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Separate visual representations in the planning and control of action

Scott Glover
Department of Psychology, Royal Holloway University of London, Egham, Surrey, TW20 0EX, United Kingdom; and Department of Psychology, University of Alberta, Alberta, Calgary, Canada.
scott.glover@rhul.ac.uk
http://www.pc.rhbnc.ac.uk/staff/scotglov.html

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-

SCOTT GLOVER is a Lecturer in the Department of Psychology at the Royal Holloway University of London, where he is currently engaged in studying the effects of TMS (transcranial magnetic stimulation) on action planning and control. He obtained his B.Sc. in psychology at the University of Lethbridge in 1996, and his Ph.D. in psychology at the University of Alberta in 2001. He has published several articles on illusion effects on action, including an opinion article in *Trends in Cognitive Sciences* in 2002. He has also published work on semantic effects on action. His interests include vision and motor control, neuropsychology, neuroimaging, attention, and philosophy.

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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

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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

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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.

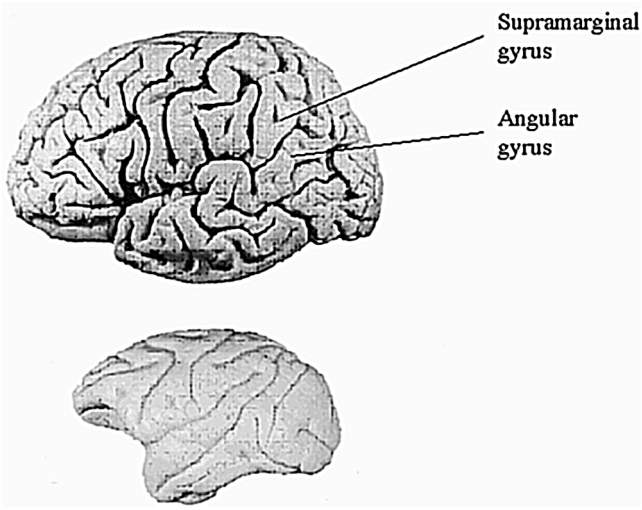


Figure 1. Comparison of the human (top) and macaque (bottom) brains. Cortical surfaces of the left hemispheres of both species are shown. Note the large area of expansion within the parietal lobes of the human brain compared to the monkey. Labeled in the figure of the human brain are the two regions 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-

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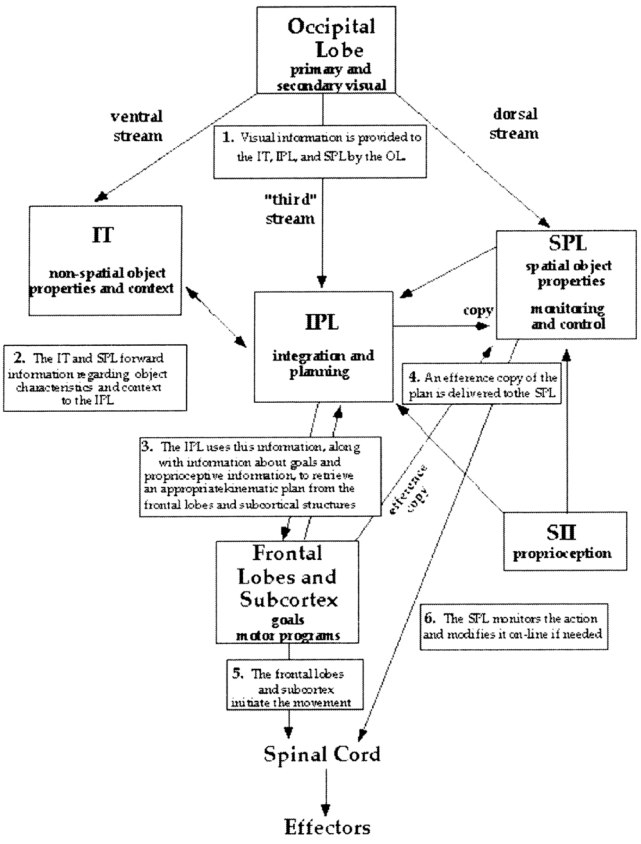


Figure 2. Schematic of the planning–control model showing the hypothesized connectivity and functions of the human visuomotor, cognitive, and somatosensory regions involved in action planning and control. Connections between early visual regions, and between visual and cerebellar regions are putative 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

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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

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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-

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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.

