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Effects of Contextual Perturbations on Natural and Pantomimed Movements

by

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Dedication

Much of the credit for this dissertation belongs to my supervisor, Peter Dixon, whose patient help and continuous encouragement were essential elements to its completion. I would also like to thank Alinda Friedman and Dallas Treit for serving on my supervisory committee and offering much in the way of constructive criticism. Gratitude is also directed towards Paul Zehr and William Prinzmetal who served as external examiners on my defense. Finally I cannot forget John Vokey and Bryan Kolb whose mentoring, though more remote in time, nevertheless was of much benefit to me in my graduate school career.

Great examples inspire courage in those who follow

Abstract

The planning/control model of action posits that separate visual representations underly each of these two stages of action. Two experiments were conducted aimed at assessing the predictions of the planning/control model. In Experiment One, reaching and grasping movements were made to a bar subject to an orientation illusion induced by a background grating. The sign of this illusion could be shifted by a corresponding shift in the grating. When the grating shifted coincident with the signal to reach (early shift condition), the illusion effect on reaching was lessened, but not reversed. A similar result occurred when the grating shifted coincident with the initiation of the movement (late shift condition). The gradual nature of the effect of shifting the grating was accommodated by a re-interpretation of the planning/control model from a discrete stage to a continuum model. In Experiment Two, the target was replaced with a two-dimensional rendition of a bar, and the task was modified such that participants were required to pantomime the reaching and grasping movement. Results were similar to those found in Experiment One, with the exception that the effect of the grating was the opposite of what it had been in Experiment One. The paradoxical effect of the grating in Experiment Two was explained as resulting from the disinhibition of competing motor programs involving movements directed towards the grating lines. This disinhibition was argued to be a consequence of the nature of the pantomiming task. The dissertation concluded with the outlines of proposals for further exploring the planning/control model.

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Chapter I. Introduction

Reaching to and grasping an object is an everyday act that most of us take for granted. Indeed, it typically appears to be such an effortless task that we might be tempted to dismiss it as unworthy of scientific study. Yet there are a large number of muscle contractions involved in any reaching and grasping movement, and achieving an adaptive timing and force of these contractions places a significant computational burden on the brain (Jeannerod, 1988; Rosenbaum, 1991). Further, there are a number of factors that can affect how a reaching and grasping movement is executed. For example, there may be a requirement to perform the movement quickly, as part of a series of movements, while attention is diverted elsewhere, or in the dark.

In the present research I examine two aspects of the visual control of action. First, I investigate the impact of changing the visual context surrounding a target at different times either prior to or coincident with movement initiation. Second, I compare the effects of these changes on two classes of action: one directed towards a real, physical target, the other a pantomimed action directed towards an image of a target. The specific purpose of the present research is to test the predictions of the planning/control model (Glover, 2000; Glover & Dixon, 2001a, 2001b, 2001c, in press a, in press b, in press c; Glover, Shah, & Dixon, 2001). More generally, it is hoped that this work will elucidate the organization of the visuomotor system.

Before describing the two experiments and their results I provide some theoretical background in the study of the visual control of action. In Chapter II, I describe the evidence for the planning/control model, and in Chapter III, the evidence for a competing model, the perception/action model. In Chapter IV I describe past research on visual illusions and actions, specifically with regards to the predictions made by the two models. To that stage, the focus will be on comparing and contrasting the planning/control and perception/action models.

However, in Chapters V (overview of the present study) through VIII (Experiments 1 and 2, and the general discussion), the focus is on the planning/control model alone. This narrowing of theoretical focus allows me to attempt to accommodate the unexpected results of the two experiments within the planning/control model. Finally, the thesis ends with a section on future directions of research on the planning/control model (Chapter IX), followed by a brief summary and conclusions section (Chapter X).

Chapter II. The planning/control model

The origins of the planning/control model date back to Woodworth (1899), who observed the beneficial effects of visual feedback in the on-line correction of actions. Woodworth had participants draw lines of specified lengths either with or without visual feedback. Woodworth observed that the lines were drawn more accurately when visual feedback was available versus when it was not available for times as short as 400 ms. However, when participants were required to complete the lines in less than 400 ms, there was no difference in accuracy whether or not visual feedback was available.

Woodworth concluded from these observations that movements could be decomposed into two distinct stages. The first, or "initial impulse" stage, involved the selection of a motor program that specified a large proportion of the upcoming movement. Woodworth considered this component of the action to be ballistic and immutable. At some time after the initial impulse stage came the "current control" stage. Here, Woodworth believed that visual and proprioceptive feedback were used to adjust the movement, making it more accurate.

In our adaptation of Woodworth's model, each stage of action uses its own specialized visual representation (Glover & Dixon, 2001a, in press a, in press b, in press c). In the first of these stages, a pre-movement or "planning" stage, a motor program is selected based on a broad range of factors, including the long-range goals of the action (Gentilucci, Negrotti, & Gangitano, 1997; Haggard, 1998; Rosenbaum, Vaughn, Barnes, & Jorgensen, 1992), memories of past experiences (cf. Rosenbaum, Loukopoulos, Meulenbroek, & Engelbrecht, 1995), the spatial characteristics of the target (e.g., its size, shape, orientation, and distance from the hand – Brenner, Smeets, & de Lussanet, 1998; Jeannerod, 1981, 1984; Klatzky, Fikes, & Pellegrino, 1995), and the non-spatial characteristics of the target (e.g., its weight, function, temperature, fragility – Fikes, Klatzky, & Lederman, 1994; Gordon, Forssberg, Johansson, & Westling, 1991; Klatzky, McCloskey, Doherty, Pellegrino, & Smith, 1987; Klatzky, Pellegrino, McCloskey, & Doherty, 1989; Weir, MacKenzie, Marteniuk, Cargoe, & Frazer, 1991). Plans also require a consideration of other objects near the hand, the target, or along the trajectory between them. These non-target, contextual objects can often present obstacles that must be avoided in order for the movement to be successful (Ruud, Meulenbroek, Rosenbaum, Jansen, Vaughan, & Vogt, in press)

Although a large proportion of the muscle contractions underlying any given action can be thought of as being pre-planned, the planning/control model also assumes that actions are monitored and sometimes adjusted in flight. There is a significant advantage in having an independent "control" stage of action during its execution. Simply put, plans may go awry for any of a number of reasons. Noise in the neuromuscular system, unexpected forces acting on the body, changes in the location of the target, etc., can all disrupt even the most accurately computed plan. In such cases, visual and proprioceptive feedback (and possibly efference copy) become important adjuncts to the planning of actions by allowing for the on-line guidance of the effector(s).

Beyond these external factors, plans may simply be faulty due to limitations of the internal processes involved. Specifically, perceptual and cognitive influences can have maladaptive effects on the planning of an action. To give one example, word meanings can cause an action to take on the characteristics of that word (such as opening the hand wider when a target is labeled "large"), even when the target does not share that same characteristic (Gentilucci & Gangitano, 1998; Gentilucci, Benuzzi, Bertolani, Daprati, & Gangitano, 2000; Glover & Dixon, 2001c). Further, the visual context surrounding a target can exert an influence on planning similar to the influence exerted on perceptually-based judgments (Glover & Dixon, 2001a, 2001b, in press a, in press b, in press c). All of these cognitive and perceptual influences must be corrected if an action is to be successful.

The control stage of action may operate best by focusing its computational power on the moment-to-moment spatial characteristics of the target and their relations to the effector, and by ignoring the other sources of information, such as the overarching goal of the movement, the non-spatial characteristics of the target, or the context surrounding the target. In brief, the goal of the on-line control system may be to minimize the spatial error of the movement. This simplicity of purpose allows on-line control to operate quickly and flexibly.

In the planning/control framework, then, movements are decomposed into two stages. A pre-movement planning stage involves the consideration of four main factors: 1) the overarching goal of an action; 2) the spatial characteristics of the target; 3) the non-spatial characteristics of the target; and 4) the visual context surrounding the target. Planning also benefits from the use of stored memories of past experiences. In one computational model, for example, the current situation is compared to past experiences in the selection of a motor program (Rosenbaum et al., 1995).

The on-line control phase, on the other hand, is used to minimize the spatial error of the movement, and thus is focussed solely on the spatial characteristics of the target. On-line control is constrained in memory to the storage of immediate or short-term (about 2 s) visual representations. As a consequence, when movements are made after a delay of 2s or more between offset of the visual stimulus and movement initiation, the control stage of action does not occur – actions are carried out "as planned", whether accurate or not.

Functional evidence for the planning/control model

In this section, I will provide evidence that planning is indeed affected by the overarching goals of an action, the visual context, and both the spatial and non-spatial characteristics of the target. I will also show that on-line control is exquisitely sensitive to the spatial characteristics of the target, but apparently to none of the other factors that affect planning.

Evidence that the overarching goal of an action is considered when that action is planned was obtained in a classic study by Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas (1987). Marteniuk et al. had participants reach to and grasp a chip with one of two purposes in mind. In one condition, participants had to "place" the chip carefully into a small receptacle. In the other condition, participants were instructed to "toss" the chip into a large container. Depending on the action required with the chip, the kinematics of the movement made *towards* the chip itself (i.e., prior to picking it up) were different. When the goal was to "place" the chip, the movement towards the chip took much longer, and was marked by a much slower approach phase. Conversely, when the goal was to "toss" the chip, the movements were faster, and there was less deceleration in the approach phase. Similar results have been obtained in other studies involving different types of goal specifications (e.g., Gentilucci et al., 1998; Haggard, 1998); and were even obtained when the ultimate goal of the action was two or more steps away (Rosenbaum et al., 1992).

Evidence that planning considers the visual context surrounding the target comes from two main sources. One source of evidence, studies involving visual illusions, is described in detail in a later section, and thus will be passed over here. Another source of evidence is the observation that the motor system avoids obstacles along the path to the target (e.g., Jackson, Jackson, & Rosicky, 1995). Although this appears to be a rather mundane observation given everyday experience, the fact that the trajectories of the hand begin to account for the position of the obstacle from the *beginning* of the reach is consistent with the notion that the obstacle's presence is encoded in the action plan.

Evidence that planning considers the spatial characteristics of the target comes from studies showing that elements of the final posture of a movement are evident well before the movement is completed (e.g., Glover & Dixon, 2001a, 2001b; Jakobson & Goodale, 1991; Jeannerod, 1984; Marteniuk et al., 1987; Wing, Turton, & Fraser, 1986). For example, the opening and closing of the thumb-finger aperture in grasping an object is correlated with the size of the target well before the target is contacted (Glover & Dixon, 2001c, in press c; Glover et al., 2001; Jakobson & Goodale, 1991; Jeannerod, 1984; Wing et al., 1986). Early scaling has also been observed for many other kinematic parameters, including hand shaping (Klatzky et al., 1995), velocity/acceleration (Gentilucci et al., 1997; Klatzky et al., 1995), and hand orientation (Desmurget, Prablanc, Arzi, Rossetti, Paulignan, & Urquizar, 1996; Glover & Dixon, 2001a, in press a, in press b; Jeannerod, 1981).

Despite the wealth of evidence supporting the notion that spatial characteristics affect planning, the empirical evidence that the non-spatial characteristics of an object are accounted for in action planning is comparatively scarce. Perhaps this is because these effects are so intuitively obvious that they do not seem to require confirmation. To give examples, people normally grasp tools by the handle when one is available; people are careful when contacting very hot objects or when running their hands over sharp surfaces; people generally treat fragile objects more gently than they do sturdy objects, etc.. A limited empirical corollary of these everyday observations was provided by Klatzky et al. (1989), who observed that participants had an awareness of the kinds of interactions that could sensibly be had with given objects. Indirect evidence for the importance of non-spatial target characteristics in action comes from studies of ideomotor apraxics, who often grasp and/or use objects inappropriately, despite being able to recognize them and understand their function (Heilman & Gonzalez Rothi, 1993).

In contrast to the large number of variables that seem to affect planning, the visual information used during control seems much more limited (albeit in a highly specialized sense). The control representation seems focussed on just the spatial characteristics of the target. The highly specialized function of on-line control has been observed in a number of studies.

Perturbation studies have involved a change in a particular spatial characteristic of the target (typically its size or its location) coincident with the onset of a reaching movement. In such cases, the motor system was able to adapt to the sudden change in the object very quickly. For example, a change in the location of the target resulted in a change in the trajectory of the hand within 100 ms (Paulignan, Jeannerod, MacKenzie, & Marteniuk, 1991). Similarly, a change in the size of the target was reflected in the grip aperture (i.e., distance between thumb and forefinger in grasping), in as short as 100 ms (Savelsburgh, Whiting, & Bootsma, 1991), but more commonly after 150-200 ms (e.g., Castiello, Bennett, & Stelmach, 1993; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991).

What is also interesting about these studies is that the adaptive motor processes appear to be initiated without conscious awareness. In fact, it appears that the initiation of adaptive motor responses actually *precede* conscious awareness of the change in the target (Castiello & Jeannerod, 1991). Further, if the change in the target is small enough (Savelsburgh et al., 1991), or occurs during a saccade (Goodale, Pelisson, & Prablanc, 1986; Prablanc & Martin, 1992), the adaptive motor response can actually occur without any conscious awareness of either the change in the spatial characteristic of the target or the adaptive motor response itself. Put simply, the hand reacts to the change in the target before the actor realizes it.

These very fast motor responses to target perturbations are consistent with the speed of motor adjustments based on visual feedback (Paulignan et al., 1991b, Elliot & Allard, 1985; Zelaznik, Hawkins, & Kisselburgh, 1983), and proprioceptive feedback (Goodale et al., 1986; Khan, Franks, & Goodman, 1998; Prablanc & Martin, 1992), and it seems likely that these feedback components play a key role in the fast on-line control processes. Motor adjustments may also depend partly on "feedforward" or "efference copy" mechanisms by which a "blueprint" of an upcoming motor plan is delivered to regions of the brain responsible for its execution. This efference copy may then be compared with an ongoing action to determine the need for adjustments (Desmurget & Grafton, 2000; Evarts & Vaughn, 1978; Jones, 1974; Paillard & Brouchon, 1968; von Helmholtz, 1866).

Thus, there is strong evidence that the control system is exquisitely sensitive to changes in the spatial characteristics of the target, even more so than the conscious perceptual system. Further, the control system is able to adjust ongoing motor behavior incredibly quickly based on visual and proprioceptive feedback, and possibly efference copy. These findings are consistent with the planning/control model.

Of course, the fact that the control system is sensitive to changes in the spatial characteristics of the target is not conclusive proof in favor of the planning/control model. The planning/control model also holds that the control system should be immune to the influences of the other three factors said to be involved in planning: the goals, the context, and the non-spatial characteristics of the target.

As always, negative predictions are difficult to prove. And indeed, the evidence to support two of these three predictions is rather non-existent. For example, there is no evidence that the control system is insensitive to any changes in the overarching goals of the action. And on the face of it, it may be too strong a prediction. Certainly people can change their minds after they begin an action, and either call off the action or proceed to another action. However, it is highly unlikely, in my opinion, that such changes in goals will be able to influence an action in as short a time as do changes in the spatial characteristics of the target.

There is also little evidence that the control system is insensitive to changes in the non-spatial characteristics of a target. And such an occurrence would seem to be well nigh impossible under natural conditions. That is, it is extremely hard to imagine an object's identity could change within the time it takes to act on it, in the same way that its position could change. But it may be just this kind of impossible situation that could be used to test the predictions of the planning/control model (by means of a virtual reality display for example – see Chapter IX). According to the planning/control model, a change in an object's non-spatial characteristics (i.e., identity) should not be accommodated within the short time frames that normally apply to changes in its spatial characteristics. Rather these changes ought to require the formulation of a new plan that should take much longer to enact than a fast on-line adjustment.

Finally, there is the question of whether or not the context affects on-line control. As this question will be addressed in detail later, I will hold myself at this point to simply saying that the answer appears to be "no", although this statement will have to be qualified following the two experiments!

In sum, the functional evidence supporting the separation of the planning and control stages of action is strong. Planning appears to be a relatively slow, deliberate process that considers many aspects of the target and the environment. It draws heavily on visual information, spatial and non-spatial, target and contextual, and attempts to achieve the overarching goal of the action through the selection of an appropriate motor program. Once initiated, the plan comes under the influence of the control system. The control system uses visual, proprioceptive, and possibly efference information to monitor and correct the aspects of the action related to the spatial characteristics of the target. The overall result is an action that is selected on the basis of what is known about the target and the overarching goal of the action, but can be quickly adjusted on-line if necessary to make the action as spatially accurate as possible.

Neuroanatomical evidence for planning and control

Aside from the functional evidence supporting the planning/control model, there are also clear indications that planning and control utilize separate (though connected) regions of the brain. In a previous work (Glover, 2000), I proposed that the visual representations underlying planning and control resided in the inferior and superior parietal lobes, respectively. Here, I will review that evidence and also describe some of the other brain regions that appear to be involved in planning and control.

In the planning/control framework, the greater part of the visual analysis supporting action occurs in the posterior visual association areas (Glover, 2000). These association areas are concentrated in three main regions: the inferior parietal, superior parietal, and inferotemporal regions. In the planning/control model, the inferior parietal lobes are responsible for action planning, and the superior parietal lobes are responsible for action control. Figure 1 shows the proposed flow of information over the course of the planning and control of an action.

As can be seen in Figure 1, the inferotemporal region is responsible for the coding of spatial and non-spatial object characteristics, and the visual context. The superior parietal region is responsible for coding spatial object characteristics only. The frontal lobes are responsible for formulating the long-range goals of the upcoming action(s). Each of these regions feeds information to the inferior parietal lobe, which integrates these sources of information with proprioceptive information gained from somatosensory association areas (SII). The inferior parietal region then integrates these various sources of information, and in concert with the frontal lobes, uses them to select an appropriate action plan. An efference copy (blueprint) of the plan is forwarded to the superior parietal lobes.

Once the plan is initiated, the superior parietal lobes assume control. The superior parietal lobes use their own visual information about the spatial characteristics of the target, along with visual and proprioceptive feedback, to monitor and correct the action in flight. Where errors are detected or the spatial characteristics of the target change, the action is adjusted.

This assignment of duties to different brain regions finds support from both brain imaging studies and neuropsychology. Brain imaging studies have shown that planning is associated with increased activity in the inferior parietal lobe, whereas control is associated with increased activity in the superior parietal lobe (Castiello, Bennett, Egan, Tochon-Danguy, Kritikos, & Dunai, 1999; Deiber, Ibanez, Sadato, & Hallett, 1996; Grafton, Fagg, & Arbib, 1998; Grafton, Mazziotta, Woods, & Phelps, 1992; Krams, Rushworth, Deiber, Frackowiak, & Passingham, 1998).

Studies in human neuropsychology show that damage to the inferior parietal lobe in the left hemisphere can lead to ideomotor apraxia (Clark, Merians, Kothari, Poizner, Macauley, Gonzalez Rothi, & Heilman, 1994; Poizner, Clark, Merians, Macauley, Gonzalez Rothi, & Heilman, 1995; Poizner, Mack, Verfaellie, Gonzalez Rothi, & Heilman, 1990), a disorder of purposeful movement that cannot be traced to difficulties with language comprehension or conceptual understanding. Damage to the inferior parietal lobe in the right hemisphere can result in hypokinesia (Mattingley, Hussein, Rorden, Kennard, & Driver, 1998), a slowness in initiating movements. These deficits I have argued relate to the planning role of the inferior parietal lobe (Glover, 2000; see also Heilman, Rothi, & Valenstein, 1982; Liepmann, 1920).

