

Frames of Reference for Perception and Action in the Human Visual System

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GOODALE, M. A., A. HAFFENDEN. *Frames of reference for perception and action in the human visual system*. NEUROSCI BIOBEHAV REV 22(2), 161–172, 1998.—A growing body of evidence demonstrates that vision for perception and vision for action are mediated by separate neural mechanisms. After briefly reviewing the neuropsychological evidence for this division of labor in the human visual system, we explore the evidence for a dissociation between perception and action in neurologically intact individuals. A number of studies have shown that unseen visual events can sometimes elicit movements of the hand and limb, despite the fact that subjects have no visual phenomenology of those events. Other work has shown that perceptual judgements about the location and size of objects can be quite different from the scaling of skilled actions directed at those objects. For example, size-contrast illusions, such as the Ebbinghaus illusion, have been shown to have little effect on the scaling of the grasp. Similar dissociations have been demonstrated in other studies in which psychophysical judgements about the dimensions of objects in the far peripheral field bear little relation to the calibration of grasping movements directed at those objects. Together with the neuropsychological work (and neurophysiological studies in the monkey), these findings provide compelling evidence for the operation of separate visual mechanisms in everyday life. In other words, what we think we see is not always what guides our actions. © 1998 Elsevier Science Ltd. All rights reserved.

Vision Perception Action Motor control Illusions Visual streams

1. INTRODUCTION

PERFORMING everyday tasks while thinking of other things is second nature for all of us. Sitting at our desk reading an article, we might, for example, reach out for a pencil to jot down a note, or pick up a cup of coffee to take a sip. Even though we are deeply engrossed in the article we are reading and not really attending to the pencil or the cup, our hand will nevertheless reflect the properties of the object we are attempting to pick up. If we reach for our coffee cup, our hand will open wider than if we reach for the pencil and the posture of our fingers will be quite different. All of this happens quite “automatically” while we continue to read the article. Of course, we could attend to the task of picking up the pencil or the cup, and perhaps we would be able to perform these actions even more efficiently. However, and this is the main thesis of this article, we would never really experience the actual visual information that is being used to program and control the movements of our fingers, hand, and limb as we reach out and pick up each of these objects. It is not simply a question of attention; no matter how much we attend to the cup, for example, we will never perceive what it is about that cup that determines the posture and trajectory of our hand and fingers as we reach out and lift it from our desk. This does not mean that we are unaware of the size, shape, and orientation of the cup or its position on the desk, but rather that the computations that use various object parameters to generate the appropriate movements of

our hand and fingers are quite different from those that generate our conscious perception of the cup. Indeed, the main reason we remain unaware of the visual information controlling the movements of our hand is that the visuo-motor systems mediating this control operate quite independently from those that allow us to perceive the objects and events that make up our experience of the visual world.

The assertion that the visual control of skilled actions and the visual perception of objects depend on different mechanisms might appear counter-intuitive. After all, it seems self-evident that the actions we direct at objects are controlled by the perceptions that we have of those same objects. Evidence from neurological patients tells us otherwise however. Consider the case of DF, a young woman who developed a profound visual form agnosia following carbon monoxide-induced anoxia (45). Even though DF’s “low-level” visual abilities are reasonably intact, she can no longer recognize common objects on the basis of their form or even the faces of her friends and relatives; nor can she identify even the simplest of geometric shapes. (If an object is placed in her hand, of course, she has no trouble identifying it by touch, and she can recognize people from their voices.) Remarkably, however, DF shows strikingly accurate guidance of her hand and finger movements when she attempts to pick up the very objects she cannot identify. Thus, when she reaches out to grasp objects of different sizes, her hand opens wider mid-flight for larger objects than

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it does for smaller ones, just as it does in people with normal vision (26). Similarly, she rotates her hand and wrist quite normally when she reaches out to grasp objects in different orientations, and she places her fingers correctly on the boundaries of objects of different shapes (24,26). At the same time, she is quite unable to describe or distinguish between any of these objects when they are presented to her in discrimination tests. In other words, DF's visual system is no longer able to deliver any perceptual information about the size, shape, and orientation of objects in the world. Yet at the same time, the visuomotor systems in DF's brain that control the programming and execution of visually guided actions remain sensitive to these same object features. Although the damage in DF's brain is quite diffuse, the ventrolateral regions of her occipital lobe are particularly compromised; her primary visual cortex, however, appears to be largely spared.

There is evidence that patients with damage to other visual areas in the cerebral cortex, such as the superior regions of the posterior parietal cortex, show a pattern of visual behaviour that is essentially the mirror image of that of DF. Such patients cannot use visual information to rotate their hand or scale the opening of their fingers when reaching out to pick up an object, even though they have no difficulty describing the size or orientation of objects in that part of the visual field (24,35,48,49).

These neurological dissociations suggest that the human visual system does not construct a single representation of the world for both visual perception and the visual control of action. Instead, vision for perception and vision for action appear to depend on separate neural mechanisms that can be differentially affected by neurological damage. Goodale and Milner (25) have proposed that this distinction can be mapped onto the two prominent pathways or "streams" of visual projections that have been identified in the cerebral cortex of the monkey: a ventral stream, which arises from primary visual cortex and projects to inferotemporal cortex, and a dorsal stream, which also arises from primary visual cortex but projects instead to the posterior parietal cortex (54). Additional support for this proposal comes from electrophysiological and behavioural studies in the monkey (for review, see (43,44)). Although some caution must be exercised in generalizing from monkey to human (14), it seems likely that the visual projections from primary visual cortex to the temporal and parietal lobes in the human brain may involve a separation into ventral and dorsal streams similar to that seen in the monkey.

Ungerleider and Mishkin (54) originally proposed that the ventral stream plays a special role in the identification of objects, whereas the dorsal stream is responsible for localizing objects in visual space. Goodale and Milner's (25) re-interpretation of this story places less emphasis on the differences in the visual information that is received by the two streams (object features versus spatial location) than it does on the differences in the transformations that the streams perform upon that information (22,25,43,44). According to their account, both streams process information about object features and about their spatial locations, but each stream uses this visual information in different ways. In the ventral stream, the transformations deliver the enduring characteristics of objects and their relations, permitting the formation of long-term perceptual representations. Such representations play an essential role in

the identification of objects and enable us to classify objects and events, attach meaning and significance to them, and establish their causal relations. Such operations are essential for accumulating a knowledge-base about the world. In contrast, the transformations carried out by the dorsal stream deal with moment-to-moment information about the location and disposition of objects in egocentric coordinates and thereby mediate the visual control of skilled actions, such as manual prehension, directed at those objects. In some ways then, the dorsal stream can be regarded as a cortical extension of the subcortical visual structures, such as the superior colliculus, that mediate visually guided movements in all vertebrates. Of course, the two systems work together in controlling the rich stream of behaviour that we produce as we live our complex lives. Their respective roles in this control differ however. The perceptual representations constructed by the ventral stream are part of a high-level cognitive network that enables an organism to select a particular course of action with respect to objects in the world; the visuomotor networks in the dorsal stream (and associated cortical and subcortical pathways) are responsible for the programming and on-line control of the particular movements that the selected action entails.

