



Review

Transforming vision into action

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ABSTRACT

Traditionally, research on vision focused on its role in perception and our cognitive life. Except for the study of eye movements, which have been regarded as an information-seeking adjunct to visual perception, little attention was paid to the way in which vision is used to control our actions, particularly the movements of our hands and limbs. Over the last 25 years all of that has changed. Researchers are now actively investigating the way in which vision is used to control a broad range of complex goal-directed action – and are exploring the neural substrates of that control. A new model of the functional organization of the visual pathways in the primate cerebral cortex has emerged, one that posits a division of labor between vision-for-action (the dorsal stream) and vision-for-perception (the ventral stream). In this review, I examine some of the seminal work on the role of vision in the control of manual prehension and on the visual cues that play a critical role in this important human skill. I then review the key evidence for the perception–action model, particularly with reference to the role of the dorsal stream in the control of manual prehension, touching on recent work that both reinforces and challenges this account of the organization of the visual system.

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Our brain is an organ of action that is directed toward practical tasks.

Santiago Ramón y Cajal (1897).

1. Introduction

In most people's minds, including the minds of many philosophers and scientists, vision is identified with visual perception. The critical role that vision plays in the planning and control of movements is largely ignored. Twenty-five years ago this view was prevalent even amongst those researchers who were studying vision and the organization of the visual pathways. In a 1983 book chapter entitled *Vision as a Sensorimotor System*, I ventured the opinion that “most contemporary theories of perception share with Descartes the view that the function of the visual system is to provide us with an internal representation of the outside world and the objects and events within it... a point of view [that] has resulted in a theoretical stance and a methodological tradition... that has limited our understanding of how the neural pathways comprising the visual system are organized” (Goodale, 1983). I still believe that this was an accurate observation of the mindset of most of the research community studying vision at that time. In

the late 1970s and early 1980s, vision researchers were trying to figure out how the internal representation of the outside world was constructed – not only from the rapidly changing information dancing across the retina but also from the rich memories of past visual experiences. Thus, for the most part, theoretical debates were centered on the relative contributions of these bottom-up and top-down sources of information. Theorists with a strong physiological orientation, like Marr (1975, 1976) emphasized a bottom-up analysis in which early visual processing was thought to play the major role in the construction of the percept. More cognitively oriented theorists, like Gregory (1970), favoured a top-down model in which “the retinal image does little more than select the relevant stored data.” Other theorists were somewhere in between – and many psychophysicists adopted a largely atheoretical stance with respect to this issue. But whatever the particular articulation of the underlying processes might have been, for most vision researchers at that time, vision was identified with visual perception – and its direct role in the control of movement was essentially ignored.

One reason why researchers were stuck on the idea of vision as perception is that it resonates so remarkably well with phenomenology. Our perception of the world beyond our bodies is such a compelling experience that it seems obvious that this must be the main, if not the exclusive, reason vision evolved. But as I have argued elsewhere (Goodale, 1983, 1996), vision began not as a system for perceiving the world, but as a system for the distal control of movement. Yet with the notable exception of eye movements, which have typically been regarded as an information-seeking

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adjunct to visual perception, little attention was paid to the way in which vision is used to control our actions, particularly the movements of our hands and limbs. Indeed, amongst vision researchers at the time, there was little acknowledgment of the fact that the functional organization of the visual system (like the rest of the brain) has been ultimately shaped by the role it plays in the control of movement.

A complete account of the visual system requires as much attention to the organization of motor output as to the processing of sensory input. But 25 years ago, a sharp division was drawn between sensory and motor systems in classical psychology and physiology. The chapters in undergraduate textbooks dealing with vision were quite separate from those discussing how the motor system works. Similar divisions existed in scientific societies, journals, and symposia – and sometimes within university departments. It is true that one could find the occasional book that talked about ‘sensorimotor integration’ and the occasional meeting that brought together researchers from both fields but, in general, sensory and motor systems were two solitudes. Instead, the prevalent belief was that the visual machinery of the brain is dedicated to constructing an internal model of the external world, a kind of simulacrum of the real thing that serves as a perceptual foundation for all visually-driven thought and action.

Although the same state of affairs still exists to some extent today, particularly within hardcore psychophysics, considerable progress has been made both in specifying the visual information that is used to control skilled movements of the hands and limbs and in identifying the neural pathways that mediate this control. In short, there has been a real revolution in the way in which vision research is conducted and disseminated. In this review, I attempt to trace the lines of research over the last 25 years that have provided fundamental insights into the role of vision in the programming and control of action, and have made the study of vision-for-action a vibrant part of the vision research enterprise. I will focus largely on the visual control of manual prehension (reach-to-grasp movements) while acknowledging that enormous strides have also been made in the study of the visual control of locomotion (for review of the latter, see Patla, 1997; Warren & Fajen, 2004).

I begin by introducing research on the control of grasping and the visual cues that play a critical role in that control. I then move on to a discussion of work on the neural substrates of this control, offering a speculative account of the selection forces that have shaped the organization of the visual pathways in the primate brain, and reviewing the evidence for a duplex model of visual function that contrasts vision-for-action with vision-for-perception. I will focus particularly on the role of vision-for-action (and its neural substrates) in the control of reaching and grasping. Finally, I touch on some of the most recent work that both reinforces and challenges the perception–action model – again focusing on the way in which this model can account for the goal selection, motor planning, and online control in the context of visually guided reaching and grasping.

2. The visual control of manual prehension

Human beings are capable of reaching out and grasping objects with great dexterity, and vision clearly plays a critical role in this important skill. Consider what happens when we perform the deceptively simple act of reaching out and picking up our morning cup of coffee. After identifying our cup amongst all the other objects on the table, we begin to reach out with our hand towards the cup, choosing a trajectory that avoids the box of cereal and the glass of orange juice. At the same time, our fingers begin to conform to the shape of the cup’s handle well before we make con-

tact with the cup. As our fingers curl around the handle, the initial forces we generate to lift the cup are finely tuned to its anticipated weight – and to our predictions about the friction coefficients and compliance of the material from which the cup is made. Over the last 25 years, researchers have provided important insights into the nature of the visual information that is used to perform actions such as these – and how our brains transform that information into the appropriate motor outputs for successful performance.

Pioneering work by Jeannerod (1981, 1984, 1986, 1988) provided evidence for the idea that the reaching component of a grasping movement is relatively independent from the formation of the grip itself. Using high-speed movie film, Jeannerod (1981) found that when a person reached out to grasp an object, the size of the opening between the fingers and thumb was positively correlated with the size of the object. This relationship could be clearly seen at the point of maximum grip aperture, which is achieved well before contact is made with the object. Jeannerod went on to show that unexpected changes in object size led to corresponding changes in shaping of the hand. Yet despite these changes in grip formation, the resultant velocity profiles for the reach remained unchanged by the experimental manipulations of object size. But when the goal objects were placed at different distances from the grasping hand, the peak velocity of the reach increased for movements of greater amplitude. Jeannerod (1981) concluded from these findings that the reach and grip components of a prehension movement are generated by independent visuomotor channels, albeit ones that are temporally coupled.¹

According to Jeannerod’s (1981) account, the kinematics of the reach component of a grasping movement are largely determined by visual cues that are extrinsic to the goal object, such as its distance and location with respect to the grasping hand. In contrast, the kinematics of the grasp component reflect the size, shape, and other intrinsic properties of the goal object. This so-called ‘dual-channel’ hypothesis has become the dominant model of human prehension. Even though later studies (e.g., Chieffi & Gentilucci, 1993; Jakobson & Goodale, 1991) went on to show that the visual control of the reach and grip components may be more integrated than Jeannerod originally proposed, there is broad consensus that the two components show a good deal of functional independence and (as I will argue later) are mediated by relatively independent visuomotor circuits in both the posterior parietal and premotor cortex.

The most direct challenge to Jeannerod’s (1981) dual-channel hypothesis has come from Smeets and Brenner (1999, 2001, 2009), who have proposed instead that the movements of each of the digits that constitute a grasping movement are programmed and controlled independently. Thus, in the execution of a precision grip the index finger is directed to one side of the object and the thumb to the other. The apparent scaling of grip aperture to object size is nothing more than an emergent property of the fact that the two digits are moving towards their respective end points. Moreover, because both digits are attached to the same limb, the so-called transport component is simply the joint movement of the two digits towards the object. Simply put, it is location rather than size that drives grasping – and there is no need to separate grasping into transport and grip components that are each sensitive to different visual cues.

Although Smeets and Brenner’s (1999, 2001) “double-pointing” hypothesis has the virtue of being parsimonious, it is not without its critics (e.g., Dubrowski, Bock, Carnahan, & Jungling, 2002; Mon-Williams & McIntosh, 2000; Mon-Williams & Tresilian, 2001; van de Kamp & Zaal, 2007). Van de Kamp and Zaal, for exam-

¹ Several models of how the reach and grip components are temporally coupled have been proposed (e.g., Hu, Osu, Okada, Goodale, & Kawato, 2005; Mon-Williams & Tresilian, 2001; Vilaplana, Batlle, & Coronado, 2004).

ple, showed that when one side of an object was perturbed as the grasping hand moved towards it, the trajectories of both digits were adjusted in flight, a result that would not be predicted by Smeets and Brenner's model but one that is entirely consistent with Jeannerod's (1981) dual-channel hypothesis. Moreover, as we shall see later, the organization of the neural substrates of grasping as revealed by neuroimaging and neuropsychology can be more easily explained by the dual-channel than the double-pointing hypothesis.

Almost all the studies of grasping discussed above have used rather unnatural situations in which the goal object is the only object present in the workspace. In the real world, however, the workspace is usually cluttered with other objects, some of which could be potential obstacles for a goal-directed movement. Nevertheless, our hand and arm rarely collide with these objects when we reach out and grasp the target. The simplicity of this behavior hides what must be a sophisticated obstacle avoidance system that encodes possible obstructions to reaching and grasping movements and incorporates this information into motor plans. The few investigations that have examined obstacle avoidance have revealed an efficient system that is capable of altering the spatial and temporal trajectories of goal-directed reaching and grasping movements to avoid other objects in the workspace in a fluid manner (e.g., Castiello, 2001; Jackson, Jackson, & Rosicky, 1995; Tresilian, 1998; Vaughan, Rosenbaum, & Meulenbroek, 2001). There has been some debate as to whether the non-goal objects are always being treated as obstacles or whether they are treated as potential targets for action (e.g., Tipper, Howard, & Jackson, 1997) or even as frames of reference for the control of the movement (e.g., Diedrichsen, Werner, Schmidt, & Trommershauser, 2004; Obhi & Goodale, 2005). By positioning non-goal objects in different locations in the workspace with respect to the target, however, it is possible to show that most often these objects are being treated as obstacles and that when individuals reach out for the goal the trial-to-trial adjustments of their trajectories are remarkably sensitive to the position of obstacles both in depth and in the horizontal plane, as well as to their height (Chapman & Goodale, 2008, 2010). Moreover, the system behaves conservatively, moving the trajectory of the hand and arm away from non-target objects, even when those objects are unlikely to interfere with the target-directed movement.

3. Visuomotor psychophysics of grasping

Part of the reason for the rapid growth of research into the visual control of manual prehension has been the development of reliable technologies for recording hand and limb movements in three dimensions. Expensive film was replaced with inexpensive videotape in the 1970s – and over the last 25 years, the use of accurate recording devices based on active or passive infra-red markers, ultrasound, magnetism, instrumented gloves, and an array of other technologies has grown enormously. This has made it possible for the development of what might be termed 'visuomotor psychophysics' in which investigators are exploring the different visual cues that are used in the programming and control of grasping.

One of the most powerful set of cues used by the visuomotor system in mediating grasping comes from binocular vision (e.g., Servos, Goodale, & Jakobson, 1992). Even though binocular vision has been studied by scientists and philosophers since the time of Euclid (for review, see Howard & Rogers, 1995), the vast majority of this work has concentrated on perceptual judgements about the visual world and has ignored its role in the planning and execution of skilled movement. One prominent exception to this has been research on binocular vision in lower animals, particularly in invertebrates and amphibia, where the role of binocular vision in the control of prey-catching and other species-specific behavior

has been studied (e.g., Collett & Harkness, 1982; Collett, Udin, & Finch, 1987; Corrette, 1990; Kral, Vernik, & Devetak, 2000). In these studies, investigators have typically studied the movements made by these animals while the availability of binocular cues and other sources of visual information are manipulated. As it turns out, when the same approach is taken to the study of the visual cues used in the programming and control of reaching and grasping in humans, binocular cues emerge as being the most important.