Damage to the superior parietal lobe, on the other hand, is associated with deficits in the on-line control of actions. Patients with lesions in this region were found to have difficulties in accurately reaching to targets (Perenin & Vighetto, 1983, 1988), in orienting their hands to pass them through a slot (Perenin & Vighetto, 1988), and in scaling their hands to the size of objects (Jakobson, Archibald, Carey, & Goodale, 1991; Jeannerod, 1986; Jeannerod, Decety, & Michel, 1994). Two factors are particularly indicative of control deficits in these cases: First, deficits are most apparent in the second half of the movement (Jakobson et al., 1991; Jeannerod, 1986), when on-line control mechanisms are held to be responsible for the smooth execution of the action. Second, deficits can be ameliorated, at least in one reported case, with the substitution of familiar, everyday objects in place of neutral "laboratory" objects (Jeannerod et al., 1994). This result suggests that a much more accurate initial plan could be retrieved from memory when the target was a familiar one, and that in such a case the importance of on-line control was minimized.

Case DF, with damage from carbon monoxide poisoning focused in the ventral stream (i.e., that part that projects to the inferotemporal cortex and thus indirectly to the inferior parietal lobe), suffers not only from impairments in form perception, as Milner and Goodale (1995) have emphasized in their work, but also has deficits in planning. For example, DF can be made to grasp tools in a manner inappropriate to their use by simply misorienting the object relative to the canonical (Carey, Harvey, & Milner, 1996). That is, when the handle is near, DF grasps the objects by the handle, when the handle is further away, DF grasps the objects by whatever end is nearer (e.g., the claw of the hammer). Further, DF is unable to make accurate movements to targets after the imposition of a delay between offset of the visual stimulus and initiation of the movement (Goodale, Jakobson, Milner, Perrett, Bensen, & Hietanen, 1994). DF is also slow to initiate movements (Milner, Perreti, Johnston, Benson, Jordan, Heeley, Betucci, Mortara, Mutan, Terazzi, & Davidson, 1991). These deficits are, however, coupled with more or less intact control (Goodale, Meenan, Bulthoff, Nicolle, Murphy, & Racicot, 1994; Goodale, Milner, Jakobson, & Carey, 1991; Milner et al., 1991). For example, DF is able to orient her hand appropriately to post a card into a slot (Goodale et al., 1991; Milner et al., 1991). Thus, the pattern of deficits and spared performance in the patient DF can also be explained within the planning/control framework.

Apart from the inferior parietal and superior parietal regions, other brain regions can also be associated with planning and control. For one, the same brain imaging studies cited above indicate that planning is associated with prefrontal, premotor, supplementary motor, and basal ganglia regions (Deiber et al., 1996; Grafton et al., 1992, 1998; Krams et al., 1998). The evidence from neuropsychology is also consistent with the role of these areas in planning. For example, long-term planning can be disrupted by damage to the prefrontal region; shorter-term planning (i.e., the planning of an immediately upcoming movement) can be disrupted by damage to the premotor areas; damage to the supplementary motor areas can lead to deficits in sequencing of complex movements; and Parkinson's disease, which leads to impairments in the functioning of the basal ganglia, is associated with deficits in planning (Kolb & Whishaw, 1995).

Conversely, control is linked through brain imaging with the cerebellum and primary motor and somatosensory regions (Deiber et al., 1996; Grafton et al., 1998; Krams et al., 1998). Consistent with this, cerebellar damage can lead to ataxias similar to those observed after damage to the superior parietal lobe and damage in the primary motor region causes loss of fine finger control (Kolb & Whishaw, 1995).

The evidence reviewed thus supports the neurological independence of planning and control. On the one hand, planning appears to rely on a visual association area in the inferior parietal lobe that operates in concert with prefrontal, premotor, and supplementary regions of the frontal lobes, as well as the basal ganglia and somatosensory areas. On the other hand, control appears to rely on a visual association area in the superior parietal lobe that operates in concert with the cerebellum and somatosensory areas.

In closing this section, it can be said that both functional and neuroanatomical evidence support the notion of separate planning and control stages in action. Each stage can be argued to serve different purposes. Planning appears to consider both the spatial and non-spatial characteristics of the target, as well as the visual context in its role of achieving the overarching goal(s) of the action. Control, however, appears to consider only the spatial characteristics of the target in its role of minimizing the spatial error of the action. Each stage can also be linked with brain regions not involved (or at least less involved) in the other stage. Planning involves a visual representation located in the inferior parietal lobe, along with a broad range of frontal lobe, basal ganglia, and somatosensory structures. Control, on the other hand, involves a visual representation located in the superior parietal lobe, along with cerebellar and somatosensory areas.

Chapter III. The perception/action model

The planning/control model can be contrasted with a model of visual processing that currently enjoys wide popularity. As with the planning/control model, I will first introduce the perception/action model before going on to describe the functional and neuroanatomical evidence in favor of it. The perception/action model (Goodale & Milner, 1992; Milner & Goodale, 1995) posits the existence of quasi-independent visual processing streams in the posterior half of the brain. A dorsal stream is thought to encode such visual information that would be needed for carrying out visually-guided actions. A ventral stream is thought to encode the visual information that underlies our conscious perception of the world.

The perception/action model had its early origins in the work of Schneider (1967), who observed a duality of visual processing in the golden hamster. Schneider found that selective lesioning of the visual cortex or optic tectum in the hamster leads to deficits in either perceptual discrimination or motor behavior, respectively. This work was later followed up extensively by Ingle, and then later by Goodale, the latter of whom spent his early career attempting to elucidate the existence of specific visuomotor modules – regions of the brain involved in a particular type of motor task. Several studies supported the idea that several specialized visuomotor modules existed in animals, each adapted to a different behavioral purpose (e.g., Goodale, 1983a, 1983b; Ingle, 1973, 1982).

In one study, Ingle (1973) observed that the visuomotor channels subserving prey-catching and locomotion in the frog were relatively independent of one another. Damage to one of these channels disrupted prey-catching behavior, whereas damage to the other channel disrupted locomotion. In each case, one of the two behaviors was left intact by the lesion that disrupted the other behavior – a classic double dissociation.

The perception/action approach, while still in its infancy, received further impetus from the proposal of the "two streams hypothesis" by Ungerleider and Mishkin (1982; Mishkin, Ungerleider, & Macko, 1983). This model suggested that the efferent outputs of the primary visual cortex in the primate brain diverged into two main pathways, or streams (Figure 2). One of these, the dorsal stream, terminating in the parietal lobe of the monkey, was argued to support spatial or "where" vision. The other, ventral stream was argued to support object identification or "what" vision (note that these are similar to the functions of encoding spatial and nonspatial object characteristics as proposed in the planning/control model.

This proposed "what/where" model was based largely on work done on brain-damaged monkeys, work that was later to receive sharp criticism from Milner and Goodale (1995). However, the greater part of the motivation for Milner and Goodale's re-casting of the functions of the two streams was to come from neurophysiological studies of the dorsal stream in the awake monkey in the1980s and 1990s. Other important empirical components of the perception/action model were the purported dissociations between perception and action demonstrated in the patient DF, who it will be recalled suffered from a damaged ventral stream associated with carbon monoxide poisoning. Further, there were behavioral dissociations between perception and action in healthy pariticipants that strengthened the case of Milner and Goodale (1995).

Functional evidence for perception and action

Much of the functional evidence for a separation between the visual processing centers underlying perception and action is the same evidence I have used to argue for a separation between planning and control. This evidence can be summed up as belonging to two main categories: 1) Reaching movements made to a target that had been perturbed during a saccade, the consequence having been that the change in target location was not available to conscious awareness, were nevertheless quickly and accurately adapted to the new position of the target (e.g., Goodale et al., 1986; Prablanc & Martin, 1992)—these studies were cited in connection with the fast on-line corrections described in Section II; and 2) Movements made to targets subject to a visual illusion were often less susceptible to the illusion than were perceptually-based judgments. This group of studies is described in detail in Chapter IV.

Essentially, the planning/control and perception/action models differ only in how these studies are interpreted. On the one hand, the planning/control model argues that these studies show dissociations between perception and control, highlighting the fast specialized processes underlying the control stage. On the other hand, the perception/action model argues that these dissociations are between perception and action (which presumably includes both planning and control).

Neuroanatomical evidence for perception and action

The evidence used to support the perception/action model has been largely drawn from neurophysiological recordings in monkeys, and in the patient DF. Little discussion of the evidence from brain imaging has come from proponents of the perception/action model, perhaps because such evidence is less than compelling (indeed, the perception/action proponents have been criticized for paying so little attention to the brain imaging data –e.g., Carey, 1998; Jeannerod, 1999). This section thus focuses on the evidence from neurophysiological and neuropsychological studies as they have been taken as evidence in favor of the perception/action model.

Neurophysiological recordings taken from the brain of awake, responding animals were not made possible until the late 1970s due to limitations in technology. Once these methods became possible, however, numerous researchers began to demonstrate the role of the posterior parietal lobes in visuomotor behavior. For example, Tiara, Mine, Georgopolous, Murata, & Sakata (1990) and Sakata, Taira, Kusunoki, Murata, & Tanaka (1997) found cells in the dorsal stream of the monkey brain whose activity was linked to reaching behavior, and (Murata, Gallese, Kaseda, & Sakata, 1996) observed similar linkages between cells in the dorsal stream and grasping. Further, the activity of cells in the dorsal stream of monkeys has been shown to be sensitive to changes in motor plans (Gnadt & Andersen, 1988; Snyder, Batista, & Anderson, 1997, 1998). Such findings, while consistent with a role of the posterior parietal lobes in spatial processing as put forth by Ungerleider and Mishkin (1982), emphasized its role in motor behaviors. Specifically, it was demonstrated that particular regions of the dorsal stream were related to particular behaviors, such as reaching, grasping, and eye movements (for a review, see Jeannerod, Arbib, Rizzolatti, & Sakata, 1995), similar to the specialized visuomotor modules discovered in rodents by Schneider (1967), Ingle (1973, 1982), and Goodale (1983a, 1983b).

The pattern of deficits and spared behaviors in patient DF have been taken as strong evidence that perception and action rely on different visual systems, this despite the fact that she represented only a single case study. DF has been repeatedly shown to have apparently intact motor performance coincident with severely impaired perception of form. When asked to verbally report the orientation of a slot, for example, she was completely at chance in her performance. However, when asked to post a card into the slot, her performance was much more accurate (Goodale et al., 1991; Milner et al., 1991).

Other demonstrations seemed to confirm DFs relatively intact visuomotor skills. In one study, DF was able to accurately select adaptive grasping points (cf. Arbib, 1991) on different objects without being able to accurately describe them visually (Goodale et al., 1994c). Further, she was near normal in her performance when asked to grasp small blocks, even though she was unable to verbally discriminate among them (Goodale et al., 1994b). Notably, however, she was unable to accurately pantomime movements to targets that were no longer present (Goodale, Jakobson, & Keillor, 1994).

Complementary to the patient DF are ataxic patients who, as mentioned in connection with the planning/control model, show impairments in the visual guidance of actions (e.g., Jeannerod, 1986; Perenin & Vighetto, 1983, 1988). Here, as with most of the lines of evidence concerning the planning/control and perception/action models, the differences are mainly those of interpretation of the evidence. For example, the perception/action model considers ataxics as having a general deficit in carrying out visually-guided actions (including both the planning and control thereof), whereas the planning/control model argues that this deficit is limited to the on-line control stage only.

Note that this dispute over the specialty of "action" versus "control" also applies to the interpretation of fast on-line adjustments. Whereas the perception/action model posits that these adjustments represent the operation of an "action" system, the planning/control model posits that such a system only operates during a movement's execution, and not during the pre-movement planning of such an action. In essence, the planning/control model holds that the "action" system of the perception/action model is nothing more than an on-line control system, and is distinct functionally and anatomically from planning. The next section is an attempt to examine these different interpretations with regards to the particular line of evidence that leads up to the two experiments included in this thesis, the effects of context-induced optical illusions on action.

Chapter IV. Context-based visual illusions and action

Before describing the results of the studies of illusion effects on action, it is worthwhile to review the predictions made by the planning/control and perception/action models. On the one hand, the planning/control model predicts that illusion effects will be present on indices of action related to the planning phase, but not on indices of action related to the control phase. On-line control, being focused on the spatial characteristics of the target, should only be able to correct for those aspects of action dependent on the spatial characteristics of the target.

The planning/control model can also be used to make predictions for movements directed towards "targets" that are either not present, or are two-dimensional. These acted or "pantomimed" movements would not involve the kinds of normal three-dimensional targets that are the special province of the on-line control system. Rather, such a "target", for example a two-dimensional image or an imagined object, would not induce an on-line control stage in the action. As such, these pantomimed movements would not benefit from the on-line corrections that normally occur with the purpose of minimizing the spatial error of the movement.

In general, there are three main implications of the tenets of the planning/control model: 1) visual illusions should affect *all* aspects of action related to the non-spatial characteristics of the target; 2) visual illusions should affect the *early* portions of the aspects of action related to the spatial characteristics of the target, but not the later portions; and 3) pantomimed movements, or movements made to imaginary targets, will not be corrected on-line. As a consequence, large effects of illusions on action should remain present throughout the movement for these behaviors.

Compare this to the predictions made by perception/action model. A simple version of this model would predict that illusions should always have larger effects on perceptions than on actions. This is because the context is held to be important in perception, but not in action. As will be seen, this simple interpretation quickly runs afoul of the data, and it has become necessary to invoke the existence of interactions between perception and action. These interactions were originally argued to be necessary when the action system required perceptual information in order to carry out its task, such as when the task involved grasping a tool appropriately for its use, or when it requires a movement to a remembered target, or a pantomimed movement. It will become evident, however, that these interactions must be extended to rather implausible lengths in order to account for some of the findings regarding the effects of visual illusions on action.

Illusion studies supporting both the perception/action and planning/control models

Much of the interest in the effects of context-induced visual illusions (i.e., those induced by the relation between the target and its surrounding visual context) on action arose from the results of early studies that suggested that some indices of action were less affected by illusions than were perceptions (Aglioti, DeSouza, & Goodale, 1995; Bridgeman, Kirch, & Sperling, 1979). These early studies were taken as strong evidence in favor of the perception/action model. However, later studies showed that illusions did affect some indices of action as much as they affected perception (Brenner & Smeets, 1996; Jackson & Shaw, 2000; Smeets & Brenner, 1995; van Donkelaar, 1999), and studies I conducted in collaboration with Peter Dixon suggested that the earlier stages of action were more affected by illusions than the later stages (Glover & Dixon, 2001a, in press a, in press b, in press c).

The seminal study of illusion effects on action was conducted by Bridgeman et al. (1979), who examined the impact of Roelef's effect on perception and action (Figure 3). Roelef's effect refers to the apparent motion induced in a target object caused by a shift in the surrounding frame. For example, when the surrounding frame is shifted to the left, the target appears to move to the right, and vice-versa. This effect is so strong that a target that has actually moved can appear to have remained stationary if the frame has been shifted in the same direction. In this case, the actual motion and the apparent motion will effectively "cancel each other out", and leave the impression that the target has not moved when it in fact has.

Bridgeman et al. (1979) had subjects either reproduce the distance the target had appeared to have moved (a perceptually-based judgment), or point to the target's new location with a hand-held pointer (an action task). Bridgeman et al. found that although subjects' perceptual judgments were affected by Roelef's illusion, the accuracy of their pointing movements was not affected. This result suggested a distinction between "motor" and "cognitive" (i.e., perceptual) visual representations.

Aglioti et al. (1995) extended Bridgeman et al.'s (1979) work to the domain of grasping. In this study, Aglioti et al. examined the impact of the Ebbinghaus size-contrast illusion on the size of the maximum grip aperture (i.e., the greatest distance between the thumb and forefinger in grasping). Aglioti et al. found that the Ebbinghaus illusion (Figure 4) had a significantly smaller effect on the maximum grip aperture than it had on perceptually-based judgments. This supported the perception/action model. Follow-up studies by Haffenden and Goodale (1998) and Hu and Goodale (2000), under conditions in which visual feedback was eliminated, confirmed that maximum grip aperture was less affected by size illusions than were perceptually-based judgments. Similar results were obtained by Jackson and Shaw (2000) and Brenner and Smeets (1996; but see Franz, Gegenfurtner, Bulthoff, & Fahle; 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farne, 1999).

Note that the results of these studies also support the planning/control model. As size and location both represent spatial characteristics of the target, movement parameters related to these ought to be corrected on-line, even though they should be affected in the planning stage. However, what is critical about the studies employing pointing accuracy and maximum grip aperture as indices of action, from a planning/control perspective, is that these indices take place well into the control phase of the movement. As such, it is quite possible that some correction process has gone on as the hand neared the target.

It appeared from these studies that a simple distinction between perception and action provided the most elegant account of the relative lack of illusion effects on action. In each case, actions were less affected by visual illusions than were perceptions. Yet more recent studies have shown that some indices of action are just as affected by illusions as are perceptually-based judgments. For example, the forces applied in grasping and lifting an object (which depends on its mass – a product of its volume and density) are normally dependent on the target size (Gordon et al., 1991), and each was affected by a size illusion (Brenner & Smeets, 1996; Jackson & Shaw, 2000).

According to the planning/control model, these findings reflected the limitation of the control system in only being able to correct those aspects of the action related to the spatial characteristics of the target. When weight (a non-spatial characteristic) was the relevant feature of the target, it was affected by a size illusion. Proponents of the perception/action model attempted to explain the effects of illusions on lifting and grasping force by positing the existence of interactions between perception and action systems, and in this case at least such explanations appeared plausible. Estimating an object's weight normally requires information related to the object's density, which in turn requires knowledge of its identity, and this would fall into the domain of perception. By this logic, illusion effects on the aspects of action related to the target's weight occur because the action module is insufficiently equipped to estimate the target's weight for the purposes of carrying out the action. Thus, identity information must be imported from the perception module, and this information is influenced by visual illusions.

The studies reviewed so far thus support both the planning/control and perception/action models. Both models can be used to predict the smaller effects of illusions on grip aperture and pointing accuracy, as well as the larger effects of illusions on grasping force and lifting force. The relative value of the two models could not be compared on the basis of these studies, because the crucial distinction (i.e., in whether or not planning is more affected by illusions than control) was not tested. In the next section, I will discuss several studies that suggested that action planning was affected by illusions, but action control was immune to such effects.

Illusion studies suggesting a planning/control distinction

One difference between the planning/control and perception/action models is that only the planning/control model argues that illusions affect planning. Here it will be seen that at least two indices that could plausibly be assumed to reflect planning processes, reaction times and movement times, are indeed affected by illusions to a significant degree. Further, it will also be seen that visual feedback aids in the on-line correction of illusion effects on action. Note that none of these effects would be predicted on the basis of the perception/action model,

van Donkelaar (1999) examined the time spent in executing a movement directed towards a target subject to the Ebbinghaus size illusion (Figure 3). This experiment was a strong test of the hypothesis that planning is affected by illusions, because the time taken to execute a movement is largely determined during the planning stage. According to Fitts' Law (Fitts, 1957), speeded movements directed towards smaller targets are programmed to take longer than are movements directed towards larger targets.

van Donkelaar found that the Ebbinghaus illusion had a significant effect on movement times. Participants moved faster to the targets that appeared larger, and slower to the targets that appeared smaller, even though these targets were in fact the same size. This result was in accord with the notion that planning is affected by illusions (although a later study by Fisher, 2001, failed to replicate this effect). Effects of illusions on movement times have also been observed (Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Smeets & Brenner, 1995). An effect of an illusion on reaction times has also been observed (Smeets & Brenner, 1995). We can conclude from these studies that, in general, illusions impact not only the reaction times of a movement, but also the planning of the velocity of a movement, and thus movement times.