This division of labour in visual processing requires that different transformations be carried out on incoming visual information by the two streams. Consider first the task of the perceptual mechanisms in the ventral stream. To generate long-term representations of objects and their relationships, perceptual mechanisms must be 'object-based' so that constancy of size, shape, color, lightness, and relative location can be maintained across different viewing conditions. Some of these mechanisms might use an array of viewer-centered representations of the same object (e.g. (9)) others might use a set of canonical representations (e.g. (47)); still others might generate representations that are truly "object-centered" (42). However, whatever the particular coding might be, it is the identity of the object, not its disposition with respect to the observer that is of primary concern to the perceptual system. This is not the case for the visuomotor mechanisms in the dorsal stream, and other related structures, that support actions directed at that object. Here the underlying visuomotor transformations must be viewer-centered; in other words, both the location of the object and its disposition and motion must be encoded relative to the observer in egocentric coordinates, that is in retinocentric, head-centered, torso-centered, or shoulder-centered coordinates. Some object-based computations, such as those related to size, must be carried out, but even here the computations must reflect the nature of the effector system to be used. Finally, because the position and disposition of a goal object in the action space of an observer is rarely constant, such computations must be carried out on each occasion an action is performed (for a discussion of this issue, see (23)). To use a computer metaphor, the action systems of the dorsal stream do most of their work on-line; only the perception systems of the ventral stream can afford to work off-line. To summarize then, while similar (but not identical) visual information about object shape, size, local orientation, and location is available to both systems, the transformational algorithms that are applied to these inputs are uniquely tailored to the function of each system. According to the Goodale and Milner (25) proposal, it is

the nature of the functional requirements of perception and action that lies at the root of the division of labour in the ventral and dorsal visual projection systems of the primate cerebral cortex.

The differences in the visual abilities of the neurological patients described earlier are certainly consistent with these ideas. Thus, DF who has relatively intact visuomotor abilities despite her compromised visual perception has a pattern of brain damage that suggests that her ventral stream is not functioning properly. In contrast, patients with posterior parietal damage, which would interfere with dorsal stream function, show normal visuoperceptual performance but poor visuomotor control (49). However, if visual perception and the visual control of action depend on different neural mechanisms in the human cerebral cortex, then it should be possible to demonstrate a dissociation between these two kinds of visual processing with the right kind of task even in neurologically intact individuals. In other words, the visual information underlying the calibration and control of a skilled motor act directed at an object might not always match the perceptual judgements made about that object. In this review, we will explore the evidence for this kind of dissociation in normal subjects and discuss some of the ecological reasons why such dissociations might arise.

2. RESPONDING TO UNSEEN VISUAL EVENTS

If two visual stimuli of unequal intensity occur at the same time, the more intense stimulus often “masks” the less intense one. In other words, the less intense stimulus is more difficult to detect than when presented alone. This masking effect can be observed even if the more intense stimulus precedes (“forward masking”) or follows (“backward masking”) the less intense stimulus, provided the interval between the two is short enough (18). Although the degree of masking varies inversely with the inter-stimulus interval, some backward masking has been reported with intervals as long as 100 ms.

However, even though the perception of a visual event might be masked by such procedures, a variety of voluntary motor outputs can still be driven by the very stimulus that subjects fail to detect. For example, Fehrer and Biederman (16) found that detection of a test stimulus (a 5 ms blanking of a steady dim light) could be masked by a bright flash presented some 50 ms later. Nevertheless, subjects continued to show a voluntary motor response to the test stimulus; moreover, their reaction times were little different than those obtained on trials in which the test stimulus was presented by itself. This result has been replicated in a number of other studies that used a somewhat different interference paradigm, metacontrast, in which the contours of the test stimulus are adjacent to those of the mask (17,33,50). In all these studies, subjects initiated a motor response to a visual event that they did not perceive.

Motor responses to unseen stimuli can be relatively complex. In one experiment, Taylor and McCloskey (53) required subjects to initiate simultaneous or sequential movements of the two hands when a small light was turned on. The muscle groups required to make the actions in each hand were quite different and subjects had to pay close attention to the instructions. Despite the complexity of

the movements, subjects continued to initiate them in response to the small light even when it was presented in a backward masking paradigm that left it unavailable to perceptual report. In other words, subjects could generate relatively complex motor acts in response to unseen visual stimuli.

Although the mechanisms of backward masking are not well understood (for review, see (5)), the results of the experiments just described suggest that the neural processing giving rise to the perception of a visual event may not be complete before a motor act triggered by that event has been initiated. Thus, the subsequent presentation of a masking stimulus may interfere only with the perception of the earlier visual stimulus and not with the programming of the movements constituting the motor act. Libet (40,41) has argued that conscious perception of a sensory stimulus might require as much as 500 ms of processing time: far longer than the typical reaction time of most motor responses to that same sensory stimulus. However it may not be simply a question of length of processing time. As was suggested earlier, it could be the case that visual perception and visuomotor control are mediated by independent visual pathways, the ventral and dorsal stream, with different information transmission times and different processing requirements.

Even when a visual event is perceived, there is evidence that the time required to deliver that perception is quite a bit longer than the time required for a motor reaction to the same stimulus. A hint of this difference in processing time was observed in a study by Paulignan et al. (48), in which subjects reported that they did not notice a sudden and unpredictable displacement in the position of an object which they were attempting to pick up until their hand, whose trajectory they had already adjusted, was nearly at the target. This temporal dissociation between the motor adjustment and perceptual report was studied more formally by Castiello et al. (11). In this study, subjects were asked to indicate (using a vocal response) when they perceived the displacement in the position of the object they were attempting to grasp. On displacement trials, in which the object was displaced at the onset of the grasping movement, the vocal response was emitted 420 ms after the onset of the movement. In contrast, adjustments to the trajectory of the grasping movement could be seen in the kinematic records as little as 100 ms after movement onset, i.e. more than 300 ms earlier than the vocal response. The authors concluded that the delay between motor correction and the vocal response reflects the fact that perceptual awareness of a visual stimulus takes far longer to achieve than adjustments to the ongoing motor activity provoked by the visual stimulus. Processing time, of course, is likely to be a much more critical constraint for visuomotor networks than for the perceptual networks supporting conscious awareness. To catch a rapidly moving insect or to block the blow of a competitor, for example, an animal would have to be able to make extremely rapid adjustments in the trajectory of its limb movements in response to sudden and unpredictable changes in the position of the target. Such temporal demands would not be placed on the perception of these changes; indeed, in many instances, the changes might not have to be perceived at all, provided the requisite adjustments were made in the animal's motor responses.

