can be observed is the 1/3 sec time-scale. This is the embodiment level. Computations at this level govern the deployment of the body's sensors and effectors.

Suppose that one looks at a scene and, through eye focusing, selects a part of it for further processing. The resulting brain representation is about (i.e., refers to) that part of the scene. When an internal representation refers to an object through such a deictic representation, this is a "deictic reference." Thus, when fixating a location, the neurons that are linked to the fovea refer to information computed from that location. The object present at that location is the referent of the deictic reference. The act of fixation assigns to this object a pointer that allows object individuation and tracking; this is due to the fact that the fixation of the gaze creates a reference to a point in space and time and the properties of the referent can enter computations as a unit. It should be noted that the term "object," as used here, does not denote the objects of our experience. Rather, being the content of the SPL-r, the referent has only the content that is stored there. In this sense, the "objects" referred to above are really segmented perceptual three-dimensional viewer-centered surfaces.

Strong modularity and circular reasoning pervade the planning–control model

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Abstract: We believe the dichotomy of processes introduced in the target article is highly speculative, because the dichotomy is shaped by the questionable assumption of modularity and the complementary assumption of locality. As a result, the author falls into a line of circular reasoning that biases his analysis of the experimental and neuropsychological data, and weakens the proposed model.

The planning–control model proposed by Glover in the target article explores the existence of two distinct but interacting psychological processes for controlling reaching-grasping movements directed toward environmental objects. We believe the evidence provided is simply not compelling enough to warrant the assumption of two distinct processes (planning and control) under the control of distinct neurocognitive modules (located in the IPL and SPL, respectively). The functional and structural dichotomy between control and planning processes defended by Glover, is only one among different interpretations that could be drawn considering the evidence provided. We believe that the planning–control model reflects certain epistemological and ontological biases related to the concept of modularity, and that Glover offers a circular line of reasoning according to which experimental and neuropsychological evidence serves as proof for the processes that are supposed to explain the evidence.

Critically, Glover seems to hold a strong modular approach that precedes the analysis of the evidence, which in turn is portrayed as supporting the modular properties of the processes included in the model. Both control and planning are believed to be independent processes because of their reliance on two different sets of information (i.e., two different visual representations) about the spatial and nonspatial characteristics of the object. The separation between the processes is justified by the assumed informational encapsulation of the two modules.

This strong modularity assumption pervades the design and interpretation of experiments conducted to test the planning–control model, in terms of a separation between different movement parameters associated with each process. Although Glover recognizes the methodological difficulties inherent in finding a task that targets only one of the processes, he insists upon defending the independence of the processes. The proposed independence leads him to introduce indeterminations in the assessment of the experimental evidence. Among them, parameter crossover – when one movement parameter (e.g., hand orientation) represents the effects of planning during some part of the movement, and control during some other part of the movement – is vaguely stated.

Particularly troubling to us is that no means is offered for determining at what time(s) a given parameter reflects either planning or control. Furthermore, the fact that 29 of the 52 entries listed in Glover's Table 2 are characterized as reflecting either "mostly" control or "mostly" planning is, we believe, diagnostic of the fact that so-called planning and control processes are not distinct. Moreover, parameter crossover seems to reflect the kind of interactivity that violates the *additive-factors logic* demanded by the modularity assumption (cf. Van Orden et al. 2001). The interaction between processes is systematically neglected in Glover's account, opening the door to the counterargument that planning and control may as well be two extremes in the on-line unfolding

of a single, more complex process, rather than being two independent processes.

Glover's model also seems to depend on the *locality assumption* – the position that planning and control processes (in this case) are independently implemented in two distinct brain areas, the IPL and SPL, respectively. According to this assumption (and central to Glover's model), damage to one of those brain areas will produce a discrete impairment that can be identified with and circumscribed to the affected module without affecting critically the workings of the remaining components of the system (Farah 1994). The IPL and SPL, however, are believed to be part of the fronto-parietal network, which functions as an integrated system during the execution of movements (Wise et al. 1997). Glover's use of neuropsychological evidence to support the planning–control model relies on the locality assumption. Glover assumes that local damage to the brain produces only a selective behavioral impairment, which can be identified with the malfunction of a distinct cognitive process. It is one thing to assume the independence of the brain centers putatively responsible for planning and control, but it is another to assume that the planning and control processes are thus *necessarily* independent (Farah 1994). The functional distinctions drawn on the basis of anatomical evidence artificially reduces the complexity of movement control to a dichotomy in the planning–control model, even though the brain system responsible for the execution of reaching-grasping is believed to be distributed among a complex network of connections linking different brain centers (Ietswaart et al. 2001).

Glover presents a host of neuropsychological case studies to support his planning–control model. His strategy is one of establishing a double dissociation: Damage to the IPL disrupts planning, but not control, and damage to the SPL disrupts control, but not planning. That double dissociation is supposed to provide evidence that planning and control reflect the activity of independent neurocognitive modules, respectively located in the IPL and SPL. But the argument for the existence of independent neurocognitive modules for planning and control based on double dissociations entails a circular reasoning (see Shallice 1988) – double dissociations are assumed to occur only in the case of modular architectures, and therefore cannot be used to verify the existence of neurocognitive modules (Van Orden et al. 2001).

In addition, Glover explicitly states that the neuropsychological evidence he provides is inconsistent and in some cases may fit the alternative model (perception–action) as well as the planning–control model. Nevertheless, that evidence is included because of its parallels with the results of PET studies. The taxonomy of cases used is strongly reminiscent of the classical model proposed by Liepmann (1900), even though Liepmann's model and the line of reasoning introduced by it are recognized as an oversimplification (Cubelli et al. 2000). This is not an innocent fact, given the similarities between Glover's and Liepmann's models. (Liepmann's model stresses the importance of the division between two separate stages in the production of movement: the formulation of a motor plan – planning, in this case – and the implementation of the planned spatio-temporal sequence of movements – control, in this case.) The argument for the existence of representations or memories of movement is a critical point of discussion in the neuropsychological literature; it is conceived by some authors as a bottleneck in the study of apraxia (Iestwaart et al. 2001).

We feel that Glover's model is constrained by the assumptions of neurocognitive modularity and locality, while the experimental evidence is either inconsistent with these assumptions (e.g., parameter crossover), or inconclusive with respect to them (e.g., the neuropsychological case studies). These assumptions have been criticized by several authors (e.g., Farah 1994; Uttal, 1998; 2000; Van Orden et al. 2001; Weldon 1999) and seem, in this case, to lead us down the wrong path in our efforts to understand movement control.

Is efficient control of visually guided movement directly mediated by current feedback?

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Abstract: The main issue addressed here concerns the central notion of a forward internal model, through which efficient control and planning are linked together and to the related online predictive error processing. The existence of such a model has strong implications in action production and may question Glover's model.

Glover's approach to hand-reaching follows a view current since Woodworth (1899), Fitts (1957), Keele and Posner (1968), and Meyer et al. (1988), according to which the movement results from two basic components: one planned action determining the gross organization of the response and a final part including a fine control of the hand movements based on the simultaneous vision of the hand and target (in Glover's model, supposed to involve, respectively, the IPL and SPL). The extent to which visually guided movements are planned in advance or controlled on-line during the execution, is still a matter of debate. Whereas many studies have searched for the origin of planning errors (see Desmurget et al. [1998] for a review), another series of experiments have tried to identify whether the so-called planning phase was really planned and not under the control of either central or peripheral feedback. These studies have been carried out in normal subjects (Bridgeman et al. 1979; Desmurget et al. 1999; 2001; Goodale et al. 1986; Pélisson et al. 1986; Prablanc & Martin 1992), but also in deafferented patients (i.e., those who have lost the sense of position) (Bard et al. 1999). Basically, their overall finding is that a third component does exist, namely, an unconscious control applied during the first phase of the movement. In all these experiments, a target perturbation inducing a planning error was randomly introduced during the so-called saccadic suppression, making these perturbations unconsciously perceived. The specificity of the corresponding corrections was both their smoothness and their early stage as compared with the corrections observed under conscious double step experiments. In these latter experiments, despite sometimes a nonspecific early short reaction time, the path deviation indicating the corrections occurred with a normal reaction time, and with a clear double peak velocity profile (Georgopoulos et al 1981, Soechting & Lacquaniti 1983). One important point to notice is that the smooth online corrections were mostly observed for unconsciously detected errors. In Glover's planning–control model, online adjustments to perturbations of the spatial characteristics of the target should occur relatively quickly, irrespective of the nature of the perturbation.

However, this unconscious error detection may not be the only prerequisite for producing fast and smooth corrections. The delays introduced by conduction processing times at the different relays along the visuomotor stream have led some authors to postulate the existence of a "look-ahead" or Smith predictor (Hoff & Arbib 1992, Miall et al. 1993). More recently, Desmurget and Grafton (2000) have emitted the hypothesis that the correct execution of a hand movement is based mainly upon a forward internal model. This "internal model" is a predicted output of the upper limb endpoint derived from the real command signals fed to the motor apparatus, together with the updated passive visual and proprioceptive information of the end-point effector (the hand). In another paper, Prablanc et al. (2003) have also suggested that the fast error correction was not directly derived from the available retinal error signal between hand and target, but resulted from a comparison between a central representation of both the target and hand, mixing both sensory signals (visual and proprioceptive) and an efferent copy of the upper limb motor commands. According to Desmurget and Grafton (2000), if the normal vision of the hand and target is available during the motor response, the

detected errors should not be taken into account by the control system, whereas Glover's planning–control model should cope with these error signals irrespective of the existence of a correct or biased internal model.

We present the paradigm in brief here. A way to unexpectedly bias the internal model is to introduce a random shift in the initialization of the model by the most efficient inflow signal (i.e., vision of the hand and fingers in their resting state) (Revol et al. 2003). Although the initial position of the endpoint effector is defined through multisensory cues such as vision and proprioception, the weight of the former is high enough to create a bias when viewing the hand through prisms goggles. Pointing performance of control subjects were thus compared: (1) when an erroneous planning together with a biased internal model occurred (using left or right prisms to displace the initial vision of the hand); or (2) when a planning error was induced by a small target displacement throughout the saccadic suppression while the internal model remained intact. When an initially displaced vision of the hand occurred, pointing became inaccurate showing an incapability to correct the erroneous planning despite the undistorted target position and the natural visual reafferences from the moving limb. In contrast, a similar planning error induced by an intrasaccadic target jump was unconsciously corrected despite the lack of visual reafferences of the moving limb. These results are hardly compatible with Glover's planning–control theory. Rather, they fit the hypothesis that an intact internal model enables fast corrections as proposed by Desmurget and collaborators (Desmurget et al. 2001).

Glover refers to a possible generalisation of the planning–control model to the oculomotor system. In fact, the opposite should rather apply, as the most influential model of the saccadic oculomotor system since thirty years (Robinson 1975), relies on a single efference copy signal being used as a feedback signal to the saccadic controller, without any need for a visual feedback. The theoretical concept of a feedback taking into account both the efference copy of the multi-joint upper limb, and the visual and kinaesthetic reafferences and their underlying neural structures, had appeared much later, even very recently (Desmurget et al. 2001). However, one has to keep in mind that the simplicity of Robinson's saccadic model lies in the absence of a planning component: The whole saccade duration is devoted to control, whereas the control phase of Glover's model cannot operate properly without a subtle combination of coherent efferent and afferent signals reconstructing the instantaneous state of the moving limb, as explained above.

Another point raised by Glover's planning–control model is regarding the effect of illusion on movement. In contrast to the perception–action model (Milner & Goodale 1995), Glover's model suggests that only planning should be affected by the illusion of a surrounding context. Recently, Revol and Honoré (in preparation) asked control subjects to point, without any visual feedback, either at a central target or in the perceived direction of the same target under optokinetic stimulation. The pointing errors recorded were linked to the specificity of the pointing task, that is, only pointings performed at the target location were unaffected by visual illusion. These results fit neither Glover's model nor the action–perception model, but rather, suggest an action-perception gradient depending on the processing of the visual information (see Rossetti & Pisella 2002).

Parallel visual pathways from the retina to the visual cortex – how do they fit?

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Abstract: Which roles are played by subcortical pathways in models of cortical streams for visual processing? Through their thalamic relays, magnocellular (M) and parvocellular (P) projecting ganglion cells send complementary signals to V1, where their outputs are combined in several different ways. The synergic role of M and P cells in vision can be understood by estimating cell response entropy in all domains of interest.

The planning–control model proposed by Scott Glover in the target article, as well as the "what" versus "where" model of Ungerleider and Mishkin (1982) and the perception versus action model of Milner and Goodale (1995), all try to explain the roles played by the major streams of visual processing in the cerebral cortex. In these models, room must be left for the function of the subcortical visual pathways that feed the visual cortex with the essential information needed for their function. Originally, the magnocellular (M) and parvocellular (P) pathways were regarded as dedicated to specific visual functions, such as movement and visual acuity plus color vision. As such, many attempted to associate M and P activity to the functions of the dorsal and ventral cortical streams, respectively. This view was abandoned once it was demonstrated that the M and P signals mix largely inside V1; examination of the temporal and spatial requirements assigned to perception and action lent further support to this decision.