Several studies have shown that covering one eye has clear detrimental effects on grasping (e.g., Keefe & Watt, 2009; Loftus, Servos, Goodale, Mendarozqueta, & Mon-Williams, 2004; Melmoth & Grant, 2006; Servos et al., 1992; Watt & Bradshaw, 2000). People reach more slowly, show longer periods of deceleration and execute more online adjustments of both their trajectory and their grip during the closing phase of the grasp. Not surprisingly, then, adults with stereo-deficiencies from amblyopia have been shown to exhibit slower and less accurate grasping movements (Melmoth, Finlay, Morgan, & Grant, 2009). Interestingly, however, individuals who have lost an eye are as quick to initiate their reaching movements as normally-sighted individuals who are using both eyes. In fact, when grasping, the one-eyed patients appear to be making use of retinal motion cues generated by exaggerated head movements (Marotta, Perrot, Servos, Nicolle, & Goodale, 1995). The use of these self-generated motion cues appears to be learned: the longer the time between loss of the eye and testing, the more likely it is that these individuals will make unusually large vertical and lateral head movements during the execution of the grasp (Marotta, Perrot, Nicolle, & Goodale, 1995).

Computation of the required distance for the grasp has been shown to depend more on vergence than on retinal disparity cues whereas the scaling of the grasping movement and the final placement of the fingers depends more on retinal disparity than on vergence (Melmoth, Storoni, Todd, Finlay, & Grant, 2007; Mon-Williams & Dijkerman, 1999). Similarly, motion parallax contributes more to the computation of reach distance than it does to the formation of the grasp, although motion parallax becomes important only when binocular cues are no longer available (Marotta, Kruyer, & Goodale, 1998; Watt & Bradshaw, 2003). [Parenthetically, it should be noted that the differential contributions that these cues make to the reach and grasp components respectively are much more consistent with Jeannerod's (1981) dual-channel hypothesis than they are with Smeets and Brenner's (1999) double-pointing account.] Of course, even when one eye is covered and the head immobilized, people are still able to reach out and grasp objects reasonably well, suggesting that static monocular cues can be used to program and control grasping movements. Marotta and Goodale (1998, 2001), for example, showed that pictorial cues, such as height in the visual scene and familiar size, can be exploited to program and control grasping – but this reliance on pictorial cues occurs only when binocular cues are not available. In other words, binocular information from vergence and/or retinal disparity typically overrides the contributions made by monocular pictorial cues.

The role of the shape and orientation of the goal object in determining the formation of the grasp is poorly understood. It is clear that the posture of the grasping hand is sensitive to these features (e.g., Cuijpers, Brenner, & Smeets, 2006; Cuijpers, Smeets, & Brenner, 2004; Goodale, Meenan, et al., 1994; van Bergen, van Swieten, Williams, & Mon-Williams, 2007) but there have been only a few systematic investigations of how information about object shape and orientation is used to configure the hand during the planning and execution of grasping movements (e.g. Cuijpers et al., 2004; Lee, Crabtree, Norman, & Bingham, 2008; Louw, Smeets, & Brenner, 2007; van Mierlo, Louw, Smeets, & Brenner, 2009).

But understanding the cues that are used to program and control a grasping movement is only part of the story. To reach

and grasp an object, one presumably has to direct one's attention to that object as well as to other objects in the workspace that could be potential obstacles or alternative goals. Research on the deployment of overt and covert attention in reaching and grasping tasks has accelerated over the last two decades, and it has become clear that when vision is unrestricted, people shift their gaze towards the goal object (e.g. Ballard, Hayhoe, Li, & Whitehead, 1992; Johansson, Westling, Bäckström, & Flanagan, 2001) and to those locations on the object where they intend to place their fingers, particularly the points on the object where more visual feedback is required to position the fingers properly (e.g. Binsted, Chua, Helsen, & Elliott, 2001; Brouwer, Franz, & Gegenfurtner, 2009). In cluttered workspaces, people also tend to direct their gaze obstacles that they might have to avoid (e.g. Johansson et al., 2001). Even when gaze is maintained elsewhere in the scene, there is evidence that attention is shifted covertly to the goal and is bound there until the movement is initiated (Deubel, Schneider, & Paprotta, 1998). In a persuasive account of the role of attention in reaching and grasping, Baldauf and Deubel (2010) have argued that the planning of a reach-to-grasp movement requires the formation of what they call an "attentional landscape" in which the locations of all the objects and features in the workspace that are relevant for the intended action are encoded. Interestingly, their model implies parallel rather than sequential deployment of attentional resources to multiple locations, a distinct departure from how attention is thought to operate in more perceptual-cognitive tasks.

Finally, and importantly for the ideas that I discuss later in this review, it should be noted that the way in which different visual cues are weighted for the control of skilled movements is typically quite different from the way they are weighted for perceptual judgments. For example, Knill (2005) found that participants gave significantly more weight to binocular compared to monocular cues when they were asked to place objects on a slanted surface in a virtual display compared to when they were required to make explicit judgements about the slant. Similarly, Servos, Carnahan, and Fedwick (2000) demonstrated that even though people relied much more on binocular than monocular cues when they grasped an object, their explicit judgements about the distance of the same object were no better under binocular than under monocular viewing conditions. These and other, even more dramatic dissociations that I review later, underscore the fundamental differences between how vision is used for action and for perceptual report. In the next section, I offer a speculative account of the origins of vision before moving on to discuss the neural organization of the pathways supporting vision-for-action on the one hand and vision-for-perception on the other – and how these different pathways contribute to the visual control of manual prehension.

4. The origins of visual systems (a speculation)

Photosynthetic bacteria will reverse direction when they encounter a decrease in the level of ambient illumination. Such photokinetic behavior keeps the bacteria in regions of the environment where an important resource, light, is available (Gould, 1982). To explain this behavior, it is not necessary to argue that the bacteria "see" the light or that, within their primitive cytoplasmic core, they have some sort of internal model of the outside world. All that is required is the postulation of a simple servomechanism linking light level to direction of locomotion. Of course, a mechanism of this sort, although driven by light, is far less complicated than the visual systems of multicellular organisms. But even in more complex organisms, such as vertebrates, much of vision can be understood entirely in terms of the distal control of movement without reference to experiential sight or any general purpose representation of the outside world.

In vertebrates, the visual control systems for different kinds of behavior have evolved as relatively independent neural systems (for review, see Goodale, 1996; Milner & Goodale, 2006). For example, in present-day amphibians, such as the frog, visually guided prey-catching and visually guided obstacle avoidance are separately mediated by different neural pathways that extend from the retina right through to the motor networks in the brainstem that produce the constituent movements (for review, see Ingle, 1991). The visual control of prey-catching depends on circuitry involving retinal projections to the optic tectum, while the visual control of locomotion around barriers depends on circuitry involving retinal projections to the pretectum (Ingle, 1973). In addition, the pretectum also appears to modulate the prey-catching networks in the optic tectum (Buxbaum-Conradi & Ewert, 1995; Ewert, 1989). Each of these retinal targets projects in turn to different configurations of premotor and motor nuclei of the brainstem and spinal cord. In fact, evidence from several decades of work in both frog and toad suggests that there are at least five distinct visuomotor modules, each responsible for a different kind of visually guided behavior and each having separate neural pathways from retina to motor nuclei (Ewert, 1987; Ingle, 1991; Saltzman, Zacharatos, & Gruberg, 2004). Much of the coordination amongst the different modules appears to be achieved by inhibition or competition (e.g., McConville & Laming, 2007). In fact, as more and more is learned about the functional architecture of the visuomotor modules in the amphibian brain, it is becoming increasingly clear that the interactions amongst them is extremely complex (Ewert et al., 2001) – but in no sense are the different patterns of motor output guided by a single general-purpose visual representation of the world. As it turns out, the evolution of separate but interacting visuomotor modules appears to be quite an efficient way of doing things, and over the last 25 years, this biological principle has been applied a number of times to the design of control systems for autonomous robots (e.g., Arbib & Liaw, 1995; Weitzenfeld, Arbib, & Alexander, 2002).

There is evidence that the same kind of visuomotor modularity found in the frog also exists in the mammalian and avian brain (for review, see Goodale, 1996 and Jäger, 1997). For example, lesions of the superior colliculus (the mammalian equivalent of the optic tectum in amphibians, reptiles, and birds) in a variety of mammals, including rats, hamsters, gerbils, cats, and monkeys, disrupt or dramatically reduce the animal's ability to orient to visual targets, particularly targets presented in the visual periphery (see review by Goodale and Milner (1982)). Conversely, stimulation of this structure, either electrically or pharmacologically, will often elicit contraversive movements of the eyes, head, limbs, and body that resemble normal orienting movements (see review by Dean, Redgrave, and Westby (1989)). In contrast, lesions of the pretectum have been shown to interfere with barrier avoidance, leaving orienting movements relatively intact (Goodale & Milner, 1982). This striking parallel in the functional organization of the subcortical visual systems of amphibians and mammals suggests that modularity in visuomotor control is an ancient (and presumably efficient) characteristic of vertebrate brains.

But although there is considerable evidence for visuomotor modularity in all classes of vertebrates, the very complexity of the day-to-day living in many mammals, particularly in higher primates, demands much more flexible circuitry. In monkeys (and thus presumably in humans as well), many of the visuomotor circuits in the midbrain and brainstem that are shared with simpler vertebrates appear to be modulated by more recently evolved control systems in the cerebral cortex (for review, see Goodale & Milner, 2004; Milner & Goodale, 2006). Having this layer of cortical control over the more ancient subcortical networks makes it possible for primates to have much more flexible visually guided behavior, such as the skilled control of reaching and grasping discussed

in the previous sections. But even so, the behavior of primates, particularly with their conspecifics, is so complicated and subtle, that direct sensory control of action is often not enough. To handle these complexities, ‘representational’ systems have emerged in the primate brain (and presumably in other mammals as well), from which internal models of the external world can be constructed. These representational systems allow primates such as ourselves to perceive a world beyond our bodies, to share that experience with other members of our species, and to plan a vast range of different actions with respect to objects and events that we have identified. This constellation of abilities is often identified with consciousness, particularly those aspects of consciousness that have to do with decision-making and metacognition. It is important to emphasize that the perceptual machinery that has evolved to do this is not linked directly to specific motor outputs, but instead accesses these outputs via cognitive systems that rely on memory representations, semantics, spatial reasoning, planning, and communication. In other words, there are a lot of cognitive ‘buffers’ between perceiving the world and acting on it, and the relationship between what is on the retina and the behavior of the organism cannot be understood without reference to other mental states, including those typically described as “conscious”. But once a particular course of action has been chosen, the actual *execution* of the constituent movements of that action are typically carried out by dedicated visuomotor modules not dissimilar in principle from those found in frogs and toads.

To summarize: vision in humans and other primates (and perhaps other animals as well) has two distinct but interacting functions: (1) the perception of objects and their relations, which provides a foundation for the organism’s cognitive life and its conscious experience of the world, and (2) the control of actions directed at (or with respect to) those objects, in which separate motor outputs are programmed and controlled online. These competing demands on vision have shaped the organization of the visual pathways in the primate brain, particularly within the visual areas of the cerebral cortex. As I discuss in the next section, it turns out that the brain areas that mediate the visual recognition of a goal object, such as a coffee cup, are functionally and anatomically distinct from those that program and control the grasping movements directed towards that cup.

5. Two visual streams: evidence from neurological patients

Nearly 30 years ago, Ungerleider and Mishkin (1982) proposed that the complex network of cortical visual projections emanating from primary visual cortex in the macaque monkey brain could be grouped into two relatively independent streams of visual processing: a ventral stream projecting to the inferotemporal cortex and a dorsal stream projecting to the posterior parietal cortex (see Fig. 1). According to their original proposal, the ventral stream plays the critical role in the identification and recognition of objects whereas the dorsal stream is responsible for localizing those objects in space. Over the next 10 years, this account of the functional differences between the two streams, often characterized as a distinction between ‘what’ vs. ‘where’, was to become one of the most familiar (and influential) ideas in cognitive neuroscience.

Much of the support for this idea came from work with monkeys. It was claimed, for example, that lesions of inferotemporal cortex in monkeys produced deficits in their ability to discriminate between objects on the basis of their visual features but did not affect their performance on a spatially demanding “landmark” task (Pohl, 1973; Ungerleider & Brody, 1977). Conversely, lesions of the posterior parietal cortex were said to produce performance deficits on the landmark task but not on the object discrimination task (for a critique of these studies, see Goodale, 1995; Milner &

Goodale, 2006). Although the evidence for Ungerleider and Mishkin’s (1982) proposal initially seemed quite compelling, accumulating evidence from a broad range of studies in both humans and monkeys began to force a re-interpretation of the division of labor between the two streams.