Although objects, particularly animate ones, often change

their location as we reach out to pick them up, they rarely (if ever) change size. Thus, we might expect that, if an object were to suddenly shrink or expand in size as we attempted to pick it up, any adjustments that we made to grasp would be quite sluggish. In fact, Castiello and Jeannerod (10) found exactly that in an experiment in which a dowel that subjects were attempting to grasp suddenly and unpredictably increased or decreased in width as they began their grasping movement. In this situation, subjects took nearly 300 ms to make adjustments in the size of their grasp: a response time that was much longer than the 100 ms needed to respond to a shift in the location of the goal object. It is possible, as Castiello and Jeannerod suggest, that the slower responses to perturbations in object size arise because the visuomotor pathways mediating grasping are more complex than those mediating movements of the limb. It is also possible that there is little need for the ability to make rapid adjustments to abrupt changes in object size because such changes are quite uncommon in the real world. It is likely, however, that the ability to make rapid adjustments to sudden changes in the location of objects has been highly selected in primate evolution. Of course, there are situations where grip aperture and distal components of the grasp might also have to be adjusted on-line; a sudden change in the orientation of an object, for example, could require an adjustment in the posture of the hand and fingers. In any case, even though the responses to changes in object size were much slower than those to changes in object location, they were still significantly faster than the perceptual reports of the change in size. Again, subjects appeared to be adjusting their motor response to a visual event before they actually perceived it.

3. DIFFERENT SPATIAL CODING FOR PERCEPTION AND ACTION

The dissociation between motor adjustment and perceptual report has also been demonstrated in experiments in which the position of a target is moved unpredictably during a saccadic eye movement (7,8,28,32). In these experiments, subjects typically fail to report the change in the position of the target even though a later correction saccade and even a manual aiming movement directed at the target will accurately accommodate the shift in position.

To understand how these experiments have been carried out, it is necessary to consider what happens when we reach out and place our finger on a target that suddenly appears in the peripheral visual field. Not only does our arm and finger extend toward the target, but the eyes, head, and body also move in such a way that the image of the target is brought to the fovea. Even though the motor signals reach the ocular and brachial musculature at roughly the same time (4), the saccadic eye movements directed at the target are typically completed while the hand is still moving. (One reason for this, of course, is that the eye is much less influenced by inertial and gravitational forces than the limb.) The first and largest of the target-directed saccades is often completed before (or shortly after) the hand has begun to move. A second saccade, the so-called "correction saccade", puts the image of the target on the fovea. This means that during the execution of the aiming movement, the target, which was originally located in the peripheral visual field, is now located either on or near the fovea. Theoretically then, the more precise information about the position of the target

provided by central vision (coupled with extra-retinal information about the relative position of the eye, head, body, and hand) can be used to update the trajectory of the hand as it moves toward the target.

Support for this idea came from an experiment by Goodale et al. (28) in which the position of a target was changed unpredictably during the execution of the movement. Subjects were asked to move their finger from a central target to a new target (a small light) that appeared suddenly in their peripheral visual field. On half the trials, the peripheral target stayed in position until the subject had completed the aiming movement. On the remainder of the trials, however, the target was displaced to a new position 10% further out from where it had originally appeared. This sudden displacement of the target occurred just after the first saccadic eye movement had reached its peak velocity. The two kinds of trials were presented in random order, and the subjects were not told that the target would sometimes change position during the first eye movement.

The effects of this manipulation on the aiming movements and correction saccades were clear and unambiguous. As Fig. 1 illustrates, the final position of the finger on trials in which the target was displaced during the saccadic eye movement was shifted (relative to "normal" trials) by an amount equivalent to the size of the target displacement. (Similarly, the correction saccade, which followed the first saccade, always brought the target, displaced or not, onto the fovea.) In other words, subjects corrected the trajectory of their aiming movement to accommodate the displacement of the target that occurred on some of the trials. In addition, the duration of limb movements made to a displaced target corresponded to the duration of the movement that would have been made had the target been presented at that location right from the start of the trial. Thus, no additional processing time was required on displaced-target trials.

These particular findings confirm the suggestion that aiming movements are typically updated during their execution, even when the target does not change position. Although the initial programming of the movements is made on the basis of information about target location from the peripheral retina (combined with extra-retinal information about eye

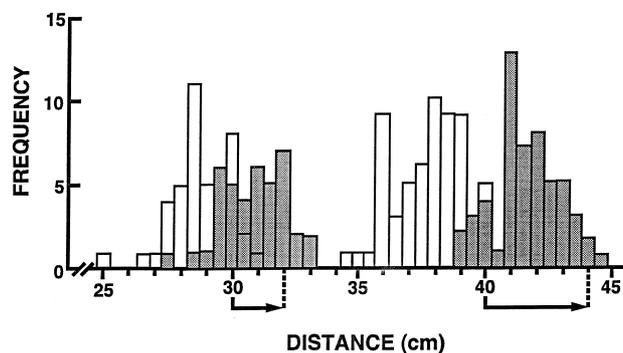


FIG. 1. Frequency distributions of the final positions of the index finger for the four subjects in single- and double-step trials for the 30 and 32 cm and the 40 and 44 cm targets. Unfilled bars indicate the final position for single-step trials. Filled bars indicate the final position for double-step trials. The extent of unfilled bars overlapped by filled bars is indicated by a horizontal line. The extents of the second displacements are indicated by the small arrows beneath the abscissa. (Adapted with permission from Goodale et al. (28).)

and head position), the trajectory of the moving limb and the amplitude of the final correction saccade is updated at the end of the first saccade, presumably on the basis of the more accurate information about target position that is available from central vision. This explains why the duration of a limb movement is the same for a given position of the target, independent of whether the target appeared there initially or was moved to that position from another during the first saccade. In either case, the same post-saccadic information would be used to update motor signals controlling the trajectory of the hand (provided the target displacement during the saccade was not too large). In other words, the apparent "correction" in the trajectory that occurred on displaced-target trials was nothing more than the normal updating of the motor programming that occurs at the end of the first saccade on an ordinary trial.