Visual information travels in a series of parallel pathways from the retina to V1. The M and P pathways are the best characterized (Silveira et al. 2003). They have their own set of bipolar cells that convey information to the M and P ganglion cells, which in turn project respectively to the magnocellular and parvocellular layers of the lateral geniculate nucleus (LGN). From there, the M and P relay thalamic neurons connected to specific V1 entrance layers. There are other ganglion cell classes connecting to the LGN koniocellular layers and pulvinar, from which visual information can reach V1 and other visual cortical areas (Hendry & Yoshioka 1994). These pathways remain separate until they reach V1 and then mix shortly after, as the information passes from V1 entrance layers to the other V1 compartments, and from the latter to the next visual cortical areas (Yoshioka et al. 1994).

All the models for visual cortical processing require the existence of multiple representations of the visual field, which are built either in egocentric coordinates or in coordinates centered with respect to the object (Milner & Goodale 1995). The information provided by the visual system is combined with a wide variety of nonvisual sensory and cognitive information to fulfill individual aims, including object perception, motor planning, and motor control. The visual information carried by light emanating from objects located in the ever-changing visual field has to be coded with enough precision in space and time to allow behavioral tasks to be adequately performed. However, because of the limits of quantum catch by the photoreceptor array, any gain in the capacity of locating an object in space more precisely is accompanied by a loss in the ability to measure precisely the moment of occurrence of a visual change, and vice versa (Land & Nilsson 2002). In addition, natural scenes are composed by singularities and periodicities, both in space and time, and the visual system has to have enough precision to evaluate not only spatiotemporal coordinates, but also their spatiotemporal frequency content. The simultaneous precision in time, temporal frequency, space, and spatial frequency is a general, basic problem in the design of measuring devices, and there is no way to increase the performance in all these domains at the same time (Gabor 1946; Silveira & de Mello 1998). All real devices, either natural or man-made, built to store, transmit, or analyze visual information, represent different degrees of compromise between precision in the space-

time domain and precision in the spatiotemporal frequency domain.

The uncertainty principle of Gabor (1946) establishes in a mathematical identity the impossibility of unlimited increase in the precision of measuring the time and temporal frequency of a phenomenon, $\Delta t \cdot \Delta f \geq 1/2$, where Δt and Δf represent the uncertainty in any measurement carried out simultaneously in the time and temporal frequency domains. The number of terms in this identity, called joint entropy in Gabor's information theory, can be expanded to accommodate the six dimensions of the retinal image or the eight dimensions of the visual field or the praxic field.

The visual coding required for perception of objects, motor planning, and motor control will vary with the function performed: No single brain representation of the space-time will fulfill all requirements. For instance, good spatial frequency discrimination can be critically important for some tasks, such as the recognition of a tree by its foliage; or precise representation of spatial coordinates might be essential to reach and grasp an object. Building a representation of the visual world adequate to the task to be performed is therefore essential to models like the planning–control model. This cannot be done by using a single retinal ganglion cell class to convey the information from the photoreceptor array to the visual cortex, because each retinal ganglion cell class is bound to a particular joint entropy combination. However, having two or more cell classes, such as the M and P cells, can solve the problem. What is needed is to combine their output in different ways in accordance with the task to be performed.

The synergic role of M and P cells in vision can be understood by estimating the cell response entropy in all domains of interest. For this, it is necessary to measure their impulse function in the domains of space and time, using discrete, localized stimuli. In addition, extended, periodic stimuli in the domains of spatial frequency and temporal frequency can be used to measure cell frequency response. The results are critically dependent on cell eccentricity; once M and P cell dendritic fields change dramatically with distance from fovea, it is hypothesized that all the functional properties would change accordingly. In addition, it has been shown that retinal illuminance also influences the response time course and receptive field size of retinal ganglion cells. The evidence so far indicates that the M and P cell responses differ in all domains, though displaying a considerable degree of overlap. The M and P cell properties in space and time, spatial frequency and temporal frequency, are complementary and result in different loci in Fourier space. Each pathway represents a particular trade-off to reduce joint entropy, and the visual system codes the spatiotemporal content of natural scenes more efficiently by using two or more channels having different entropy loci in the information diagram. M and P cells perform simultaneous and overlapping analyses of the visual field using different strategies to minimize entropy. This enables higher order visual neurons, similar to those of the dorsal and ventral cortical streams to combine M and P information in different ways and could explain why M and P outputs converge in the visual cortical pathways.

The requirements for perception, motor planning, and motor control are such that refined information about target location, time of occurrence of an event, and spatial and temporal frequency discrimination are needed in different degrees for each task. Each subcortical pathway conveys information with different degrees of precision in each dimension. The information is combined in V1 and sent to the different cortical streams as requested to build visual representations for perception and action. Each representation is a trade-off in the information space optimum for each task.

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The control process is represented in both the inferior and superior parietal lobules

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Abstract: Glover postulates that the inferior parietal lobule (IPL), along with the frontal lobes and basal ganglia, mediates planning, while the superior parietal lobule (SPL), coupled with motor processes in the cerebellum, regulates the control process. We demonstrate that the control process extends beyond the cerebellum and SPL into regions hypothesized to represent planning.

The target article by Scott Glover separates planning and control processes into distinct, separate representations spanning multiple cortical and subcortical networks. In particular, Glover argues that the planning process initiates and selects an adaptive motor program in the context of environmental and task goals, whereas the control process is focused on the on-line correction of the spatial parameters of the action. The specific thrust of Glover's thesis states that the inferior parietal lobule (IPL), along with the frontal lobes and basal ganglia, mediates planning, while the superior parietal lobule (SPL), coupled with motor processes in the cerebellum, regulates the control process. Two lines of empirical evidence suggest that this dichotomy may be too simplistic to completely understand the complex integrity of human brain function in the control of movement.

The first line of evidence is developed from research in patients with Parkinson's disease (PD). PD results from a loss of dopaminergic neurons in the substantia nigra pars compacta, leading to abnormal basal ganglia outflow from the substantia nigra pars reticulata and the internal segment of the globus pallidus to the thalamus (Albin et al. 1989; Wichmann & DeLong 1996). PD patients were shown to have more variable force output than age-matched healthy control subjects during a continuous grip force production task that required on-line visuomotor processes (Vaillancourt et al. 2001). Also, Ghilardi and colleagues (2000) found that movement kinematics and accuracy were similar between PD subjects and controls in the absence of visual feedback, but movements of individuals with PD had a shorter transport phase and reduced velocity compared with control subjects with on-line visual feedback. Direct neural recordings from primates have shown that a considerable number of globus pallidus neurons specifically respond to a visually-guided reaching task (Mushiake & Strick 1995). The findings on PD and the work from primate electrophysiology suggest that Glover's control process is associated with basal ganglia function – a region hypothesized by Glover to only mediate the planning process.

The second line of evidence comes from work in human neuroimaging. We conducted a whole brain echo-planar functional magnetic resonance imaging study at 3 Tesla (Vaillancourt et al. 2003), in which human subjects controlled continuous force output by grasping an apparatus with their middle finger and thumb. Subjects produced force at 15% of their maximum for 30 sec blocks while using on-line visual feedback, and rested by fixating on the visual target. Figure 1 depicts a group map of the significant activation found in the parietal cortex during the comparison of force with on-line visual feedback compared with rest. Both the inferior and superior parietal lobules were active bilaterally during the force control task. The task of producing force to the target required subjects to initiate the force, acquire the force target, and regulate force for the remainder of the 30 sec block. All subjects initiated force and acquired the target within 500 msec, and this time period was not included in the analysis shown in Figure 1. Only the force control period was included in Figure 1. According to Glover's definition, the task used in Figure 1 would fall

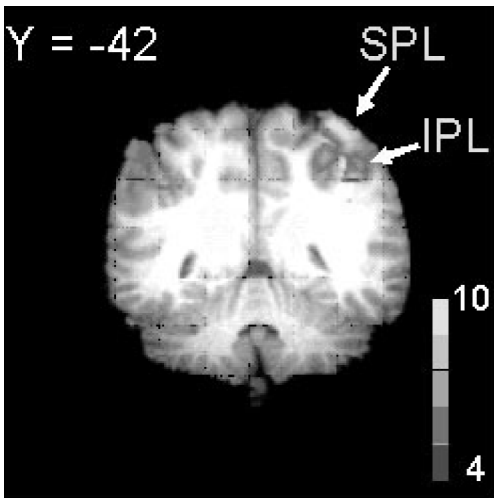

Figure 1 (Vaillancourt et al.). Visuomotor Process in IPL and SPL. The group functional map was obtained from a group Fisher test of the force with visual feedback minus rest t-map across the ten subjects. The group map was overlaid on a single subject's Talairach transformed brain. The image is shown from a radiological perspective.

under the control process – and include the activation of the superior parietal lobule and the cerebellum. However, the findings from that study demonstrate that the control process may also occur in the inferior parietal lobule. Although not depicted in Figure 1, a distributed network within the anterior prefrontal cortex, premotor cortex, putamen, lateral cerebellum, intermediate cerebellum, and the dentate nucleus assisted the parietal lobules in regulating the on-line visual control of force.

The implications from the work in PD and the findings from the neuroimaging studies lead us to two possible conclusions: (1) that Glover's control process occurs in a more widely distributed network that includes multiple cortical and subcortical regions; or (2) that the on-line visual control of the force task includes a planning component not recognized within Glover's theoretical framework. To reconcile these differences we turn to a postulated model of the visual control of force that may support the latter conclusion.

Slifkin and colleagues (2000) examined the influence of intermittent visual feedback on the variability and frequency of continuous force production. During the force task, subjects received visual feedback at different frequencies that were presented at intervals as slow as every 5 sec to as fast as every .04 sec. Slifkin and colleagues found that there was a hyperbolic reduction in the dominant frequency of force output at 1–2 Hz, reaching asymptotic values near a visual feedback frequency of 6.4 Hz (or 150 msec). Slifkin et al. proposed a model where force error is accumulated at a maximum frequency of 6.4 Hz. Each successive force error is then held in short-term storage (with a maximum temporal capacity of 1–2 sec (Elliott & Madalena 1987; Vaillancourt & Russell 2002), and, after approximately one second, an error correction signal is computed. In the context of Glover's theory and the Slifkin et al. model of continuous force production, the control process would operate at a fast time scale where the maximum is 6.4 Hz, and the planning process computes the error signal about once per second.

In summary, the above explanation reconciles the apparent contradictory findings with Glover's postulated dichotomy of planning and control processes. While the proposed dichotomy of planning and control elegantly links historical models of Woodworth (1899) with theories of perception and action (Milner & Goodale 1993), the model does not account for the fact that the visuomotor feedback network extends into multiple cortical and subcortical regions (Vaillancourt et al. 2003).

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Further evidence for, and some against, a planning–control dissociation

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Abstract: We summarize a number of recent results from our own experiments as well as those from other laboratories. Some of these results support Glover's planning/control dissociation and some are at odds with it. We suggest that the model needs to be further refined and expanded.

In his target article, Glover has provided a welcome alternative theory for the evidence related to the perception-action/dorsal-ventral visual stream controversy. Like many new theories, it leads to more questions than answers, but this is not necessarily a bad thing, if it motivates those of us doing sensorimotor research to delve more deeply into the issues surrounding this controversy. Indeed, because Glover's planning–control dichotomy appears to map onto a circumscribed set of brain areas, it makes several predictions regarding activation patterns or the effects of lesions. For example, he suggests that transcranial magnetic stimulation (TMS) delivered to sensorimotor areas underlying planning or control should lead to corresponding deficits in these behaviors under appropriate conditions. A recent study from one of our labs has addressed this very question in the context of the perception-action debate (Lee & van Donkelaar 2002). Subjects were asked to point to the central circle in an Ebbinghaus display while TMS was delivered to either dorsal or ventral stream sites. Previously, we had shown that when the target circle appeared to be large, pointing movement times were shorter and velocities were greater than when the circle appeared to be small (van Donkelaar 1999). When TMS was delivered over either dorsal or ventral stream sites, this effect was significantly reduced. Interestingly, dorsal but not ventral stream stimulation also reduced the effects of target size even in a control condition without surrounding circles.

We interpreted these findings, taken together, to suggest that the dorsal stream contribution to the effect was mainly related to the motor aspects of the task, a conclusion that does not appear to differ drastically from Glover's point of view. A key issue with respect to his theory, however, is whether we were stimulating in the IPL or the SPL. According to the planning–control model, processing that occurs within the IPL is proposed to underlie the planning of the motor response and thus be susceptible to illusion effects. By contrast, SPL processing is thought to contribute to on-line control and to correct for any illusion effects induced during planning but to otherwise be immune to their influence. Therefore, according to the planning–control model, TMS over the IPL should significantly reduce the illusion effect because of a disruption of the planning process. By contrast, SPL stimulation should actually enhance the effect because of a disruption to the on-line control underlying the corrections in response to the illusion. Clearly, we observed the former result, which implies that we were in fact stimulating the IPL.