Some of the most telling evidence against the what vs. where distinction came from studies of neurological patients – particularly when one examines what happens when these patients make (or attempt to make) visually guided reaching and grasping movements. It had been known since the pioneering work of Bálint (1909) and Holmes (1918) that patients with damage to the posterior parietal cortex (in what is thought to be the human homolog of the dorsal stream) often have great difficulty reaching out and grasping objects under visual control (even though they have no difficulty touching different parts of their body indicated by the experimenter). Clinically, this deficit is known as optic ataxia. Holmes, a distinguished (and eloquent) English neurologist, characterized the mis-reaching that often accompanies damage to the posterior parietal cortex as symptomatic of a general failure of spatial vision (what he referred to as a ‘disturbance of visual orientation’). His persuasive account proved to be enormously influential and was echoed decades later in Ungerleider and Mishkin’s formulation of dorsal-stream function. But several other observations of the behavior of these patients suggest a very different interpretation. First, as can be seen in Fig. 2A, some (but not all) patients with damage to posterior parietal cortex not only fail to reach in the right direction but also fail to orient their hand and form their grasp appropriately (Goodale, Meenan, et al., 1994; Jakobson, Archibald, Carey, & Goodale, 1991; Perenin & Vighetto, 1983, 1988; Rondot, de Recondo, & Ribadeau Dumas, 1977). Second, as can again be seen in Fig. 2A, patients with optic ataxia are often able to describe the orientation, size, shape, and even the relative spatial location of the very objects they are unable to reach out and grasp correctly (Perenin & Vighetto, 1988). Third, in some patients the deficit is apparent in one hand but not the other (Perenin & Vighetto, 1988). In fact, Bálint’s original patient showed mis-reaching to visual (but not tactile) targets only when using his right hand; when he used his left hand, his visually guided reaches were relatively normal. And even when reaching is impaired whichever hand is used, some patients with optic ataxia are still able to direct their eyes accurately toward targets that they cannot accurately reach for (Ratcliff & Davies-Jones, 1972; Riddoch, 1935). Clearly, this pattern of deficits and spared abilities cannot be explained by appealing to an over-arching deficit in spatial vision. As Bálint himself recognized, the deficit is neither purely visual nor purely motor and is better characterized instead as a visuomotor problem. [One possible reason why Bálint’s ideas had so little impact on the Anglo-American neurological community – as opposed to Holmes’ visual disorientation hypothesis – is that Bálint’s (1909) paper was written in German and was not translated into English until 1995 (Bálint & Harvey, 1995)!.]

Over the last two decades, reports on the visual deficits (and spared visual functions) of patients with ventral-stream damage also began to challenge Ungerleider and Mishkin’s (1982) what vs. where hypothesis. Investigations of the visually driven behavior of one patient, known as DF, have been especially illuminating (Goodale, Milner, Jakobson, & Carey, 1991; Milner et al., 1991). DF, now in her early 50s, had the misfortune at age 34 to suffer irreversible brain damage as a result of near-asphyxiation by carbon monoxide. When she regained consciousness, it was apparent that DF’s visual system had been badly damaged from the hypoxia she had experienced. She was unable to recognize the faces of her relatives and friends or identify the visual form of common objects. DF could not tell the difference between even simple geometric shapes such as a square and a triangle. At the same time, she had no difficulty recognizing people from their voices or identifying

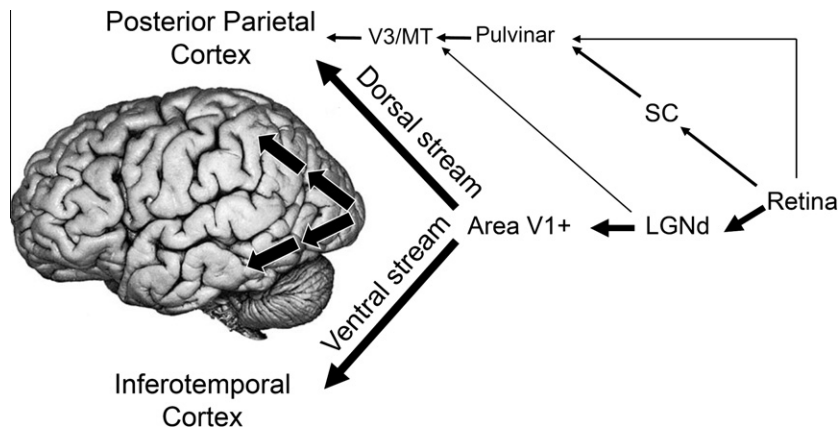


Fig. 1. The two streams of visual processing in human cerebral cortex. The retina sends projections to the dorsal part of the lateral geniculate nucleus (LGNd), which projects in turn to primary visual cortex. Within the cerebral cortex, the ventral stream arises from early visual areas (V1+) and projects to the inferotemporal cortex. The dorsal stream also arises from early visual areas but projects instead to the posterior parietal cortex. Recently, it has been shown that the posterior parietal cortex also receives visual input from the pulvinar via projections to MT (middle temporal area) and V3, as well as from the interlaminar layers of LGNd via projections to MT and V3. The pulvinar receives projections from both the retina and from the superior colliculus (SC). The approximate locations of the two streams are shown on a 3-D reconstruction of the pial surface of the brain. The two streams involve a series of complex interconnections that are not shown. Adapted from Goodale, M. A. and Westwood, D. A. (2004). An evolving view of duplex vision: separate but interacting cortical pathways for perception and action. *Current Opinion in Neurobiology*, 14, 203–211.

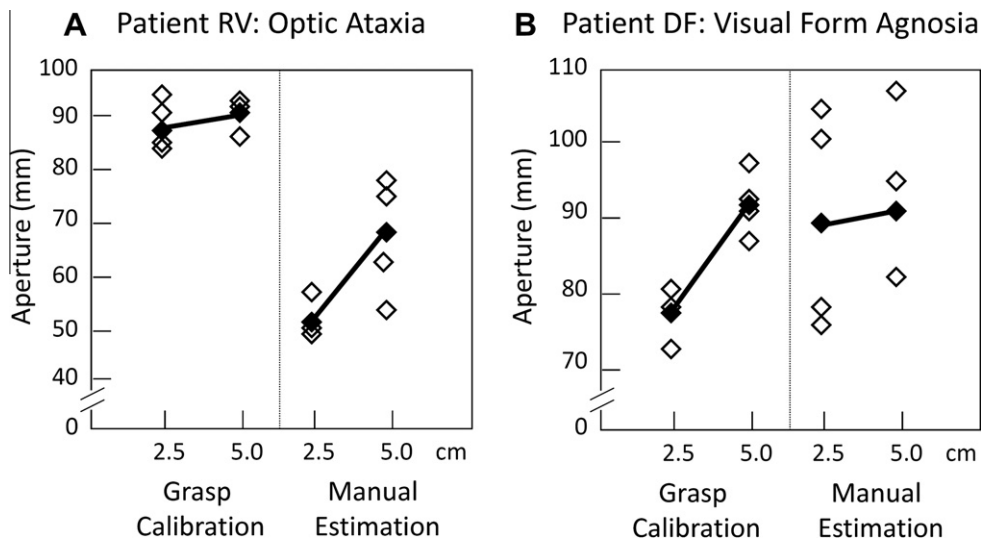


Fig. 2. Graphs showing the size of the aperture between the index finger and thumb during object-directed grasping and manual estimates of object width for RV, a patient with optic ataxia, and DF, a patient with visual form agnosia. Panel A shows that RV was able to indicate the size of the objects reasonably well (individual trials marked as open diamonds), but her maximum grip aperture in flight was not well-tuned. She simply opened her hand as wide as possible on every trial. In contrast, Panel B shows that DF showed excellent grip scaling, opening her hand wider for the 50 mm-wide object than for the 25-mm wide object. D.F.'s manual estimates of the width of the two objects, however, were grossly inaccurate and showed enormous variability from trial to trial.

objects placed in her hands; her perceptual problems appeared to be exclusively visual. DF still perceived motion and she could also distinguish amongst objects on the basis of their color and visual texture; it was the *form* of the objects that defeated her. Even today, more than 20 years after the accident, she remains quite unable to identify objects or drawings on the basis of their visual form. In fact, DF's deficit in form vision is so complete that she has great problems describing or discriminating the orientation or form of any visual contour, no matter how that contour is defined. Thus, she cannot identify shapes whose contours are defined by differences in luminance or color, or by differences in the direction of motion or the plane of depth. Nor can she recognize shapes that are defined by the similarity or proximity of individual elements of the visual array.

DF's basic deficit in form vision is not unique. Several other patients have been described in the literature, the most famous of which is probably Mr. S., who "was found stuporous on the

bathroom floor after having been exposed to leaking gas fumes while showering" (Benson & Greenberg, 1969). Like DF, Mr. S. had profound deficits in object and pattern recognition; he failed to recognize familiar faces, and was unable to identify or copy line drawings of common objects or even simple geometric shapes. When he was shown real objects, however, again like DF, he was sometimes able to make reasonable guesses at the object's identity by virtue of surface properties such as color, reflectance, and texture (Efron, 1969). Benson and Greenberg coined the term, visual form agnosia, to refer to the specific deficit in form vision shown by Mr. S. and DF.

Remarkably, however, even though DF can no longer discriminate between objects on the basis of their size, shape, and orientation she is able to scale her hand to the size, shape, and orientation of these same objects when she reaches out to pick them up (Goodale et al., 1991; Goodale, Meenan, et al., 1994; Milner et al., 1991). For example, when she was presented with a series of

rectangular blocks that varied in their dimensions but not in their overall surface area, she was unable to say whether or not any two of these blocks were the same or different. Even when a single block was placed in front of her, she was unable to indicate how wide the block was by opening her index finger and thumb a matching amount (see Fig. 2B). Nevertheless, when she reached out to pick up the block using a precision grip, the opening between her index finger and thumb was scaled in flight to the width of the object, just as it is in people with normal vision (see Fig. 2B). Furthermore, DF exhibits normal visuomotor control in other tasks, including stepping over obstacles during locomotion, despite the fact that her perceptual judgments about the height of these obstacles are far from normal (Patla & Goodale, 1997).

But where is the damage in DF's brain? As it turns out, even though DF shows diffuse loss of tissue throughout her cerebral cortex (consistent with hypoxia), she also shows prominent focal lesions bilaterally in the lateral occipital cortex, a region of the human ventral stream that we now know is involved in the visual recognition of objects, particularly their geometric structure (James, Culham, Humphrey, Milner, & Goodale, 2003; see Fig. 3). It is presumably this selective damage to her ventral stream that has disrupted her ability to perceive the form of objects. But these lesions have not interfered with her ability to use visual information about form to shape her hand when she reaches out and grasp objects. The preservation of normal visually guided grasping in the face of ventral-stream damage, suggests that other parts of her brain are able to process information about the size, shape, and orientation of the objects that she is able to grasp.

Since the original work on DF, other patients with ventral-stream damage have been identified who show strikingly similar dissociations between vision-for-perception and vision-for-action. Thus, Patient SB, who suffered several bilateral damage to his ventral stream early in life, shows remarkably preserved visuomotor skills (he plays table tennis and can ride a motorcycle) despite having profound deficits in his ability to identify objects, faces, colors, visual texture, and words (Dijkerman, Lê, Démonet, & Milner, 2004; Lê et al., 2002). Recently, another patient, who sustained bilateral damage to the ventral stream following a stroke, was tested on several of the same tests that were given to DF more than a decade ago. Remarkably, this new patient (JS) behaved almost identically to DF: in other words, despite his inability to perceive the shape and orientation of objects, he was able to use these same object features to program and control grasping movements directed at those objects (Karnath, Rüter, Mandler, & Himmelbach, 2009; see Fig. 4). Finally, it is worth noting that if one reads the

early clinical reports of patients with visual form agnosia, one can find a number of examples of what appears to be spared visuomotor skills in the face of massive deficits in form perception. Thus, Campion (1987), for example, reports that patient RC, who showed a profound visual form agnosia after carbon monoxide poisoning, “could negotiate obstacles in the room, reach out to shake hands and manipulate objects or [pick up] a cup of coffee”.

Although it is somewhat of a gloss, one might say the pattern of visual deficits and spared abilities in DF (and in SB, JS, and other patients with visual form agnosia) is the mirror image of that observed in the optic ataxia patients described earlier. DF, for example, who has damage in her ventral stream, can reach out and grasp objects whose form and orientation she does not perceive, whereas patients with optic ataxia, who have damage in their dorsal stream, are unable to use vision to guide their reaching and/or grasping movements to objects whose form and orientation they perceive. This ‘double dissociation’ cannot be easily accommodated within the traditional what vs. where account. Instead, to make sense of these data, a new formulation of the division of labor between the ventral and dorsal streams is required.

6. Two visual streams: a new perception–action framework

In the early 1990s, David Milner and I proposed a functional distinction between the two streams that focused on the differences in the output systems served by each stream. According to our account, the ventral stream plays the major role in constructing a perceptual representation of the visual world and the objects within it, while the dorsal stream mediates the visual control of actions directed at those objects (Goodale & Milner, 1992; Milner & Goodale, 1993). Thus, the ventral stream (together with associated cognitive networks) allows us to identify objects and events, attach meaning and significance to them, and establish their causal relations. Such operations are essential for accumulating and accessing a visual knowledge-base about the world. As I will discuss later, it is the ventral stream that provides the perceptual foundation for the offline control of action, projecting action into the future and incorporating stored information from the past into the control of current actions. In contrast, processing in the dorsal stream does not generate visual percepts; it generates skilled actions (in part by modulating processing in more ancient visuomotor modules described earlier).