However, the most remarkable thing about these experiments was the dissociation between what the subjects did when the target was displaced and what they actually perceived was happening. Even though the subjects' motor output was exquisitely sensitive to changes in the position of the target, the subjects remained quite unaware of the fact that the target had jumped to a new location while they were reaching towards it. Indeed, even when subjects were told that the target would be displaced during the eye movement on some trials and were asked to indicate after each trial whether or not such a displacement had occurred, their performance was no better than chance. Of course, the failure to perceive stimulus change, particularly position, during saccadic eye movements is well-known and is sometimes termed "saccadic suppression" (e.g. (56,6)). However, in this case, subjects could not even detect that the target had changed position at the end of their first saccade. These and other experiments using similar paradigms (for review, see (21)) have consistently shown that subjects fail to perceive changes in target position even though they modify their visuomotor output to accommodate the new position of the target.

In fact, had the subjects perceived the change in target position that occurred on displaced-target trials and, on the basis of this perception, consciously altered the trajectory of their reach, then one might have expected the duration of the movements on these trials to have fallen outside the amplitude-duration curve observed on normal trials where no displacement occurred. The fact that this did not occur is additional evidence that the subjects were treating normal trials and displaced-target trials in an identical fashion and suggests that the "correction" observed on displaced-target trials is nothing more than the fine-tuning of the trajectory that occurs at the end of the first saccade in the normal course of events. Later experiments by Denis Pélisson (personal communication 1989) have shown that if the displacement of the target during the first saccade is made large enough, subjects will perceive the change in target position. When this happens, the subjects show a large re-adjustment in the trajectory of their reach that falls well outside the normal amplitude-duration curve for movements to targets that are initially presented in those locations. In other words, if the change in target position is perceived, then subjects fail to make efficient on-line adjustments in their motor output. Efficient on-line adjustments would appear to occur only if the subjects fail to perceive the displacement of the target.

Complementary dissociations between perception and action have also been observed in which the perception of

a visual stimulus is manipulated while visuomotor output remains unaffected. Bridgeman et al. (7) have shown that even though a fixed visual target surrounded by a moving frame appears to drift in a direction opposite to that of the frame, subjects persist in pointing to the veridical location of the target. Similar observations have been made using saccadic eye movements rather than pointing. In an experiment by Wong and Mack (58), for example, a small target was presented within a surrounding frame and after a 500 ms blank, the frame and target re-appeared, but now with the frame displaced a few degrees to the left or right. The target itself was presented at exactly the same location as before. In this case, however, instead of perceiving the frame as having changed position, subjects had the strong illusion that it was the target that had moved, in a direction opposite to that of the actual displacement of the frame. This illusion was maintained even when the target was displaced in the same direction as the frame, but by only one third of the distance. In this latter condition, the perceived change in target position following the blank period and the actual change of target position on the retina were in opposite directions. Yet despite the presence of this strong illusory displacement of the target, subjects consistently directed their saccades to the true location of the target. In short, an illusory displacement of target position occurred without any change in the spatial organization of the target-directed motor output.

Taken together, these findings suggest that the mechanisms mediating the perception of object location operate largely in allocentric coordinates whereas those mediating the control of object-directed actions operate in egocentric coordinates. In other words, perception uses a coordinate system that is world-based in which objects are seen as changing location relative to a stable or constant world; the systems controlling action systems, however, cannot afford these kinds of constancies and must compute the location of the object with respect to the effector that is directed at that target. Thus, in the experiments by Bridgeman et al. (7) and Wong and Mack (58), the target within the moving or displaced frame was perceived as moving relative to the frame while the frame itself, which was the only large visible feature in the field of view, was perceived as a stable background. The visuomotor systems computing the saccadic eye movements (or the aiming movements) directed at the target simply ignored the movement of the frame and computed the actual position of the target in retinocentric (and perhaps also in head and/or shoulder-centered) coordinates. In the experiments by Goodale et al. (28), in which the position of the target was changed unpredictably during a saccade, the subjects' failure to perceive the displacement of the target was probably a reflection of the broad tuning of perceptual constancy mechanisms: mechanisms which preserve the identity of a target as its position is shifted on the retina during an eye movement. When no other reference points are available in the field of view, the perceptual system assumes that the position of the target (which was stable at the beginning of the saccade) has not changed. Such an assumption has little consequence for perception and is computationally efficient. The visuomotor systems controlling saccadic eye movements and manual aiming movements cannot afford this luxury. At the end of the first saccade, they must re-compute the position of the target (within egocentric frames of reference) so that the

appropriate correction saccade and amendment to the trajectory of the moving hand can be made. In short, visuomotor control demands different kinds of visual computations than visual perception. As we suggested earlier, it is this difference in the computational requirements of the visual control of action and visual perception that explains the division of labour between the two streams of visual processing in the primate cerebral cortex.

4. PERCEPTUALLY DRIVEN MOTOR OUTPUTS

Until now, we have emphasized the fact that motor outputs, such as saccadic eye movements and aiming movements with the limb, are directed to the location of targets within egocentric frames of reference. These egocentric locations may or may not be coincident with the perceived location of the target. There are special circumstances, however, where motor output can be driven by the perceived position of a target rather than by its actual location in egocentric coordinates. One of the clearest demonstrations of the effect of perception on motor output comes from work by Wong and Mack (58), in which they employed the same paradigm they had used to demonstrate a dissociation between perception and motor control. In that paradigm, the target was displaced in the same direction as the surrounding frame but by only one third of the distance. Subjects moved their eyes correctly in the direction of the target displacement but perceived the target as having moved in the opposite direction. In Wong and Mack's second experiment, subjects were asked to look back to the "original" location of the target after making their saccade to its new location. These memory-driven saccades were made to a location in perceptual, not retinal, coordinates. In other words, the "look-back" saccade was made to a location that corresponded with the subjects' perceptual judgement about the previous location of the target: a judgement that was determined by the relative location of the target in the frame rather than by its absolute location in egocentric space.

The suggestion that memory-driven saccades may be driven by visual information that is different from that driving normal target-directed saccades (and by inference, may depend on separate neural pathways) is consistent with a number of other observations showing that the kinematic profiles and trajectories of saccades to remembered targets can be very different from those of target-directed saccades. Thus, saccades made 1–3 s following the offset of a target light were 10–15 ms longer and achieved lower peak velocities than saccades directed towards an identical target that remained illuminated (3). In addition, the coupling between peak velocity and movement amplitude also appears to be much more variable in saccades made to remembered rather than to visible targets (51). Memory-driven saccades also appear to be less accurate than those made to visible targets (20): these errors were seen even when the delay between target offset and the initiation of the saccade was as short as 100 ms. Moreover, the amplitude of the errors increased as the delay was lengthened systematically up to 2 s. This observation led Gnadt et al. to propose that a transition occurs in the oculomotor system between visually linked and memory-linked representations during the first 800–1000 ms following offset of a visual target and that "the 'memory' of intended eye-movement

targets does not retain accurate retinotopic registration" (20), p. 710). In summary, these differences in saccadic dynamics and accuracy suggest that the neural subsystems for the generation of saccades to remembered locations are to some degree independent from those subserving normal target-driven saccades (see, for example, (30,59)). Indeed, if, as the work by Wong and Mack (58) described above suggests, memory-driven saccades are computed in allocentric rather than egocentric coordinates, then the visuomotor transformations mediating those saccades may use the same visual information that underlies perceptual reports of spatial location.