The importance of visual feedback of the hand and target during reaching to targets subject to visual illusions has also been noted. In one study, Gentilucci et al. (1996) measured the accuracy of pointing movements subject to the Muller-Lyer illusion (Figure 5). Here, participants began with their fingertip on one end of a Muller-Lyer shaft, and pointed as quickly and accurately as possible to the other end. Visual feedback was manipulated through the use of four vision conditions. In one condition, full visual feedback of the hand and target was allowed. In a second condition, vision was occluded (by turning off the lights in the room) coincident with the movement of the participant's hand off of the starting position. In a third condition, vision was occluded coincident with the signal to move (roughly 400 ms prior to the actual start of the movement). In a fourth condition, vision was occluded a full five seconds before the signal to move.

Gentilucci et al. (1996) found that removing visual feedback led to larger illusion effects on pointing accuracy. Further, the longer the time between the removal of visual information and the onset of the movement, the greater the effect of the illusion. A similar finding was observed by Westwood, Heath, & Roy (2000) in a study of grasping movements subject to the Muller-Lyer illusion, and in our work, we extended this finding to movements of the lower limbs (Glover & Dixon, 2001b). Although it is interesting that the clearest evidence of the importance of visual feedback in correcting illusion effects on-line comes from studies employing the Muller-Lyer illusion, there is at least some indication that similar effects likely occur for other illusions as well (Glover & Dixon, in press b, in press c).

From this review, it is clear that many studies of illusions and action support the idea that visual illusions affect planning but not control. For one, the fact that reaction times and movement times are affected suggests that the time taken to plan a movement, as well as the time that the movement is programmed to take, are significantly impacted by visual illusions. For another, the fact that illusion effects on action can be smaller when visual feedback is available supports the idea that the control system is using visual feedback, at least in part, to correct for illusion effects on-line. All of these results are consistent with the planning/control model.

Yet it is difficult to incorporate such results within a perception/action model, even when one invokes the existence of interactions between perception and action. For example, there is no *a priori* reason to assume that the time to program a movement and the time to subsequently execute the movement requires the input of the perceptual system. What is more, the beneficial effects of visual feedback are very hard to explain in a model that makes no distinction between the visual information used during planning and control. Indeed, a large part of the perception/action argument vis-à-vis illusions and actions has been based on the premise that visual feedback is *not* contributing to the smaller effects of illusions on actions (see e.g., Bridgeman et al., 1979; Bridgeman, Perry, & Anand, 1997; Haffenden & Goodale, 1998; Hu & Goodale, 2000).

Taken in sum, the evidence from studies of illusions and action described so far has been almost entirely consistent with the planning/control model, but much of it has been rather inconsistent with the perception/action model. The studies described in the next section, however, leave little doubt that the planning/control model does a better job of explaining the pattern of effects and non-effects of visual illusions on action than the perception/action model.

Dynamic illusion effects in reaching and grasping

Based on much of the evidence described above, Peter Dixon and myself reasoned that the ideal means of testing the planning/control and perception/action models would be to take a continuous measure of an index of action throughout the action itself. In particular, inasmuch as a given movement parameter will normally be affected by a relevant feature of the target from early in the movement (e.g., Jakobson & Goodale, 1991; Jeannerod, 1984), it ought to be possible to induce an illusory perception of a target feature and measure its effects on the relevant parameter of the reach as it progresses from start to finish.

This continuous measure of an illusion effect over the course of a movement allows a direct test of the planning/control and perception/action models. Specifically, if the planning/control model is correct, then an illusion ought to have a large effect on the relevant movement parameter early in a reach (reflecting the influence of the visual context on planning), but a continuously decreasing effect on this parameter throughout the remainder of the reach (reflecting the lack of an influence of the visual context on control). Such a "dynamic illusion effect" would not be predicted by the perception/action model, however. In this model, most actions ought to be relatively immune to visual illusions throughout the entire reach, as actions are assumed to be both planned and control with little reference to the visual context.

We first tested this paradigm with an orientation (or "tilt") illusion. This illusion was induced by placing a target bar on a background grating (Figure 6), the orientation of which was either ten degrees clockwise (Figure 6, left) or ten degrees counterclockwise (Figure 6, right). The grating orientation affects the perception of the bar in a manner predicted by the imposition of the grating as a relative frame of reference (Gregory, 1968).

When the grating was tilted clockwise, the bar appeared to be oriented further counterclockwise than it really was, and vice-versa.

Critical to the goal of obtaining a continuous index of an illusion effect on action was finding a parameter that was dependent on the orientation of the bar. Not surprisingly, the orientation of the hand turned out to be quite a useful index. Hand orientation became reliably dependent on the orientation of the target within the first half of the reach, and so it was relatively straightforward to see how the effect of the illusion changed as the reach progressed.

In our original study (Glover & Dixon, in press a), participants reached out to and grasped a bar that was placed at one of seven orientations, ranging from 5 to 35 degrees clockwise. As mentioned, the perceived orientation of the bar was manipulated through the use of the background grating. The orientation of the hand during reaching was measured by placing two infrared emitting diodes on the back of the hand such that their axis was parallel with the large knuckles. Optical recording equipment recorded the position of these ireds during each reach, and data was stored in the computer for analysis off-line.

We observed in this study that the orientation of the hand was tied to the orientation of the bar right from the beginning of the reach. The slope of this dependence increased from roughly 0.05 to 0.25 from the beginning to the end of the reach. That is, at early in the reach, the hand was rotated approximately 0.05 degrees for every 1 degree that the bar was turned; at the end, this relationship was about 0.25 for every 1 degree.

Critically, this dependence of hand orientation on bar orientation allowed us to determine the relative impact of the orientation illusion throughout the reach. At reach onset, the illusion had an effect equivalent to a nine degree rotation of the bar on the orientation of the hand. This was quite large in comparison to the effect on perceptual judgments (which were about two degrees). Yet by the end of the reach, the effect of the illusion on hand orientation was equivalent to less than a one degree rotation of the bar (and did not differ statistically from zero). In essence, then, the illusion had a very large impact on the orientation of the hand early in the reach, but this effect declined to zero (or near zero) by the end of the reach.

This result, which we labeled the "dynamic illusion effect", was consistent with the planning/control model, in which large illusion effects on planning are counteracted during the movement by the on-line control system. However, such a result was hard to reconcile with the perception/action model, in which illusions are thought to affect perceptions but not actions. Indeed, the perception/action model could only explain this result by recourse to an interaction between perception and action systems, with the perception system playing a dominant role in the planning phase, but the action system assuming control once the movement was initiated. This type of interaction would make it hard to distinguish from the planning/control model, however.

One concern with this result was that the reduction in the illusion effect on hand orientation over time may have been the consequence of a careful and deliberate use of visual feedback by the participants. In other words, participants may have been able to overcome the illusion by guiding the hand into the target visually. However, another study of ours discounted this explanation (Glover & Dixon, in press b). Here, the dynamic illusion effect was also found in a condition in which vision of the hand and target was precluded coincident with the signal to reach. The overall effect of the illusion in this "no vision" condition was generally larger than in the control (i.e., "vision") condition, although the evidence for an effect of vision in this case was not strong. Nevertheless, the replication of the dynamic illusion effect in the "no vision" condition suggested that continuous visual information was not crucial to the correction process. Rather, it appeared that some combination of stored visual information, proprioception, and efference copy were being employed during control to correct for the illusion's effect on planning.

We also found similar results in a study that examined the effects of the Ebbinghaus size-contrast illusion on grasping (Glover & Dixon, in press c). This study was conducted both as an extension and replication of the dynamic illusion effect found with an orientation illusion, and of the studies using the Ebbinghaus illusion previously reported by Goodale and his colleagues (Aglioti et al., 1995; Haffenden & Goodale, 1998). In those studies, it was found that the Ebbinghaus size illusion had a smaller effect on the maximum grip aperture than on perceptually-based judgments. In our study, the dependent variable was the grip aperture throughout the entire course of the reach.

Similar to our previous work, in this study we observed that the size of the grip aperture was clearly dependent on the size of the target from early in the reach. In two experiments, the slope of this dependence ranged from less than 0.1 at the beginning of the reach, to a peak of roughly 0.8 from the three-quarter mark to the end of the reach. That is, early in the reach, the hand opened less than 0.1 mm for every mm change in the size of the target. By the three-quarter mark onwards, the hand opened about 0.8 mm for every mm change in the size of the target. This rise in the slope was similar whether or not vision was allowed throughout the reach.

Yet the critical result of this study was that the dynamic illusion effect was replicated with a different index of action (grasping rather than reaching), and for a different visual illusion (the Ebbinghaus rather than orientation illusion). The dynamic illusion effect was also shown to occur in grasping subject to a simple size-contrast illusion (Figure 7), in which only one contextual figure was presented along with the target (Glover et al., 2001). This consistency in results across behaviors and illusions lent further support to the planning/control model, but as mentioned already, was difficult to reconcile with the perception/action model.

In summarizing the results of illusions and actions, it can be stated rather clearly that the planning/control model does a better job of explaining the pattern of effects and non effects of visual illusions on action than does the perception/action model. Most strikingly, the dynamic illusion effect (Glover & Dixon, 2001a, in press a, in press b, in press c; Glover et al., 2001) is predicted by the planning/control model, but not by the perception/action model. The planning/control model is also favored by the results of studies showing beneficial effects of continuous vision on the accuracy of movements subject to illusions (Gentilucci et al., 1996; Glover & Dixon, 2001b; Westwood, Chapman, & Roy, 2000). Finally, there are some indices of action that are just as affected by illusions as are perceptions, including reaction times (Smeets & Brenner, 1995), and movement times (Gentilucci et al., 1996; Smeets & Brenner, 1995; van Donkelaar, 1999), and these indices can plausibly be linked to planning processes.

Note that the perception/action model can only explain the effects of illusions on action by invoking an ever-increasing list of interactions between perception and action (Milner & Goodale, 1995). On the one hand, these interactions seem eminently plausible in situations such as when the identity of the target is important (for example, when grasping a tool, or judging a target's weight). On the other hand, these interactions become rather implausible when they involve the types of information for which the action system would seem to have its own independent sources. For example, as the dorsal "action" stream receives independent (and accurate) orientation information from the early visual areas, it is unclear why it should import *illusory* orientation information from the ventral "perception" stream in order to plan the movement.

More plausible, it seems, is the idea that illusions affect planning processes through a coding of the visual scene that includes the visual context surrounding the target. Such a coding would result in the same types of effects of visual illusions as are found on perceptually-based judgments.

However, these illusions are ultimately overcome by the motor system using a visual representation that focuses almost exclusively on the target, and as such, is not affected by context-induced illusions. This single-purpose system might also be useful in correcting other types of interference with action planning caused by other types of cognitive and/or perceptual variables, such as word meanings (e.g., Gentilucci & Gangitano, 1998; Glover & Dixon, 2001c).

Chapter V. Overview of the present study

The aims of the two experiments reported here can be summarized as follows: 1) to replicate the dynamic illusion effect; 2) to investigate the impact of changing the visual context either before or coincident with movement initiation; 3) to compare the effects of 1 and 2 above in normal versus pantomimed reaching and grasping; 4) to attempt to integrate these results within the planning/control framework. The methods of the two experiments involve a basic replication of an earlier study (Glover & Dixon, in press a), but with changes in the context and/or in the nature of the task itself during certain trials.

The first aim, to replicate the dynamic illusion effect, is rather a minor one, as this effect has already been found to be quite robust and reliable (Glover & Dixon, 2001a, in press a, in press b, in press c; Glover et al., 2001). The second aim, to investigate the impact of changing the visual context, is new. This derives from the prediction of the planning/control model that the context affects planning but not control. As such, any change in the context made before the movement begins should occur during planning and thus affect the initial portion of the movement. Conversely, any change that occurs after the movement has begun should occur during on-line control, and thus not affect the movement. As will be seen, this prediction was not entirely upheld by the data.

The third aim of the study, to compare the effects of an illusion and the change in context on pantomimed reaching movements, is derived from the observations of Goodale and his colleagues (Goodale et al., 1994a; Westwood et al., 2000a). This work suggested that pantomimed movements are more "perception-driven" than are movements made to actual targets. In the planning/control context, this means that pantomimed movements cannot access the same mechanisms of on-line control that are available to "normal" movements. As such, the planning/control model would predict that pantomimed movements would not be corrected on-line. Rather, illusion effects on pantomimed movements should remain large throughout the movement, and moreover should be affected by a change in the context whether it occurs before or during the movement.

Finally, it was hoped that the results of the two experiments can be sensibly integrated into the planning/control framework. In the case of the first experiment at least, this goal was largely met. In the case of the second experiment, however, the results were much more difficult to interpret, although they were interesting all the same.

Design of the two experiments

The design of the two experiments is superficially similar to the design of our previous studies employing the orientation illusion (Glover & Dixon, 2001a, in press a, in press b). In those studies, participants reached out to and grasped a bar laid on a background grating that induced an illusion in the perceived orientation of the bar. In the present study, this basic methodology was adapted by having participants each participate in three context-change conditions.

The overall design of the procedure followed in the two experiments is summarized in Figure 8. Each of three conditions included a 1000 ms viewing phase, in which participants observed the bar laying on the background grating, the latter of which could be oriented at plus or minus 10 degrees clockwise from the sagittal plane. After this 1000 ms, the second phase was initiated by a tone signalling the participants to begin reaching. As the participants let go of a starting handle to reach out to the bar, they released a switch that initiated the third phase of the trial. Depending on the particular condition, the background grating could change or remain the same at the beginning of either the second or third phases.

In the first (control) condition, the orientation of the grating remained stable throughout the pre-movement and movement phases. That is, if the grating was oriented at +10 degrees at the beginning of the trial, it remained at +10 degrees throughout the entire trial. In the second (early change) condition, the orientation of the grating shifted (from +10 to –10 degrees, or vice-versa) at the beginning of the second phase. In the third (late change) condition, the orientation of the grating shifted at the beginning of the third phase.

In the pantomime experiment (Experiment 2), the same three conditions were employed, with the exception that the actual, physical bar was removed and replaced with a projected image of a three-dimensional bar. In this experiment, the participants' goal was just to treat the image as if it were an actual bar, and to execute and reach and grasping movement to that bar. Again, the bar did not move, but the background grating could shift either early or late (or not at all) as in Experiment 1.

Predictions of the planning/control model

Recall again the tenets of the planning/control model. In this model, the visual context is predicted to affect the planning but not control of movements made to physical (real) targets. As such, inasmuch as planning can be thought of as occurring just prior to movement onset, an early change in the grating (coincident with the signal to reach) ought to affect the initial portion of the movement. However, inasmuch as control can be thought of as occurring from between the time the movement is initiated to the time of its completion, a late change in the grating (coincident with movement initiation) ought to have no effect at all on the initial portion of the movement.

Further, in the planning/control model, the control system is thought to require an actual three-dimensional physical target in order to correct for illusion effects on action. Thus, the visual context ought to affect both the planning and control of movements made to a two-dimensional (i.e., represented by an image) target. As such, both an early and a late change in the grating ought to affect not only the initial portion of the reach, but the entire trajectory of the reach as well. In essence, the dynamic illusion effect ought to disappear in reaching to an image of a target. Instead illusion effects on the trajectory ought to be large throughout the course of the reach, and to be affected by changes in the context whenever they occur.

It will be seen that neither of the experiments bear out the predictions made by the planning/control model, and a discussion of the possible reasons for this will follow in each case. However, the data do perhaps provide an interesting set of results, and a basis for future experiments, and these will be discussed at the conclusion of this paper.

Chapter VI. Experiment 1

Experiment 1 was aimed at testing the predictions of the planning/control model regarding the impact of the visual context on the trajectory of a reaching and grasping movement. According to this model, the context ought to affect the planning of the reach, but not its on-line control. A logical extension of this prediction is that a change in the visual context ought to have an impact if it occurs while the movement is being planned (i.e., prior to its initiation), but not if it occurs during movement execution.

Method

Participants

Twenty University of Alberta undergraduates served as participants in the experiment. All participants reported being right-handed, and having normal or corrected-to-normal vision. All participants were naive as to the purpose of the experiment and gave their informed consent prior to testing.

Apparatus

Participants sat on an adjustable chair at a 100 x 60 cm table and viewed the table through round, 2.50 cm diameter shutters mounted on a stand at a height of 32 cm. The shutters were opened and closed electronically. The visible surface of the table when the shutters were open was roughly a 46 cm by 40 cm (41.48° by 36.01° visual angle) area horizontally and in the forward planes, respectively.

A 2.5 cm horizontal plane by 8.0 cm forward plane microswitch was positioned 11 cm from the participants' edge of the table. This switch also served as a starting handle that participants grasped at the beginning of each trial. When the handle was grasped, the circuit was closed, whereas releasing the handle activated the switch. This switch served to indicate the beginning of the reach in the late change trials. The table top was covered with black construction paper to prevent reflections. A circular area 19 cm in diameter (23.74° visual angle) was cut out of this paper, centered 29 cm from the center of the starting handle. An 8 x 2 cm black cylindrical bar (10.49° by 2.64° visual angle) was laid on the center of the circular area.

Computer-generated images of gratings (1.05 cyc/deg) were projected from under the table onto the surface of a plexiglass sheet inlaid in the table top. The plexiglass was covered with a thin layer of acetate, also meant to prevent reflections. The overall effect of the stimulus display was of a black bar sitting on an image of a grating in the circular area cut out of the black construction paper.

The table top was illuminated with indirect diffuse lighting. The luminance of the black mat surface during testing was 0.3 cd/m2. The illumination of the plexiglass surface (i.e., the circular area where the target was placed and background was projected) was 1.4 cd/m2.

The table top was monitored with an overhead infrared video camera which fed into an Iscan tracking system. The calibration of the tracking system was accomplished using a method based on Haggard and Wing (1990). Two ireds were attached to a bar at a distance of 12 cm from one another and moved forward and sideways over the workspace from various starting positions while the reported distance between the two ireds was recorded. The standard deviation of these measurements was less than 1.2 mm in both the forward and horizontal planes.

Procedure

Participants wore two ireds attached to their right (reaching) hand. The ireds were taped to the back of the hand, along an axis parallel with the knuckles, but about one-third of the way from the knuckles to the wrist. The ireds were alternately illuminated at 60 Hz, and the position of the lit ired was detected electronically every video frame and recorded by computer for analysis off-line.

Participants were required to begin each trial by grasping the starting handle with their thumb and fingers, such that their thumb contacted the right side of the handle and their fingers the left side (from their perspective). The first and second fingers also served to hold down the switch while the participant awaited the signal to reach.

When the shutters were opened, the participant was able to see the background grating with the bar on top of it. After a 1s delay, a tone signalled the participants to begin. Coincident with this tone, the background screen went blank for 50 ms, after which the grating could re-appear either in the same (control and late change conditions) or opposite (early change condition) orientation. When the participants released the switch to begin reaching, the background screen again went blank, after which the grating re-appeared in either the same (control and early change conditions) or opposite (late change condition) orientation.

In half the trials, the grating orientation was initially at +10 degrees, in the other half it was initially at –10 degrees. For each of these grating conditions, the bar was placed at one of 5, 15, 25, or 35 degrees orientations. Each participant performed four blocks of each combination of two background x three change x four bar conditions (24 trials) for a total of 96 trials. Six randomly-determined practice trials preceded the test trials for each participant.

Data Analysis

The dependent variable on each trial was the orientation of the hand (i.e., the axis connecting the two ireds) throughout the course of the movement. Data were analyzed by first passing the position recordings through a custom filter that excluded artifacts. For each video frame, the position of the ired that was not lit during that frame was interpolated between the measurements for the succeeding and following frames. The angle between the two ireds was then computed for each sampled position. The criterion velocity for the onset and offset of the movement was set at 0.050 m/s. An average of the position of the two ireds was used to determine velocity. Trials were excluded if either the reaction time or movement time was less than 200 ms or greater than 1500 ms. Over 90% of all trials were included in the final analysis.