Localizing TMS sites is not the most exact science, but various clues can be used to make good approximations. For example, the site of stimulation in our study was 7 cm posterior to the motor hot point. By comparison, in a study by Desmurget and colleagues (1999) examining the effects of TMS on on-line corrections within

the posterior parietal cortex (PPC), a site 4 cm posterior and 0.5 cm medial to the motor hot point was stimulated. This difference in the relative locations of the stimulation sites in the two studies and the typical underlying layout of the intraparietal region suggest that we were in fact affecting IPL processing. The results from our TMS study therefore appear to be consistent with Glover's planning–control model.

More generally, however, we feel that Glover's theory does not place enough emphasis on the contributions to planning and control from areas such as the premotor cortex, supplementary motor area, and motor cortex. There is a tendency in the target article to focus on the functional distinctions between the SPL and IPL, with only a limited discussion of some of the areas to which these dorsal stream sites project. Indeed, perhaps a more appropriate approach is to think of planning/decision-making as a parietal-prefrontal process and control/execution as a motor area process with an evolution from planning to control as one moves from input to output areas. For example, one criterion for control/execution should be the ability to elicit responses by direct stimulation. This definitely holds for motor areas such as the motor and premotor cortex, and (for eye movements) the frontal eye fields and superior colliculus. Moreover, there is clear evidence that control processes can occur within the motor cortex. In particular, Desmurget and colleagues (2001) have used brain imaging to demonstrate that the motor cortex (along with the cerebellum and PPC) is activated specifically during the on-line control of reaching movements. It would therefore seem that control can occur at even fairly low levels in the sensorimotor system. We think that it is vital to expand the model to include the contributions from these levels to the control process.

Finally, although Glover explicitly states that the planning–control model is not meant to generalize to eye movements, we feel that the well-documented relationships between hand and eye movements can provide further insights with which to judge the model. For example, Glover uses the results of a study on the Roelofs illusion (Bridgeman et al. 1997) as evidence for his planning–control model of reaching – while the illusion does affect movements to remembered targets, movements with no delay are presumably corrected through on-line control so that the illusion's effect on planning is eliminated. However, recent work here (Dassonville & Bala 2002) demonstrates that saccadic eye movements show the exact same pattern of accurate and inaccurate localizations for immediate and remembered saccades, respectively. Given the ballistic nature of saccades, though, on-line control cannot be used in an analogous way to explain the lack of illusory effects for immediate saccadic responses. It follows that either the saccadic system uses an altogether different mechanism to overcome the illusion than does the manual motor system, or that they both use a single mechanism that is not based on a planning–control distinction – to us, the latter possibility seems more parsimonious. Thus, a better understanding of the relations between eye and hand under illusory conditions (e.g., Binsted & Elliot 1999) will undoubtedly provide further insight into this issue. For now, though, it seems that the jury is still out.

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Human vision focuses on information relevant to a task, to the detriment of information that is not relevant

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Abstract: Glover offers an account for why some pictorial illusions influence early but not late phases of an action. His proposed corrective control process, however, functions normally in the absence of continuous visual information, suggesting that the stimulus is registered veridically prior to action onset. Here I consider an alternative account, based on differing informational constraints of behaviors (and phases of behaviors).

Glover's planning-versus-control (PVC) model provides an intriguing explanation as to why pictorial illusions affect some behaviors much more than others. Earlier theories, most notably the Milner and Goodale (1995) perception-versus-action (PVA) model, have described the presence of separate visual streams for "perception" and "action," and acknowledged that the two streams must, of course, interact with one another. However, the form of that interaction has been only vaguely described. The PVC approach takes on the important task of describing the details of this interactive process.

The PVA model could be extended in some straightforward ways to account for most of the findings reviewed by Glover, if one simply presumes that the "perception" stream is involved in planning and early execution of actions, and the "action" stream controls the final stages of a behavior. This tremendous flexibility of the PVA theory, however, is one of its great limitations. The PVC model makes far more precise predictions – predictions that could potentially be refuted by further experimentation because of their specificity. Only by increasing the precision of our models do we make progress toward developing a better understanding of human perception and action.

With these strengths in mind, there are some decided limitations to the PVC approach that should be noted in the realm of size-mediated judgment versus reaching, described in much detail in this commentary. As Glover summarizes, it is generally believed that pictorial illusions exert large effects on (a) judgments and the early stages of visuomotor actions, while exerting small or nonsignificant effects on (b) the latter portions of a visuomotor action. The PVC approach claims that the planning of a reaching action is strongly influenced by pictorial illusions, and a corrective control process removes that error during the course of the reach. Implied by this theory is a closed-loop action control process that uses information from a "quickly updated visual representation in the SPL, coupled with visual and proprioceptive feedback, and an efference copy of the movement plan" (sect. 1.1, para. 2). Glover later states, "Put simply, the control system is focused on the on-line correction of the spatial parameters of the action" (sect. 1.1.3, para. 6).

One property of visuomotor actions from Glover's own studies, however, does not fit well with this story. Even when the view of the stimulus is removed at the onset of the action, the corrective process proceeds normally, just as when the stimulus is fully visible. Glover specifically states that the "dynamic illusion effects" are apparent when vision of the hand and target are blocked during the reach (Glover & Dixon 2001c; 2002a). If the control system operates by providing on-line corrections to the process, then having visual information available on which to base the correction should be important. The fact that it is not suggests that the information for fully specifying the action, including the correction, is available before the action begins, that is, during the planning phase.

My collaborators and I have pursued an alternative account for the differences in the effects of pictorial illusions on judgment versus reaching behaviors based on the differences in the informational demands of the tasks (Vishton & Fabre 2003; Vishton et al. 1999; submitted). For nearly all judgment tasks that have been

studied in this context, participants compare multiple elements of the display. For instance, the Titchener circles illusion is commonly assessed by asking participants to compare the sizes of the two central disks. Nearly all action tasks in these studies, however, involve a two-finger pincer grip, which is mediated by the size of only one element of the display. While the judgment versus reaching difference between these two tasks has been highlighted, this "one versus two elements" difference provides an alternative explanation for the observed effects.

We have repeatedly found that if judgments are based on a single element, the effects of pictorial illusions are greatly reduced, often to the same levels observed with reaching behaviors. Conversely, in some situations, we have found that when actions are simultaneously based on multiple elements of a display, actions are more strongly influenced by pictorial illusions (Fig. 1). Whereas the studies related to this approach cited by Glover used only two-dimensional stimuli (Vishton et al. 1999), leaving the findings open to the interpretation that they were specific to "pantomime" reaches, we have more recently extended these results to reaches for three-dimensional targets as well (Vishton & Fabre 2003; Vishton et al., submitted). These effects are not present at the very conclusion of the reaching action, when the size of the target object determines the size of the grasp, but the effects are apparent well past the midpoint of the reach. This work has also suggested that the familiarity of a task plays an important role in determining the effects of an illusion. For most people, reaching is a far more common, familiar task than overt judgment.

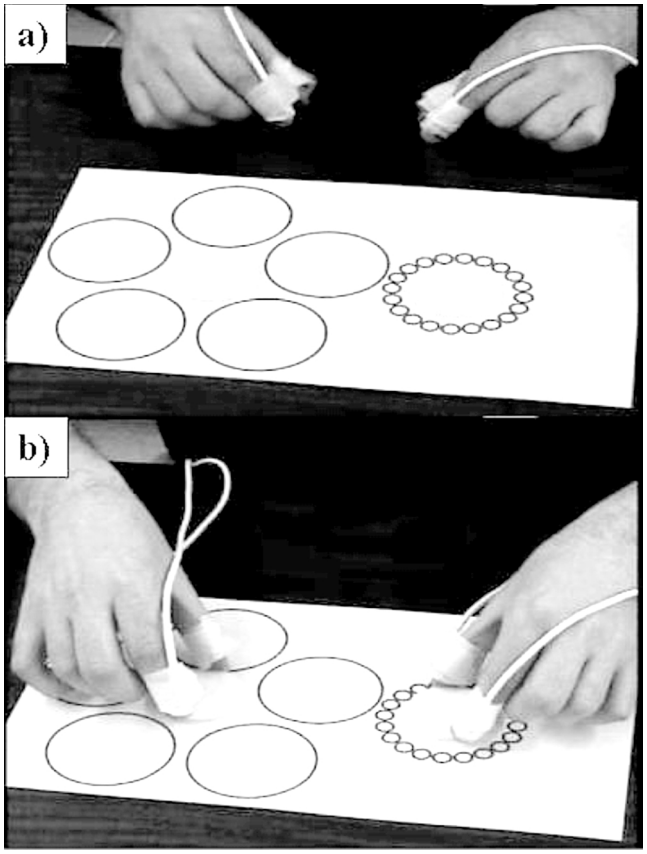

Figure 1 (Vishton). The start (a) and end (b) of a reach mediated by sizes of two target elements. The grip-scaling component of one-handed, pincer grip reaching is largely immune to the effects of the Titchener circles illusion, but, if a two-handed reach is made, based simultaneously on both central disks in the display, the effects are significantly larger. For both "perception" and "action," it thus seems that illusions are small when based on a single element of a display and large when based on multiple elements.

This account is not directly at odds with the PVC model, per se. My claim here is that there are facets of the interaction between response task and illusion magnitude that are better explained by alternative approaches. The PVC distinction may be present, but other important factors must be included in any complete understanding of how visually registered information leads to precise action choice, planning, and implementation.

Glover's focus on how different phases of an action are influenced by different sources of information (e.g., contextual vs. spatial information) is quite consistent with our approach, advancing it to a much more precise level. As Glover clearly points out, the choice of an action plan is mediated by different information than the control of the action once the general action plan has been set. We should therefore expect the distribution of visual attention to be different at these two moments. Differences such as these may influence how pictorial illusion displays are processed, whether separate visual processing streams are involved or not.

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Planning, control, and the illusion of explanation

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Abstract: Several aspects of Glover's planning–control model (PCM) appear incompatible with existing data. Moreover, there is no logical reason to suppose that separate visual representations should be required for the "planning" and "control" of actions in the first place. Although intuitively appealing, the PCM appears to lack strong empirical support.

No need for separate representations. It seems clear that different types of information are relevant for regulating different aspects of an action. However, it is not clear why separate visual representations of the same object feature (e.g., size) should be necessary for the initial programming and the on-line control of the same aspect of the action (e.g., grip aperture). On-line control requires a representation of the desired state of the effector (e.g., the desired grip aperture), a representation of the current state of the effector (e.g., the moment-to-moment size of the grip), a comparator, and a means by which to influence the effector. Of these components, visual information about the target object can be used to update only the desired state of the effector. Once an action has been initiated, however, no new sources of visual information about the target become available. Even if the target were to change in some way during the action (e.g., increase or decrease in size), the computations necessary to derive the size of the object are not any different than if the object were to change size before the action was initiated. That is, the precise (and absolute) metrics of the target object can be computed in the same way before and during the action. Why, then, would it not be advantageous for the motor system to make use of the same computations (or, the same "visual representation," in Glover's parlance) for movement programming and on-line control?

Nonspatial object features. Glover proposes that a putative action planning system "is responsible . . . for all movement parameters relating to nonspatial target characteristics" (sect. 1.1.2, para. 4). According to Table 1 in the target article, the specification of grasping and lifting forces should be the domain of the action planning system – a system that accesses a host of cognitive information about the object. One would suspect, then, that larger grasping and lifting forces should be observed when the actor picks up an object that is judged to be heavier (or larger) than an-

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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http://www.cogsci.uci.edu/personnel/chubb/chubb.shtml

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

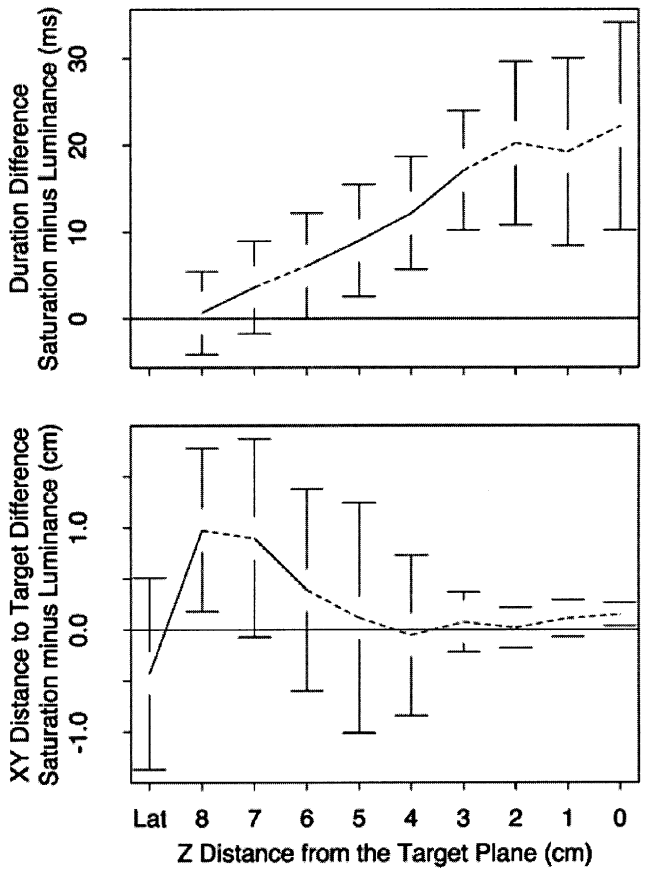

Figure 1 (Wright & Chubb). This figure summarizes differences in the trajectories of movements to matched gray and green targets based on more than 4,000 movements (~500 each for eight participants). The two panels of this figure share the same abscissa: Z distance. Z distance is the (perpendicular) 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 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.