Like eye movements, manual aiming movements are most accurate when directed to still-visible targets, and errors accumulate as the length of the delay period between target viewing and movement initiation increases (15,34). Indeed, Elliot and Mandelena (15) have suggested that a visual representation of the environment which would be useful for guiding manual aiming movements does not persist for longer than 2 s. It seems likely that the action systems underlying the control of pointing, like those underlying the control of saccadic eye movements, work optimally in "real time" with visible targets. Once the target is gone and some time has elapsed (2 s or more), the production of a aiming movement, like the saccadic eye movements discussed earlier, may have to be referred to earlier perceptual representations of the target: representations that depend on neural circuitry quite separate from that mediating aiming movements to visible targets.

5. DIFFERENTIAL SIZE CODING FOR PERCEPTION AND ACTION

Just as the perception of object location appears to operate within relative or allocentric frames of reference, so does the perception of object size. Although we often make subtle judgements of the relative sizes of objects,

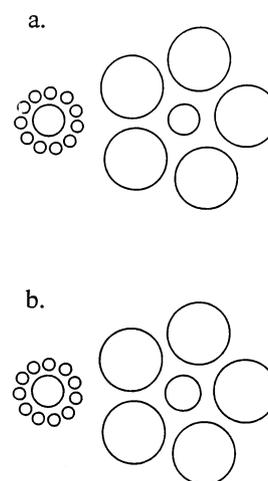


FIG. 2. The "Ebbinghaus" illusion. Panel a shows the standard version of the illusion in which physically identical target circles appear perceptually different. Most people judge the target circle surrounded by the annulus of smaller circles to be larger than the other target circle. Panel b shows a version of the illusion in which the target circle surrounded by the annulus of larger circles has been made physically larger than the other target, compensating for the effect of the illusion. Most people now see the two target circles as equivalent in size. (Adapted with permission from Aglioti et al. (1).)

we rarely make judgements of their absolute size. Indeed, our judgements of size appear to be so inherently relative that we can sometimes be fooled by visual displays in which visual stimuli of the same size are positioned next to comparison stimuli which are either much smaller or much larger than the target stimuli. Such size-contrast illusions are a popular demonstration in many introductory textbooks in psychology and perception. One such illusion is the so-called Ebbinghaus Illusion (or Titchener Circles Illusion) in which two target circles of equal size, each surrounded by a circular array of either smaller or larger circles, are presented side by side (Fig. 2). Subjects typically report that the target circle surrounded by the array of smaller circles appears larger than the one surrounded by the array of larger circles, presumably because of the difference in the contrast in size between the target circles and the surrounding circles. Although the illusion is usually depicted in the way just described, it is also possible to make the two target circles appear identical in size by increasing the actual size of the target circle surrounded by the array of larger circles (Fig. 2).

While perception is clearly affected by these manipulations of the stimulus array, there is good reason to believe that the calibration of size-dependent motor outputs, such as grip aperture during grasping, would not be. After all, when we reach out to pick up an object, particularly one we have not seen before, our visuomotor system must compute the object's size accurately if we are to pick it up efficiently. It is not enough to know that the target object is larger or smaller than surrounding objects; the visuomotor systems controlling hand aperture must compute its real size. Moreover, the visual control of motor output cannot afford to be fooled by an accidental conjunction of contours in the visual array that might lead to illusions of size or location. For these reasons therefore, one might expect grip scaling to be insensitive to size-contrast illusions.

To see just how insensitive grip scaling might be to such an illusion, Aglioti et al. (1) developed a three-dimensional version of the Titchener circles illusion in which two thin "poker-chip" disks were used as the target circles. In this experiment, trials in which the two disks appeared perceptually identical but were physically different in size were randomly alternated with trials in which the disks appeared perceptually different but were physically identical. Subjects were given the following instructions. If you think the two disks are the same size, pick up the one on the left; and if you think they are different in size, pick up the one on the right. (Half the subjects, of course, were given the opposite instructions.) The aperture between their index finger and thumb was monitored using opto-electronic recording.

All the subjects remained sensitive to the size-contrast illusion throughout testing. On trials in which the disks were physically identical, their choice indicated that they thought the disks were different in size; on trials in which the disks were physically different, they behaved as though they were the same size. Remarkably, however, the scaling of their grasp was affected very little by these beliefs. Instead, the maximum grip aperture, which was achieved approximately 70% of the way through the reach towards the disk, was almost entirely determined by the true size of that disk. As Fig. 3 illustrates, the difference in grip aperture for large and small disks was the same for trials in which the subject believed the two disks were equivalent in size (even

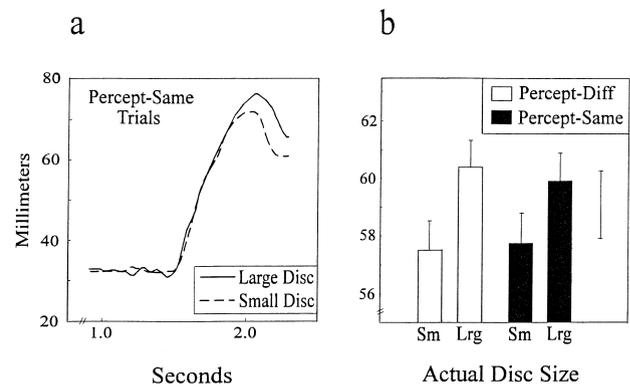


FIG. 3. Panel a shows representative grip aperture profiles for one subject picking up a large disk and a small disk on separate trials in which he judged the two disks to be identical in size (even though, of course, the two disks were physically different). In both cases, the disk was located on the left hand side of the display. Panel b shows the mean maximum grip aperture for the 14 subjects in different testing conditions. The two solid bars on the right indicate the maximum aperture on trials in which the two disks were judged to be perceptually the same, even though they were physically different in size. The two open bars on the left indicate the mean maximum aperture on trials in which the two disks were judged to be perceptually different, even though they were physically the same size (either two small disks presented together or two large disks presented together). The line on the extreme right of the graph indicates the average difference in disk size that was required to achieve perceptual equivalence as determined in a pretest. The difference between the maximum grip aperture achieved for large disks was significantly greater than the maximum grip aperture for small disks independent of whether or not the subject perceived the disks to be the same or different sizes ($P < 0.001$). No other comparisons were significant. Error bars indicate the standard error of the mean. (Adapted with permission from Aglioti et al. (1).)

though they were different) as it was for trials in which the subject believed the two disks were different in size (even though they were identical). In short, the calibration of grip size was largely impervious to the effects of the size-contrast illusion.