For each movement, the orientation of the hand was computed at 11 equally-spaced intervals from movement onset to offset, inclusive. These time-normalized data were averaged for each participant, bar orientation, grating orientation, and grating shift condition. Three analysis were performed on the data. For the first analysis, data was converted into scaled illusion effects by dividing the raw illusion effect (i.e., difference in hand orientation in the two grating conditions) by the slope of the effect relating hand orientation to bar orientation. The data were analyzed for the scaled illusion effects on hand orientation at four times during the reach (40, 60, 80, and 100% of reach duration). The use of only four times was determined by the need to limit the degrees of freedom as a means of compensating for the lack of independence of successive measurements of hand orientation. The first time included in the analysis (at 40% of the reach duration) corresponded with the first time at which the slope relating hand orientation to bar orientation was greater than 0.025. As the slopes prior to 40% of the reach duration were all below 0.025, the scaled effects tended to be very variable at these times and did not lend themselves to ready analysis.

The second analysis was performed to compensate for the variability in the scaled effects. This analysis used the raw illusion effects on hand orientation as the dependent variable. Here, I conducted simple comparisons of grating shift conditions at each 20% of reach duration. The third analysis was performed to test for effects of the manipulated variables on reaction times and movement times.

For each analysis, the relative fits of nested linear models were compared using likelihood ratios (Dixon, 1998; Dixon & O'Reilly, 1999). In each case, a null model that excluded the effects of any variables was first compared to a simple model that included a main effect of one variable only. Further comparisons were made using models that included successive factors as variables. In each analysis, I adopted 10:1 as a criterion for strong evidence in favor of one model over another (Dixon, 1998; Dixon & O'Reilly, 1999; Goodman & Royall, 1988).

Results

Figure 9 shows the orientation of the hand for each bar orientation at each ten percent of the reach duration, and Figure 10 shows the slope of the effect relating hand orientation to bar orientation over time. As we have previously found (Glover & Dixon, 2001a, in press a, in press b), the orientation of the hand became increasingly dependent on the orientation of the bar as the movements progressed. It can be seen in Figure 10 that the slope relating the orientation of the hand to the orientation of the bar was miniscule at the outset of the reach, rose to roughly 0.025 by the 40% mark, and rose further to roughly 0.25 by the end of the reach.

Figure 11 shows the scaled effects of the illusion on hand orientation for each grating shift condition at 40, 60, 80, and 100% of reach duration. Note that positive numbers indicate an illusion effect relative to the *initial* orientation of the grating on each trial. It can be seen in Figure 11 that the dynamic illusion effect was only clearly evident in the control condition, and not in the early grating shift or late grating shift conditions.

The first analysis of the data from Experiment 1 was conducted on the scaled illusion effects shown in Figure 11. A null model that included no effects of any variables was first compared to a model that included a constant effect of the illusion. The likelihood ratio comparing these two models was very large, $\lambda > 207.9$. That is, the data were more than 200 times as likely on the assumption that the illusion had an effect on hand orientation than on the assumption of no such effect. When an effect of time was added into the model, the fit was better still, $\lambda > 1000$. Adding in an effect of grating shift condition also improved the fit, $\lambda = 80.6$. Finally, adding in the interaction between grating shift and time improved the fit immensely, $\lambda >$

1000. In sum, the data showed evidence for a constant effect of the illusion that was itself affected by grating shift condition, and that changed over time. Further, there was clear evidence that the change in the illusion effect on hand orientation over time was different in the three grating shift conditions.

The second analysis of the data compared the raw illusion effects in the three grating shift conditions at each 20% of reach duration (Figure 12). Clear evidence of a difference in the raw illusion effects in the different grating shift conditions was found only at 20% and 40% of reach duration ($\lambda = 22.3$ and $\lambda = 15.9$ for the 20% and 40% times, respectively). For the 0%, 60%, 80%, and 100% times, the grating shift conditions did not clearly differ ($\lambda = 3.2$; $\lambda = 1.5$, $\lambda = 1.7$, and $\lambda=2.4$ for the 0%, 60%, 80% and 100% times, respectively).

The third analysis concerned the effects of bar orientation, grating orientation, and grating shift condition on reaction times and movement times. The reaction times and movement times for each bar and grating shift condition in the two grating conditions are shown in Figure 13 and Figure 14, respectively. For the reaction times, the planning/control model predicted no effect and the data supported this. The likelihood ratio comparing a null model to a model that included an effect of grating shift condition was very small, $\lambda = 1.0$. Adding in the effects of grating orientation and the shift x orientation interaction did little to improve the fit, $\lambda = 1.1$.

For the movement times, the planning/control model also predicted no effect, but the data seemed to indicate an interaction between bar, grating, and grating shift condition (see Figure 14). The model that fit the data well included a two-way interaction between bar orientation and grating orientation, with movements in the 5 degree bar orientation and +10 degree grating orientation being faster than movements in all the other conditions, which were assumed to have taken an equal amount of time. The likelihood ratio comparing this interaction to the null model that included no effects of any variables was very large, $\lambda > 1000$. The F-ratio of the variance not accounted for by this model was small, $F = 1.43$.

Discussion

The dynamic illusion effect observed in the control condition of Experiment 1 replicates the findings of previous studies employing different illusions and variables, including the orientation illusion used here (Glover & Dixon, 2001a, in press a, in press b), the Ebbinghaus illusion (Glover & Dixon, in press c), and a simple size-contrast illusion (Glover et al. 2001). This result supports the notion, inherent in the planning/control model, that the visual context affects how movements are planned but not how they are controlled on-line.

The lack of a clear illusion effect at 40% duration in the early grating shift conditions was not predicted. Rather, I had suggested that the early shift would result in the selection of a new motor program based on the updated information on the grating caused by the shift. This should have resulted in data that mirrored the data in the control condition; a large, but negative, early effect. The fact that the effect was not clearly different from zero suggested that the original grating orientation still had a large impact on how the movement was planned.

Data from the late shift condition were also inconsistent with the predictions I had made based on the planning/control model. In the late shift condition, I had predicted that the shift would have no effect on the magnitude of the illusion effect. This was because the shift would have occurred in the control stage, in which visual processing is supposed to be largely independent of the context. Instead, the illusion effect at 40% duration was decreased in the late shift condition relative to the control condition. This suggests that the shift affected the early portion of the movement even though this was ostensibly a part of the control phase.

The illusion effect in the late shift condition seems to suggest one of two possibilities: 1) that movement planning continues during execution (see e.g., Castiello et al., 1993; Paulignan et al., 1991a, 1991b), with the attendant contextual influences; or 2) that on-line control is affected, at least to some extent, by the orientation illusion. The first of these notions accommodates the results by arguing that planning is not a ballistic, immutable stage as was first argued by Woodworth (1899). Rather, planning is a more fluid process that can accommodate new information as it comes in, even when this new information arrives after the movement has been initiated. In the present case, the new information would be the change in grating. The second notion simply argues that the context has some constant, albeit small effect during on-line control.

Of the two possibilities, I would favor the first. It may be that drawing strong lines between when one process stops and another starts may be elegant, but inaccurate. Rather, the distinction between planning and control might better be thought of as operating along a continuum, with certain aspects of the visual processing (e.g., context) being assigned greater weight early in a movement, and others (e.g., egocentric size or orientation) being assigned more weight later in a movement. Figure 15 illustrates the comparison between the "discrete stage" and "continuum" versions of the planning/control model.

The second notion, that on-line control is affected by the orientation illusion, is discounted by the lack of illusion effects at the end of all three conditions, as well as in several other studies similar to the control condition of Experiment 1 here (Glover & Dixon, 2001a, in press a, in press b). Rather, these studies all support the idea that on-line control is relatively unaffected by the orientation illusion, and is much more sensitive to the veridical spatial information regarding the target. Taken in sum, these arguments support the continuum version of the planning/control model. In short, variables affecting planning have their greatest impact early in the reach, but can also have an impact later in the reach. However, the extent of this impact becomes increasingly smaller as the reach nears completion and comes more under the influence of the control system.

The impact of shifting the grating orientation in the early and late shift conditions relative to the control conditions suggests that a strict separation between planning and control stages may not be correct. Rather, it would seem from these data that planning and control may operate along a continuum, with the early stages of action more affected by planning (and the variables that affect it), and the late stages of action more affected by control. For the data in Experiment 1, the results clearly support the continuum version of the model rather than the discrete stage version.

Both the discrete stage and the continuum version of the planning/control model can accommodate the results in the early shift condition, but only the continuum model can explain the results in the late shift condition. Specifically, either version of the planning/control model could be used to predict that the early change in the context results in a smaller illusion effect early in the movement if one assumes that planning utilizes visual information from the entire time frame before the movement, i.e., including the 1000 ms preview stage. On this analysis, the initial orientation of the grating would also have a large influence on how the movement was planned, despite being shifted coincident with the signal to reach. The end result of such a shift would be a moderation of the illusion effect early in the movement.

However, only the continuum version of the planning/control model can explain the decrease in the illusion effect at 40% duration in the late shift relative to the control condition. In the continuum version, contextual information continues to have a large influence in the early portion of the reach. In the separate stage version of the model, the contextual information would be ignored starting from the time the movement was initiated, and data in the late shift condition would not differ from that in the control condition. In sum, then, the data favor the continuum version of the planning/control model.

Another result that was of interest was the presence of an illusion effect at 20% of reach duration in the control condition (Figure 12), despite the lack of significant scaling of the orientation of the hand to that of the bar at that time (Figure 10). Needless to say, this result is rather counterintuitive, and further has not been observed in any of the previous studies conducted using the orientation illusion and reaching (Glover & Dixon, 2001a, in press a, in press b). Also puzzling is the fact that the effect was present in the control condition only, and not in the early shift or late shift conditions.

These results might be interpreted to suggest that the grating orientation has its impact earlier in the trajectory than the orientation of the target. The reasons for this effect occurring only in the control condition would have do with the occurrence of the grating shift in the other two conditions; in the latter cases, this shift would tend to "neutralize" the effect of the initial grating orientation.

The interaction between bar orientation and grating orientation on movement times was also unexpected and without precedence in our studies of illusions and action. The fact that movements were faster in the right grating/5 degree bar orientation condition might have been due to the fact that this was the only case in which the orientation of the bar was counterclockwise relative to the orientation of the grating. As such, this may have allowed participants to more easily retrieve these experiences from past memory because there would be fewer instances in which the grating/bar relation was such. However, if this were true one would then expect a reduction in reaction times also, and this was not the case. In sum, this result is difficult to account for, and must be considered as anomalous, especially as this grating by bar interaction on movement times did not occur in our other studies employing the same orientation illusion (Glover & Dixon, 2001a, in press a, in press b).

In closing, the data from Experiment 1 were inconsistent with the original formulation of the planning/control model, in which the two stages of action were thought to be discrete. In the scaled data, illusion effects early in the movement were smaller in the early shift and late shift conditions relative to the control condition, but were not reversed in the early shift relative to the control condition, as would have been predicted by the discrete stage version. These data could, however, be accommodated within a continuum version of the planning/control model, in which the two stages are thought to operate along a continuum of increasing/decreasing influence.

Another result of interest was the effect of the grating in the control condition at 20% duration of the movement, prior to any significant scaling of the hand to the bar. This may have occurred as a consequence of a reliance of the hand on the grating as opposed to the bar itself in the early portion of the reach. This is also consistent with a continuum version of the planning/control model. Finally, the bar by grating effect on movement times was an anomalous result, not predicted by either version of the planning/control model.

Chapter VII. Experiment 2

The planning/control model (or more specifically, the continuum version of the planning/control model) was able to account for the major portion of the results of Experiment 1, in which illusion effects on the early portion of a reaching trajectory were lessened by a shift in the orientation of the background grating. In Experiment 2, the same methods were applied to study the planning and control of pantomimed movements. Three studies relevant to the present thesis have been conducted and are discussed below.

Goodale et al. (1994a) examined pantomimed movements in healthy participants and in the patient DF. As will be recalled, DF showed severe deficits in form perception, yet had relatively intact on-line guidance of her hand to a target. In the Goodale et al. study, participants were allowed a 5s view of an object before closing their eyes. After a 2s delay, participants opened their eyes. Now the object had been removed, and the participants had to pantomime a grasping movement towards the previous location of the object, as if the object were still physically present. A control condition had the participants actually reach out and grasp the object (which in this case was left on the table) for comparison.

In healthy participants, many of the kinematic markers indicative of a movement to a physically present object were altered in the pantomime condition. These changes included an increase in movement times and a lower peak grip aperture in the pantomimed condition relative to the normal condition. But in DF, the pantomimed movements in no way resembled normal movements. Rather, DF showed no scaling to the actual size of the remembered target in the pantomimed movements. Goodale et al. argued from these results that the normal on-line visuomotor transformations were not used in pantomimed movements. Rather, the movements were programmed using a stored "percept" of the target, and in DF's case this percept was of course inadequate.

A second study related to Experiment 2 was conducted by Westwood et al., (2000a). Westwood et al. examined the effects of the Muller-Lyer illusion on grasping behavior. Participants were allowed a 2s preview of the target, after which they had to either: a) reach out and grasp the target with full vision, or b) pantomime a reach and grasp to the previous position of the target following a 3s delay (during which the target was removed from the table). Westwood et al. observed that, whereas the maximum grip aperture (i.e., distance between thumb and finger) in natural grasping movements was not significantly affected by the Muller-Lyer illusion, the maximum grip aperture in pantomimed movements made to remembered targets was affected. On the basis of this result, Westwood et al. argued that pantomimed movements were programmed on the basis of the "perceptual" input of the ventral visual stream.

Another relevant study that involved pantomimed movements was conducted by Vishton, Rea, & Cutting (1999). Vishton et al. had participants complete imaginary grasps of two-dimensional triangular or square figures. The figures had inverted 'T's drawn on them to induce the illusion that vertical lines appear longer than horizontal lines of the same extent. In this study, there was a greater vertical than horizontal distance in the final placement of the thumb and fingers in a pantomimed three-fingered grasp of the two-dimensional figures. This suggested that pantomimed movements were affected by the horizontal-vertical illusion, even at the end of the movement.

The results of Goodale et al. (1994a), Westwood et al. (2000a), and Vishton et al. (1999) all support the distinction between perception and action inasmuch as pantomimed movements to imaginary targets can be explained as requiring the use of a perceptual representation. Yet these results can also be quite easily incorporated into the planning/control model. In the planning/control model, the argument is that it is specifically the on-line control processes that require the presence of a physically present target object. In other words, plans are similar whether or not a movement to an actual target is to be made, but control cannot operate without the presence of a three-dimensional physical object. As such, the two models make similar predictions.

Naturally, the results of only three studies cannot be taken as firm evidence that either of these interpretations are the correct ones. Indeed, there are many other factors besides a lack of a physically present target that might affect how a movement is planned and controlled. For one, the presence of a physical target also allows for haptic feedback that would not be received from a target image (although visual feedback would still be available). For another, movements may operate under different constraints when a pantomime movement is made to a two-dimensional target image as compared to a movement directed towards a three-dimensional object.

As none of the aforementioned studies examined an index of action throughout the movement, it was clear that the question of how pantomimed movements are planned and controlled required further exploration. In Experiment 2, I replicated the methods used in Experiment 1, but substituted a virtual image of a bar for the three-dimensional bar used in Experiment 1.

As the discrete stage version of the planning/control model has been largely discounted based on the results of Experiment 1, I will here focus on the predictions offered by the continuum version. According to this model, the virtual image ought to be insufficient to evoke the operation of the on-line control system. As such, illusion effects on hand orientation ought to remain large throughout the movement. Further, as the early illusion effects seemed to depend on the relative amount of time spent observing each grating in two shift conditions, the continuum version of the planning/control model would predict that the shift manipulation would have a similar effect on the early portion of the reach itself whether the movement was real or pantomimed. In essence, the only difference expected between the results of Experiments 1 and 2 would be that the effect of the grating should remain large throughout the movements. When the grating was shifted, the new grating orientation should henceforth have a large effect on the orientation of the hand.

Methods

Participants

Twenty new University of Alberta undergraduates served as participants in the experiment. All participants reported being right-handed, and having normal or corrected-to-normal vision. All participants were naive as to the purpose of the experiment and gave their informed consent prior to testing.

Apparatus

The same apparatus was used here as was used in Experiment 1, with two exceptions. First, the black bar was replaced with an image of a dark grey bar of the same shape and size. Two examples of the computer-generated images used in Experiment 2 are given in Figure 16. Second, in the 50 ms intervals between grating shift epochs, the screen was blank and the bar image was absent in Experiment 2; whereas in Experiment 1 the bar of course remained present during these intervals.

Procedure

The same procedure was followed here as in Experiment 1, with the exception that the instructions to the participants were altered to reflect the different nature of the task in Experiment 2. Specifically, in Experiment 2 the instructions were altered to emphasize the "pretend" nature of the task.

Data Analysis

As with Experiment 1, the scaled illusion effect analysis will be dealt with first, followed by the analysis of the raw illusion effects, then the analysis of the reaction times and movement times.

Results

The effect of bar orientation on hand orientation is shown in Figure 17 and the slope of this effect is shown in Figure 18. It can be seen by comparing Figure 17 to Figure 9 from Experiment 1 that the overall nature of the pantomimed movements (at least with respect to hand orientation) very closely mimicked movements made to real targets. Participants in Experiment 2 did, however, exhibit a slight tendency to "overact" when pantomiming movements: The hand turned more, and scaled to a greater extent in Experiment 2 as compared to Experiment 1. Yet overall, this scaling of the hand to the target followed a very similar pattern whether or not an actual physical bar was present or not (compare Figure 18 to Figure 10).

The similarities in the general organization of normal and pantomimed movements were in stark contrast with the different effects of the grating on the movement, however. The scaled illusion effects on hand orientation from 40% of the duration of the reach onwards are shown in Figure 19. Note that positive numbers indicate an illusion effect relative to the initial orientation of the grating on each trial. It can be seen from Figure 19 that a large negative illusion effect occurred at 40% of reach duration in the control condition. This early effect was nearer to zero in the late shift condition, and was positive in the early shift condition.

The first analysis of the data from Experiment 2 was conducted on the scaled illusion effects shown in Figure 19. The likelihood ratio comparing a null model that included no effects of any variables to a model that included an effect of time only was large, $\lambda = 59.2$. Adding in an effect of grating shift increased the fit substantially, $\lambda = 289.2$. Adding an interaction between time and grating shift to this model also improved the fit, $\lambda > 1000$. Finally, adding in a constant effect of the illusion did little to improve the fit of the model, $\lambda = 3.0$. From this analysis, the best-fitting model included effects of time and grating shift and their interaction, but not a constant effect of the illusion. Overall, the effect of the illusion was of the greatest magnitude (whether positive or negative) at 40% of reach duration, and increased or decreased towards zero by the end of the reach.

The second analysis of the data compared the raw illusion effects in the three grating shift conditions at each 20% of reach duration (Figure 20). Clear evidence of a difference in the raw illusion effects in the different grating shift conditions was found at 0%, 20% and 40% of reach duration ($\lambda = 271.2$, $\lambda = 213.8$, and $\lambda = 44.0$ for the 0%, 20% and 40% times, respectively). For the 60%, 80%, and 100% times, the grating shift conditions did not clearly differ ($\lambda = 1.7$, $\lambda = 1.8$, and $\lambda = 4.7$ for the 60%, 80% and 100% times, respectively).

