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

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

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

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

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

# Author's Response

## Planning and control in action

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

### R1. Introduction

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

### R2. The definition and characterization of planning

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



https://doi.org/10.1017/S0140525X04520022 Published online by Cambridge University Press

### *R2.1. Planning is not perception*

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

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

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

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

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

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

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

### *R2.3. Planning is not monolithic*

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

### *R2.4. Planning and grip force*

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


https://doi.org/10.1017/S0140525X04520022 Published online by Cambridge University Press

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

## R3. The definition and characterization of control

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

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

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

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

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

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

### *R3.2. The nature of on-line adjustments*

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



https://doi.org/10.1017/S0140525X04520022 Published online by Cambridge University Press

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

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

## R4. Evolution, neurophysiology, and development

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

### *R4.1. Humans are not scaled-up macaques*

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

### *R4.2. The evolution of planning*

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

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

### *R4.3. Differences across species*

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

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


https://doi.org/10.1017/S0140525X04520022 Published online by Cambridge University Press

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

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

#### *R4.4. The neurophysiology of planning and control*

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

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

#### *R4.5. Ontogeny follows phylogeny*

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

### R5. Visual illusions and context in action

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

#### *R5.1. Evaluating models of illusions and action*

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

*Table R1.* Illusions and actions: Models and predictions

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



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

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

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

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

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

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

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

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

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

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


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

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

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

### *R5.3. Visual feedback and illusions*

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

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

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

### *R5.4. Illusions and patients*

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

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

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

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



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

#### *R5.5. Context in planning and control*

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

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

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

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

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

#### *R6.1. Is the IPS special for anything?*

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

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

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

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

#### *R6.2. Planning and control in fMRI*

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


https://doi.org/10.1017/S0140525X04520022 Published online by Cambridge University Press

cuted the pointing movement to the target when it appeared.

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

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

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

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

## R7. Evidence from human neuropsychology

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

### *R7.1. Optic ataxia*

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

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

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

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

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

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

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



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

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

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

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

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

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

### *R7.2. The apraxias*

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

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


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

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

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

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

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

### *R7.3. Basal ganglia in planning versus control*

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

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

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

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

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

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

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

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



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

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

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

## R8. Conclusions

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

### *R8.1. What goes into planning and control?*

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

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

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

### *R8.2. Visual illusions and planning versus control*

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

### *R8.3. Evidence from brain evolution and function*

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

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

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


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

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

### *R8.4. Conclusions*

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

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


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https://doi.org/10.1017/S0140525X04520022 Published online by Cambridge University Press