Note that this division of labor reflects the competing demands on vision outlined in the last section: the perception of objects and

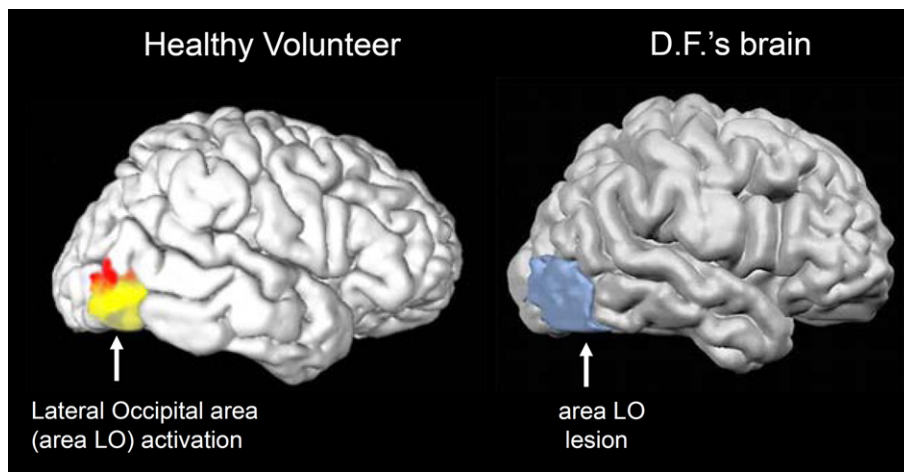


Fig. 3. Area LO, a ventral-stream area implicated in object recognition (particularly object form), has been localized on the brain of a healthy control subject by comparing fMRI activation to intact versus scrambled line drawings. Note that the lesion (marked in blue) on patient D.F.'s right cerebral hemisphere encompasses all of area LO. Area LO in D.F.'s left hemisphere is also completely damaged. Adapted with permission from Goodale and Milner (2004).

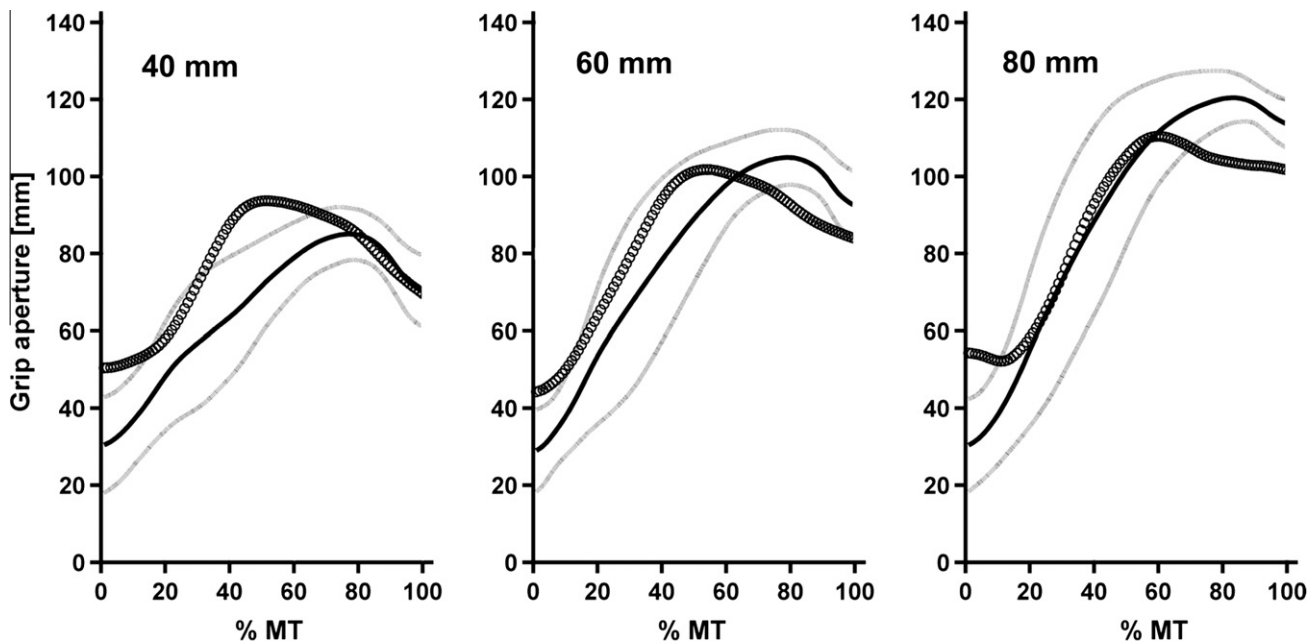


Fig. 4. The time courses of the mean grip aperture for patient JS grasping target objects with three different widths (40 mm, 60 mm, 80 mm). The horizontal axis shows the normalized movement time. The thick black line represents the mean aperture of the control group with one SD (indicated as gray lines) below and above each mean value. The circles represent the mean aperture for patient JS. Note that despite his difficulty in perceiving the width of objects, his grip aperture still scales to the size of the objects relatively normally (although he opens his hand slightly wider than normal for the smaller objects). Adapted with permission from Karnath et al. (2009).

their relations on the one hand and the control of actions directed at (or with respect to) those objects on the other. Note too that this is *not* the distinction between ‘what’ and ‘where’ that was originally put forward by Ungerleider and Mishkin (1982). In our scheme, the structural and spatial attributes of goal objects are processed by both streams, but for different purposes. In the ventral stream, information about a broad range of object parameters is transformed for perceptual purposes; in the dorsal stream, some of these same object parameters are transformed for the control of actions. This is not to say that the distribution of visual inputs does not differ between the two streams, but rather that the main difference lies in the nature of the transformations that each stream performs on those two sets of inputs. Of course, the two streams are not hermetically sealed from one another. Indeed, they work together in controlling our behavior as we live our complex lives – but they play separate and complementary roles in the production of adaptive behavior (for a detailed discussion of this issue, see Milner & Goodale, 2008). Thus, in the context of coffee cup example that was discussed earlier, the ventral stream plays the major role in enabling us to identify our cup, whereas the dorsal stream mediates the visual control of the movements we make as we pick it up.

Not only does this new proposal account for the neurological dissociations observed in patients with damage to the ventral and dorsal streams, but it is also supported by a wealth of anatomical, electrophysiological, and lesion studies in the monkey too numerous to review here (for recent reviews, see Andersen & Buneo, 2003; Cohen & Andersen, 2002; Milner & Goodale, 2006; Tanaka, 2003). But perhaps some of the most convincing evidence for the perception–action proposal has come from functional magnetic resonance imaging (fMRI) studies of the dorsal and ventral streams in the human brain.

7. Neuroimaging the ventral stream

As the organization of the human visual system beyond V1 began to be revealed with the advent of fMRI (Menon et al., 1992; Ogawa et al., 1992), it soon became apparent that there was a

remarkable correspondence between the layout of extrastriate visual areas in monkeys and humans, including the separation of these areas into dorsal and ventral streams (Tootell, Tsao, & Vanduffel, 2003; Van Essen et al., 2001). In the ventral stream, regions have been identified that seem to be selectively responsive to different categories of visual stimuli. Early on, an area was isolated within the ventrolateral part of the occipital cortex (the lateral occipital area or LO) that appears to be involved in object recognition (for review, see Grill-Spector, 2003). As mentioned earlier, DF has bilateral lesions in the ventral stream that include area LO in both hemispheres (see Fig. 5).

Not surprisingly therefore, an fMRI investigation of activity in DF’s brain revealed no differential activation for line drawings of common objects (vs. scrambled versions) anywhere in D.F.’s remaining ventral stream, mirroring her poor performance in identifying the objects depicted in the drawings (James et al., 2003; see Fig. 5). Again, this strongly suggests that area LO is essential for form perception, generating the geometrical structure of objects by combining information about edges and surfaces that has already been extracted from the visual array by low-level visual feature detectors.

In addition to LO, other ventral-stream areas have been identified that code for faces, human body parts, and places or scenes (for review, see Milner & Goodale, 2006). Although there is a good deal of debate as to whether these areas are really category-specific (e.g. Downing, Chan, Peelen, Dodds, & Kanwisher, 2006) or instead are particular nodes in a highly distributed system (e.g. Cant, Arnott, & Goodale, 2009; Cant & Goodale, 2007; Haxby et al., 2001; Op de Beeck, Haushofer, & Kanwisher, 2008), the neuroimaging work continues to provide strong support for the idea that the ventral stream plays the major role in constructing our perceptual representation of the world. Indeed, processing within ventral-stream areas, such as LO, exhibits exactly the characteristics that one might expect to see in such a system. For example, LO shows selective activation for objects irrespective of whether the objects are defined by differences in motion, texture, or luminance contrast (Grill-Spector, Kushnir, Edelman, Itzchak, & Malach, 1998). Moreover, LO also appears to code the overall geometric shape of an

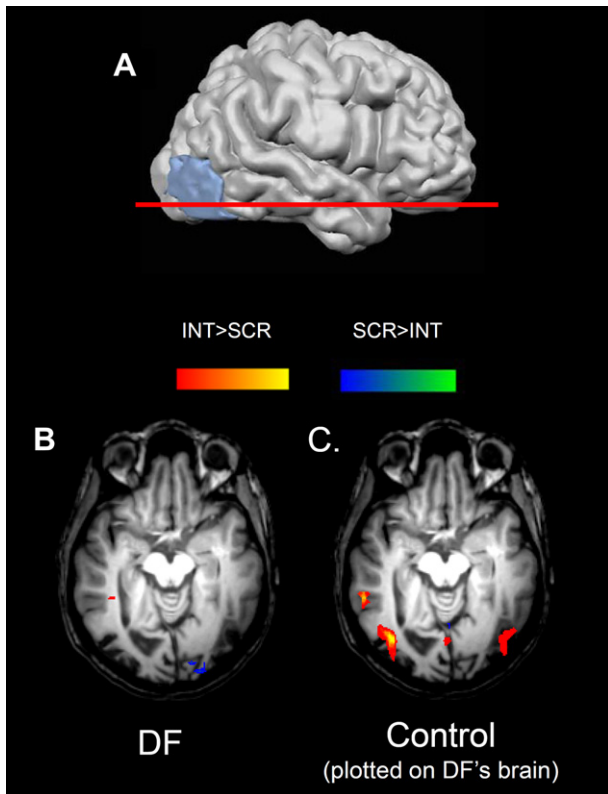


Fig. 5. Neuroimaging in DF's ventral stream. Panel A shows a right lateral view of DF's brain, with the lesion in LO marked in blue. Panel B shows fMRI activation for line drawings (vs. scrambled drawings) plotted on a horizontal section through DF's brain at the level of the red line on Panel A. DF shows no selective activation for line drawings either in area LO or in neighboring areas. As can be seen in Panel C, a control subject shows robust activation to the same drawings. The activation in the control subject's brain, which has been mathematically morphed onto DF's brain, coincides well with her LO lesions. Adapted with permission from James et al. (2003).

object rather than simply its local contours (Kourtzi & Kanwisher, 2001). Although there is evidence that area LO shows some sensitivity to changes in object viewpoint (Grill-Spector et al., 1999), at least part of area LO appears to be largely insensitive to such changes and treats different views of the same object as equivalent (James, Humphrey, Gati, Menon, & Goodale, 2002; Valyear, Culham, Sharif, Westwood, & Goodale, 2006). Importantly, area LO does not appear to play an essential role in the programming and online control of grasping movements. As described earlier, DF, who has large bilateral lesions of area LO, is still capable of generating well-formed grasping movements that reflect the size, shape, and orientation of the goal object. But in addition, fMRI studies of object-directed grasping in neurologically-intact individuals typically show no selective activation in area LO, even when the hand has to be scaled for objects of different sizes (Cavina-Pratesi, Goodale, & Culham, 2007; Culham, 2004; Culham et al., 2003). Of course, when individuals are asked to discriminate between sizes of objects, rather than pick them up, area LO is now activated – just as one would expect of an area involved in the perception of object features (Cavina-Pratesi et al., 2007).

In summary, the neuroimaging work on the human ventral stream reinforces the idea that this set of pathways plays a fundamental role in constructing our perceptual representations of the world – but is not essential for the programming and online control of visually guided actions, such as reaching and grasping, that are directed at the goal objects that the ventral stream has helped to identify.