The third analysis concerned the effects of bar orientation, grating orientation, and grating shift condition on reaction times and movement times. The reaction times and movement times for each bar and grating shift condition in the two grating conditions are shown in Figure 21 and Figure 22, respectively. For the reaction times, the planning/control model predicted no effect, but in fact, reaction times were faster in the control condition than in the two grating shift conditions. The likelihood ratio comparing a null model to a model that included an effect of grating shift condition was large, $\lambda = 47.3$. Adding in the effects of grating and bar orientation did little to improve the fit, $\lambda = 2.5$. There was little to indicate that any of the two-way interactions or the three way interaction had an effect on reaction times.

The grating shift effect on reaction times was anomalous, especially in that the reaction times were faster in the control condition relative to both grating shift conditions, even though the late shift condition was identical to the control condition right up to the point of movement initiation. As such, a further posthoc test was done that collapsed the data in the control and late shift conditions. The likelihood ratio comparing a null model that included only an effect of participants to a model that added in the effect of grating shift was moderate, $\lambda = 9.4$, but certainly not overwhelming. This analysis suggested that the apparent effect of grating shift condition on reaction times may have simply been a result of random noise in the data.

For the movement times, I also predicted no effect, but the data seemed to indicate an effect of grating (see Figure 22). When a null model was compared to a model that included an effect of grating, the likelihood ratio was moderate, $\lambda > 11.4$. Movements made when the grating was oriented at -10° were generally slightly faster than movements made when the grating was oriented at $+10^\circ$. There appeared to be no other effects of any variables on movement times.

Discussion

The results of Experiment 2, in which participants pantomimed a reaching and grasping movement to a virtual image of a bar, were surprising. The continuum version of the planning/control model predicted that the illusion would have a large positive effect early in the movements in the control condition because the pantomimed movement ought to have been susceptible to the movement. It also predicted that the illusion effect would remain high throughout the course of the movement, because on-line control mechanisms would be inoperative when reaching to a non-physical target. It also predicted no effects of any variables on reaction times or movement times. Finally, the continuum version of the planning/control model predicted that the illusion effect would be smaller in the late shift condition and smaller yet in the early shift condition relative to the control condition.

The data were difficult to reconcile with the planning/control model, however. The illusion effect was large and negative in the control condition, small and negative in the late shift condition, and small and positive in the early shift condition. These results were exactly opposite to what was found in Experiment 1. The results are also inconsistent with the planning/control model in two ways:

First, the illusion effects early in the reach were reversed relative to Experiment 1, whereas the planning/control model predicted these effects would be roughly similar in both experiments. Second, the illusion effects in Experiment 2 also moderated towards zero by the end of the reach, whereas the planning/control model predicted that the effects would remain high (as a consequence of the lack of an on-line control stage when the target was two-dimensional).

The results of Experiment 2 are puzzling in any case, in that the effect of the grating in Experiment 2 was in the opposite direction to what would be expected based on its effects on perceptions and on normal reaching (for example, in Experiment 1). Moreover, the decrease in the effect of the illusion in the late grating shift condition and further decrease in the early grating shift condition of the normal reaching task of Experiment 1 were mirrored by corresponding increases in these two grating shift conditions in the pantomime task of Experiment 2.

Superficially, these results struck me as bizarre and unexpected. Certainly, there was no *a priori* reason to suspect that the illusion effect would be reversed in the pantomimed reaching task. Yet at least one possible explanation can be given for this reversal of the illusion effect in pantomimed reaches, and this refers to the idea that the grating excited competing motor programs pertaining to the affordances offered by the environment (Gibson, 1971; Tipper, Lortie, & Baylis, 1992).

According to this notion, the brain is ever ready to respond to objects present in the environment, and the relevant motor programs are primed by the affordances offered by the surroundings. Naturally, however, most of these programs are inhibited and never executed, so that organisms are not responding to everything in the environment all the time. It is only by an act of intention that the motor program relevant to the particular immediate goal of the organism is released from this inhibition, and that action is executed. At the same time as the willed action is selected, the unwanted motor programs are suppressed.

In the present case, it is worth pointing out that whereas Gibson was concerned exclusively with the potentiality of "real" movements to 3-D targets, I here expand on his notion to take into account the particular constraints of the movement in question (a similar extension was applied to pointing movements by Tipper et al., 1992). In the present case, the motor programs that would be excited would be *pantomime* programs, and as such, two-dimensional targets would take precedence.

To consider this hypothesis as it applies to the present study, then, let us imagine that each of the stimuli in the environment evoke the selection (but not necessarily execution) of a motor program relevant to that stimuli. In Experiments 1 and 2, the stimuli were nearly identical apart from the replacement of a real bar in Experiment 1 with a two-dimensional rendition of a bar in Experiment 2. Thus, in both experiments, either the grating lines or the target bar (or its rendered equivalent) were potential targets of action.

In both experiments the task required that the motor program aimed at picking up the bar (or pantomiming the picking up of the bar) be selected and the program aimed at pantomiming a movement aimed at grasping one or more of the grating lines be inhibited. Under normal circumstances, three-dimensional targets take precedence over two-dimensional ones. Thus, there was no tendency to implement the motor program aimed towards the grating line(s) in Experiment 1.

However, in Experiment 2, the two types of target (bar and grating) presented the motor system with a problem in that it could not easily distinguish them as belonging to target and non-target classes. In this case, the planning of the movement was interfered with, and early in the movement the grating played the role of a competing target for the moving hand. This then explains why the effect of the grating in Experiment 2 was the opposite of what it was in Experiment 1.

The notion that the grating was a competing target early in the reach of Experiment 2 is supported by the fact that the grating had an effect independent of the bar at the onset and at 20% of reach duration. This effect would have been expected only if the grating had been taken as a possible target early in the reach. Although a similar effect of grating had also occurred at 20% of reach duration in Experiment 1, in Experiment 2 this effect occurred even earlier, and had an opposite effect.

This explanation, admittedly speculative, is able to account for the results of Experiment 2 with regards to the grating's effect on hand orientation early in the movements. It is clear at this time, however, that this phenomenon requires clarification with further research.

Reaction times in Experiment 2 were faster in the control condition than in the two grating shift conditions. It is possible to explain this result when one compares the control to the early shift condition. In this case, the difference in reaction times may reflect the use of the grating as a competing target: When the grating shifted, a new set of competing motor programs was enacted, and integrating these into the updated motor plan may have required some time.

This explanation would not suffice when one compares the control to the late shift condition, however, because here, the change in grating occurs after movement is initiated. As such, there is no reason to expect that reaction times should differ for the two conditions, and a further post hoc analysis showed the effect to be, in reality, marginal.

Movement times in Experiment 2 were slightly faster when the grating was oriented at –10° than when it was at +10°. Why this occurred is also a mystery, although the evidence for this effect was not overwhelmingly convincing either. Perhaps the effect resulted from the fact that the grating at –10° was less likely to present the participants with an easily "grasped" target (it is rather uncomfortable to orient the hand at –10°), and as such, actually interfered less with the movement than when it was oriented at +10°.

Chapter VIII. General discussion

The two experiments provided many novel and interesting findings. First of all, in both Experiments1 and 2 there was a pattern of illusion effects early in the reach that suggested that the original, discrete stage version of the planning/control model was incorrect. Whereas the discrete stage model predicted that the illusion effect early in the reaches would depend only on the grating orientation just prior to movement initiation, it was found that the illusion effect was smaller, but not reversed, when the grating was shifted either coincident with the signal to reach or coincident with movement initiation.

The data were better accounted for by assuming that planning and control operate along a continuum, with planning having a decreasing influence as a movement progresses, and control having an increasing influence. On this account, illusion effects early in a reach ought to reflect a weighted average of pre-movement and early movement influences.

Second, in both Experiments 1 and 2 the grating had an effect earlier in the movement than did the bar. That is, the grating effect was present even when the orientation of the hand was not appreciably scaled to the orientation of the bar. This suggested that in both experiments the grating served as a cue (albeit a faulty one) to the planning system as to the orientation of the target, and that this cue was in use before there was clear information available regarding the actual orientation of the bar. This again is more consistent with the continuum version of the planning/control model than with the discrete stage version, inasmuch as the former allows for the influence of different components of the visual scene to evolve over time.

Third, the illusion effect in the early portion of the reach in Experiment 2 was the opposite of what was predicted based on its perceptual effects and effects on reaching in past studies (and in Experiment 1 of the present study). I argued that this resulted from the interference of a competing motor program aimed at pantomiming a reach and grasp of one or more of the grating lines. On this analysis, the grating lines themselves became candidate targets early in the reach, but this tendency was overcome as the reach progressed. Consistent with this notion was the fact that the (negative) effect of the grating was present at reach onset in Experiment 2, whereas it was not present until 20% of reach duration in Experiment 1.

Finally, there were anomalous effects of the manipulated variables on movement times in the two experiments. In Experiment 1, there was a tendency towards faster movement times when the bar was oriented at 5 degrees and the grating at 10 degrees. Inasmuch as movement times can be regarded as being largely pre-planned (e.g., Fitts, 1957), this result suggests that the faster movements in this particular condition were a consequence of its unique characteristic of having the bar oriented further counterclockwise than the grating. However, it is not clear why this effect occurred only in Experiment 1, and did not also occur in either Experiment 2, or in any of the other studies conducted using the orientation illusion (Glover & Dixon, 2001a, in press a, in press b).

Movement times in Experiment 2 were affected by the grating condition, with movements being made faster when the grating was oriented at –10° than when it was at +10°. This result was quite difficult to explain, was not found in Experiment 1 or in any other study using the orientation illusion (Glover & Dixon, 2001a, in press a, in press b), and so might reflect either some unique characteristic of the pantomiming of movements, or might represent random noise in the data.

This summary of the results relates a number of unexpected findings that occurred in the present study. Although explanations can also be thought of for these surprising results, these explanations are largely based on speculation. Yet there is one particular result of the present study that I believe has clear implications for the future not just of the planning/control model, but perhaps even of motor performance in general.

Support for the Continuum Version of the Planning/Control Model

Up to and including the early portions of the present work, I have routinely suggested that planning and control represent distinct and more-or-less independent stages of action. Yet (and perhaps with some benefit of hindsight) there has always been a sense in which this discrete stage model has been more of an heuristic than a solid model. At some time in the evolution of the planning/control model, it was likely that this model would need to be replaced with something more flexible. Presently, the continuum model addresses this need. By arguing that planning and control influence action in a weighted fashion, the elegance of the original discrete stage model is lost, yet the increased predictive power of the continuum model is gained in compensation.

Past studies have upheld both versions of the planning/control model because illusions have affected the early portions of a reaching movement more than the later portions (Glover & Dixon, 2001a, 2001b, in press a, in press b, in press c; Glover et al., 2001). However, the present study supports only the continuum version. Here, illusion effects on planning depended not only on the relative amount of time different grating orientations were visible on any given trial prior to reaching, but were also influenced by a change in the grating coincident with movement initiation.

According to the discrete stage version of the planning/control model, the control stage begins coincident with movement initiation and as such, changes in the context at this time should have no effect. However, according to the continuum model, the boundary between the planning and control stages is ill-defined, or rather, non-existent. Instead, one stage gradually transforms into the other. The data from the two experiments reported here support the continuum model, but not the discrete stage model. In both experiments, changing the context coincident with movement initiation had an effect on the orientation of the hand early in the movement.

Other studies also support the continuum model over the discrete stage model. For example, in one study (Glover et al., 2001), we examined the importance of the discriminability of the target's contours in the on-line correction of a size illusion. If, as was argued by Arbib (1981), grasping involves the placement of the thumb and finger on contact points on the target's surface, then removing visual information regarding the location of these contact points might have been expected to reduce the ability of the motor system to correct for the effects of a size illusion on grip aperture. Indeed, such a result did occur: Illusion effects on grasping were larger when the edges of the target contrasted very little with the background (and were thus difficult to discriminate, tending to "blend in" with the background), than when the edges of the target contrasted strongly with the background.

However, this "contrast" effect was only present at the very end of the movement, and not earlier in the movement. This result suggests that the use of contour localization information is paramount only at the very end of the movement, even further reinforcing the notion that different visual information has different influences at different times during the movement. Note that a strict interpretation of the discrete stage version of the planning/control model would predict that such a contrast effect would be present from early on in the reach, as such information would be important from the beginning of the control phase.

Chapter IX. Future directions

What type of experiments might be done in the future to explore the predictions of the planning/control model? Although there are many possible avenues of research that could be pursued, I here briefly describe what I believe to be three of the more interesting ones. The first involves a more detailed examination of the role of the context in pantomimed reaches, specifically as it may excite competing motor programs in the planning of actions. The second is an attempt to connect the dynamic illusion effect to the neural underpinnings of planning and control using patients with brain damage. The final proposal deals with varying the time course of the information available during the (pre-movement) planning of an action as a further test of the discrete stage and continuum versions of the planning/control model.

The context as a competing target in pantomimed reaches?

As described earlier, contextual objects have been hypothesized to excite competing motor programs in reaching (e.g., Gibson, 1971; Tipper et al., 1992). Further, it is possible that these competing motor programs may be more influential in pantomimed versus actual movements, and/or more influential in movements towards neutral rather than real targets. If these notions are true, a competing motor program may have been responsible for the paradoxical illusion effect found for pantomimed reaches in Experiment 2.

In order to test this hypothesis further, I propose an experiment somewhat along the lines of Experiment 2, but using a 2x2x2 design. One independent variable would be (as it was in Experiment 2) the valence of the grating, i.e., whether it is oriented clockwise or counterclockwise. A second independent variable would be the magnitude of the rotation of the grating. Specifically, the grating could be oriented at either 20 or 40 degrees in either direction. Finally, a third independent variable would be the frequency of the grating, which would either be high frequency (as in Experiment 2) or a lower frequency.

If the competing motor program hypothesis is correct, then manipulating the magnitude of grating rotation ought to induce smaller or larger effects of the grating on pantomimed reaches. That is, the difference in hand orientation for gratings at either +/-40° ought to roughly double the difference for gratings at +/-20°. Further, a lower frequency grating would provide fewer competitors, and thus ought to invoke less interference than a higher frequency grating. These are just two possible manipulations that could be used to further examine the rather surprising results of Experiment 2.

Visual illusions and patients

One way of integrating the neural and behavioral tenets of a model is to test whether or not a behavioral phenomenon can cross over to the domain of brain-damaged patients (e.g., Posner, Walker, Friedrich, & Rafal, 1984). In the present case, there are indeed very interesting predictions that would be made based on the planning/control model. Specifically, as will be argued below, it may be possible for brain damage to actually improve one's performance!

One possible experiment would involve the use of patients with deficits in control. Ideomotor apraxics, thought to have a deficit in action planning (Glover, 2000; Heilman et al., 1982; Liepmann, 1920) might be tested for their ability to reach out to and grasp objects subject to an optical illusion. A simple design would involve the control condition of Experiment 1 in which the grating remains the same throughout the movement. If apraxics indeed have deficits in planning actions, it ought to be necessary for them to rely on a strategy of online control (i.e., one heavily dependent on visual and/or proprioceptive feedback). And if such a strategy were necessary, then based on the planning/control model, one would expect to see a lack of an illusion effect at any point during the movement.

The complementary study to this would involve the testing of optic ataxic patients, that I have hypothesized have a deficit localized to the control stage. If these patients are indeed suffering from disrupted control processes, the exact opposite might be expected from them as is expected from apraxics. Specifically, optic ataxics ought to show large effects of the illusion at all points throughout the movement. These two studies together would make up not only a startling pair of results, but a double dissociation of the neural substrates of the planning and control of action.

Time course of adjustments to changes in spatial and non-spatial target characteristics

There are many interesting ways in which one could alter the visual information available during either the planning and/or control of an action, and I here focus on one particular method only for the sake of brevity. These experiments would involve the use of virtual reality equipment that might impose its own limitations, and thus the proposal is made cautiously.

In the past, participants have been shown to react very quickly to changes in the size of a target in flight by adjusting their grip aperture accordingly (e.g., Castiello et al., 1993; Castiello, Bennett, & Chambers, 1998; Paulignan et al., 1991a). I propose here that these adjustments in grip aperture are possible only because size represents a spatial characteristic of the target. However, a similar change in size would also imply a change in weight (a non-spatial target characteristic), and it would be interesting to see whether such changes would be accommodated by the motor system as quickly.

To test this, a target's apparent size would be manipulated using a virtual reality device. As the participant reached out to grasp the target, a change in size would occur. The dependent measures would be the grip aperture and the vertical force applied in lifting the object. According to the planning/control model, the grip aperture ought to begin adapting to the change within 150 ms (consistent with past studies), whereas lifting force ought to require longer, perhaps 250 ms (similar to the time required to plan and initiate a movement). Such a result would be strong evidence in favor of the notion that control is tuned to minimizing the spatial error of the movement only, while other components of action require more time to be re-programmed.

Chapter X. Conclusions

This dissertation can be summarized as having two major parts. In Chapters I through IV the focus was on comparing the planning/control and perception/action models. In the (original) planning/control model, actions are decomposed into two stages. In a pre-movement planning stage, a motor program is selected based on several factors, including memories of past experiences, the overarching goals of the action, the visual context surrounding the target, and both the spatial and non-spatial characteristics of the target. On initiation, movements come under the influence of the control system. This system utilizes only the spatial characteristics of the target and aims to minimize the spatial error of the movement. One striking prediction of this model is that visual illusions will have greater effects early in a movement than later in a movement, provided these illusions affect a spatial characteristic of the target.

The perception/action model, on the other hand, argued that actions are both planned and controlled by reference to a single visual representation underlying actions, and separate from perceptions. This model predicts that dissociations should occur between vision for perception and vision for action. Regarding visual illusions, the perception/action model predicts that illusions should have small or non-existent effects on most actions, unless that action requires input from the perceptual system.

The planning/control model is able to account for all of the data held as support for the perception/action model. Furthermore, only the planning/control model is able to account for the dynamic illusion effects found in several studies (Glover & Dixon, 2001a, in press a, in press b, in press c; Glover et al., 2001), and for a similar type of effect found with word meanings (Glover & Dixon, 2001c). In these studies, a visual illusion (or word meaning) was found to have a large impact early in a reach, but a continuously decreasing impact as the reach progressed. The comparison of the two models was concluded by suggesting that the planning/control model provided a better account of the data.

Chapters V through VIII dealt with the description and analysis of two experiments manipulating the timing of a shift in an illusion-inducing background grating on either a reaching and grasping movement to a physical bar (Experiment 1) or a pantomimed movement to an image of a bar (Experiment 2). The shift could occur early (coincident with the signal to reach), late (coincident with movement initiation), or not at all (control condition). According to the original, discrete stage version of the planning/control model, only the early grating shift ought to have had an impact on the magnitude of the illusion effect early in the reach. The late grating shift ought to have had no effect at all, as this would have occurred during the control phase.

In Experiment 1, and in contrast to the predictions of the discrete stage model, it was found that both grating shifts impacted the effect of the illusion early in the reach. In neither shift condition did the illusion effect actually reverse, as had been predicted for the early shift condition. Rather, the illusion effect was lessened somewhat in both conditions relative to the control condition. These results were contrary to the predictions of the discrete stage version of the planning/control model.

In order to account for the results of Experiment 1, I proposed a modification of the planning/control model from the discrete stage version to a continuum version. According to the continuum version, planning and control both have influences on an action during the course of that action. The degree of influence of the two inputs, however, depends on the time course of the action itself. Early in the action, planning systems have the greatest impact. As the action progresses, the planning systems have an ever-decreasing influence, and the control systems have an ever-increasing influence.