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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,

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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)

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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).

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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-

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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.

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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).

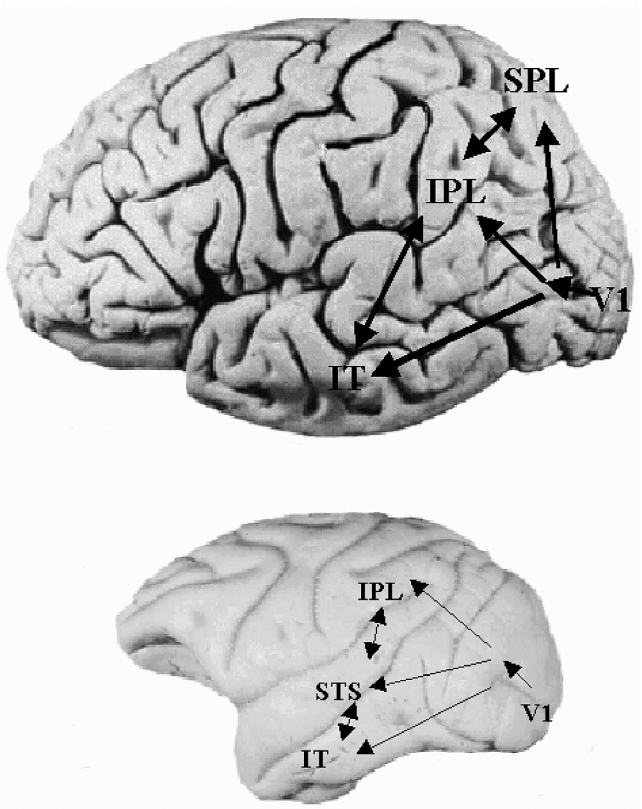


Figure 3. Illustration of putative visual pathways in the posterior regions of the human brain (top), and macaque brain (bottom – based on Boussaoud et al. 1990; Mishkin et al. 1983). Note that whereas the dorsal stream in the macaque brain terminates in the inferior parietal lobule, in the human brain 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-

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

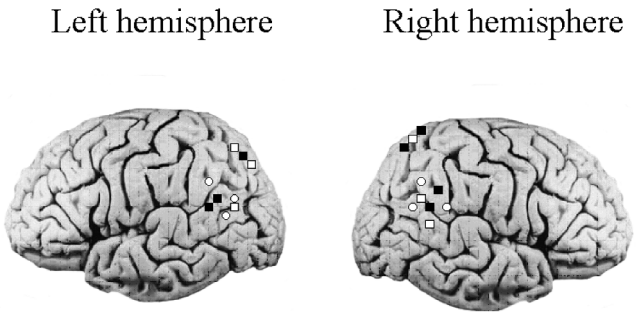


Figure 4. Summary illustration of increases in brain activity in the posterior parietal lobe related to motor planning, on-line control, and motor imagery. Filled squares: increased activity related to planning; empty squares: increased activity related to on-line control; filled circles: increased activity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

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.

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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-

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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

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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

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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.

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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

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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-

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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

Jos J. Adam and Ron F. Keulen

Department of Movement Sciences, Maastricht University, 6200 MD Maastricht, The Netherlands. **jos.adam@bw.unimaas.nl ron.keulen@bw.unimaas.nl www.personeel.unimaas.nl/jos.adam**

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

P. Paolo Battaglini[a], Paolo Bernardis[b], and Nicola Bruno[b]

[a]*Dipartimento di Fisiologia e Patologia and BRAIN Center for Neuroscience, Università di Trieste, 34143 Trieste, Italy;* [b]*Dipartimento di Psicologia and BRAIN Center for Neuroscience, Università di Trieste, 34143 Trieste, Italy.*
battagli@univ.trieste.it bernardis@psicoserver.univ.trieste.it nick@psico.univ.trieste.it http://www.units.it/~brain/

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

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