8. Neuroimaging the dorsal stream

Ever since the pioneering work of Mountcastle, Lynch, Georgopoulos, Sakata, and Acuña (1975), evidence has continued to accumulate showing that neurons in the dorsal stream of the macaque monkey play a central role in transforming visual information into the appropriate coordinates for motor acts (for reviews, see Andersen & Buneo, 2003 and Sakata, 2003). Thus, an area in the lateral bank of the intraparietal sulcus (area LIP) in the posterior parietal cortex appears to play a primary role in the visual control of voluntary saccadic eye movements, whereas a quite separate area, located more anteriorly within the intraparietal sulcus (area AIP) is involved in the visual control of object-directed grasping movements. The visual control of reaching engages networks in the medial bank of the intraparietal sulcus (MIP) and in the parieto-occipital sulcus (area V6A). More recent work suggests that this neat division into areas responsible for eye movements, areas responsible for grasping, and still other areas responsible for reaching may be too simplistic – and that the interactions between these different areas in the performance of different visuomotor actions may be much more complex than originally envisaged. For example, Fattori and colleagues have shown that area V6A in the monkey may play a pivotal role in the control of grasping as well as reaching (Fattori, Breveglieri, Amoroso, & Galletti, 2004; Fattori et al., 2010).

Just as was the case for visuo-perceptual areas in the ventral stream, the advent of fMRI has led to the discovery in the human dorsal stream of visuomotor areas that appear to be largely homologous with those in the monkey brain (for reviews, see Castiello, 2005; Culham & Kanwisher, 2001; Culham & Valyear, 2006) (see Fig. 6). Early on, an area in the intraparietal sulcus was identified that appeared to be activated when subjects shifted their gaze (or their covert attention) to visual targets. This area is thought by many investigators to be homologous with area LIP in the monkey, although in the human brain it is located more medially in the intraparietal sulcus than it is in the monkey (Culham, Cavina-Pratesi, & Singhal, 2006; Grefkes & Fink, 2005; Pierrot-Deseilligny, Milea, & Muri, 2004). Studying eye movements in the magnet is relatively easy, but using fMRI to study the activity in brain areas mediating the visual control of reaching and grasping movements has proved to be a more difficult task. As soon as limbs are moved

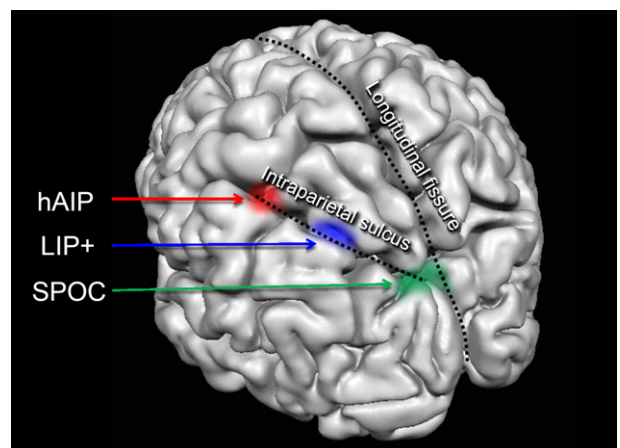


Fig. 6. Illustration of the approximate locations of human anterior intraparietal areas (hAIP), the putative homologue of the monkey lateral intraparietal area (termed LIP+ in the human), and the superior parieto-occipital area (SPOC). Notice that LIP+ is actually located on the medial bank of the intraparietal sulcus in the human brain. hAIP has been implicated in the visual control of grasping, LIP+ in the visual control of saccadic eye movements and shifts of attention, and SPOC in the visual control of reaching movements.

in the magnet there is a much greater likelihood of movement artefacts and perturbations in the magnetic field of the scanner. For this reason, most studies of this kind use slow-event related designs so that the real-time artefacts can be easily identified and removed from the data analysis. There is also the challenge of presenting real objects that people can grasp while lying in the magnet. To overcome this problem, Culham and her colleagues devised a pneumatically driven apparatus that presents real 3-D graspable objects within the bore of a high-field magnet. Using this device, they were able to compare reach-to-grasp movements with simple reaching movements directed at target objects that varied in orientation and size (Culham, 2003; Culham et al., 2003). They identified an area in the anterior part of the intraparietal sulcus that was consistently activated more by reaching out and grasping objects than by simply reaching out and touching them with the back of the fingers. This area, which they called human AIP (hAIP), appears to be the same area that Binkofski et al. (1998) had earlier shown was activated when subjects grasped objects in the scanner. This latter group also showed that patients with damage to this area showed deficits in grasping but little disturbance in reaching. Several more recent studies have also shown that hAIP is differentially activated during visually guided grasping (e.g., Cavina-Pratesi et al., 2007; Frey, Vinton, Norlund, & Grafton, 2005). As discussed earlier, there was no evidence for selective activation of area LO in the ventral stream when subjects reached out and grasped objects (Cavina-Pratesi et al., 2007; Culham, 2004; Culham et al., 2003). This suggests that hAIP and associated networks in the posterior parietal and premotor cortices are able to program and control grasping movements quite independently. This inference is considerably strengthened by the fact that patient DF, who has large bilateral lesions of area LO, shows robust differential activation in area hAIP for grasping (compared to reaching) similar to that seen in healthy subjects (James et al., 2003).

There is preliminary fMRI evidence to suggest that when binocular information is available for the control of grasping, dorsal-stream structures can mediate this control without any additional activity in ventral-stream areas such as LO – but when only monocular vision is available, and reliance on pictorial cues becomes more critical, activation increases in LO along with increased activation in hAIP (Verhagen, Dijkerman, Grol, & Toni, 2008). This observation is consistent with the psychophysical work reviewed earlier showing that binocular vision plays the major role in the programming and control of manual prehension – and helps to explain why DF has great difficulty grasping objects under monocular viewing conditions (Marotta, Behrmann, & Goodale, 1997).

But what about the visual control of reaching? As we saw earlier, the lesions associated with the mis-reaching that defines optic ataxia have been typically found in the posterior parietal cortex, including the intraparietal sulcus and sometimes extending into the inferior or superior parietal lobules (Perenin & Vighetto, 1988). More recent quantitative analyses of the lesion sites associated with mis-reaching have revealed several key foci in the parietal cortex, including the medial occipito-parietal junction, the superior occipital gyrus, the intraparietal sulcus, and the superior parietal lobule as well as parts of the inferior parietal lobule (Karnath & Perenin, 2005). As it turns out, these lesion sites map nicely onto the patterns of activation found in a recent fMRI study of visually guided reaching that showed reach-related activation both in a medial part of the intraparietal sulcus (near the intraparietal lesion site identified by Karnath and Perenin) and in the medial occipito-parietal junction (Prado, Clavagnier, Otzenberger, Scheiber, & Perenin, 2005). In a more recent study, it was found the reach-related focus in the medial intraparietal sulcus was equally active for reaches with and without visual feedback, whereas an area the superior parietal occipital cortex (SPOC) was particularly active when visual feedback was available (Filimon,

Nelson, Huang, & Sereno, 2009). This suggests that the medial intraparietal region may reflect proprioceptive more than visual control of reaching whereas SPOC may be more involved in visual control.

Just as is the case in the monkey, there is evidence to suggest that SPOC may play a role in some aspects of grasping, particularly wrist rotation (Grol et al., 2007; Monaco, Sedda, Fattori, Galletti, & Culham, 2009). But at the same time, it seems clear from the imaging data that more anterior parts of the intraparietal sulcus, such as hAIP, play a unique role in visually guided grasping and appear not to be involved in the visual control of reaching movements. Moreover, as was reviewed earlier, patients with lesions of hAIP have deficits in grasping but retain the ability to reach towards objects (Binkofski et al., 1998), whereas other patients with lesions in more medial and posterior areas of the parietal lobe, including SPOC, show deficits in reaching but not grip scaling (Cavina-Pratesi, Ietswaart, Humphreys, Lestou, & Milner, 2010). The identification of areas in the human posterior parietal cortex for the visual control of reaching that are anatomically distinct from those implicated in the visual control of grasping, particularly the scaling of grip aperture, lends additional support to Jeannerod's (1981) proposal that the transport and grip components of reach-to-grasp movements are programmed and controlled relatively independently. None of these observations, however, can be easily accommodated within the double-pointing hypothesis of Smeets and Brenner (1999).

As mentioned earlier, not only are we adept at reaching out and grasping objects, but we are also able to avoid obstacles that might potentially interfere with our reach. Although to date there is no neuroimaging evidence about where in the brain the location of obstacles is coded, there is persuasive neuropsychological evidence for a dorsal-stream locus for this coding. Thus, unlike healthy control subjects, patients with optic ataxia from dorsal-stream lesions do not automatically alter the trajectory of their grasp to avoid obstacles located to the left and right of the path of their hand as they reach out to touch a target beyond the obstacles – even though they certainly see the obstacles and can indicate the midpoint between them (Schindler et al., 2004). Conversely, patient DF shows normal avoidance of the obstacles in the same task, even though she is deficient at indicating the midpoint between the two obstacles (Rice et al., 2006).

But where is the input to all these visuomotor areas in the dorsal stream coming from? Although it is clear that V1 (both directly and via V2) has prominent projections to the motion-processing area MT and other areas that provide input to dorsal-stream networks, it has been known for a long time that humans (and monkeys) with large bilateral lesions of V1 are still capable of performing many visually guided actions despite being otherwise blind with respect to the controlling stimuli (for review, see Milner & Goodale, 2006; Weiskrantz, 1997; Weiskrantz, Warrington, Sanders, & Marshall, 1974). These residual visual abilities, termed 'blindsight' by Sanders, Warrington, Marshall, and Weiskrantz (1974), presumably depend on projections that must run outside of the geniculostriate pathway, such as those going from the eye to the superior colliculus, the interlaminar layers of the dorsal lateral geniculate nucleus, or even directly to the pulvinar (for review, see Cowey, 2010; see Fig. 1). Some of these extra-geniculate projections may also reach visuomotor networks in the dorsal stream. It has recently been demonstrated, for example, that a patient with a complete lesion of V1 in the right hemisphere was still capable of avoiding obstacles in his blind left hemifield while reaching out to touch a visual target in his sighted right field (Striemer, Chapman, & Goodale, 2009). The avoidance of obstacles in this kind of task, as we have already seen, appears to be mediated by visuomotor networks in the dorsal stream (Rice et al., 2006; Schindler et al., 2004). Similarly, there is evidence that such patients show some evidence

for grip scaling when they reach out and grasp objects placed in their blind field (Perenin & Rossetti, 1996). This residual ability also presumably depends on dorsal-stream networks that are being accessed by extrageniculostriate pathways. There is increasing evidence that projections from the superior colliculus to the pulvinar – and from there to MT and area V3 – may be the relay whereby visual inputs reach the visuomotor networks in the dorsal stream (e.g. Berman & Wurtz, 2010; Lyon, Nassi, & Callaway, 2010). Projections from the interlaminar regions of the LGNd to extrastriate cortical areas may also play a role (Schmid et al., 2010; Sincich, Park, Wohlgenuth, & Horton, 2004). Some have even suggested that a direct projection from the eye to the pulvinar – and then to MT – might be responsible (Warner, Goldshmit, & Bourne, 2010). But whatever the pathways might be, it is clear that the visuomotor networks in the dorsal stream that are known to mediate grasping and obstacle avoidance during reaching are receiving visual input that bypasses V1. It seems likely that these pathways did not evolve to be a ‘back-up’ if V1 happened to be damaged but instead play a central role in the control of actions such as reaching and grasping. The nature of that control, however, remains unspecified. What is needed is more experimental work in which reaching and grasping is studied in monkeys with reversible lesions of the retino-recipient and tecto-recipient regions of the pulvinar and in neurological patients who have sustained damage to this structure.

In summary, the neuropsychological and neuroimaging data that have been amassed over the last 25 years suggest that vision-for-action and vision-for-perception depend on different and relatively independent visual pathways in the primate brain. In short, the visual signals that give us the percept of our coffee cup sitting on the breakfast table are *not* the same ones that guide our hand as we pick up it up! The programming and control of such actions depend instead on signals processed by dedicated visuomotor networks in the dorsal stream.

Before leaving this section, it is important to acknowledge that in this review, I have focused entirely on the role of dorsal-stream structures in the visual control of skilled actions, such as reaching and grasping. But it is clear that these posterior-parietal structures also play a critical role in the deployment of attention as well as in other high level cognitive tasks, such as numeracy and working memory. Nevertheless, a strong argument can be made that these functions of the dorsal stream (and associated networks in premotor cortex and more inferior parietal areas) grew out of pivotal role that the dorsal stream plays in the control of eye movements and goal-directed limb movements (for more on these issues, see Moore, 2006; Nieder & Dehaene, 2009; Rizzolatti & Craighero, 1998); Rizzolatti, Riggio, Dascola, & Umiltá, 1987).