Experiment 2 investigated the effects of the grating shifts on pantomimed movements. *A priori*, it was assumed that pantomimed movements would not evoke the control mechanisms used to interact with real objects, based on the results of past studies (Goodale et al., 1994; Vishton et al., 1999; Westwood et al., 2000a). Rather, it was expected that the illusion would have a large influence on the action throughout its course, and also that the grating shift would contribute to that influence. This was not what was found, however.

Paradoxically, the effect of the grating on pantomimed reaching was actually the opposite of its effect on reaching to an actual target. That is, where reaching to an actual target had been subject to a large illusion effect early in the reach, but an ever-decreasing effect as the reach was executed, in Experiment 2 the effect of the grating on hand orientation was opposite to the effect of the illusion! Apart from this result, however, the results did show a remarkable similarity between normal and pantomimed reaches, even to the point of the relative magnitude of the illusion effect (whether positive or negative as the case was for Experiments 1 and 2) on reaching.

This paradoxical effect of the grating in Experiment 2 was completely unexpected, but may be explainable if one adopts the notion that non-target objects in the environment excite competing motor programs (Gibson, 1971; Tipper et al., 1992). As an extension of this notion, I hypothesized that these competing motor programs produce their greatest interference when the task is ill-defined, as is the case with pantomiming. Certainly in normal reaching one would be less inclined to consider the grating as a potential target, as it cannot be grasped. Yet in pantomimed reaching the grating may in fact have played such a role.

The results of the two experiments were unexpected and required at least some re-interpretation of the planning/control model. The newer continuum version of the planning/control model sacrifices some of the elegance of the discrete stage version for an increase in flexibility and intuitive sensibility. It may indeed turn out that the picture of how the brain organizes, monitors, and adjusts movements is much more complex still. In future, methodological and theoretical innovations will be needed to assess the time course of various influences (both internal and external) on the planning and control of action.

Figure 1. The hypothesized neural flow of information in the planning/control model. Adapted from Glover (2000).

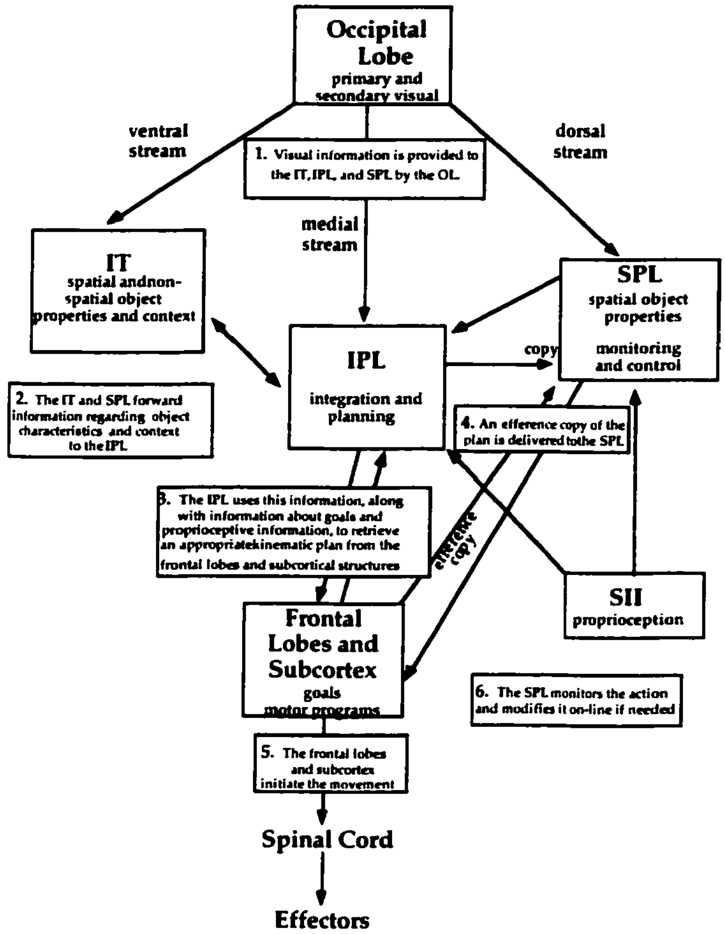


Figure 2. The two-stream model proposed by Ungerleider & Mishkin (1982). A dorsal stream terminates in the inferior parietal lobe and carries visuospatial information. A ventral stream terminates in the inferotemporal cortex and carries identity-related information. Adapted from Glover (2000).

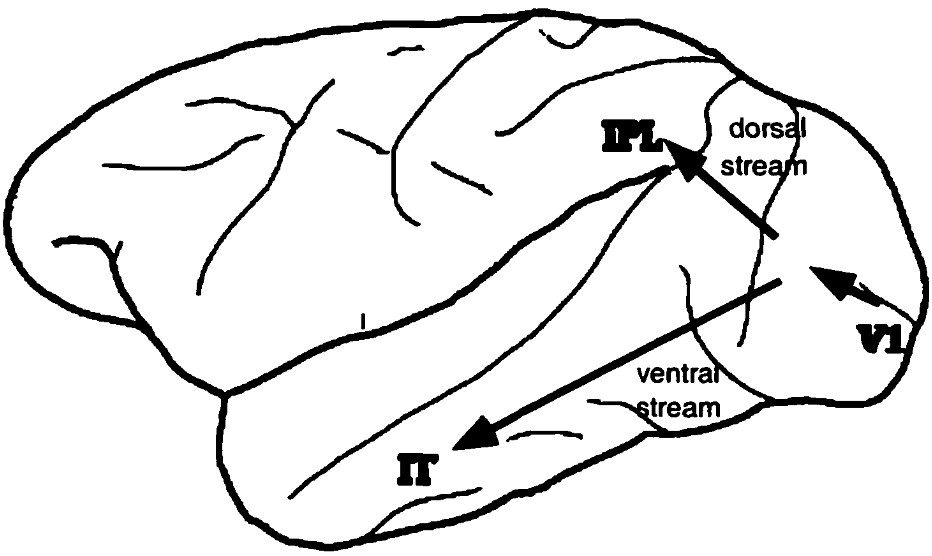


Figure 3. The Roelef's effect: The two target 'x's are vertically aligned, but owing to the positioning of the frames, the top 'x' appears to be to the left of the bottom 'x'.

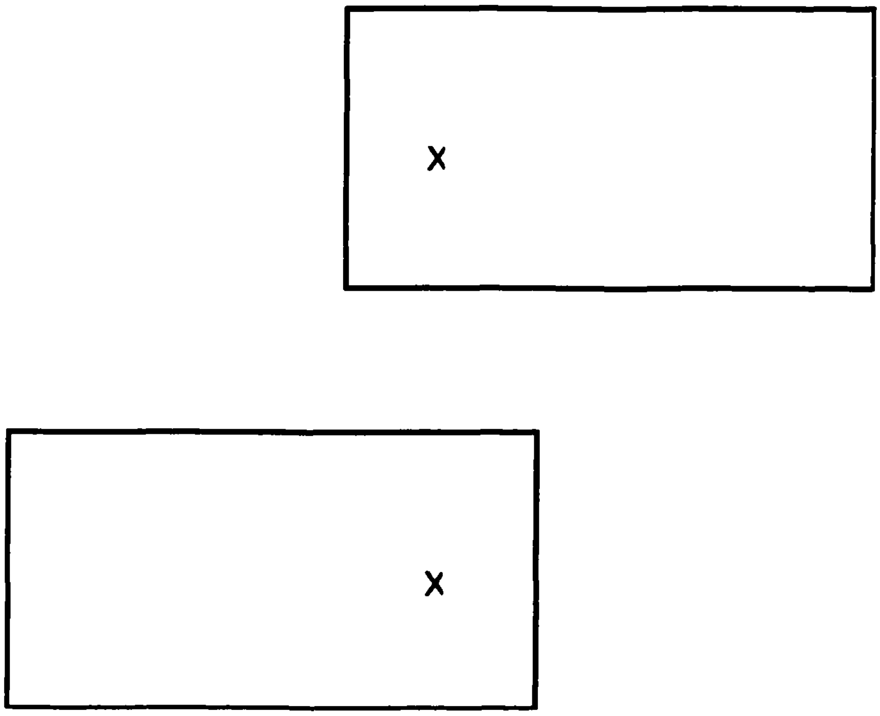


Figure 4. The Ebbinghaus circles illusion. The two target circles are identical in size, but the target surrounded by smaller circles (top) appears larger than it really is, and the target surrounded by larger circles (bottom) appears smaller than it really is.

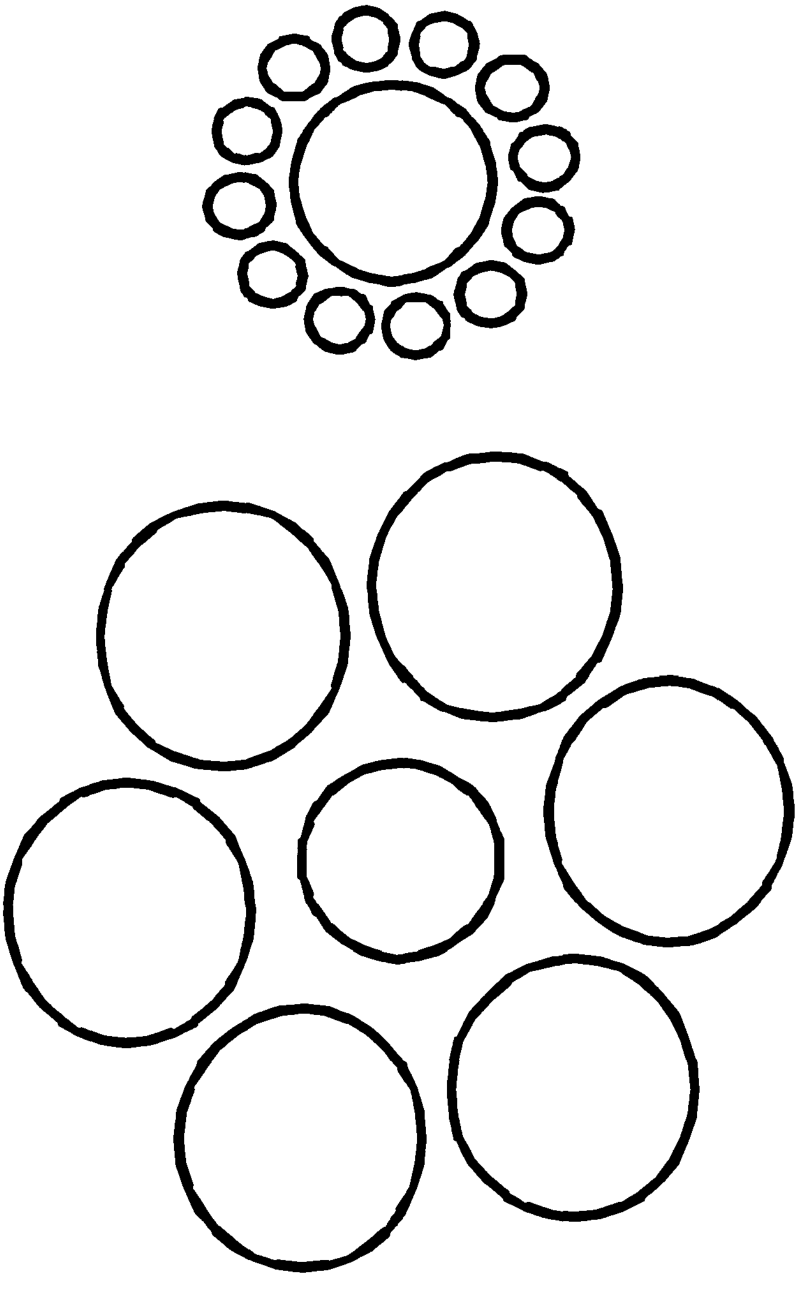


Figure 5. The Muller-Lyer illusion. The two vertical lines are of equal length, but the vertical line on the left (with the attached fins pointing inwards) appears shorter than the vertical line on the right (with the attached fins pointing outwards).

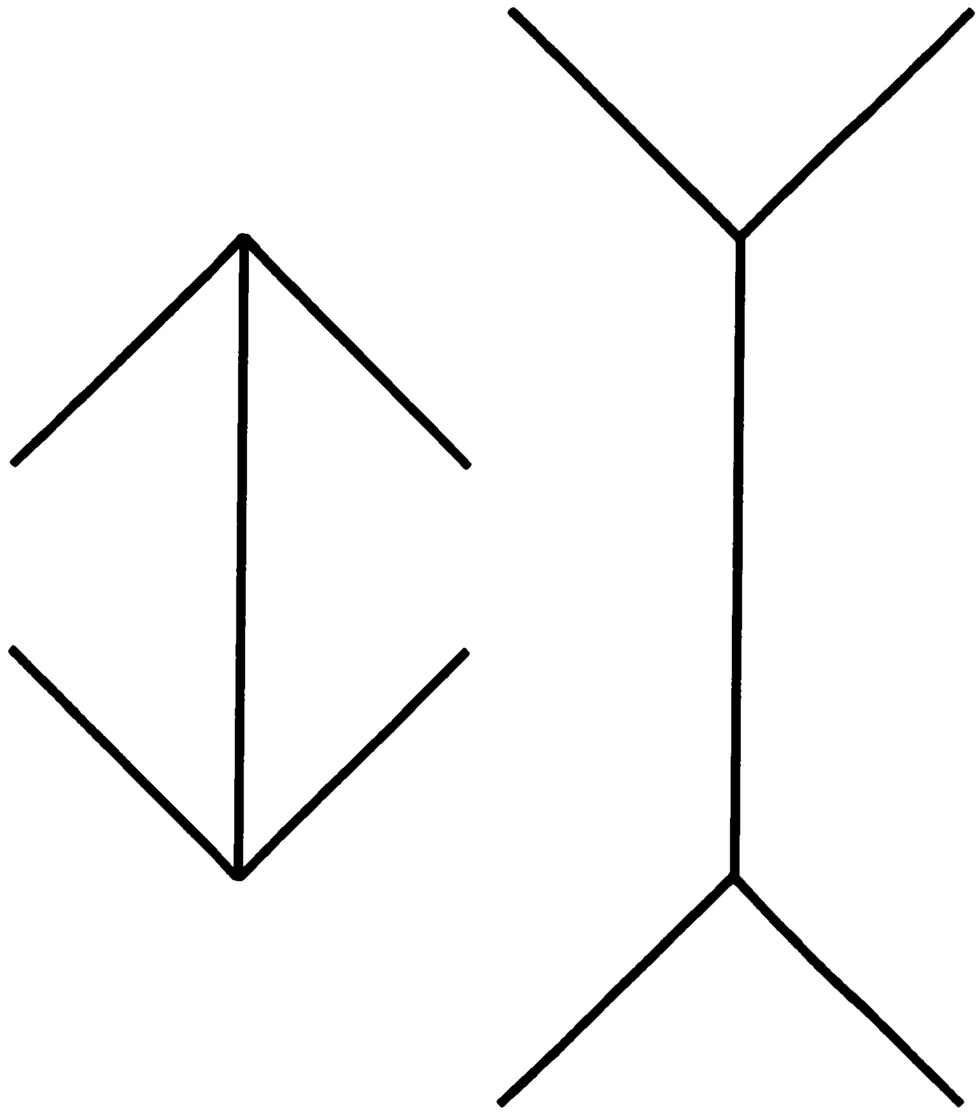


Figure 6. The orientation illusion used in Glover & Dixon (2001a, in press a, in press b), and in Experiment 1 here. On the left, the grating is oriented at +10 ° clockwise; on the right, the grating is oriented at –10° clockwise. Both bars are drawn vertical, but each appears to be slightly misoriented in the direction opposite to that of the background grating.

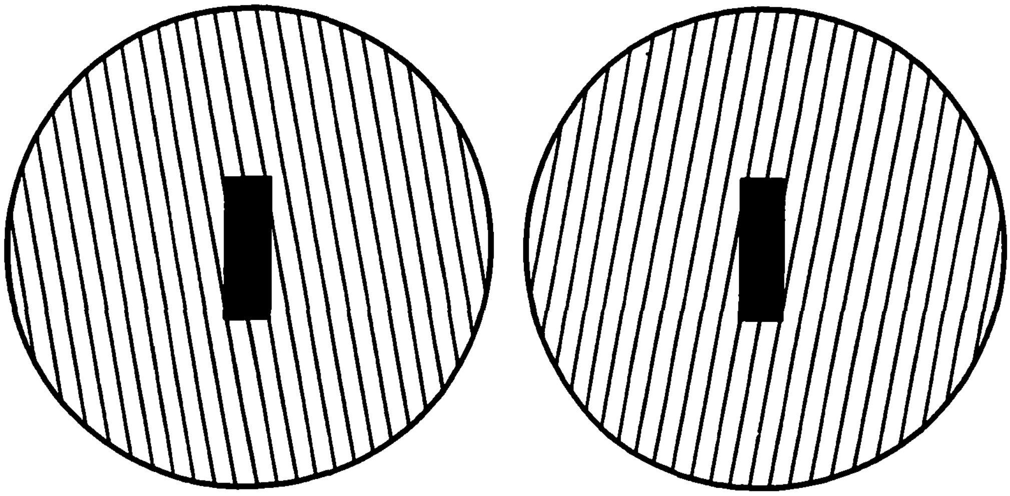


Figure 7. A single distractor size-contrast illusion. The two identical targets are on the right side of each pairing. The target situated next to a large distractor (top) appears smaller than the target situated next to a small distractor (bottom).

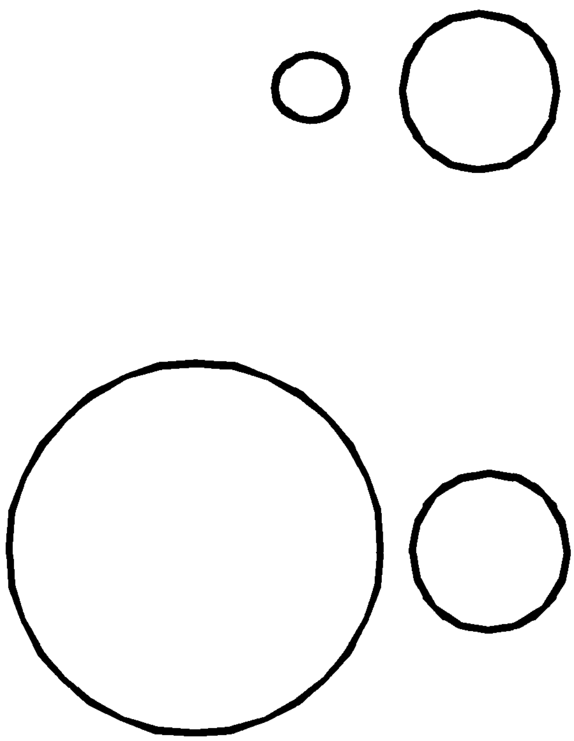


Figure 8. Summary of the design of the two experiments. Given are examples of the control (top), early grating shift (middle), and late grating shift (bottom) conditions.