ACKNOWLEDGMENT

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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

contradicted by the well-established on-line corrections to unexpected slippage of objects (Johansson & Cole 1992). When a subject repeatedly lifts a fixed weight with his or her hand, an unexpected change in weight leads to fast on-line corrections triggered by skin mechanoreceptors. Responses in FA II afferents trigger the corrective reactions that compensate for the unanticipated slippage at a short latency. Not only does object slippage trigger feedback control, but it also updates memory of the object properties to be used in the next lift, thus demonstrating the strict interconnection between planning and control.

There are other examples of the difficulty of ascribing specific kinematic or kinetic parameters to distinct stages of planning and control. Consider reaching for a visual target with the hand. Visual information about target location must be transformed into commands that specify the patterns of muscle activity bringing the hand to the target. Movement endpoint must be specified, but what about arm trajectory? Is there a kinematic plan that includes a specification of the path and law of motion of the limb? There is no consensus on this issue.

At the phenomenological level, a number of lawful relationships have been described for the kinematic trajectories of the hand in external space, and of the individual limb segments in the angular coordinates of the joints. Thus, the spatial trajectories of both the hand and the joints are essentially unaffected by wide changes in speed and load. In point-to-point movements, the velocity profile of the hand tends to be bell-shaped, while the velocity profiles of shoulder and elbow angular motions tend to be temporally correlated. In curved movements, the instantaneous tangential velocity of the hand is inversely related (by a power law) to the local curvature of the path (for a review, see Lacquaniti 1997). However, these kinematic regularities could arise either from the explicit specification of limb kinematics provided by a detailed kinematic plan, or from the implicit inner working of the execution control stage. Therefore, they could arise from optimization principles. Optimization may involve endpoint trajectory or joint angular trajectories; it could involve kinematic or kinetic criteria. One interesting optimization idea, the minimum variance principle, collapses together planning and control (Harris & Wolpert 1998). This principle states that the neural control signals are corrupted by noise whose variance increases with the size of the control signal. In the presence of such signal-dependent noise, the shape of a trajectory could be selected to minimize the variance of the final arm position.

Neurophysiology. Is there evidence for explicit representations of desired trajectories prior to the execution phase of a motor task, as predicted by the planning/control dichotomy? Such an explicit representation should be apparent in the neural activity during an instructed-delay period, when information about the direction and distance of an upcoming movement is presented prior to the instruction to start the movement. One would expect that, during this instructed-delay period, trajectory planning should take place as soon as movement metrics are specified, with no need to recapitulate after the Go signal. Instead, during this period, the cortical neural activity does not differ appreciably from that seen during simple reaction tasks (Crammond & Kalaska 2000). Glover claims that the planning stage relies on the inferior parietal lobule (IPL), whereas control relies on the superior parietal lobule (SPL). However several recent electrophysiological studies in the monkey indicate that both SPL and IPL neurons participate during all stages of motor organization, not just the execution phase (Battaglia-Mayer et al. 2000; 2001; Buneo et al. 2002; Hyvärinen & Poranen 1974; Mountcastle et al. 1975; Snyder et al. 1997). Many neurons in different parts of the SPL, such as areas 7m, PEc and V6A (Battaglia-Mayer et al. 2000; 2001) are thus involved during both the delay time preceding movement onset and during movement execution. Similarly, in different areas of the IPL, neurons fire not only during memorized delays, but also during movement time (Mountcastle et al. 1975; Snyder et al. 1997). Finally, neural activity in area 7a is modulated by hand-tracking movements (Hyvärinen & Poranen 1974), a task that Glover considers to be mostly dependent on on-line control. It is worth mentioning that a recent fMRI study (Astafiev 2003) has found regions activated by preparation for pointing in both the SPL and the IPL, as well as in the premotor cortex. The same study has reported a good spatial correspondence between parietal areas in humans and monkeys, suggesting that the same architectural and evolutionary plan underlies the organization of the parietal cortex in both species, contrary to what is assumed by Glover.

Burnod et al. (1999) proposed that different classes of reach-neurons are not confined within individual cortical areas of the parieto-frontal-network, but are common to different areas, with gradient tangential distribution of eye and hand signals related to both planning and execution. Computation of commands for the combined eye-hand movements occurs as a simultaneous recruitment of discrete populations of neurons sharing similar properties in different cortical areas, rather than as a serial process from vision to movement, engaging different areas at different times.

Author's Response

Planning and control in action

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Abstract: The views expressed in the commentaries challenge many of the tenets of the planning–control model as espoused in the target article. This response is aimed at addressing the most serious of these challenges as well as clarifying errors of interpretation. It is argued that the majority of the challenges from brain and behavior, although meritorious, can nonetheless be incorporated within the planning–control model. It is concluded that only some minor revision of the model with regard to anatomy is necessary at this time.

R1. Introduction

The target article has elicited a number of stimulating and challenging commentaries. I here endeavour to address what I see as the main issues raised with the planning–control model: (1) the definition and characterization of "planning"; (2) the definition and characterization of "control"; (3) the evolutionary, neurophysiological, and developmental aspects of the model; (4) the effects of visual illusions (and contextual information in general) on actions; (5) the neuroimaging of planning and control; and (6) the neuropsychology of planning and control. In many cases, apparent discrepancies between the views propounded in the target article and the views held by the commentators appear to have arisen quite accidentally and require only a clarification of the model's tenets. In other cases, there are challenges to the model that require attention.

R2. The definition and characterization of planning

A number of commentators have addressed the definition and characterization of "planning" in the target article. To begin with, certain clarifications are required.

R2.1. Planning is not perception

Given that the planning–control model was proposed as an alternative to the two-stream perception-action model, it is perhaps understandable that **Bridgeman**, **Goodale & Milner**, **Raftopoulos**, and **Wright & Chubb** have all inferred that planning and control must also use the same two "ventral" and "dorsal" systems. Specifically, they seem to have inferred that planning in the planning–control model can be equated with perception in the perception-action model. However, the planning–control model is not simply a reformulation of the two-stream hypothesis. Rather, the posterior regions of the cortex involved in planning are held to be centered in the inferior parietal lobe (the IPL, the terminus of the putative "third" visual stream). Because the IPL receives visual input from both the ventral and dorsal streams, the output of planning often possesses characteristics of both. The implication is that ventral stream processes can influence planning, but that is not the same thing as equating planning with perception. For example, when Wright & Chubb argue that color coding should affect planning because it is a ventral stream function, they appear to be equating planning with perception, when, in reality, planning is its own process. Although color may affect planning when color is associated with a spatial characteristic of the target in long-term memory (Haffenden & Goodale 2000), there is nothing in the planning–control model to suggest that color perception in and of itself should affect planning.

R2.2. Kinematic planning is subject to cognitive/ perceptual influences

Goodale & Milner have correctly identified the clearest point of difference between the planning–control and perception-action models. In the planning–control model, planning and control are entirely separate: Cognitive and perceptual influences are posited to potentially impact the planning of movement kinematics – but never their on-line control. Conversely, in the perception-action model, both the planning and the control of movement kinematics should be immune to cognitive and perceptual influences.

Although this reflects a clear understanding of one of the main differences between the planning–control and perception-action models, it is surprising that **Goodale & Milner** choose to contest this point. Indeed, not only has it been shown that many kinematic parameters are affected by cognitive and perceptual variables (including visual illusions – e.g., Aglioti et al. 1995; Brenner & Smeets 1996; Glover & Dixon 2001a; and semantics – e.g., Gentilucci et al. 2000a; Glover et al. 2004), but even data from their own studies supports the planning–control model. For example, Haffenden and Goodale (2000; 2002a; 2002b) showed that learned associations between a cue and a characteristic of a target (e.g., between a color and a target's size) can affect the kinematics of movements directed towards the target.

Indeed, the Haffenden and Goodale (2000; 2002a; 2002b) studies seem remarkably consistent with what I have claimed as the role of long-term memories (presumably encoded in either the ventral stream or the IPL) in the kinematic planning of actions; and in fact, such a role for long-term memories was acknowledged by Haffenden and Goodale in these studies. However, this is in contrast to **Goodale & Milner**'s traditional view (e.g., Milner & Goodale 1995), which holds that the dorsal stream is wholly responsible for movement kinematics made to visible targets through computations carried out de novo each time a movement is made.

Goodale & Milner have often addressed the inconsistency between de novo (i.e., based entirely on low-level visual inputs and independent of "representations") planning and the varied effects of cognitive/perceptual factors on planning by invoking the idea that the ventral and dorsal streams can "interact" (e.g., Haffenden & Goodale 2000; 2002a; Milner & Goodale 1995; Milner et al. 2003). However, they have been much less clear on what circumstances should lead to an interaction. To an outsider, their general approach seems to be this: If an action is immune to a cognitive or perceptual variable, it is because the dorsal stream is planning and controlling the action (this supports the perception-action model). On the other hand, if an action is affected by a cognitive variable, it is because of an "interaction" between the ventral and dorsal streams (this also supports the perception-action model).

As pointed out by **Phillips**, **Triggs & Meehan** (**Phillips et al.)** and **Latto**, however, such "interactions" provide weak, post hoc explanations. In contrast to this, the planning–control model has the virtue of making strong, a priori predictions. Cognitive and perceptual variables will often affect planning but will never affect on-line control. A characteristic of a strong approach such as this is that the predictions can be contradicted. This allows for many challenges to the planning–control model, such as appeared in some of the commentaries, for example, in the cases of the optic ataxics who show direction errors from early in the trajectory (**Gentilucci & Chieffi**, **Goodale & Milner**, and **Newport**, **Pears & Jackson** [**Newport et al.**]), or in cases in which the context has been shown to influence both planning and control (**Coello & Rossetti**). In contrast, it is unclear what evidence, if any, could ever be found to falsify the perception-action model.

R2.3. Planning is not monolithic

Coslett & Buxbaum, **Longo & Bertenthal**, and **Goodale & Milner** suggest that the definition of planning in the target article is too vague and does not take into account many of the various processes that go into planning. They argue that my characterization of *planning* is monolithic and thus incomplete. In some sense, this is not an unreasonable criticism; certainly a single article cannot fully explore the many components of a system as diverse as action planning. However, I did touch on planning's complexity when I described the various deficits that can occur following damage to the planning regions, from hypokinesia in Parkinson's disease following damage to the basal ganglia (Zigmond et al. 1999), to ideational apraxia following damage to the premotor cortex (Heilman & Gonzalez Rothi 1993), to ideomotor apraxia following damage to the left IPL (e.g., Clark et al. 1994). Even so, there can be many variants of planning deficits, and each is instructive as to the overall organization of the brain, as Coslett & Buxbaum and Longo & Bertenthal elucidate.

R2.4. Planning and grip force

Vaillancourt, **Mayka & Corcos** (**Vaillancourt et al.**), **Westwood**, and **Zago**, **Lacquaniti**, **Battaglia-Meyer & Caminiti** (**Zago et al.**) voiced concerns regarding the role

of planning and control in the application of grip force, arguing that both systems appear to influence grip force. To reiterate my own views, grip force is dependent on weight (a nonspatial target characteristic) and therefore falls within the domain of the planning system. Just as with any planning parameter, grip force can adapt over a number of trials on the basis of memories of past experiences (the size-weight illusion adaptation – Flanagan & Beltzner 1999). This is not surprising, given that grip force computations rely heavily on past experiences whether or not a size-weight illusion is present (Johansson & Westling 1984; 1988). Naturally enough, when grip force is calculated erroneously by the planning system, it can still be adjusted once the target has been contacted and lifted (Johansson & Westling 1988). However, it is unlikely that the application of grip force corresponds with activity in the "control" system as I define it. For one, the adjustment to target slippage has been shown to be too rapid to involve processing in the CNS (Eliasson et al.1995). For another, neurologically induced deficits in maintaining a constant grip force most likely reflect an elementary motor deficit also outside the domain of the "control" system (e.g., Fellows et al. 1998; Nowak & Hermsdorfer 2003).

R3. The definition and characterization of control

The criticisms leveled by commentators at the description of the control system in the target article can be classified into two main categories: the use of immediate visual feedback by the control system (**Goodale & Milner**; **Vishton**) versus the existence of a short-term memory in the visual representation used by the control system (**Binsted & Heath**; **Westwood**); and the nature and timing of on-line corrections (**Gaveau & Desmurget**; **Gentilucci & Chieffi**). Because the issue of visual feedback also pertains to illusion and action studies, I will address it in section R4.