As we saw earlier, however, the control of skilled movements is not completely isolated from perception. There is no doubt, for example, that the perceived function of an object can affect the nature of the grasp that we adopt when we pick it up. Moreover, we often pick up the same object differently depending on what we plan to do with it. Thus, the grasp we use to pick up a glass of wine we are going to drink from is usually quite different from the grasp we use when placing the glass on a serving tray. It is perhaps not surprising, therefore, that perception had some effect on grip scaling even in the Titchener circles illusion task, at least on those trials in which subjects perceived the two disks to be different in size when, in fact, they were identical. On some of these trials, some subjects opened their fingers slightly more for the disk surrounded by the small circles than they did for the disk surrounded by the large circles. Nevertheless, this perceptual effect on grip aperture was quite variable and was significantly smaller than the size difference that was required to achieve perceptual equivalence between the two disks in judgement tasks. In other words, the effect of the illusion on grip size was much smaller and more variable than the effect of the illusion on perceptual judgements of size. In contrast, as we have already seen, all subjects showed a strong effect of real object size on the calibration of their grip, independent of

whether or not it was on perceptually different or perceptually identical trials.

It is remotely possible, of course, that the accurate scaling of the grasp was simply due to the fact that the subjects were, somehow, comparing their grip aperture with the diameter of the target disk in flight. This is unlikely for several reasons however. For one thing, as can be seen in Fig. 3, the maximum grip aperture was actually much larger than the diameter of the disk: more than twice as large on most trials. However, just as has been observed in many previous studies of grasping (see (36,37)) maximum grip aperture was still well correlated with the size of the target. Secondly, subjects remained susceptible to the illusion throughout the experiment, despite the fact that they were scaling their grasp to the real size of the target disk. If they were adjusting their grasp on the basis of information delivered by the same visual networks that they used to make their perceptual judgements, then one might expect to see some weakening of the illusion over the course of the experiment. No such weakening was observed. Thirdly, the calibration of maximum grip aperture is largely determined by motor programming that is carried out before the hand has actually left the table (36), and as we saw earlier, can be modified by new information only late in the trajectory (10). In fact, on a few occasions, subjects expressed surprise when they handled the disk after they had picked it up, claiming that it seemed larger or smaller than they had thought it was, even though their grasp had been calibrated accurately in flight.

Nevertheless, it seemed important to eliminate the possibility of on-line modulation, since adjustments to the grasp were undoubtedly occurring at least in the final portion of the reach trajectory. In addition, there was another, perhaps more serious, problem with the Aglioti et al. (1) study: the measure of the effect of the illusion on perception was essentially dichotomous, while the measure of its effect on the grasp was continuous. For these reasons, in a subsequent experiment (31), we replicated the Aglioti et al. (1) study, but with two modifications. Firstly, the entire experiment was run in "visual open-loop". In other words, as soon as subjects had made their choice about whether the disks were the same or different in size and had begun to move their hand toward one of the disks, the lights were turned off, leaving them with no opportunity to use vision to modify their grip aperture on-line. Secondly, an additional condition was added to the experiment in which subjects were asked not to pick up the disk after making their choice, but rather to estimate the diameter of the disk by opening their index finger and thumb a matching amount. This response, which was also run in open loop, gave a continuous measure of the subjects' perception of disk size that could be more directly compared to the calibration of the grasp. The results of this study were clear and unambiguous. The scaling of grip aperture was again correlated with the true size of the disk, even though the subjects were now grasping the disk without the benefit of any visual feedback. The subjects' manual estimations of disk size, however, were strongly biased in the direction of the illusion.

However, why should perception be so susceptible to this illusion, whereas the calibration of grasp is not? The mechanisms underlying the size-contrast illusion are not well understood. It is possible that it arises from a straightforward relative size judgement, whereby an object that is

smaller than its immediate neighbors is assumed to be smaller than a similar object that is larger than its immediate neighbors. It is also possible that some sort of image-distance equation is contributing to the illusion in which the array of smaller circles is assumed to be more distant than the array of larger circles; as a consequence, the target circle within the array of smaller circles will also be perceived as more distant (and therefore larger) than the target circle of equivalent retinal image size within the array of larger circles. In other words, the illusion may be simply a consequence of the perceptual system's attempt to make size constancy judgments on the basis of an analysis of the entire visual array (13,29).

Mechanisms such as these, in which the relations between objects in the visual array play a crucial role in scene interpretation, are clearly central to perception. In contrast, the execution of a goal-directed act like prehension depends on metrical computations that are centered on the target itself. Moreover, the visual mechanisms underlying the control of the grasping movements must compute the real distance of the object (presumably on the basis of reliable cues such as stereopsis and retinal motion). As a consequence, computation of the retinal image size of the object, coupled with an accurate estimate of distance, will deliver the true size of the object for calibrating the grasp. The relative insensitivity of reaching and grasping to pictorial illusions has been demonstrated in several other recent experiments employing a number of different classical illusions, including the horizontal-vertical illusion (55), the Ponzo illusion (Ian Whishaw, personal communication 1994), and the Müller-Lyer illusion (19). What is particularly interesting about the last of these studies is that the introduction of a 5 s delay between viewing the display and responding significantly increased the effect of the illusion on the calibration of the final motor response. As was discussed earlier and as will be explored further in the next section, motor responses to remembered stimuli appear to rely more on a perceptual than an action-based frame of reference.

6. GRASPING OBJECTS THAT ARE NO LONGER THERE

Skilled actions are not entirely immune to the influences of perception and cognitive factors. As was mentioned earlier, the perceived functions of objects, such as hammers, pens, wine glasses, and telephones, can have clear effects on the way we pick them up. In other words, the posture of our hand anticipates what we intend to do with an object that we are about to pick up. Nevertheless, a good deal of the metrical calibration of the final grasp depends on computations that are largely impervious to such perceptual and cognitive influences. Moreover, these metric computations are generated according to a "just-in-time" rule; they are not prepared ahead of time but only when an action is about to occur. The reasons for this are clear. Observers and goal objects rarely stay in the same location with respect to one another; i.e. the egocentric coordinates of a goal object often change dramatically from one moment to the next. It would make sense, therefore, to compute the required coordinates for action immediately before the movements are initiated and it would make little sense to store these coordinates (or the resulting motor programs) for more than a few milliseconds before executing the action.