9. Different neural computations for perception and action

But why did two separate streams of visual processing evolve in the primate brain? Or, to put it another way, why couldn't one “general purpose” visual system handle both vision-for-perception and vision-for-action? The answer to this question lies in the computational requirements of vision-for-perception and vision-for-action. As I suggested earlier, perception and action require quite different transformations of the visual signals. To be able to grasp our coffee cup successfully, for example, it is essential that the brain compute its actual size and its orientation and position with respect to the hand we intend to use to pick it up. Some of these computations could reflect the metrics of object (its size, for example) while others, particularly those involved in determining the location of the object, might depend more on learned “look-up tables” that engage topological representations of the target or even ordered geometries (Thaler & Goodale, 2010). In other words,

the generation of a visually guided reach would require only a link between neurons that code the location of the target in space and neurons that code the desired state of the limb. The time at which these computations are performed is equally critical. Observers and goal objects rarely stay in a static relationship with one another and, as a consequence, the egocentric location of a target object can often change radically from moment-to-moment. For these reasons, it is essential that the required coordinates for action be computed at the very moment the movements are to be performed.

Perceptual processing needs to proceed in a quite different way. Vision-for-perception does not require the absolute size of objects or their egocentric locations to be computed. In fact, such computations would be counter-productive because our viewpoint with respect to objects does not remain constant. For this reason, it would be better to encode the size, orientation, and location of objects relative to each other. Such a scene-based frame of reference permits a perceptual representation of objects that transcends particular viewpoints, while preserving information about spatial relationships (as well as relative size and orientation) as the observer moves around. The products of perception also need to be available over a much longer time scale than the visual information used in the control of action. We may need to recognize objects we have seen minutes, hours, days – or even years before. To achieve this, the coding of the visual information has to be somewhat abstract – transcending particular viewpoint and viewing conditions. By working with perceptual representations that are object- or scene-based, we are able to maintain the constancies of size, shape, color, lightness, and relative location, over time and across different viewing conditions. Although there is much debate about the way in which this information is coded, it is pretty clear that it is the identity of the object and its location within the scene, not its disposition with respect to the observer that is of primary concern to the perceptual system. Thus current perception combined with stored information about previously encountered objects not only facilitates the object recognition but also contributes to the control of goal-directed movements when we are working in off-line mode (i.e. on the basis of our memory of goal objects and their location in the world).

Although much of the evidence for the idea that vision-for-action and vision-for-perception engage different brain systems has come from human neuropsychology and neuroimaging (as well as from work with non-human primates), evidence for fundamental differences in the computations underlying these two kinds of visual processing has come primarily from studies in normal human observers.

There is evidence that observers tend to perceive the shape of objects in a configurational or ‘holistic’ manner, so that a given dimension cannot be perceptually isolated from the other dimensions of the object. Thus, Ganel and Goodale (2003) found that when people were asked to make perceptual judgements about the width of different rectangular-shaped objects, their judgements were always affected by differences in the length of those objects. In other words, vision-for-perception always took into account the overall shape of the objects. But when the same people were asked to pick up the objects, something quite different happened. Now, their grasping movements were unaffected by the differences in the non-relevant dimension of the objects. In other words, vision-for-action focussed on only the most relevant dimension of the goal object (in this case its width) without being influenced by its length.

Interestingly, when subjects in the Ganel and Goodale (2003) experiment were asked to pantomime the grasping movements without actually touching the target objects, their grasping was now affected by the differences in the length of the object, just as it was in the perceptual judgement task. This presumably reflects the fact that the production of a pantomimed movement utilizes perceptual rather than direct visuomotor processing. DF, for

example, has great difficulty pantomiming an action to an object she saw moments before even though her real-time grasps to the same object are essentially normal (Goodale, Jakobson, & Keillor, 1994). Taken together, these results lend support to the idea that in contrast to the configural and scene-based processing associated with perception, visuomotor systems are able to process the action-relevant dimension while at the same time ignoring changes in other, irrelevant, dimensions.

The differences in the metrics and frames of reference used by vision-for-perception and vision-for-action have also been demonstrated in experiments with pictorial illusions, particularly size-contrast illusions. Aglioti, DeSouza, and Goodale (1995), for example, showed that the scaling of grip aperture in flight was remarkably insensitive to the Ebbinghaus illusion, in which a target disk surrounded by smaller circles appears to be larger than the same disk surrounded by larger circles (see Fig. 7). They found that maximum grip aperture was scaled to the real not the apparent size of the target disk. A similar dissociation between grip scaling and perceived size was reported by Haffenden and Goodale (1998), under conditions where participants had no visual feedback during the execution of grasping movements made to targets presented in the context of an Ebbinghaus illusion. Although grip scaling escaped the influence of the illusion, the illusion did affect performance in a manual matching task, a kind of perceptual report, in which participants were asked to open their index finger and thumb to indicate the perceived size of a disk. [This measure is akin to the typical magnitude estimation paradigms used in conventional psychophysics, but with the virtue that the manual estimation makes use of the same effector that is used in the grasping task.] To summarize then, the aperture between the finger and thumb was resistant to the illusion when the vision-for-action system was engaged (i.e. when the participant grasped the target) and sensitive to the illusion when the vision-for-perception system was engaged (i.e. when the participant estimated its size).

This dissociation between what people say they see and what they do underscores the differences between vision-for-perception and vision-for-action. The obligatory size-contrast effects that give rise to the illusion (in which different elements of the array are compared) presumably play a crucial role in scene interpretation, a central function of vision-for-perception. But the execution of a goal-directed act, such as manual prehension, requires computations that are centered on the target itself, rather than on the relations between the target and other elements in the scene. In fact, the true size of the target for calibrating the grip can be computed from the retinal-image size of the object coupled with an accurate estimate of distance. Computations of this kind, which do not take into account the relative difference in size between different objects in the scene, would be expected to be quite insensitive to the kinds of pictorial cues that distort perception when familiar illusions are presented.

The initial demonstration by Aglioti, DeSouza, and Goodale (1995) that grasping is refractory to the Ebbinghaus illusion engendered a good deal of interest amongst researchers studying vision and motor control – and over the last 15 years, there have been numerous investigations of the effects (or not) of pictorial illusions on visuomotor control. Some investigators have replicated the original observations of Aglioti et al. with the Ebbinghaus illusion (e.g., Amazeen & DaSilva, 2005; Fischer, 2001; Kwok & Braddick, 2003) – and others have observed a similar insensitivity of grip scaling to the Ponzo illusion (Brenner & Smeets, 1996; Jackson & Shaw, 2000), the horizontal-vertical illusion (Servos et al., 2000), the Müller-Lyer illusion (Dewar & Carey, 2006), and the Diagonal illusion (Stöttinger & Perner, 2006; Stöttinger, Soder, Pfusterschmied, Wagner, & Perner, 2010). Others have reported that pictorial illusions affect some aspects of motor control but not others (e.g., Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Daprati & Gentilucci, 1997; Biegstraaten, de Grave, Brenner, & Smeets, 2007; Glazebrook et al., 2005; van Donkelaar, 1999). And a few

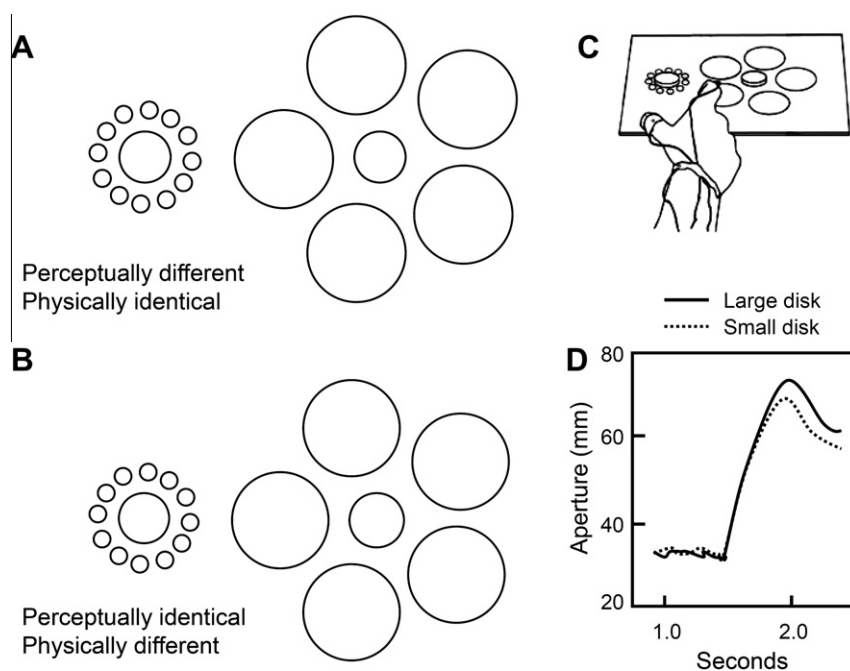


Fig. 7. The effect of a size-contrast illusion on perception and action. (A) The traditional Ebbinghaus illusion in which the central circle in the annulus of larger circles is typically seen as smaller than the central circle in the annulus of smaller circles, even though both central circles are actually the same size. (B) The same display, except that the central circle in the annulus of larger circles has been made slightly larger. As a consequence, the two central circles now appear to be the same size. (C) A 3-D version of the Ebbinghaus illusion. Participants are instructed to pick up one of the two 3-D disks placed either on the display shown in Panel A or the display shown in Panel B. (D) Two trials with the display shown in Panel B, in which the participant picked up the small disk on one trial and the large disk on another. Even though the two central disks were perceived as being the same size, the grip aperture in flight reflected the real not the apparent size of the disks. Adapted with permission from Aglioti et al. (1995).

investigators have found no dissociation whatsoever between the effects of pictorial illusions on perceptual judgments and the scaling of grip aperture (e.g., Franz, Bulthoff, & Fahle, 2003; Franz, Gegenfurtner, Bulthoff, & Fahle, 2000). A recent meta-analysis studies of grasping in the context of the Müller-Lyer illusion showed that grasping is less affected than perceptual judgements, but only when online visual feedback is available during execution of the grasping movement (Bruno & Franz, 2009).²

Demonstrating that actions such as grasping are sometimes sensitive to illusory displays is not by itself a refutation of the idea of two visual systems. One should not be surprised that visual perception and visuomotor control can interact in the normal brain. Ultimately, perception *has* to affect our actions or the brain mechanisms mediating perception would never have evolved! The real surprise, at least for monolithic accounts of vision, is that there are clear instances where visually guided action is apparently unaffected by pictorial illusions, which, by definition, affect perception. But from the standpoint of the duplex perception–action model such instances are to be expected (see Goodale, 2008; Milner & Goodale, 2006, 2008). Nevertheless, the fact that action has been found to be affected by pictorial illusions in some instances has led a number of authors to argue that the earlier studies demonstrating a dissociation had not adequately matched action and perception tasks for various input, attentional, and output demands (e.g., Smeets & Brenner, 2001; Vishton and Fabre, 2003) – and that when these factors were taken into account the apparent differences between perceptual judgments and motor control could be resolved without invoking the idea of two visual systems. Other authors, notably Glover (2004), have argued that action tasks involve multiple stages of processing from purely perceptual to more ‘automatic’ visuomotor control. According to his planning/control model, illusions would be expected to affect the early but not the late stages of a grasping movement (Glover, 2004; Glover & Dixon, 2001a, 2001b).

Some of these competing accounts, particularly Glover’s (2004) planning/control model, can simply be viewed as modifications of the original perception–action model. Nevertheless, Glover’s model fails to distinguish between planning in the sense of deciding upon one course of action rather than another, and planning in the sense of programming the actual constituent movements of an action (see Milner & Goodale, 2006). Milner and I would not dispute that vision-for-perception (and thus, the ventral stream) is involved in the former kind of planning, but would argue that the other kind of planning (i.e. programming) is mediated by vision-for-action (and thus, the dorsal stream). In fact, Glover and Dixon’s (2002) claim that perceptual processing intrudes into the early part of motor programming for grasping movements is based on findings that have been difficult to replicate (e.g., Danckert, Sharif, Haffenden, Schiff, & Goodale, 2002; Franz, 2003). Nevertheless, there are a number of other studies whose results cannot easily be reconciled with the two-visual-systems model, and it remains a real question as to why actions appear to be sensitive to illusions in some experiments but not in others.

There are several reasons why grip aperture might appear be sensitive to illusions under certain testing conditions. In some cases, notably the Ebbinghaus illusion, the flanker elements can be treated as obstacles, influencing the posture of the fingers during the execution of the grasp (de Grave, Biegstraaten, Smeets, & Brenner, 2005; Haffenden, Schiff, & Goodale, 2001; Plodowski & Jackson, 2001). In other words, the apparent effect of the illusion

on grip scaling in some experiments might simply reflect the operation of visuomotor mechanisms that treat the flanker elements of the visual arrays as obstacles to be avoided. Another critical variable is the timing of the grasp with respect to the presentation of the stimuli. When targets are visible during the programming of a grasping movement, maximum grip aperture is usually not affected by size-contrast illusions, whereas when vision is occluded before the command to initiate programming of the movement is presented, a reliable effect of the illusion on grip aperture is typically observed (Fischer, 2001; Hu & Goodale, 2000; Westwood & Goodale, 2003; Westwood, Heath, & Roy, 2000). As discussed earlier, vision-for-action is designed to operate in real time and is not normally engaged unless the target object is visible during the programming phase, when (bottom-up) visual information can be immediately converted into the appropriate motor commands. The observation that (top-down) memory-guided grasping is affected by the illusory display reflects the fact that the stored information about the target’s dimensions was originally derived from the earlier operation of vision-for perception (for a more detailed discussion of these and related issues, see Bruno et al., 2008; Goodale, Westwood, & Milner, 2004).