R3.1. Visual feedback and the transience of the control representation

The planning–control model argues that a short-term visual representation subserves on-line control such that on-line corrections are possible for up to two seconds following the removal of visual information. New evidence described by **Binsted & Heath** appears to contest this point, however. From this evidence it appears that the control process is impaired immediately upon removal of visual input, as is shown by an increase in the correlation between hand position early and late in a movement when visual feedback is unavailable. Further and more important, this impairment appears to be identical after a zero-second delay to after a five-second delay. Similarly, Adamovich et al. (1998; 1999) have also noted that on-line corrections do not appear to occur when visual feedback is unavailable. Conversely, Westwood et al. (2001a) found that errors in accuracy accumulated gradually over increasingly long delay periods.

Whereas the majority of the aforementioned results suggest that on-line visual feedback is crucial to the control process, other results suggest differently. Perhaps the most dramatic of these instances was in Goodale et al. (1986), described in section 2.5.1 of the target article, in which on-line corrections were made to a target that had jumped during a saccade, despite the fact that vision of the hand was not allowed. This result using the saccadic suppression paradigm has been upheld several times since then (e.g., Bard et al. 1999; Prablanc & Martin 1992), and so seems reliable. How then to reconcile these on-line corrections with the lack of corrections found in more recent studies?

One way to do this relies on the fact that whereas vision of the moving limb is absent in all the aforementioned studies, vision of the target *was* available throughout the movement in the saccadic suppression studies. Similarly, it has been shown that on-line vision of the target can be an important factor in making in-flight corrections in visual illusions (Gentilucci et al. 1996; Glover & Dixon 2001c), and that vision of the hand can be important in making on-line corrections under normal (i.e., nonillusory) conditions (e.g., Carlton 1981). No doubt a number of factors feed into on-line corrections, not just vision but also proprioception (Gentilucci et al. 1994; Jackson et al. 2000; Jeannerod et al. 1984; Sainburg et al. 1993), and efference copy (Craggo et al. 1976; Evarts & Vaughn 1978), and the respective contributions of these factors remain to be fully teased apart.

What then, does this imply for the current characterization of the control system? On the one hand, it does appear that under some circumstances at least some continuous visual input is important for on-line corrections to occur. As yet, however, it is less clear exactly what these circumstances are, or what the crucial visual input is. Clearly, more work will be needed in order to elucidate the respective roles of visual feedback of the hand/target, proprioception, and efference copy, in on-line control.

R3.2. The nature of on-line adjustments

Whereas **Silveira** acknowledged the need for distinct visual information in the on-line control of actions, **Gaveau & Desmurget** and **Revol & Prablanc** raised the issue of the nature and timing of on-line adjustments. Gaveau & Desmurget argued that on-line corrections are, in fact, planned, and therefore no evidence is available that two separate processes occur. The argument for this is based largely on evidence from the perturbation paradigm, in which large adjustments were required (Paulignan et al. 1991a). In that study, subjects were made to grasp a target that on some trials could be switched with another target of larger or smaller size coincident with the onset of the movement. In the case of a switch from a small to a large target, the adjustment was paradoxical, inasmuch as, rather than showing an immediate increase in the size of the grip aperture, there was instead a brief deceleration of the opening of the hand (see also Castiello et al. 1993; Glover et al., in press). Paulignan et al. (1991a) took this as suggesting that the adjustment was planned. However, such "backwards" effects are anomalous in the perturbation literature. One possibility is that the size perturbation paradigm is a rather unnatural circumstance. Whereas it may be relatively common for targets to change their position after a movement has begun (imagine potential food running away!), it is much less common for them to change their size. Indeed, an unfortunate coincidence of the size-perturbation paradigm as developed by Paulignan et al. is that the target changes quite drastically, not only in size, but in the vertical position at which it can be grasped (a narrow cylinder – the small target – protrudes out of a broad cylinder – the large target – and either one or the other is lit from beneath). The small target is therefore grasped at a higher ver-

tical position than the large target. Hence, the apparent replanning of the movement seen in this case need not be considered as representative of control in a more "natural" setting. An experiment using virtual reality could address this issue by maintaining a constant vertical height (reaching component) while manipulating target size (grasping component).

Even if one is convinced that control involves some advance planning, this is not at all troublesome for the planning–control model. Rather, what the model emphasizes is the existence of distinct visual and cognitive inputs into the two stages, not that the outputs of the two stages must necessarily be implemented in fundamentally different ways. One could easily argue that whereas both are pre-planned, the "planning" system uses a much richer and detailed visual representation than the "control" system.

R4. Evolution, neurophysiology, and development

Although the issue of evolution is an interesting one, I did not delve into it in the target article as much as I would have liked because of space restrictions. **Goodale & Milner** argue that biological continuity should be supposed until evidence suggests otherwise; but, in fact, the evidence already does suggest otherwise – quite dramatically so (Kolb & Whishaw 1995; Tootell et al. 2003; Van Essen et al. 2001; Zeki 1993; 2003). Indeed, given that macaques belong to a different biological family (*Cercopithecidae*) than humans (*Hominidae*), and that the two families diverged tens of millions of years ago, is it really sensible to assume that macaques and humans have very similar brains? Instead, I think the question really should be: Where do we draw the line? How much of what goes on in the macaque brain should we assume also goes on in the human brain? And just as important, when similar processes exist, should we assume that the same processes go on in the same place in both brains?

R4.1. Humans are not scaled-up macaques

In the target article, I argued that given the differences between humans and macaques, both neurological and behavioural, strong parallels should not be drawn between the two species. For one, the human parietal lobes have expanded considerably compared with the macaque, and this is evident in the expansion of visual areas in the human brain relative to the macaque – this expansion is especially apparent in "higher order" visual areas such as exist in the parietal lobes (Van Essen et al. 2001). For another, the human IPL seems to be important in the human propensity for tool use, and hence should play an important part in planning as well. The macaque parietal lobes have no such area that seems critical for tool use, in contrast; thus there exists at least one fundamental difference in how the two species plan actions. Similarly, as pointed out by **Kawai**, macaques show no evidence of advance planning, and therefore one can only conclude that the planning regions of the macaque brain are relatively undeveloped as compared to the planning regions of the human brain (or, for that matter, the chimpanzee). It is indeed notable that available evidence suggests that macaques do not plan even simple reaching and grasping actions in the way that humans do (Fogassi et al. 1991). Whereas humans scale their movements to the size and distance of a target (Jeannerod 1984), macaques do not.

R4.2. The evolution of planning

Kawai makes an interesting behavioural contribution to this argument by showing that certain planning processes go on in chimpanzees as they do in humans, but are not apparent in macaques. In his commentary, he explains how chimpanzees (another member of the *Hominidae* family) appear to be aware of the consequences of future actions and to be able to plan accordingly, a skill that humans also develop quite early in life. Macaques, however, have never been shown to possess this skill. The evolution of such skill clearly shows that humans and macaques differ more so, than do humans and chimpanzees, but what does this imply about how macaques and humans plan their actions?

There has long been evidence of pre-movement kinematic planning in the brains of macaques (e.g., Gentilucci et al. 1988; Kettner et al. 1996). Generally speaking, activity in the frontal lobes of the macaque follows a progression from rostral to caudal as movement initiation looms (e.g., Crammond & Kalaska 1996; Godschalk et al. 1981). Given the consequences of damage to various regions of the frontal lobes in humans, one may assume a general similarity across species, though the human system is clearly more elaborate. Damage to more rostral regions of the frontal lobes in humans impairs planning in the longer term – in the case of the "frontal syndrome," linked with damage to the prefrontal cortex, this may be evident over the course of a day's errands (Shallice & Burgess 1991). In contrast, damage to more caudal areas such as the premotor and supplementary motor cortex tends to lead to more immediate planning deficits; deficits in the sequencing of actions (Heilman & Gonzalez Rothi 1993).

R4.3. Differences across species

What makes humans and macaques different? For one, it appears that laterality largely evolved with the human brain. This laterality is the most obvious in functions that are (more or less) uniquely human, such as language, which is strongly left-lateralized (Kimura 1979). However, it is also evident in functions that would appear to be more basic. A deficit in the seemingly basic function of attention is manifest in humans as unilateral neglect. Neglect tends to follow damage to the right hemisphere in humans, most often including the right IPL and temporal-parietal junction (Bisiach & Vallar 1988). Although Rizzolatti and his colleagues have proposed a neglect syndrome in the macaque (Rizzolatti & Berti 1990; Rizzolatti et al. 1983), this differs from the human syndrome of neglect in at least two ways: First, the macaque version of neglect is strictly motor, characterized by a hypokinesia of movement into the contralesional hemispace. Second, whereas the human version is most common following damage to the parietal lobes, macaque "neglect" follows damage to the frontal lobes. Another deficit following damage to the IPL is ideomotor apraxia, described in the target article. This deficit follows damage to the left hemisphere, most often including the left IPL (Heilman & Gonzalez Rothi 1993). As of yet, there is not even the remotest candidate for a macaque model of ideomotor apraxia.

What is even more interesting is that the monkey model for optic ataxia, though often touted as evidence that humans and macaques have very similar dorsal streams, is in fact an approximate model at best. Whereas humans with

optic ataxia most often show a visual field *and* a hand effect (wherein damage affects movements in the contralateral visual field and executed with the contralesional hand), monkeys tend to show only a hand effect (Jeannerod 1988). Further, macaques tend to make errors in the direction of the lesion, regardless of target position (Lamotte & Acuna 1978), whereas humans tend to show errors towards fixation. Further, monkeys with optic ataxia generally are more accurate when visual feedback is available than when it is not (Lamotte & Acuña 1978; but see Rushworth et al. 1997a). Conversely, humans with optic ataxia may be equally inaccurate regardless of whether or not visual feedback is available (Jakobson et al. 1991; Perenin & Vighetto 1983), and are sometimes even worse when visual feedback *is* available (Buxbaum & Coslett 1997; Damasio & Benton 1979).

Despite these differences, much has been made of the properties of cells in the monkey posterior parietal cortex, and given that macaques show deficits in action that are at least coarsely similar to those seen in humans with optic ataxia, these studies are of interest. However, many of those who study macaque vision have cautioned against drawing clear links between human and macaque vision (e.g., Tootell et al. 2003; Van Essen et al. 1993; Zeki 1993; 2003); and arguing for human homologues of areas in the macaque that differ both functionally and neurologically, appears to me to be considering the problem a bit too simplistically.

R4.4. The neurophysiology of planning and control

Putting aside the clear differences across species, I find it interesting to consider the monkey data when it comes to the planning and control of goal-directed movements, as the characteristics of the planning and control of kinematics are the main point of contention between the planning–control and perception–action models. According to the planning–control model, different areas of the brain ought to be involved in the two stages of action; according to the perception–action model, both planning and control should be represented uniformly within the dorsal stream.

Many cells in the monkey parietal cortex respond differentially prior to movement initiation (i.e., during planning) versus its execution (i.e., during control). For example, the Fattori et al. (2001) study, discussed by **Battaglini**, **Bernardis & Bruno** (**Battaglini et al.**), showed that whereas only 30% of responsive cells in the macaque area V6A were active during the planning phase, a much greater percentage (70%) were active during the control phase. This represents a significant change in activity related to the two stages of action. Similarly, Johnson et al. (1996) observed greater activity in cells in the superior parietal lobe (SPL) during execution, whereas cells in more lateral areas of the parietal lobe showed greater activity during the premovement (planning) phase. Therefore, even if one insists on holding to the biological continuity belief, as **Goodale & Milner** seem to, there appears to be a ventral-dorsal gradient of activity between planning and control even in the macaque.

R4.5. Ontogeny follows phylogeny

Not only phylogeny but ontogeny is instructive when it comes to planning and control, as **Káldy & Kovács** point out. The study described by **DeLoache** is an excellent example of the immaturity of the planning system early in life. This follows the principle that more recently evolved systems tend to develop later in life. DeLoache and her colleagues observed that children presented with scaled down versions of real objects (e.g., a toy car) often attempt to interact with the object as if it were its usual size. Surprisingly, the actual movements made towards the scaled-down version acknowledge the real spatial characteristics of the target, such that a child who tries to get into a toy car will actually grasp the toy door accurately despite the insensibility of the entire act! The fact that the children not only make scale errors in movement selection, but then go on to execute the same movements with splendid precision, nicely illustrates the dissociation between planning and control. It can be argued from this that the planning process likely matures at a later date than the control process in humans, just as it seems to have evolved later in evolution along the primate lineage.

R5. Visual illusions and context in action

A number of commentators discussed the effects of visual illusions on action, and this is not surprising given the amount of research that is being conducted in this area, and the controversy that has arisen. Table R1 summarizes the various interpretations of this research and the predictions that follow.