If visuomotor computations occur in “real time,” then movements directed to remembered objects (objects that were present in the visual array, but are no longer there) might be expected to look rather different from movements directed to objects that remain visible. Indeed, as we have already discussed, there is a good deal of evidence to suggest that this is the case for aiming movements and saccades made to remembered targets. In fact, the trajectories of such movements appear to reference stored perceptual representations of the target location rather than the location of the target in egocentric coordinates. A recent experiment by Goodale et al. suggests that the same is true for grasping movements directed at remembered objects (23). Their experiment was run as follows. Subjects were first shown a rectangular block, the size and distance of which varied from trial to trial. Automated shutters located in front of the subjects’ eyes were then closed for 2 s and the block was removed. The shutters then opened and the subjects were required to reach out and pretend to pick up the block as if it were still there. In other words, subjects were being asked to pantomime a grasping movement, but only 2 s after last seeing the intended goal object. Subjects performed these pantomimed actions in a manner that was quite different from the way in which they executed natural, goal-directed grasping movements. Their mimed actions consistently reached lower peak velocities, tended to last longer, followed more curvilinear trajectories, and undershot target location, compared to normal reaches. Moreover, subjects consistently opened their hand less when miming than when reaching for objects which were physically present, although their grip aperture was still highly correlated with the size of the object they had viewed just 2 s before.

It is perhaps worth emphasizing that pantomiming a grasp to a no-longer visible object after seeing it 2 s earlier does not resemble the kind of grasp that is observed when subjects reach in visual open loop; i.e. when the lights are turned off as the movement begins. The kinematics of open-loop grasping are much more similar to the kinematics of

normal closed-loop grasping directed to visible targets (36). In fact, where open-loop grasping does differ from closed-loop grasping is in grip aperture; open-loop grasps typically achieve a larger maximum aperture, presumably to compensate for the absence of visual feedback in the closing phase of the grasp. Pantomimed grasps, of course, have smaller maximum grip apertures than closed-loop grasps.

The programming of pantomimed movements must rely, not on current visual information, but rather on a stored representation of the previously seen object and its spatial location: a representation that was presumably derived from earlier perceptual processing of the visual array. As was argued earlier, the perceptual system, which plays a major role in object recognition, is designed to represent objects and their spatial locations over quite long periods of time. For perception, a retention interval of 2 s is trivial. Clearly we are capable of remembering the characteristics of objects we have seen only once for extremely long periods of time. If pantomimed movements depend on perceptual representations, then it is possible to make an interesting prediction about DF, the young woman with visual form agnosia described at the beginning of this article, whose perception of the size, shape, and orientation of objects is severely impaired. She should have real trouble pantomiming grasping movements to objects seen only 2 s earlier, even though, as was described earlier, she has no difficulty grasping objects in real time. As Fig. 4 illustrates, this is indeed the case. After a delay of 2 s, DF appeared to have “lost” all information about object size needed to preshape her hand in flight. Of course, this is not all that surprising since DF had no “percept” of the object in the first place. When no object was present to drive her real-time visuomotor control systems, she could not fall back on the stored information about object size that was available to normal subjects.

Because visuomotor control systems not only operate in real time but also within egocentric frames of reference, we would expect them to be ill-equipped to deal with a significant spatial displacement of the required output coordinates

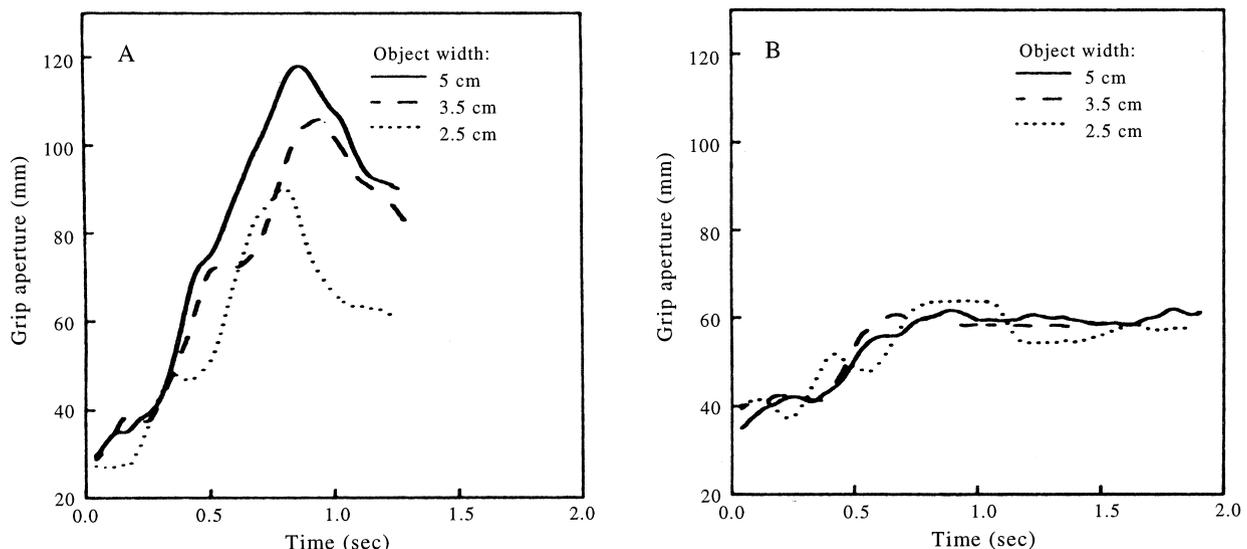


FIG. 4. Profiles of DF's grip aperture without (A) and with (B) a 2 s delay. While peak velocity and movement amplitude continue to be scaled for target distance during the delay condition, all evidence of anticipatory hand shaping for target size is lost. Thus, the relationship between the maximum opening of the patient's hand in flight and the size of the target object seen without a delay does not endure when a delay is imposed. (Adapted with permission from Goodale et al. (23).)

with respect to the actual coordinates of the target. Not surprisingly then, requiring normal subjects to pantomime a grasping movement beside an object, as opposed to grasping it directly, resulted in the same kind of change in the kinematics of the movements as was seen in the movements directed to remembered objects. Moreover, since these pantomimed movements were presumably also driven by perceptual representations of the target object rather than on-line visuomotor control systems, DF was unable to perform them as well as normal subjects (23).