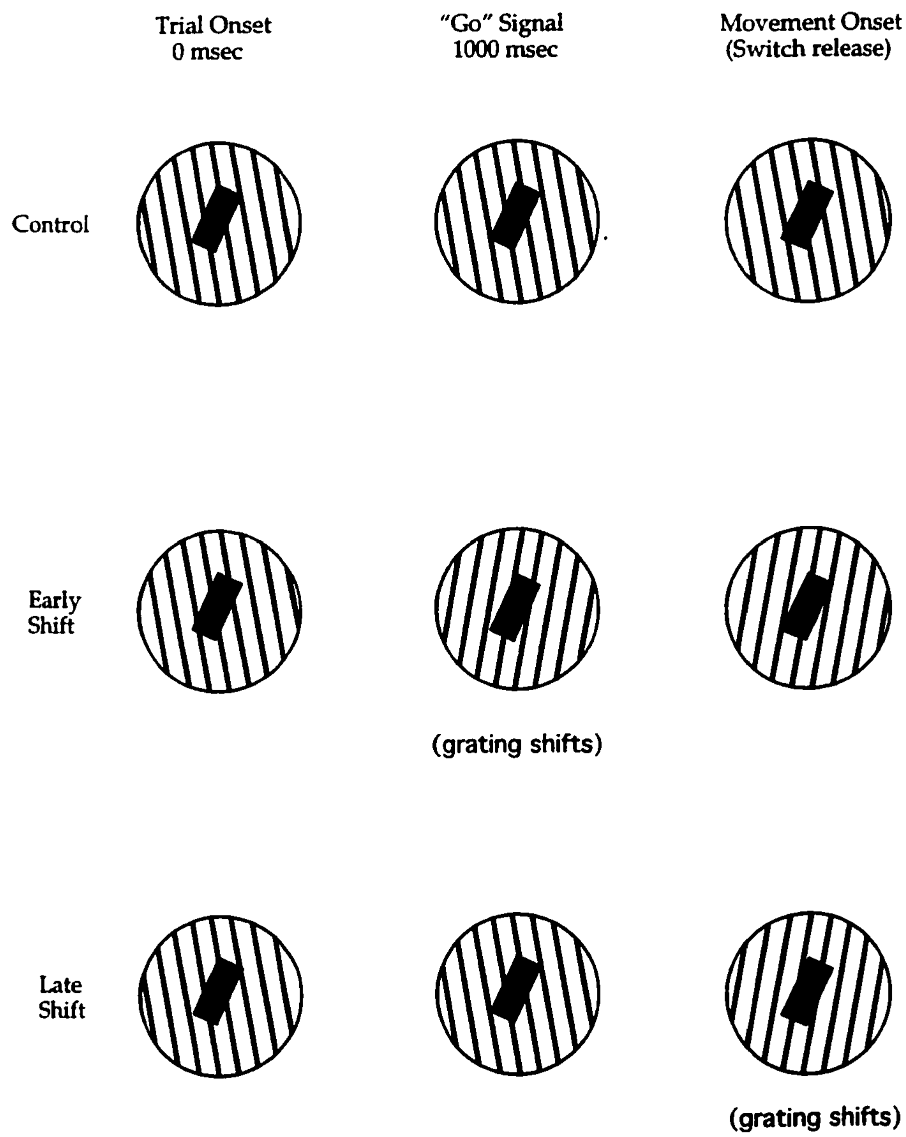


Figure 9. Experiment 1: Hand orientation as a function of bar orientation for each 10% of reach duration.

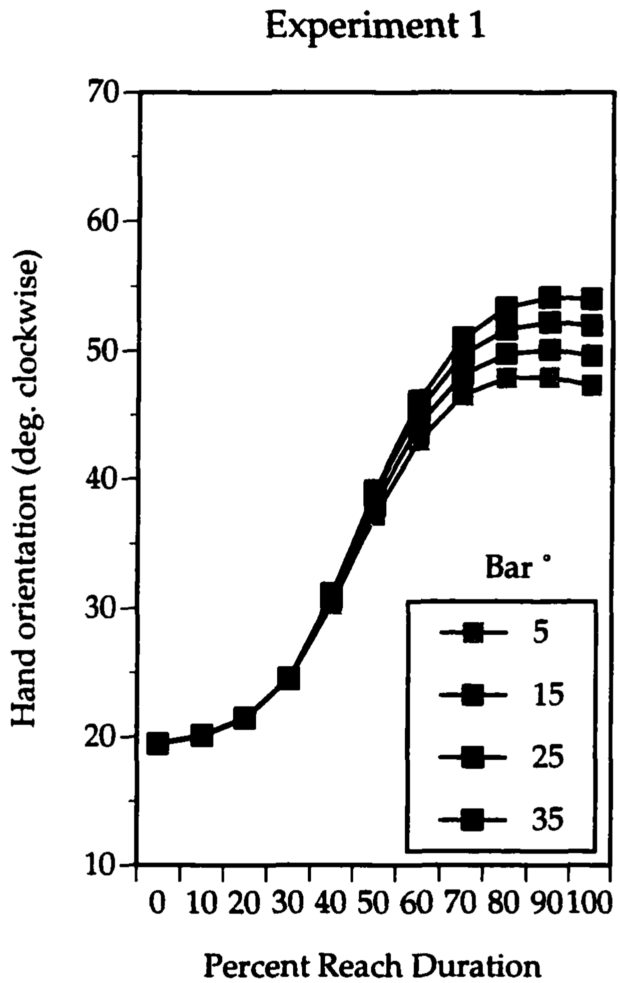


Figure 10. Experiment 1: Slope of the dependence of hand orientation on bar orientation for each 10% of reach duration.

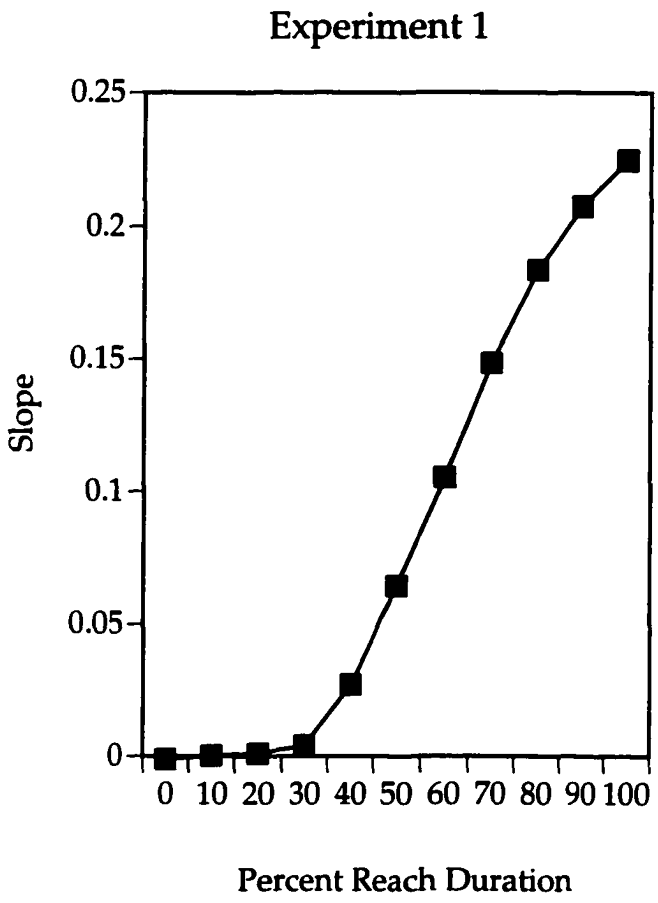


Figure 11. Experiment 1: Scaled illusion effect on hand orientation over time for each of the control, early grating shift, and late grating shift conditions for times from 40% to 100% of reach duration. Note that positive numbers indicate an illusion effect relative to the *initial* orientation of the grating on each trial. Error bars represent standard errors of the means.

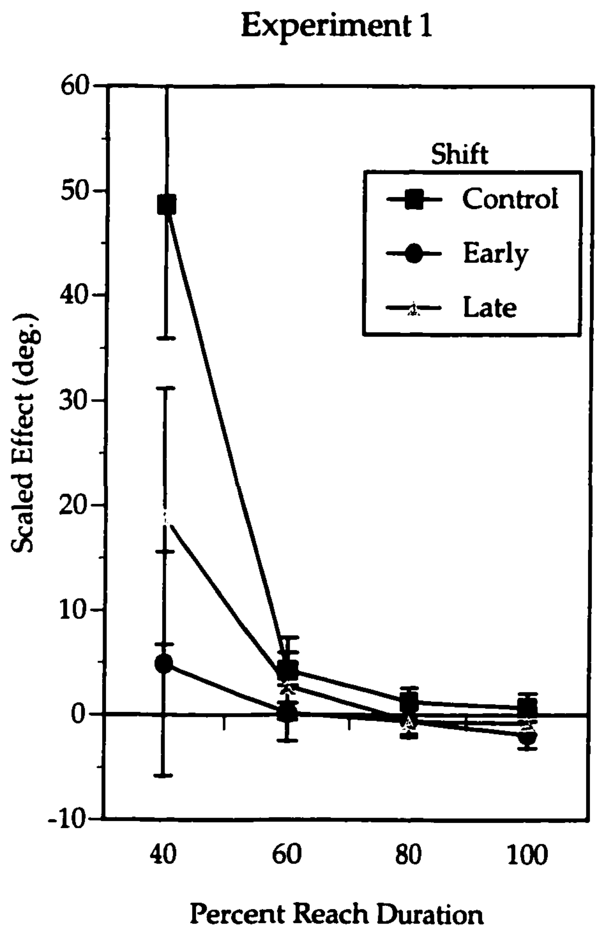


Figure 12. Experiment 1: Raw illusion effect on hand orientation over time for each of the control, early grating shift, and late grating shift conditions for times from 20% to 100% of reach duration. Error bars represent standard errors of the means.

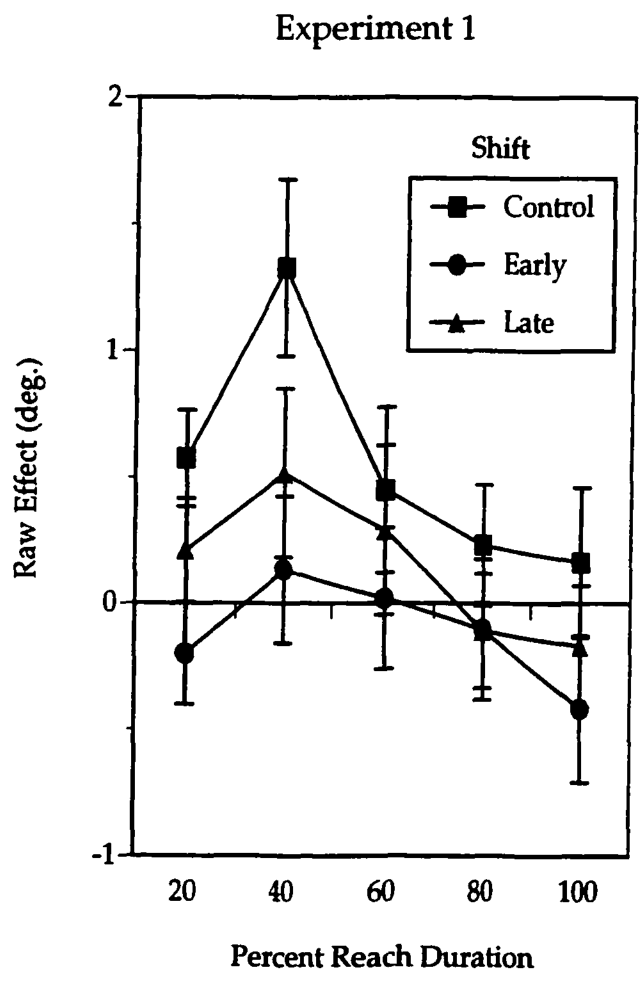


Figure 13. Experiment 1: Reaction times for each bar orientation by grating shift condition in the −10° grating (left) and +10° grating (right) conditions. Error bars represent standard errors of the mean.

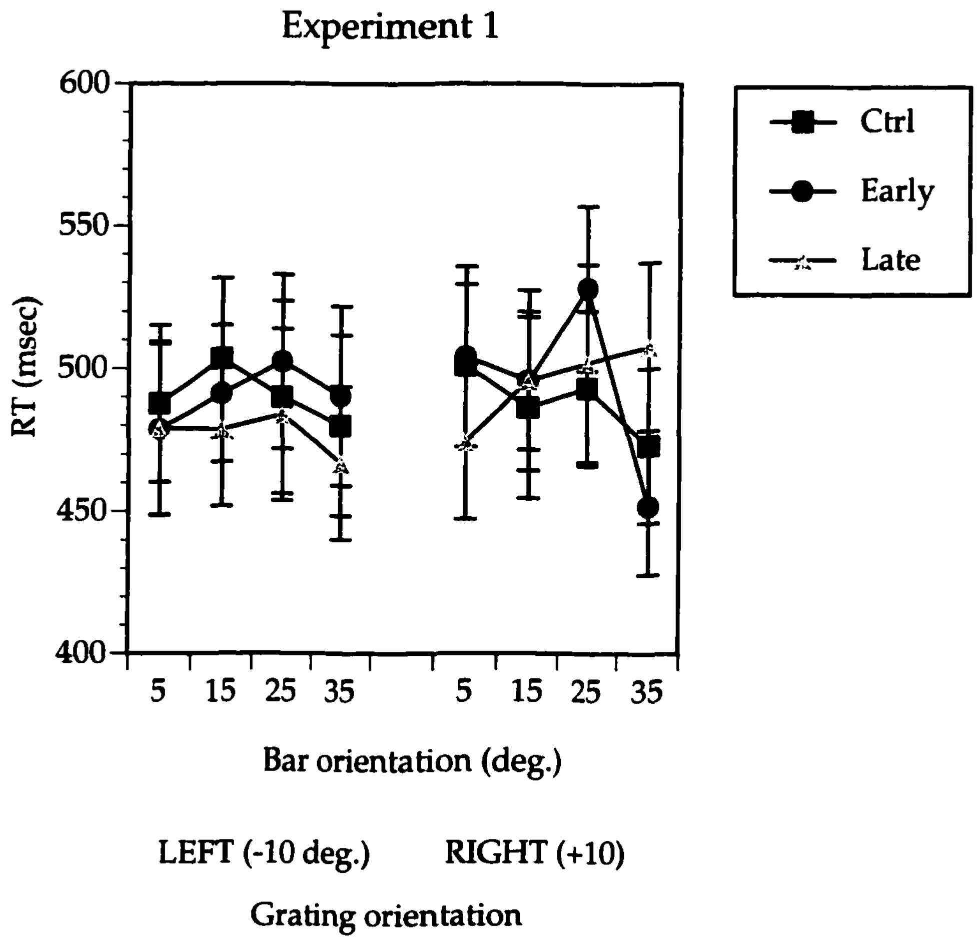


Figure 14. Experiment 1: Movement times for each bar orientation by grating shift condition in the –10° grating (left) and +10° grating (right) conditions). Error bars represent standard errors of the mean.

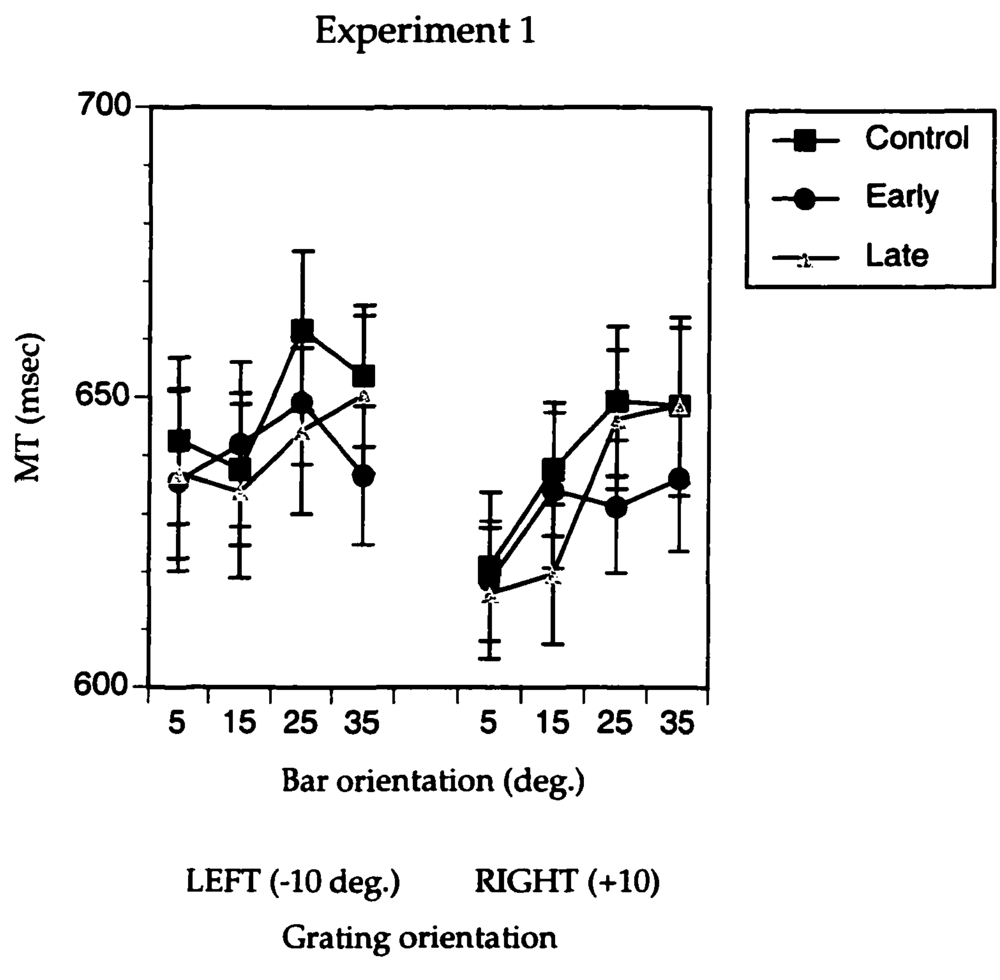
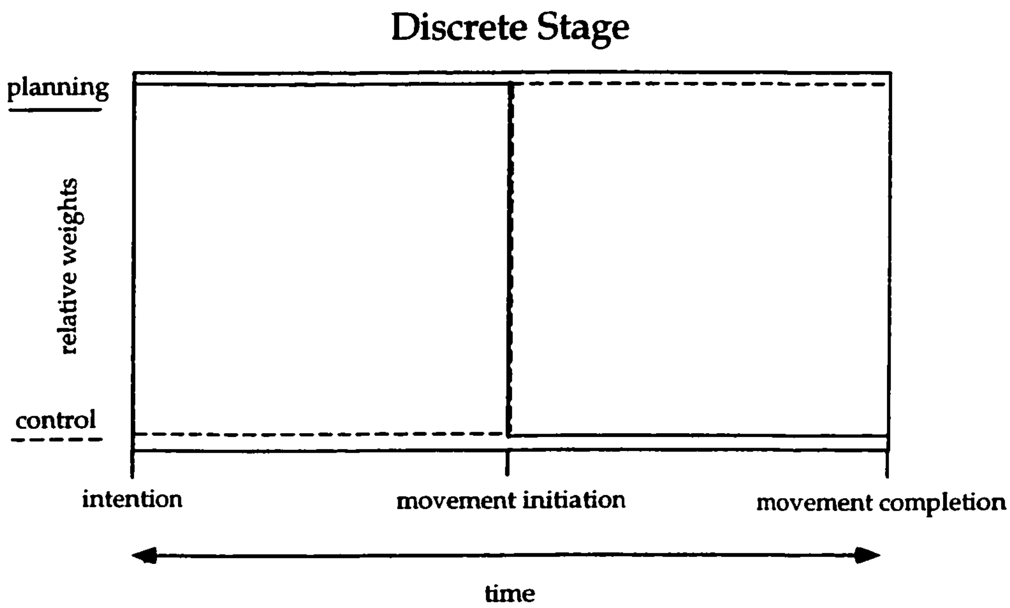


Figure 15. Schematic of the two versions of the planning/control model. On the top is the original, "discrete stage" version, on the bottom is the "continuum" version.