R5.1. Evaluating models of illusions and action

How to evaluate these numerous models? In one sense, they each postulate a dissociation between illusory and nonillusory visual information (with the exception of the common representation model, which postulates *no* such dissociation). The question is under what circumstances illusions

Table R1. Illusions and actions: Models and predictions

Contrast	Predictions	Basic References
Planning vs. Control	Illusions affect planning of actions but are corrected on-line	Glover & Dixon (2001a) Glover (2002)
Perception vs. Action	Illusions have small or nonexistent effects on actions	Bridgeman et al. (1979) Aglioti et al. (1995)
Absolute vs. Relative	Illusions affect relative judgments but not absolute judgments	Vishton et al. (1999) Bruno (2001)
Common Representation	Illusions affect both perceptions and actions equally	Franz (2001) Franz et al. (2001)
Task Demands	Illusions affect actions when they utilize the affected characteristic	Brenner & Smeets (1996)
Allocentric/ Egocentric	Illusions affect actions more, the less – or less recent – visual information is available	Daprati & Gentilucci (1997) Gentilucci et al. (1996)

should affect actions and why. It is clear from Table 2 in the target article that illusions often do have effects on action, and any simple interpretation based on a perception-action dissociation, with illusions affecting the former and not the latter, must therefore be incorrect as **Coello & Rossetti** point out. However, there are ways in which the perception–action model may be reincarnated to accommodate these findings (e.g., Carey 2001), through invoking numerous "interactions" between perception and action. In cases where illusions have effects on action, this is said to be because the "perception" system is being used to guide the action on account of some inherent limitation of the action system.

A problem with most of the other models is that they seem to explain only the data with which they are presented (e.g., the absolute/relative model, the allocentric/egocentric model), without any attempt to integrate their predictions with the results of the broad wealth of studies on illusions and actions. For example, how would any of these models explain the dynamic illusion effect, in which illusions have large effects early in a trajectory that dissipate as the hand approaches the target? In both cases, there must be presumed a shift between a relative/allocentric representation and an absolute/egocentric representation during the course of the movement. Of course, this is analogous to what the planning–control model already holds, thus making these explanations redundant.

The task demands model (e.g., Brenner & Smeets 1996), advocated in the commentary of **Brouwer**, **Brenner & Smeets** (**Brouwer et al.**), attempts to explain the dynamic illusion effect as resulting from a crossover of sorts between the visual information used when the trajectory is initiated, and the visual information used to guide the hand to the target. For each case of the dynamic illusion effect, there is a new way of modelling how the effects might be observed in a way consistent with the task demands model (Smeets et al. 2002; 2003). As a consequence, the task demands model becomes increasingly cumbersome and ad hoc.

One might criticize the planning–control model for not explaining the entire set of results presented in Table 2 of the target article. Indeed, it is hard to deflect this criticism if only because many of the results contradict one another. For example, Aglioti et al. (1995) found significant effects of the Ebbinghaus illusion on grasping, as did Franz et al. (2000) and Glover and Dixon (2002a), whereas Haffenden and Goodale (1998; Haffenden et al. 2001) do not. It is therefore not surprising that a model has difficulty accommodating 100% of the results of such studies; this is what makes the area controversial. The question then becomes: Why are these results so contradictory? The ensuing section will attempt to address this issue with respect to the dynamic illusion effect.

R5.2. The dynamic illusion effect depends on (proper) methodology

Goodale & Milner, **Elliott & Meegan**, and **Franz** have criticized the dynamic illusion effect (Glover & Dixon 2001a; 2001b; 2001c; 2002a) by arguing that an analysis of their own data does not show these effects. However, a careful examination of their methods leads one to question this assertion. For example, Danckert et al. (2002 – cited by **Goodale & Milner**) reported no evidence that the effect of the Ebbinghaus illusion on grasping changed over time, except in one case in which the effect actually seemed to increase over time! Why did they find this result and not the dynamic illusion effect found by Glover and Dixon (2002a) using the very same illusion?

One very good reason, already alluded to in section 2.6.7 of the target article, is that Danckert et al. did not scale the illusion effect by the relevant parameter relating grip size to target size. This is absolutely vital in determining the real impact of the illusion over time. This can be made clear if one considers what a "raw" illusion effect really represents. For instance, when the hand is at rest prior to beginning a trial, one would expect to see no effect of either the size of the target or of the illusion on the size of the grip aperture. As the hand begins its movement towards the target, the effect of target size on grip aperture slowly and gradually increases until the target is grasped (Glover & Dixon 2002a; 2002b). Given the gradual evolution of this target-grip size effect, there is no reason to expect a large raw illusion effect early in the movement. Rather, one would expect the illusion effect to evolve gradually along with the effect of target size. One would not expect the hand to suddenly open very quickly (for a "large" illusion) at the outset of the movement, or remain completely closed (for a "small" illusion) at the outset of the movement simply because of the presence of the illusion. Instead, the effects of the illusion and the effects of target size should both evolve over roughly the same time course.

Therefore, the correct way to measure the impact of the illusion over time is to scale it by the effect of the actual size of the target (Franz 2003; Franz et al. 2000; 2001; Glover & Dixon 2001a; 2001b; 2001c; 2002a). One may do this most correctly by using Fieller's theorem, as advocated by **Franz**, although it seems unlikely from Franz's Figure 1 that this will make a significant difference to using the method of Glover and Dixon (2001a; 2001b; 2001c; 2002a) at any time point other than 0% MT (movement time).

Another shortcoming of the Danckert et al. study is the lack of any power analysis. If one is going to argue on the basis of a null effect, as Danckert et al. do, then one must at least prove that there existed sufficient power to detect the effect in the first place (Cohen 1988; Loftus 1996)! A similar argument can be made for the lack of dynamic illusion effects reported by **Franz** and by **Elliott & Meegan**.

Another shortcoming of the Danckert et al. (2002) and Franz (2003) studies is that they omit any movement period following the maximum grip aperture (i.e., after roughly two-thirds of the way through the reach), even though these are the very times at which the on-line control system is known to be most active, and in which evidence for the dynamic illusion effect is most likely to be observed. Their arguments for this are that the hand may be contacting the object after the maximum grip aperture is achieved, and by then there would be no reason to expect an illusion effect due to the influence of haptic feedback. However, there certainly does exist a significant period of time between when the maximum grip aperture is achieved and the target is contacted (Glover & Dixon 2002a; 2002b; Glover et al. 2004; Jakobson & Goodale 1991; Jeannerod 1988; Wing & Fraser 1983; Wing et al. 1986), and it is important to include measures from this period. Further, it is incorrect to criticize the Glover and Dixon studies (Glover & Dixon 2001a; 2001b; 2001c; 2002a) for including "100%" MT, because those studies used a velocity criterion of at least 5 centimeters per second forward velocity of the thumb, and thus

the measured duration of the movement ended before the target was contacted by the thumb, much less before the forefinger closed around it. Indeed, even when we conducted an analysis that excluded 100% MT, but retained 95% MT, a dynamic effect was still observed (Glover et al. 2004).

Other considerations include validating the normalization procedure itself. In our studies, we always ensured both that movement times were not affected by the direction of an illusion, and that the baseline kinematics of the hand (i.e., acceleration, velocity) did not differ across illusion conditions (we did not always report these null effects in our papers). These considerations are important in any normalization procedure, and a failure to meet them could result in artifacts in the data. For example, grip aperture normally corresponds with the distance travelled by the hand, so that the closer the hand moves to the target, the larger the grip (at least to the point of maximum grip aperture). Therefore, if the hand (for whatever reason) moves faster in one condition than in another, then normalizing both together will result in a spurious effect of condition, which is in fact an artifact of the hand's velocity.

So what guidelines are important for examining the effects of illusions over the course of a movement? First and foremost, the effect of the illusion (or any cognitive/perceptual variable for that matter) must be scaled by the effect of the target feature it corresponds to (e.g., size) on the effector (Franz 2003; Franz et al. 2000; 2001; Glover & Dixon 2001a; 2001b; 2001c; 2002a; 2002b; Glover et al. 2004). The most rigorous statistical procedure for doing this is Fieller's theorem, as advocated by **Franz**. Second, the study must possess sufficient statistical power to be able to detect a dynamic illusion effect. This can be estimated before the study is begun, using the method given by Cohen (1988). Third, the analysis must include as much as the movement as possible. Finally, there must be equivalence in movement times/kinematics across conditions of interest. It is only after all of these factors have been adequately accounted for that fair tests of the dynamic illusion effect will be possible.

R5.3. Visual feedback and illusions

Goodale & Milner appear to agree that visual feedback leads to smaller illusion effects on actions as compared to when no visual feedback is available, a finding reported often throughout the literature (e.g., Gentilucci et al. 1996; Glover & Dixon 2001c; 2002a; Glover et al. 2004; Westwood et al. 2000c). Implicitly, then, Goodale & Milner seem to agree that the on-line control system is able to use visual feedback to correct for illusion effects on actions. Yet, they then go on to argue that this does not support the planning–control model. Curiously, this runs counter to their earlier claim that the planning of actions is "refractory" to the visual illusion (Aglioti et al. 1995; Haffenden & Goodale 1998). Rather, it appears that having visual feedback available aids the control system in reducing or even eliminating the effects of visual illusions on actions, just as the planning–control model predicts. The comments of Goodale & Milner in this respect therefore seem to obfuscate the issue somewhat, though I am sure this was not their intention.

Vishton expresses surprise that the effects of visual illusions on action can be corrected on-line (at least partly) in the absence of visual feedback. In two studies (Glover & Dixon 2001c; 2002a), we have shown that illusions have large effects early in a movement whether visual feedback is available or not. However, we also observed that the extent to which the effect of the illusion dissipates over the course of the movements depends on the presence or absence of visual feedback. Thus, when visual feedback is available, the effect of the illusion is much less at the end of the movement than when visual feedback is unavailable.

That the illusion effect decreases over time in the absence of visual feedback, would be surprising if visual feedback were the only source of information available to the on-line control system. However, this is clearly not the case. In the target article (sects. 2.4.1, 2.4.2, and 2.4.3), it is stated that not only visual feedback, but also stored visual information, proprioception, and efference copy contribute to on-line corrections. The degree to which nonvisual sources of information can aid the on-line control process is a matter for future research, though roles for both proprioception and efference copy in on-line control have already been shown in the target article. Therefore, the presence of dynamic illusion effects in the absence of visual feedback does not imply an anomalous result. Rather, it implies that the on-line control process does not rely on visual feedback alone, a fact that has long been known.

R5.4. Illusions and patients

An interesting point was raised by **Goodale & Milner** regarding illusions and patients. They rightly pointed out that visual illusions should have similar effects on the patient D.F. (with a damaged ventral stream) as they have on normal subjects, because D.F. should not be impaired at on-line corrections of illusion effects. This is an interesting point, not least of which because of the unusual results reported by **Coello & Rossetti** for the optic ataxic patient I.G. Given that D.F. has extensive damage to her ventral stream, it might be supposed that this prediction is too strong, and it will be interesting to see what happens in this respect.

Coello & Rossetti report data from the optic ataxic I.G., who suffered bilateral damage to the dorsal stream, including large regions of the SPL, the intraparietal sulcus (IPS), and a smaller portion of the IPL. I.G., incidentally, is the same optic ataxic who showed accurate movements to stationary targets, but disrupted movements when targets jumped (Gréa et al. 2002; Pisella et al. 2000).

Surprisingly, given the extensive damage to the dorsal stream in I.G., she was just as affected by the induced Roelofs' effect as were healthy controls. Specifically, when the target position was varied along the sagittal plane, both I.G. and controls were affected by the illusion. Conversely, when the target position was varied along the frontal-parallel plane, neither I.G. nor controls were affected.

There are two possible interpretations of this result. One, offered by **Coello & Rossetti**, is that both I.G. and controls use their ventral (sic) stream to plan movements, and thus both have similar effects. A second possibility is that I.G. has spared capacities in her dorsal stream that allow her to correct for the illusion on-line, just as controls do. Of these two possibilities, I would favor Coello & Rossetti's view, although it would certainly be interesting to see these experiments repeated with other patients, and to try to localize exactly what area(s) are responsible for susceptibility/immunity to illusion effects on action, and in particular with

respect to the evolution of such effects over the course of a movement. Similarly, transcranial magnetic stimulation (TMS) may be used to selectively "knock out" the planning or control visual representations and gauge the effects of this on how the motor system responds to visual illusions, as was suggested by **van Donkelaar & Dassonville**.

R5.5. Context in planning and control

Other arguments regarding the planning–control model criticize the supposition that the context does not affect control. **Coello & Rossetti** describe data that demonstrates, rather compellingly, that the context can indeed have an impact on actions. When movements are made in a structured environment, they are much more accurate than movements made in an otherwise empty environment (e.g., Coello & Magne 2000; Magne & Coello 2002). Further, Coello & Rossetti show that the benefits of a structured visual environment are present both during the planning and the control phase. **Adam & Keulen** make similar arguments regarding the role of the context in on-line control, arguing that contextual objects must still be processed while the movement is underway in order for obstacles to be avoided. Indeed, the lack of an effect of context per se on on-line control would seem to be disproved by these studies. Therefore, the model would seem to require modification.