Nevertheless, some have argued that if the perceptual and grasping tasks are appropriately matched, particularly with respect to their scaling functions, then grasping can be shown to be as sensitive to size-contrast illusions as psychophysical judgements (Franz, 2001; Franz et al., 2000). Although this explanation, at least on the face of it, is a compelling one, it cannot explain why Aglioti et al. (1995) and Haffenden and Goodale (1998) found that when the relative sizes of the two target objects in the Ebbinghaus display were adjusted so that they appeared to be perceptually identical, the grip aperture that participants used to pick up the two targets continued to reflect the physical difference in their size. Moreover, it also cannot explain the findings of a recent study by Stöttinger et al. (2010) who showed that when one meets all the criteria that Franz argues must be satisfied before one can compare grip scaling with psychophysical judgements, grip scaling is still far less sensitive to the diagonal illusion than are perceptual judgements of target size.

The results of a recent experiment by Ganel, Tanzer, and Goodale (2008) provide evidence that is even more difficult to explain away by appealing to a failure to match testing conditions and other task-related variables. In this experiment, which used a version of the Ponzo illusion, a real difference in size was pitted against a perceived difference in size in the opposite direction (see Fig. 8). The results were remarkably clear. Despite the fact that people believed that the shorter object was the longer one (or vice versa), their grip aperture in flight reflected the real not the illusory size of the target objects. In other words, as can be seen in Fig. 9, on the same trials in which participants erroneously decided that one object was the longer (or shorter) of the two, the anticipatory opening between their fingers reflected the real direction and magnitude of size differences between the two objects. Moreover, the subjects in this experiment showed the same differential scaling to the real size of the objects whether the objects were shown on the illusory display or on the control display. Not surprisingly, as Fig. 9 also shows, when subjects were asked to use their finger and thumb to estimate the size of the target objects rather than pick them up, their manual estimates reflected the apparent not the real size of the targets. Overall, these results underscore once more the profound difference in the way visual information is transformed for action and perception. Importantly too, the results are difficult to reconcile with any argument that suggests that grip aperture is sensitive to illusions, and that the absence of an effect found in many studies is simply a consequence of differences in the task demands and/or a failure to equate for differences in scaling functions (Franz, 2001; Franz et al., 2000).

² Interestingly, a similar meta-analysis looking at studies of pointing in the context of the Müller-Lyer illusion (Bruno, Bernardis, & Gentilucci, 2008) found that pointing was largely resistant to the illusion even when vision was not available during the performance of the movement, provided that the initial programming of the movement was driven by vision rather than memory.

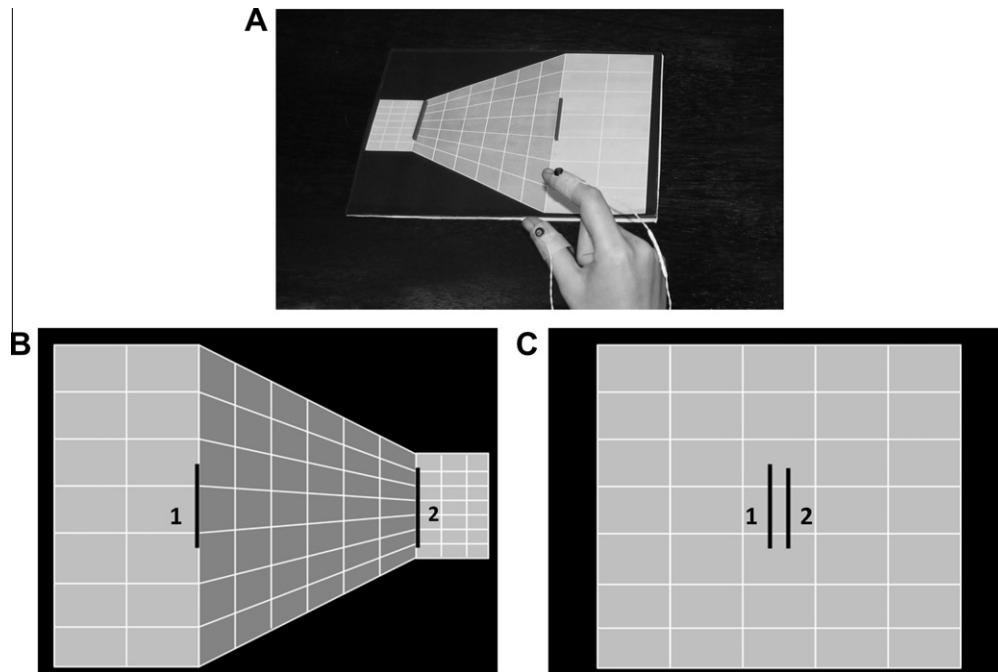


Fig. 8. Stimuli and experimental design of Ganel et al. (2008) study. Panel A shows the experimental paradigm and the version of the Ponzo illusion used. Panel B shows the arrangement of the objects on incongruent trials in which real size and the illusory size were pitted against one another. In this example, object 1 is perceived in most cases as shorter than object 2 (due to the illusory context), although it is actually longer. The real difference in size can be clearly seen in Panel C where the two objects are placed next to one another (for illustrative purposes) on the non-illusory control display. Adapted with permission from Ganel, Tanzer, et al. (2008).

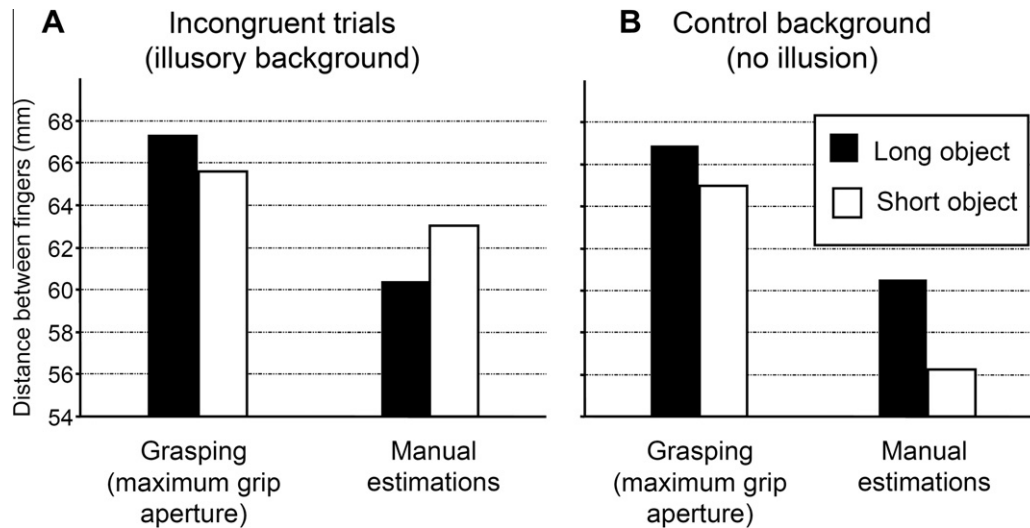


Fig. 9. Maximum grip aperture and perceptual estimates of length for objects placed on the illusory display (Panel A) and control display (Panel B). Only incongruent trials in which participants made erroneous decisions about real size are shown for the grip aperture and estimates with the illusory display. As Panel A shows, despite the fact that participants erroneously perceived the physically longer object to be the shorter one (and vice versa), the opening between their finger and thumb during the grasping movements reflected the real difference in size between the objects. This pattern of results was completely reversed when they made perceptual estimates of the length of the objects. With the control display (Panel B), both grip aperture and manual estimates went in the same direction. Adapted with permission from Ganel, Tanzer, et al. (2008).

One exceptionally interesting (and controversial) finding with respect to differences in the computations used by vision-for-perception and vision-for-action is the recent demonstration that grip scaling, unlike manual estimates of object size, does not appear to obey Weber's Law (Ganel, Chajut, & Algom, 2008). In other words, when people estimated the size of an object (either by adjusting a comparison line on a computer screen or by making a manual estimate), the JND increased with physical size in accord with Weber's Law; but when they reached out and picked up the object, the JND, as indicated by differences in grip aperture, was unaffected by vari-

ations in the size of the object (see Fig. 10). This surprising finding would appear to suggest that Weber's law is violated for visually guided actions, reflecting a fundamental difference in the way that object size is computed for action and for perception.

Of course, this finding (as well as the fact actions are often resistant to size-contrast illusions) fits well with Smeets and Brenner's (1999, 2001) double-pointing account of grasping. They argue that the visuomotor system does not compute the size of the object but instead computes the two locations on the surface of object where the digits will be placed. According to their double-pointing

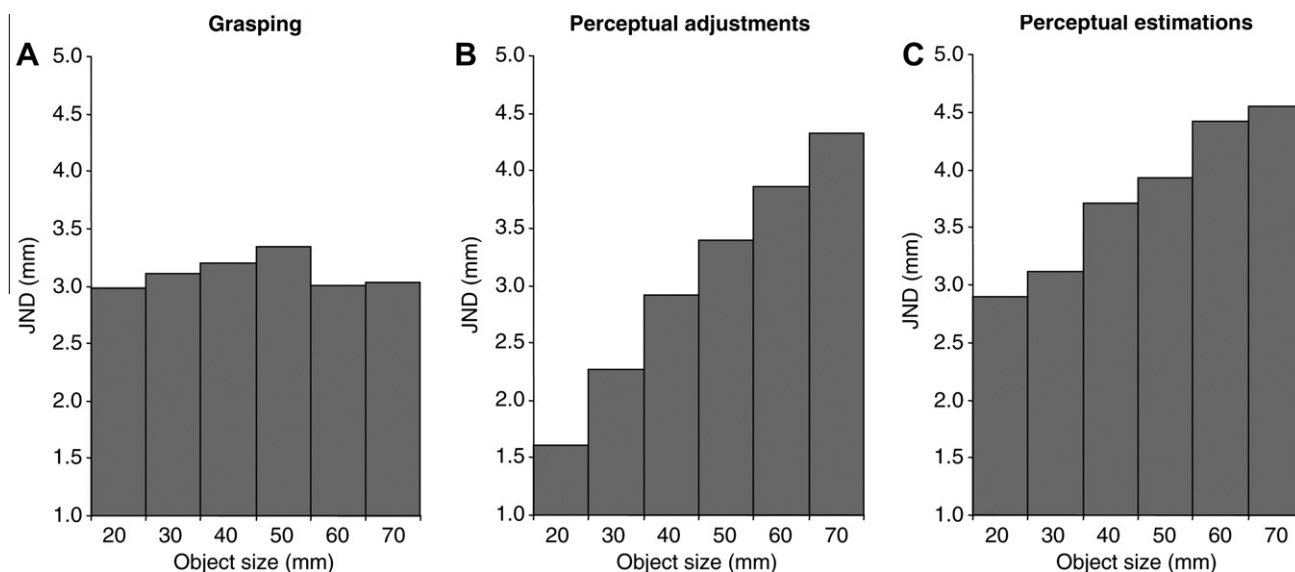


Fig. 10. Effects of object length on the visual resolution for grasping and for perceptual judgments in the experiments of Ganel, Chajut, et al. (2008). The JNDs, which represent visual resolution, are shown in Panel A the grasping, in Panel B for the perceptual adjustment, and in Panel C for the manual estimation. The JND increased linearly with the length of the target object for the two perceptual conditions but was unaffected by changes in length for grasping. Adapted with permission from Ganel, Chajut, et al. (2008).

hypothesis, size is irrelevant to the planning of these trajectories, and thus variation in size will not affect the accuracy with which the finger and thumb are placed on either side the target object. In short, Weber's law is essentially irrelevant (Smeets & Brenner, 2008). The same argument applies to grasping movements made in the context of size-contrast illusions: because grip scaling is simply an epiphenomenon of the independent finger trajectories, grip aperture would be impervious to the effects of the illusion. Although, as discussed earlier, Smeets and Brenner's account has been challenged, it has to be acknowledged that their double-pointing model offers a convincing explanation of all these findings – and would appear to seriously undermine the claim, based on data showing that grasping violates Weber's Law and is unaffected by pictorial illusions, that there is a clear distinction between vision-for-action and vision-for-perception. (Interestingly, their model would also not predict Franz's claim that grasping is as sensitive to pictorial illusions as perception is.)