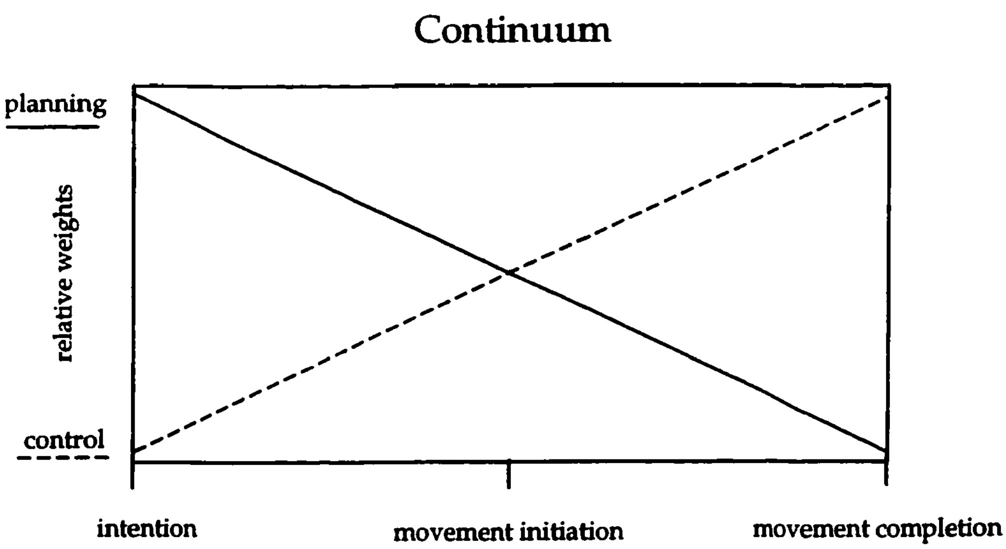


Figure 16. Examples of the stimuli used in Experiment 2. The gratings are identical to those used in Experiment 1, but the bar has now been replaced with a two-dimensional depiction of the same dimensions. The illusion still operates on these depictions.

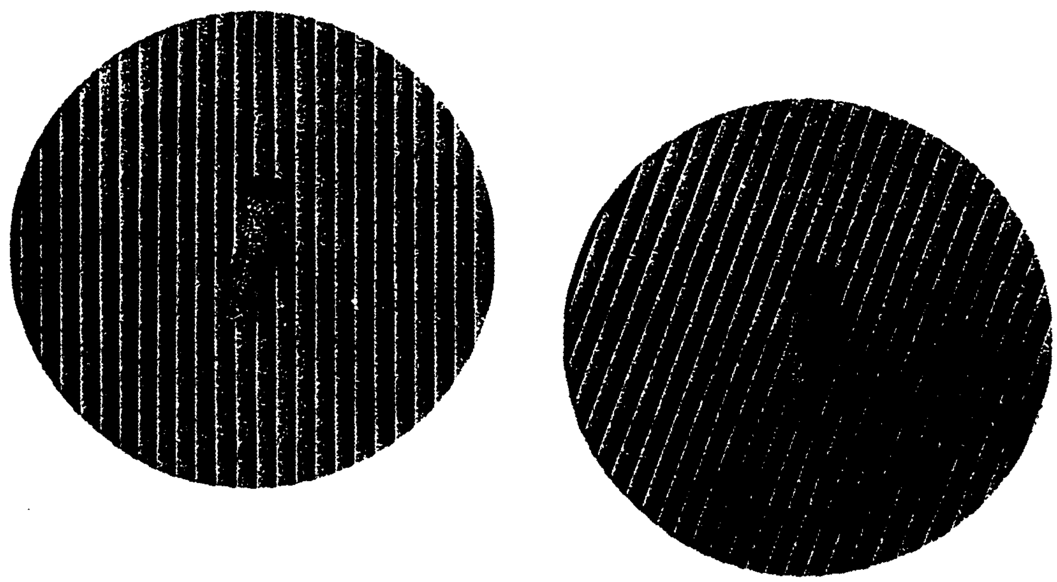


Figure 17. Experiment 2: Hand orientation as a function of bar orientation for each 10% of reach duration.

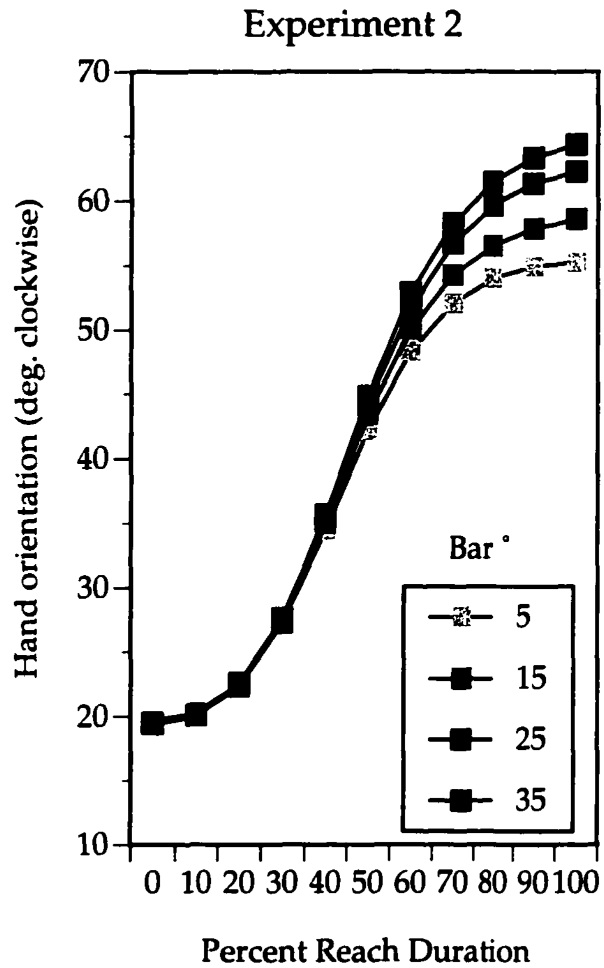


Figure 18. Experiment 2: Slope of the dependence of hand orientation on bar orientation for each 10% of reach duration.

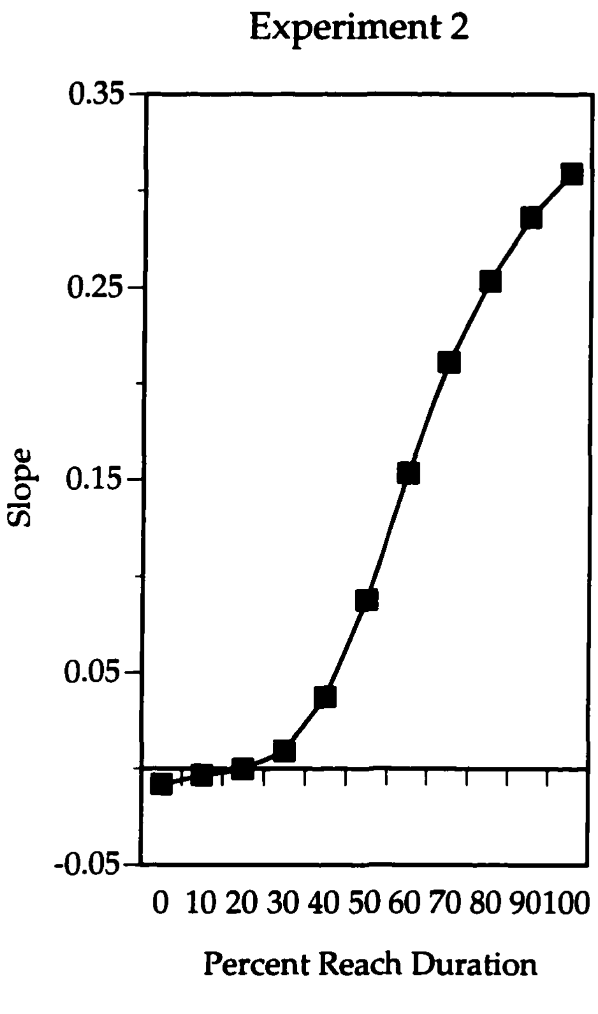


Figure 19. Experiment 2: Scaled illusion effect on hand orientation over time for each of the control, early grating shift, and late grating shift conditions for times from 40% to 100% of reach duration. Note that positive numbers indicate an illusion effect relative to the *initial* orientation of the grating on each trial. Error bars represent standard errors of the means.

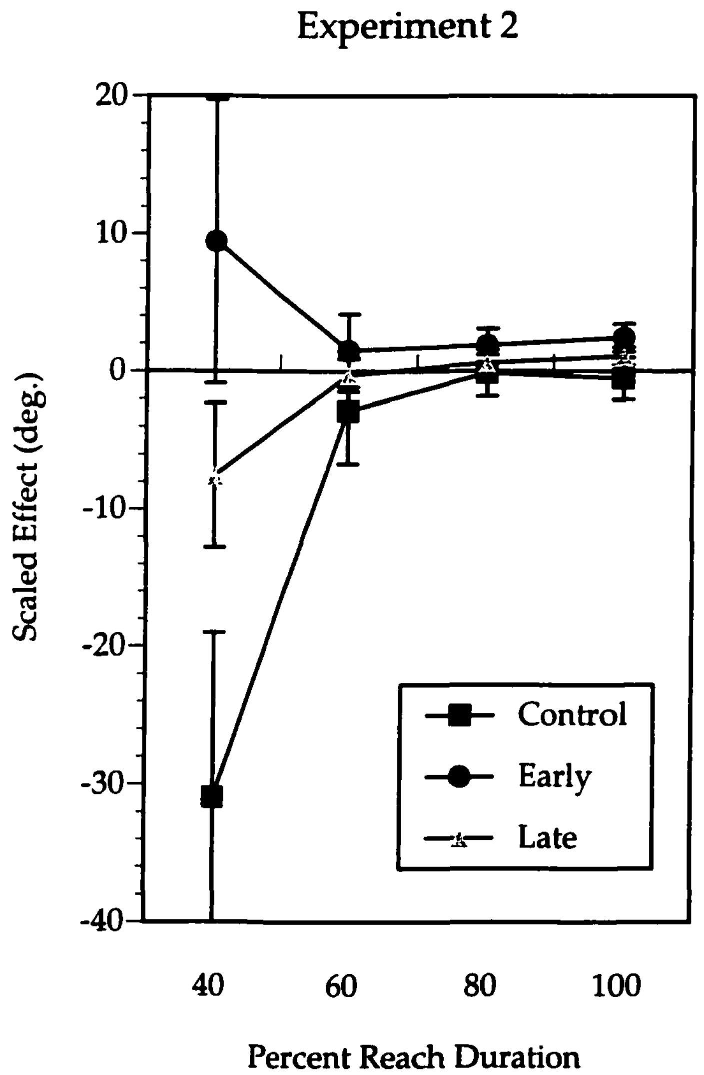


Figure 20. Experiment 2: Raw illusion effect on hand orientation over time for each of the control, early grating shift, and late grating shift conditions for times from 20% to 100% of reach duration. Error bars represent standard errors of the means.

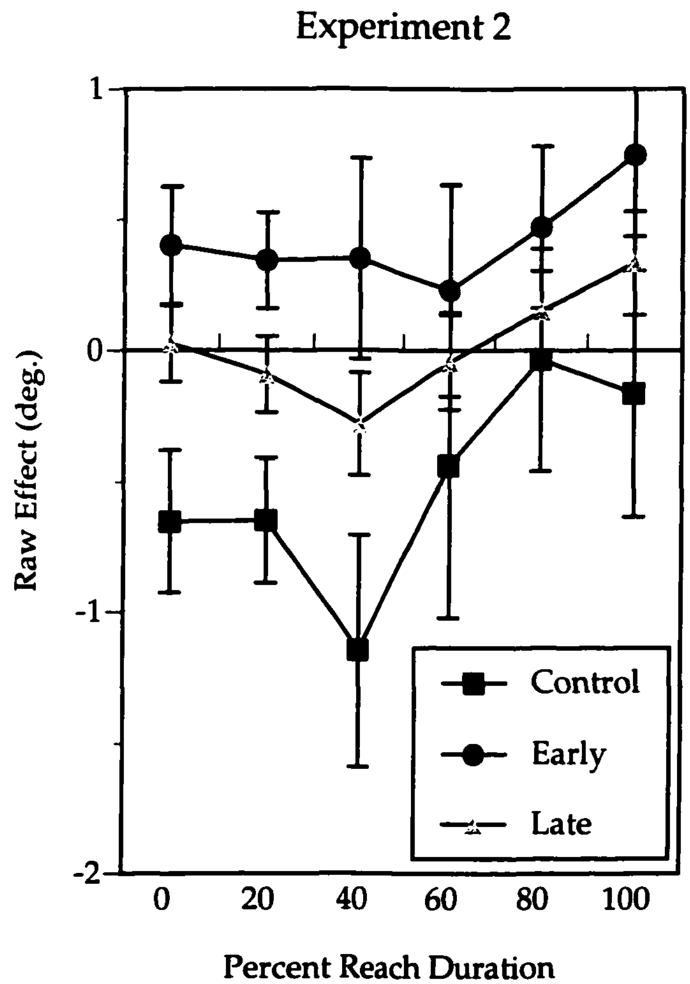


Figure 21. Experiment 2: Reaction times for each bar orientation by grating shift condition in the −10° grating (left) and +10° grating (right) conditions. Error bars represent standard errors of the means.

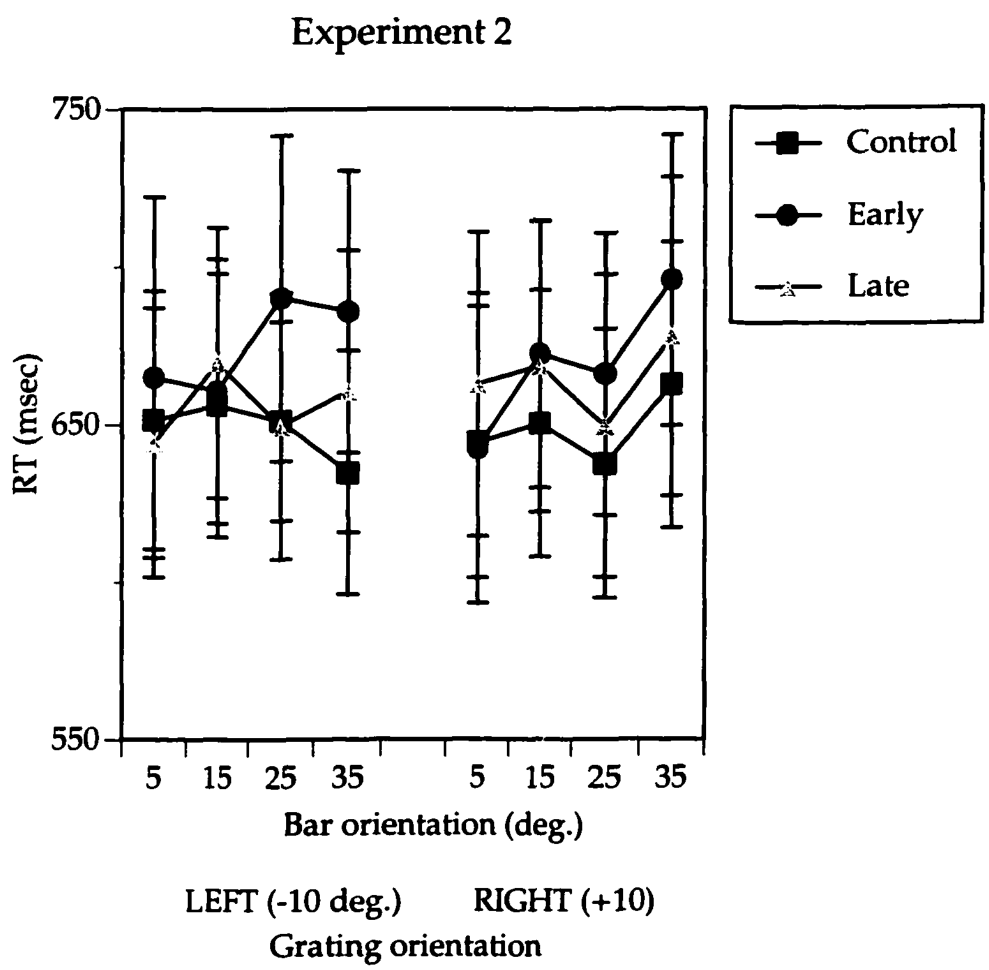
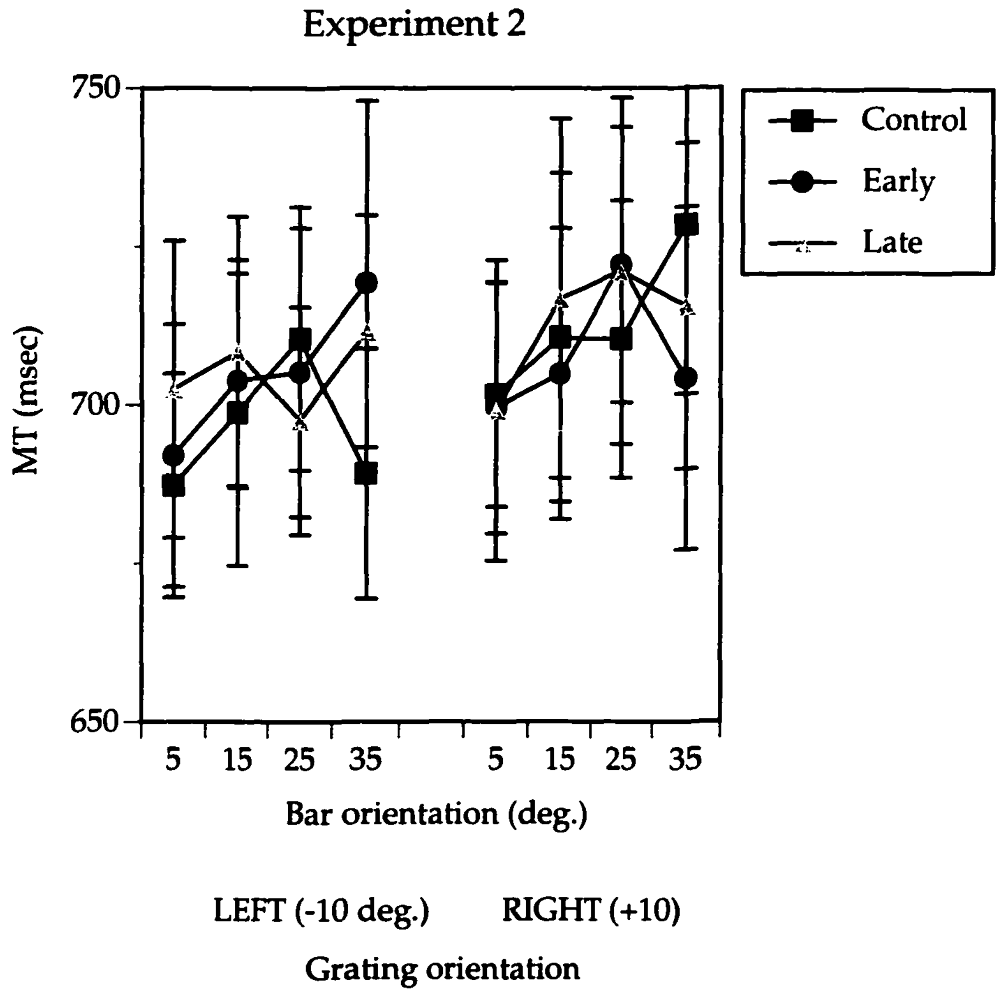


Figure 22. Experiment 2: Movement times for each bar orientation by grating shift condition in the -10° grating (left) and +10° grating (right) conditions). Error bars represent standard errors of the means.



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