The simplest way of doing this is to suppose that the contextual figures and objects influence only planning with respect to how they affect the processing of the relevant target characteristics. That is, when a contextual figure/object induces a visual illusion, this affects planning but not control. However, the context in general can affect both planning and control with regard to obstacle avoidance, and possibly may also have beneficial effects on target localization. Whether, and to what extent, the effects of non-illusion-inducing context are similar for planning and control, remains to be seen.

R6. Recent brain imaging studies of action: Planning versus control

Goodale & Milner criticize the target article for not citing a number of recent fMRI studies on action. Although it is true that I did not discuss these studies in detail, there is a good reason for this. Very few of these studies actually address the distinction between planning and control.

For example, the recent fMRI study by Culham et al. (2003) described by **Goodale & Milner** showed that both the SPL and an anterior region of the intraparietal sulcus (IPS) was activated during both reaching and grasping, but that the IPS was more active during grasping than during reaching. Further to this, areas in the frontal eye fields, occipital lobes, motor cortex, cingulate, and parietal-occipital region were also more active during grasping than during reaching. The effects of grasping in activating the anterior IPS were similar to those reported by Binkofski et al. (1998). Quite aside from some methodological issues I have with the Culham et al. study, it is unclear how that study addresses the issue of planning versus control.

R6.1. Is the IPS special for anything?

The results of Culham et al. (2003), as described by **Goodale & Milner**, seem to suggest that the anterior intraparietal sulcus (aIPS) is involved in action, and, in particular, grasping. This in turn seems to imply a human homologue for the macaque region aIPS involved in grasping (Taira et al. 1990). However, these results say little about whether the IPS/SPL is involved in planning, control, or both stages of action. Given the speeded nature of the task (reaching out to touch or to grasp objects as soon as they appeared), it is unlikely that subjects had much time to plan their movements. As movement times were not recorded, one can only assume they were at least equivalent to reaction times in a speeded task such as this one. Thus, it is not clear from this study whether IPS/SPL activity was related to planning, control, or both.

Another interesting point about the Culham et al. study is that the IPS was also activated, along with vast regions of the parietal lobes, during the so-called perception task (in particular, in the condition where scrambled images were used). Activation of the macaque IPS during perceptual judgment tasks has also been observed by Tsutsui et al. (2003). Culham et al. explained this as possibly arising as a result of task difficulty, but if this were the case, one must also wonder whether grasping an object as quickly as possible (while lying supine in a noisy scanner) is more difficult than simply pointing to it. If so, this might account for activity in the IPS during grasping that was less prevalent during reaching.

Indeed, a casual examination of the literature shows the IPS to be activated during a number of seemingly unrelated tasks. For example, the IPS has recently been shown to be more active during: (1) judgments of stimulus intensity versus judgments of stimulus duration (Ferrandez et al. 2003); (2) number versus letter or color processing (Eger et al. 2003); (3) motion perception versus rest (Dupont et al. 2003; Pelphrey et al. 2003); (4) comparisons of quantity versus rest (Fias et al. 2003); (5) demanding versus simple visual search (Coull et al. 2003; Imaruoka et al. 2003; Pollmann et al. 2003); and (6) dual-task versus single-task performance (Szameitat et al. 2003). The last four of these in particular could quite sensibly be interpreted as effects of task difficulty, and the last two could hardly be interpreted in any other way. One must therefore exercise caution before implicating the IPS in grasping versus reaching, regardless of what this implies for the planning–control model.

Another concern with interpreting effects in the IPS also relates to the vast numbers of seemingly unrelated tasks that activate it. Given the amount of tissue this region comprises and the depth of the sulcus itself, such effects might simply reflect a large amount of densely packed tissue for which any increase in activity is magnified in the analysis. One must therefore exercise caution in interpreting activations of the IPS in brain imaging studies.

R6.2. Planning and control in fMRI

A recent fMRI study that did address the planning–control issue was carried out by Astafiev et al. (2003). In this study, subjects lie supine in an fMRI scanner while being presented with a cue followed two seconds later by a target. In three conditions subjects either: (1) covertly attended to the location indicated by the cue; (2) prepared a saccade to the location indicated by the cue, then executed the saccade to the target when it appeared; or (3) prepared a pointing movement to the location indicated by the cue, then exe-

cuted the pointing movement to the target when it appeared.

When evaluating the planning–control model, the paradigm employed by Astafiev et al. (2003) has two main advantages over the immediate reaching and/or grasping tasks typically used by Goodale and his colleagues. First, the imposition of a two-second delay between cue and target presentation ensures that the scan captures mainly the planning phase rather than some combination of planning and control weighted (somewhat obscurely) towards the control phase that results when subjects have to move immediately on presentation of the target. Second, the inclusion of an "attention" condition allows one to control for the attentional demands of the tasks.

As was observed for the PET studies described in the target article (Deiber et al. 1996; Grafton et al. 1998) and elsewhere (Corbetta et al. 1993; 1996; Haxby et al. 1994; Jovicich et al. 2001; Nobre et al. 1997), high attentional demands tended to activate the SPL in the Astafiev et al. (2003) study. However, when activity in the attention condition was subtracted from activity in the pointing condition, the main areas of activation included the angular gyrus of the IPL, the superior temporal sulcus (another putative "third stream" area), and a region straddling the IPL and IPS. Although a general increase in SPL activity was present in both the attention and pointing conditions, it did not significantly differ across conditions, suggesting that the attentional demands of the pointing task were the cause of the increase.

Similar effects of attention were reported by **Adam & Keulen** (Adam et al. 2003). In their study's task, a precue was used to isolate planning processes. The presence of the cue led to activity throughout the planning network (and including the IPL), though some activation also occurred in the SPL, presumably due to the attentional demands of the task.

Future fMRI studies aimed at comparing the planning–control and perception–action models will need to consider at least two factors. First, these studies will need to carefully distinguish the action from the attention components of the activation. This can most easily be done by including an "attention" condition in which subjects need only attend to the target, not direct a movement to it (Astafiev et al. 2003). Second, researchers must be aware of the constraints imposed by their tasks. For example, it should be kept in mind that immediate movements tend to emphasize the control phase of the task and should thus lead to activity in the SPL and possibly the IPS. Conversely, including preparation periods should tend to activate the IPL more strongly, as has already been observed in both PET (Deiber et al. 1996; Grafton et al. 1998) and fMRI studies (Adam et al. 2003; Astafiev et al. 2003).

R7. Evidence from human neuropsychology

Many commentators discussed the issue of planning and control with regard to human neuropsychology. These discussions can be divided into three main categories: optic ataxia, apraxia, and the basal ganglia.

R7.1. Optic ataxia

Goodale & Milner, **Newport et al.**, and **Gentilucci & Chieffi** have pointed out results obtained from patients with optic ataxia that seem to contradict the planning–control model. The model holds that optic ataxia, commonly found after damage to the SPL/IPS control system, should lead to deficits in on-line control with a concomitant lack of effects on planning. One prediction of this is that an optic ataxic will have a relatively intact movement trajectory early in the action, but that errors will arise as the movement unfolds. Evidence in favor of this view comes from studies showing errors in grip formation that largely arise late in the movement (Binkofski et al. 1998; Jakobson et al. 1991; Jeannerod 1986); from the fact that optic ataxics are more impaired in peripheral vision than in central vision (e.g., Perenin & Vighetto 1983; 1988); that an optic ataxic was impaired at manual tracking but not pointing to stationary targets (Ferro 1984); and that an optic ataxic is near normal at pointing or grasping stationary targets, but shows a severe impairment when the position of the target is perturbed coincident with movement initiation (Gréa et al. 2002; Pisella et al. 2000).

Despite the wealth of evidence supporting the notion that optic ataxia is a deficit specific to the on-line control phase of actions (see Glover 2003, for a review; also see Rossetti et al. 2003), there are recent data described by the commentators that appear to contradict this view.

R7.1.1. Directional errors in optic ataxia. Commentators **Goodale & Milner** discuss an article by Milner et al. (2003) in which an optic ataxic was shown to make errors in direction from the outset of a movement. Similar results were described by **Newport et al.** (see Jackson et al. 2004), and by **Gentilucci & Chieffi**. As the data reported by Gentilucci & Chieffi have not been published, I will focus my discussion on Milner et al. (2003) and Jackson et al. (2004).

Milner et al. (2003) report the trajectories of two patients with optic ataxia, I.G. and A.T. Both patients suffered extensive bilateral damage to the SPL and neighboring IPS, and some damage to the adjacent angular gyrus of the IPL. When these patients were tested for their ability to point to targets in the visual periphery, they showed large errors, a common finding in patients with optic ataxia (e.g., Perenin & Vighetto 1983; 1988). Moreover, when the trajectories were measured from the outset of the movement, these showed errors consistent with the final error. That is, both planning and control appeared to be impaired in pointing to targets in the periphery.

In another interesting experiment, the target was initially presented in one of two conditions, was removed from vision for five seconds, and then could reappear in either the original position (a congruent trial), or in another position (an incongruent trial). On congruent trials, both I.G. and A.T. were accurate, suggesting that their planning system was able to take advantage of the preview of the target's position. However, on incongruent trials, both I.G. and A.T. pointed in the direction of the original target, and did not correct these errors on-line.

Newport et al. reported data from two patients, Mrs. D. (originally described by Carey et al. 1997), and J.J. (described by Jackson et al. 2004). These two patients both make errors in pointing towards fixation. Further, both Mrs. D. and J.J. made errors from the outset of the movement. Both of these patients suffered extensive damage to the SPL, the IPS, and adjacent regions of the IPL.

Although the directional errors early in the trajectory of these patients are clear evidence of a planning deficit, I do

not believe that this provides evidence against the planning–control model. Rather, there are at least two good reasons to suspect that these patients suffer from severe deficits in on-line control, as well as a relatively minor deficit in action planning.

R7.1.2. Direction coding in the IPL? The first reason relates to the anatomical loci of the patients' lesions. In all cases, the patients were reported to have large lesions of the SPL and IPS (the control system), but also lesions of the angular gyrus in the IPL. Given that the IPL plays a major role in action planning, it is difficult to accept the argument of **Newport et al.** that the planning centers have been "spared." Rather, it would appear that the planning system (IPL) was slightly damaged in these patients, though much less so than was the on-line control system. Indeed, one might note that neglect patients, with damage typically centered on the right IPL, often make directional errors early in the trajectory. However, these errors are corrected on-line, presumably because of the spared SPL (e.g., Edwards & Humphreys 1999).

One fact not acknowledged by the commentators was that the directional errors made by the optic ataxics were not only present early in the movement, but were not corrected on-line at all, even in the presence of visual feedback. For example, the optic ataxic Mrs. D. (Fig. 1 of **Newport et al.**) exhibited a consistent leftward deviation in the original heading of her movements, but these movements then became redirected (often reversing direction) towards fixation. This shows a clear distinction between planning and control phases, because the planning phase exhibited a leftward deviation, and the control phase exhibited a honing error towards the point of fixation. Further, the optic ataxics I.G. and A.T. both made significant directional errors in the early portion of the trajectory when pointing to the incongruent targets, but there is also little evidence of any on-line correction in these movements (Milner et al. 2003).

Another thing I find interesting about these patients' deficits is that whereas they all show directional errors in planning, there appear to be few if any amplitude errors (incidentally, it is also interesting that the optic ataxic I.G. had the same susceptibility to the induced Roelofs effect (IRE) as control subjects along *both* the directional and amplitude dimensions – see **Coello & Rossetti**). Given that the distinction between distance and direction coding has long been known (Rosenbaum 1980), these data suggest the intriguing possibility that the angular gyrus codes the direction component of reaching movements, but that the amplitude component may be coded elsewhere in the IPL. This possibility might be examined in a brain imaging experiment in which targets vary either along the directional (i.e., left to right) or distance (i.e., near to far) planes. The data from patients with optic ataxia suggests that the directional task would be associated with activity in the angular gyrus, whereas the distance task ought to be associated with a separate region of the IPL.

R7.1.3. Much ado about directional errors. Although the commentators make much of directional errors in optic ataxics, this would appear to be practically the only evidence against an interpretation of optic ataxia as a deficit specific to the on-line control of actions. Therefore, the second reason for doubting that directional errors early in the trajectory of optic ataxics' pointing movements refutes the planning–control model relates to the wealth of evidence showing that these patients are indeed mostly impaired at on-line control, with relatively intact planning systems. For example, I.G., who shows directional errors early in pointing to targets in the visual periphery, shows no such errors in pointing to targets in foveal vision. Further, she shows a greatly exaggerated error when pointing to a target that changes position coincident with the onset of the movement (Pisella et al. 2000). She also shows large errors in grasping targets that change position at movement onset, completing first a movement towards the original position of the target, then a secondary movement to the new target position (Gréa et al. 2002).