There are some behavioral observations, however, that cannot easily be accommodated by the Smeets and Brenner (1999, 2001) model of grasping. For example, as discussed earlier, if a delay is introduced between viewing the target and initiating the grasp, the scaling of the anticipatory grip aperture is much more likely to be sensitive to size-contrast illusions (Fischer, 2001; Hu & Goodale, 2000; Westwood & Goodale, 2003; Westwood et al., 2000). Moreover, if a similar delay is introduced in the context of the Ganel, Chajut, et al. (2008) experiments just described, grip aperture now obeys Weber's Law (see Fig. 11). These results cannot be explained by the Smeets and Brenner model without conceding that – with delay – grip scaling is no longer a consequence of programming individual digit trajectories, but instead reflects the perceived size of the target object. Nor can the Smeets and Brenner model explain what happens when unpracticed finger postures (e.g. the thumb and ring finger) are used to pick up objects in the context of a size-contrast illusion. In contrast to skilled grasping movements, grip scaling with unpracticed awkward grasping is quite sensitive to the illusory difference in size between the objects (Gonzalez, Ganel, Whitwell, Morrissey, & Goodale, 2008). Only with practice, does grip aperture begin to reflect the real size of the target objects. Smeets and Brenner's model cannot account for this result without positing that individual control over the dig-

its occurs only after practice. Finally, recent neuropsychological findings with patient DF suggest that she could use action-related information about object size (presumably from her intact dorsal stream) to make explicit judgments regarding the length of an object that she was about to pick up (Schenk & Milner, 2006). All of this, together with the neuropsychological and neuroimaging data discussed earlier, is far more consistent with Jeannerod's (1981) duplex account of manual prehension, which posits that the grasp is scaled to the size of the goal object, than it is with Smeets and Brenner's double-pointing hypothesis.³

It is worth noting that dissociations between perceptual report and action have been reported for other classes of responses as well. For example, by exploiting the illusory mislocalization of a flashed target induced by visual motion, de'Sperati and Baud-Bovy (2008) showed that fast but not slow saccades escaped the effects of the illusion and were directed to the real rather than the apparent location of the target. This result underscores the fact that the control of action often depends on processes that unfold much more rapidly than those involved in perceptual processing (e.g., Castiello & Jeannerod, 1991). Indeed, as has been already discussed, visuomotor control may often be mediated by fast feedforward mechanisms in contrast to conscious perception, which requires (slower) feedback to earlier visual areas, including V1 (Lamme, 2001).

10. Interactions between the two streams

When the idea of a separate vision-for-action system was first proposed 25 ago, the emphasis was on the independence of this system from vision-for-perception. But clearly the two systems must work closely together in the generation of purposive behavior. One way to think about the interaction between the two streams (an interaction that takes advantage of the complementary differences in their computational constraints) is in terms of a

³ It should be noted that even if Smeets and Brenner's model of grasping is correct, this would not obviate the idea of separate visual pathways for perception and action. It could be the case that real-time grasping, which is mediated by the dorsal stream, uses independent digit control whereas delayed and awkward grasping, which is mediated by the ventral stream, uses object size.

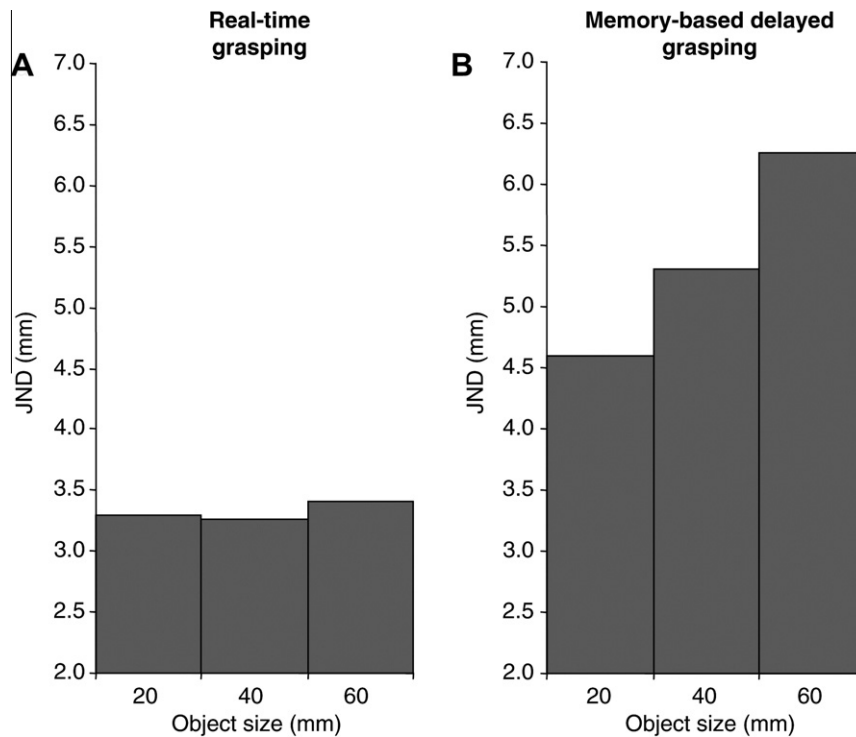


Fig. 11. Effects of object length on visual resolution during real-time and memory-based grasping in the experiments of Ganel, Chajut, et al. (2008). Panel A shows real-time grasping and Panel B shows memory-based, delayed grasping. As in the previous experiments, the JNDs were unaffected by changes in the length of the target object for real-time grasping. In contrast, memory-based grasping performance, which is known to rely on perceptual representations, showed a linear increase in the size of the JND with object length. Adapted with permission from Ganel, Chajut, et al. (2008).

'tele-assistance' model (Goodale & Humphrey, 1998). In teleassistance, a human operator, who has identified a goal object and decided what to do with it communicates with a semi-autonomous robot that actually performs the required motor act on the flagged goal object (Pook & Ballard, 1996). In terms of this tele-assistance metaphor, the perceptual-cognitive system in the ventral stream, with its rich and detailed representations of the visual scene (and links with cognitive systems), would be the human operator. Processes in the ventral stream participate in the identification of a particular goal and flag the relevant object in the scene, perhaps by means of an attention-like process. Once a particular goal object, such as the coffee cup sitting on our desk, has been flagged, dedicated visuomotor networks in the dorsal stream (in conjunction with related circuits in premotor cortex, basal ganglia, and brainstem) are then activated to transform the visual information about the cup into the appropriate coordinates for the desired motor act. This means that in many instances a flagged object in the scene will be processed in parallel by both ventral and dorsal stream mechanisms – each transforming the visual information in the array for different purposes. In other situations, where the visual stimuli are particularly salient, visuomotor mechanisms in the dorsal stream will operate without any immediate supervision by ventral stream perceptual mechanisms.

Of course, the tele-assistance analogy is far too simplified. For one thing, the ventral stream by itself cannot be construed as an intelligent operator that can make assessments and plans. Clearly, there has to be some sort of top-down executive control – almost certainly engaging prefrontal mechanisms – that can initiate the operation of attentional search and thus set the whole process of planning and goal selection in motion (for review, see Desimone & Duncan, 1995; Goodale & Haffenden, 2003). Reciprocal interactions between prefrontal/premotor areas and the areas in the posterior parietal cortex undoubtedly play a critical role in recruiting

specialized dorsal-stream structures, such as LIP, which appear to be involved in the control of both voluntary eye movements and covert shifts of spatial attention in monkeys and humans (Bisley & Goldberg, 2003; Corbetta, Kincade, & Shulman, 2002). In terms of the tele-assistance metaphor, area LIP can be seen as acting like a videocam on the robot scanning the visual scene, and thereby providing new inputs that the ventral stream can process and pass on to frontal systems that assess their potential importance. In practice, of course, the videocam/LIP system does not scan the environment randomly: it is constrained to a greater or lesser degree by top-down information about the nature of the potential targets and where those targets might be located, information that reflects the priorities of the operator/organism that are presumably elaborated in prefrontal systems.

What happens next goes beyond even these speculations. Before instructions can be transmitted to the visuomotor control systems in the dorsal stream, the nature of the action required needs to be determined. This means that praxis systems, perhaps located in the left hemisphere, need to 'instruct' the relevant visuomotor systems. After all, objects such as tools demand a particular kind of hand posture. Achieving this not only requires that the tool be identified, presumably using ventral-stream mechanisms (Valyear & Culham, 2010), but also that the required actions to achieve that posture be selected as well via a link to these praxis systems. At the same time, the ventral stream (and its related cognitive apparatus) has to communicate the locus of the goal object to these visuomotor systems in the dorsal stream. One way that this ventral-dorsal transmission could happen is via recurrent projections from foci of activity in the ventral stream back downstream to primary visual cortex and other adjacent visual areas. Once a target has been 'highlighted' on these retinotopic maps, its location could then finally be forwarded to the dorsal stream for action (for a version of this idea, see Lamme & Roelfsema, 2000). Moreover, LIP itself,

by virtue of the fact that it would be ‘pointing’ at the goal object, could also provide the requisite coordinates, once it has been cued by recognition systems in the ventral stream.

Once the particular disposition and location of the object with respect to the actor has been computed, that information has to be combined with the postural requirements of the appropriate functional grasp for the tool, which, as I have already suggested, are presumably provided by praxis systems that are in turn cued by recognition mechanisms in the ventral stream. At the same time, the initial fingertip forces that should be applied to the tool (or any object, for that matter) are based on estimations of its mass, surface friction, and compliance that are derived from visual information (e.g. Gordon, Westling, Cole, & Johansson, 1993). Once contact is made, somatosensory information can be used to fine-tune the applied forces – but the specification of the initial grip and lift forces (before any somatosensory information is available) must be derived from learned associations between the object’s visual appearance and prior experience with similar objects or materials (Buckingham, Cant, & Goodale, 2009). This information presumably can be provided only by the ventral visual stream in conjunction with stored information about past interactions with the objects.

Again, it must be emphasized that all of this is highly speculative. Nevertheless, whatever complex interactions might be involved, it is clear that goal-directed action is unlikely to be mediated by a simple serial processing system. Multiple iterative processing is almost certainly required, involving a constant interplay among different control systems at different levels of processing (for a more detailed discussion of these and related issues, see Milner & Goodale, 2006).

11. The next 25 years

As I have tried to outline in this review, the last 25 years have witnessed a sea change in research on vision and motor control. No longer regarded as separate enterprises, the two fields of research have come together on many fronts, and many researchers are now actively investigating the way in which vision is used to control, not just information-seeking eye movements, but a broad range of complex goal-directed actions, such as reaching and grasping. Indeed, a new field of research has emerged, visuomotor psychophysics, in which investigators are exploring the visual cues that are critical for the programming and online control of the skilled actions involved in both manual prehension and locomotion. At the same time, a new model of the division of labor in the primate visual system has emerged, one that posits that the neural pathways mediating vision-for-perception are quite separate from those mediating vision-for-action (Goodale & Milner, 1992). This perception–action model has provided a powerful theoretical framework for organizing a broad range of findings in neuropsychology, neuroimaging, neurophysiology, and neuroanatomy in both monkeys and humans, as well as a number of apparently contradictory findings in the psychophysics of perceptual report and visuomotor control. As I have tried to show in this review, the dorsal ‘action’ stream works in real time and, by itself, can deal only with objects that are visible when the action is being programmed – although in this limited domain it is remarkably accurate and efficient. The ventral ‘perception’ stream, however, allows us to escape the present and bring to bear information from the past – including information about the function of objects, their intrinsic properties, and their location with respect to other objects in the world. Ultimately, both streams are working to produce adaptive behavior, allowing us to reach out and grasp objects in cluttered environments with exquisite skill.

Despite all the progress that has been made, the nature of the interactions between our inner cognitive life and the control of our actions is still poorly understood. But even though the future will almost certainly see the development of more sophisticated ways of studying the complexities of these networks, a real understanding of how we get from thinking about a goal to executing the appropriate action to achieve that goal will depend as much on novel theory building (and perhaps paradigm shifts) as it will on new methods and technologies. One important step has already been taken. Many researchers now understand that brains evolved not to enable us to think but to enable us to move and interact with the world. Ultimately, all thinking (and by extension, all perception) is in the service of action. But this is a two-way street. Actions themselves (and not just eye movements) can influence our perception of the world. By interacting with objects (picking up and manipulating an unfamiliar fruit, for example), we gain new information about its intrinsic properties as signalled by other modalities, such as somatosensation, olfaction, and taste – and, with experience, learn to associate the visual appearance of objects with those properties. In short, by interacting with objects, we integrate information from many different sensory modalities. But importantly, it is vision that enables us to select objects of interest in the first place and to plan, program, and control the actions that we might wish to direct towards those objects. Over the next 25 years, I expect that research in vision will become even more closely integrated with the study of action planning and control.

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