Results such as these provide convincing evidence that the visuomotor systems underlying goal-directed actions are different from those underlying pantomimed actions, which appear to depend more on the perceptual systems mediating object recognition. This is not to suggest that memory about objects does not influence motor behaviour, or that memory is not used to optimize motor performance. After all, we can and do use information about objects, such as their function, weight, fragility, temperature, and friction coefficients, in planning movements directed at those objects (e.g. (39)). In addition, we all know that our performance of many motor skills improves with practice. Yet when we perform an action, however well-rehearsed that action is and however well-informed we might be about the intrinsic characteristics of the goal object, we still must compute the egocentric coordinates of the target object at the precise moment we execute that action. We cannot rely on memory to do this, because, of course, the location and orientation of that object with respect to our own body coordinates can vary enormously from one occasion to the next. As we saw at the outset of this section, this is the reason it would not be useful to store such coordinates (or the resulting motor programs) for more than a few moments (certainly less than 2 s) before executing the action.

7. PERCEPTION AND VISUOMOTOR CONTROL IN THE PERIPHERY

There can be little doubt that the best way to see something is to look at it. Indeed, our ability to identify objects falls off dramatically as our view becomes more and more peripheral (for reviews, see (52)). However, why are our visual fields so extensive if most of our perception of the world comes from central vision? Part of the answer, of course, is related to the need to detect biologically relevant stimuli across a wide region of visual space. Humans, like most highly visual vertebrates, typically orient their gaze (and thus their fovea) towards objects and events that suddenly appear in the visual periphery. However, this is not the only reason why our visual fields are so large. Many of the movements that humans make through the world require processing of information far into the periphery. Thus, when we walk from one place to another in our immediate environment we use the optic flow that is generated by our movement to control both our heading and our rate of locomotion (for review, see (57)). We also use optic flow to modulate our posture, particularly on uneven terrain or in situations, such as balancing on a narrow beam, where proprioceptive information is unreliable (for review, see (38)). We even seem able to pick up objects, such as coffee cups and pens, without looking at them directly.

Most of the time, we remain quite unaware of the fact that

we are using information from the visual periphery to control our actions. However, is this simply a question of attention? The evidence we have reviewed throughout this review would suggest that visuomotor control is mediated by networks that are quite separate from those delivering our perception of the world. Perhaps these visuomotor systems have privileged access to information from the visual periphery. To put it another way, even if we were directed to attend to stimuli in the visual periphery, our ability to discriminate between these stimuli would never be as good as our ability to use them to direct our actions. Recent experiments in our laboratory suggest that this is indeed the case (27,46).

In these experiments, subjects were presented with one of five different rectangular blocks for 100 ms at various positions in the peripheral visual field along the horizontal meridian, from 5° to 70° . The change in eccentric viewing was accomplished by having the subjects direct their gaze increasingly leftward at fixation points located at different distances from the target object along the same horizontal plane. Thus, although the retinal location of the target block varied from trial to trial, the location of the block, with respect to the subject's hand and body, remained constant. Sensitivity to the width of the blocks (which varied in their dimensions but not in their overall area) was measured under two response conditions: a visuomotor condition in which subjects were required to reach out and grasp the block; and a visuperceptual condition in which subjects were required to categorize the different blocks on the basis of their width.

When subjects reached out and grasped the blocks, the maximum aperture of their grasp increased with the eccentricity of the view but continued to be well-tuned to the actual width of the target block. Moreover, as Fig. 5

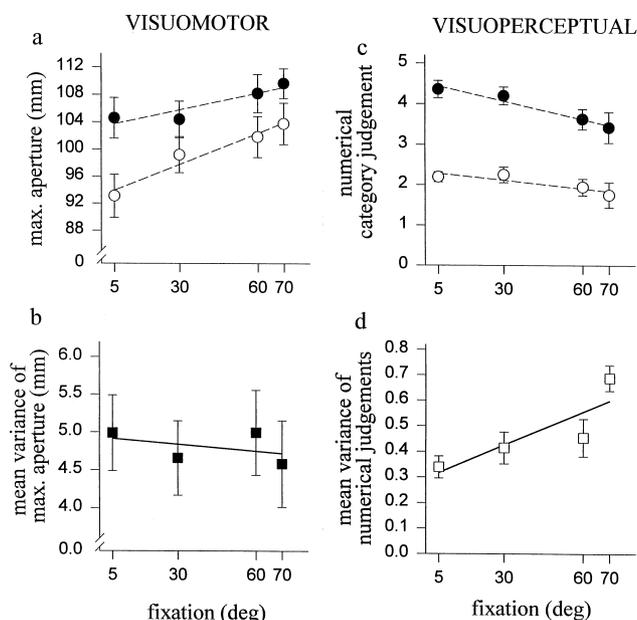


FIG. 5. Reaching to and estimating two different sizes of blocks: (a) maximum grip aperture increases with increasing retinal eccentricity, but (b) the variance seen in grip scaling remains constant. (c) in contrast to the visuomotor results, estimations of block size decrease with increasing retinal eccentricity and (d) the variance of the estimations increases. (Adapted with permission from Goodale and Murphy (27).)

illustrates, trial-to-trial variability in grip aperture did not change as a function of eccentricity. In contrast, when subjects were asked to make perceptual judgements of the width of the objects, they progressively underestimated the width of the blocks as retinal eccentricity increased. In addition, even though the subjects continued to discriminate between the blocks in the peripheral visual field, the variability of their judgements increased significantly the further away from central vision the block was viewed (Fig. 5). These and other findings (for review, see (27)) suggest that visuomotor systems may be more sensitive to stimuli in the visual periphery than the perceptual systems mediating our experience of the visual world beyond the fovea.

These behavioural observations in humans are consistent with anatomical and electrophysiological studies in the monkey showing that areas in the dorsal stream receive extensive inputs from the peripheral visual fields while inputs to the ventral stream are largely from more central regions of the visual field (for review, see (2,12)). The difference in representation of the visual field might explain why the visual control of grasping movements directed at

targets in the visual periphery is so much more reliable than perceptual judgements about those same objects; in short, the dorsal action is simply better connected with the visual periphery than the ventral perception system.

8. CONCLUDING REMARKS

The various examples of dissociations between perceptual judgement and visuomotor control that we have reviewed in this paper provide powerful evidence for the parallel operation, within our everyday life, of two types of visual processing systems. Each system has evolved to transform visual inputs for quite different functional outputs, and, as a consequence, is characterized by quite different transformational properties. The nature of the dissociations lend further support to the proposal by Goodale and Milner (25,43,44) that these two types of processing are mediated by separate visual pathways in the primate cerebral cortex. The parallel operation of these two systems lies at the heart of the paradox that what we think we “see” is not always what guides our actions.

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