In sum then, the evidence of directional errors in patients with optic ataxia does not pose a problem for the planning–control model, because this model is based on an anatomical distinction between the IPL and planning on the one hand, and the SPL/IPS and control, on the other. Whereas optic ataxia is associated to damage to the latter region, in the cases of optic ataxics showing directional errors early in the trajectory, there is a consistent involvement of the angular gyrus of the IPL (i.e., of the planning system). The commentators seem to be assuming that all optic ataxics have damage restricted to the control regions, and that none should show any errors in planning. Again, more careful correlations of the anatomical locus of brain damage with the resulting behavioural deficits are necessary before strong conclusions can be drawn. However frustrating it is for researchers that brain damage does not often restrict itself to isolable anatomical regions, it is a factor that must be considered.

R7.2. The apraxias

Goodale & Milner and **Ramenzoni & Riley** contest the identification of the planning system with apraxia, suggesting that it is much too simplistic. **Johnson-Frey** and **Coslett & Buxbaum** argue that the apraxia can also be associated with damage to the SPL, suggesting a wider distribution of the planning system. Before addressing these issues, I will first reiterate my view. In the planning–control model, planning involves regions of the frontal lobes, the basal ganglia, and the IPL. It is, in my opinion, beyond coincidence that damage to the frontal lobes or IPL often leads to various forms of apraxia, and that many of these can be equated with deficits in various aspects of planning. However, this is not the same as saying that every patient with apraxia should present the exact same deficit in planning, or that planning is a single, monolithic system, or that apraxia only follows damage to the IPL. Rather, one must again use caution in interpreting the results from human neuropsychology because of the propensity for naturally occurring lesions to disrespect our scientifically imposed anatomical boundaries.

The target article describes two of the many variants of apraxia, ideational apraxia (a deficit in action selection, sect. 4.3), and ideomotor apraxia (a deficit in executing learned actions, sect. 4.1). Each of these syndromes represents damage to different regions of the planning system, a frontal region involved in action selection, and a posterior region involved in kinematics. Similarly, I also describe Parkinson's disease as reflecting a deficit in action planning (hypokinesia).

However, many commentators have nevertheless argued that the planning system as I describe it, is monolithic and thus incomplete. Clearly this is not what was implied in the discussion of the consequences of damage to the various brain regions implicated in planning. Again, I can appreciate that the planning system is very complex and does not lend itself easily to simple descriptions or simple flowcharts. In this respect then, the commentators are correct. However, in a broader perspective, this means only that the planning system needs fleshing out (hard to do in a single article, even in *BBS*!).

Nevertheless, some interesting comments were provided on the topic of apraxia, and these deserve discussion. For example, **Longo & Bertenthal** argue that there are many instances in which apraxics perform better when the target object(s) are present than when they must simply pantomime actions in the absence of the target object(s). It is hard to imagine how this contradicts the planning–control model. Another argument raised by Longo & Bertenthal is that patients with "pantomime agnosia" are able to imitate gestures they are unable to recognize. This also does not contradict the planning–control model, because the model says nothing about how actions are recognized.

Coslett & Buxbaum argue that the planning–control model is not consistent with at least two findings relating to apraxics. For one, they argue that the model would not predict difficulty in learning new gestures (Gonzalez Rothi & Heilman 1984). It is again unclear how this is inconsistent with the model, given that the planning system is said to rely heavily on memories of past experience, and that visuokinesthetic engrams (plans) are stored in the IPL. The finding that apraxics often have difficulty in learning new gestures is therefore entirely consistent with the planning–control model.

The second point of contention raised by **Coslett & Buxbaum** is that the planning–control model would not predict the commonly observed dissociations between performance on transitive and intransitive gestures. In particular, it appears that the left IPL may be less critical for the performance of intransitive gestures than it is for the performance of transitive gestures. However, this assumes that damage to the left IPL, in the planning–control model, would result in a complete inability to plan any action, which was never suggested in the target article. Rather, I posit that the IPL is but one part (albeit an important one) of a greater planning system. My reason for focusing on the role of the IPL in planning was mainly to contrast it with the role of the SPL/IPS in control.

To summarize, the commentators have clearly added to the discussion by illustrating that planning cannot be viewed as a simple system. This should stimulate much work on the organization and function of the various components of the planning system. On the other hand, it is not clear how such dissociations between different aspects of planning contradict the planning–control model.

R7.3. Basal ganglia in planning versus control

The planning–control model holds that the basal ganglia is a part of the planning system. However, both **Gaveau & Desmurget** and **Vaillancourt et al.** commented on the possible role of the basal ganglia in on-line control, and these comments seem to suggest the need to clarify and perhaps modify the model somewhat.

First, it is not true that the distinction between planning and control means that both operate in complete isolation of the other. Thus, whereas many errors in planning can be corrected on-line, assuming an intact control system, a certain type of error may affect planning as well. One way in which the two systems overlap is in the provision and use of the *efference copy.* An efference copy is akin to a blueprint of a motor plan used by the control system in the on-line correction process. The control system uses this efference copy to encode the goal of the task, which it then fulfils using a combination of visual and proprioceptive information. In this sense, then, control relies on planning to provide an adequate efference copy. If such an adequate representation of the movement goal is not produced by the planning system, then the control system will be unable to complete its task.

Such a deficit appears to arise from damage to the basal ganglia, a planning center. Consequences of damage to the basal ganglia can include Huntingdon's disease, in which patients show an impairment in making on-line corrections (Smith et al. 2000). It is possible that this reflects a deficit in the planning system through an inability to produce an accurate efference copy of the movement, although the deficits in coding sensory input on-line would seem to suggest a role of the basal ganglia in the control phase as well.

Vaillancourt et al. argue that the distinct kinematic profiles of Parkinson's patients with or without visual feedback reflects a role of the basal ganglia in on-line control. Specifically, when visual feedback is available, Parkinson's patients show a reduction in the transport phase and velocity of their movements relative to controls. This would also seem to implicate the basal ganglia in on-line control.

To summarize, recent findings have implicated the basal ganglia not just in planning, as posited in the target article, but also in on-line control. It appears then that the planning–control model may require modification in order to accommodate these recent findings. It may be that the basal ganglia represents an important interface between the planning and control systems. However, more research will be needed to address these issues directly.

R7.4. A note on the neuropsychology of the perception–action model

As a final comment on the neuropsychology of action, I here address a concern with the perception–action model. I do this because I think the evidence from neuropsychology in favor of the perception–action model has been and continues to be scant. To illustrate this, one need only examine the evidence for the "double dissociation" between perception and action from human neuropsychology.

On the one hand, we may consider **Goodale & Milner**'s celebrated case of D.F., who suffered extensive damage to the ventral stream with a spared dorsal stream. Whereas D.F. shows severe deficits in perception, consistent with the "perception as ventral" tenet of the perception–action model, she also shows many errors in action (see sect. 4.6 of the target article). In principle, this falsifies a strict interpretation of the perception–action model based on the ventral-dorsal stream distinction because D.F.'s dorsal stream is spared. Her action system should therefore be intact, but clearly it is not. However, once again the model is salvaged, because D.F.'s impairments are said to arise on those occasions when the dorsal and ventral streams must

interact to plan and control an action. Indeed, D.F. is held as an instructive example as to when such interactions must take place. Of course this assumption has the one drawback of requiring that the model be correct in the first place.

Consider also the complementary dissociation: optic ataxia. Patients with optic ataxia have roughly the opposite pattern of brain damage as D.F.: a spared ventral stream but a damaged dorsal stream. A strict interpretation of the perception–action model then holds that they should have relatively intact perceptions coupled with severely impaired actions (at least actions under visual guidance). And yet again, the strict dissociation is not upheld by the data (see sect. 4.4 of the target article). As Rossetti et al. (2003) have most eloquently pointed out, despite suffering damage to large areas of the SPL and IPS, most clinical optic ataxics have little if any trouble going about their everyday lives – indeed much less so than D.F.! Further, many of the deficits in visual guidance are apparent only under rather artificial experimental conditions, such as in pointing to targets in the visual periphery. Again, this relative sparing of abilities related to action following damage to the dorsal stream appears very difficult to reconcile with the perception–action model, at least without recourse to interactions.

It seems much more parsimonious to describe the pattern of action deficits that arise from damage to the posterior visual areas of the brain by adopting the planning–control distinction. The reader is encouraged to review section 4 of the target article for the full treatment of the argument, only the basics of which I will reiterate here. First, action planning, including the initial kinematic planning, involves mainly the IPL, although it also draws information from the ventral stream and frontal lobe regions, as well as subcortical structures. This explains why D.F. is not completely spared in her abilities to act; rather, she has deficits in planning that can sometimes be ameliorated through a reliance on on-line control. Conversely, visual on-line monitoring and control involves the SPL (and possibly the neighbouring IPS) along with the cerebellum. This explains why optic ataxics are generally much less impaired in action than would be predicted if actions were the domain of the dorsal stream alone, and that they exhibit a pattern of spared and disrupted behaviours that are consistent with a planning–control distinction (Glover 2003; Pisella et al. 2000; Rossetti et al. 2003).

R8. Conclusions

The planning–control model, as elucidated in the target article, has provoked a number of interesting and often challenging commentaries. Unfortunately, a not insubstantial proportion of these challenges reflected misinterpretations, suggesting that the original exposition was not as clear as it could have been. I've attempted to address this shortcoming in my replies. More challenging were the commentaries that appeared to contradict the planning–control model directly. The most important of these can be reiterated here.

R8.1. What goes into planning and control?

Goodale & Milner argued that the planning and control of kinematics to visible targets are both functions of the dorsal visual stream, and are therefore relatively immune to cognitive or perceptual (i.e., ventral stream) processes. This is not consistent, however, with the evidence from visual illusions (e.g., Aglioti et al. 1995; Gentilucci et al. 1996; Glover & Dixon 2001a; 2002a), semantics (e.g., Gentilucci et al. 2000a; Glover et al. 2004), or associations in long-term memory (Haffenden & Goodale 2000; 2002a; 2002b). Rather, these types of effects are consistent with the notion that planning is susceptible to interference from cognitive and perceptual variables, whereas on-line control is not.

Others argued that the characterization of planning was too vague, with which I generally have agreed, albeit with the explanation that the target article was not meant as an all-encompassing description of "planning." Certainly some attempt had been made to at least touch on the various components of the planning system.

Finally, many cogent arguments were made regarding the use of visual feedback in the control process, and controversial arguments were also made regarding the time course of the decay of the control representation. These seem to directly challenge the notion of a gradual decay in the control system, and I look forward to seeing further investigations of these issues.

R8.2. Visual illusions and planning versus control

A number of commentators addressed the issue of the effects of visual illusions on action planning and control. Among the many arguments put forth are those that question the reliability of the dynamic illusion effect. However, in the absence of rigorous attempts to replicate the dynamic illusion effect using sound methodology, I maintain that such arguments are spurious. In particular, the issues of scaling the illusion effects, employing sufficient statistical power to detect the effects in the first place, and including time points late in the movement need to be taken seriously.

R8.3. Evidence from brain evolution and function

Controversy arose over the assertion that the brains of macaques and humans differ in significant ways. Although I suspect that the differences in planning across species far outnumber the differences in control, the evolution of the brain, in particular as it relates to the respective commonalities and differences between macaques and humans, is nonetheless an important issue that must be heeded.

Several commentators contested the characterization of planning and control with regard to human neural anatomy. Particularly challenging are the reports that many optic ataxics make errors not only in the final accuracy of pointing movements, but in the initial direction as well (Jackson et al. 2004; Milner et al. 2003). However, in these cases, damage had invariably extended into the angular gyrus of the IPL, and I suggest that the angular gyrus might represent the coding of direction. Further, the planning–control model's IPL/SPL distinction is present in a number of studies of brain imaging (e.g., Adams et al. 2003; Astafiev et al. 2003; Deiber et al. 1996; Grafton et al. 1998; Krams et al. 1998) and neuropsychology (e.g., Clark et al. 1994; Edwards & Humphreys 1999; Gréa et al. 2002; Pisella et al. 2000).

Other arguments related to the characterization of apraxia. Mainly, these suggested that the explanation given for apraxia was too simplistic. Certainly it is the case that to describe and categorize the multitude of variants of apraxia

fully requires much more space than is allotted here, and I agree with the various commentators that the complexity of this syndrome is beyond the present scope of the planning–control model. Perhaps a future expansion of the model could attempt to encompass apraxia fully.

Finally, reasoned arguments were made for including the basal ganglia in the control system as well as the planning system, and it appears that this may require a slight modification of the planning–control model. To this end I have suggested that that the basal ganglia may represent an interface between planning and control, and may indeed be responsible for the transfer of the efference copy from planning to control centers.

R8.4. Conclusions

There appear to be two main questions outstanding: First, to what extent do planning and control rely on different visual and/or cognitive information, and exactly what information goes into each stage? Second, what are the neural underpinnings of planning and control, and to what extent do these support the functional and anatomical distinctions drawn in the target article? Other questions of interest relate to the phylogeny and ontogeny of planning and control, the time course of the transformation from planning to control, and the detailed component structures of each system.

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Letters "a" and "r" appearing before authors' initials refer to target article and response, respectively.

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