Do action systems resist visual illusions?

David P. Carey

Arguments about the relative independence of visual modules in the primate brain are not new. Recently, though, these debates have resurfaced in the form of arguments about the extent to which visuomotor reaching and grasping systems are insensitive to visual illusions that dramatically bias visual perception. The first wave of studies of illusory effects on perception and action have supported the idea of independence of motor systems, but recent findings have been more critical. In this article, I review several of these studies, most of which (but not all) can be reconciled with the two-visual-systems model.

One of the principal criticisms levelled at the Milner and Goodale reformulation1 of Ungerleider and Mishkin's two visual systems hypothesis2 has been that the model was based on evidence from a single patient³, the visual form agnosic DF. This complaint is oversimplified, because much of the model draws on neurophysiological and neuropsychological work on human and non-human primates (including many of the studies referred to in the original model²). Nevertheless, this criticism has fuelled substantial interest in two lines of research on neurologicallyintact individuals that have been advanced as strong support for Milner and Goodale account. One argument proposes that requiring participants to make movements to memorized targets must require participation of ventral stream perceptual mechanisms, because sensorimotor control systems of the dorsal stream are incapable of maintaining representations of target attributes for more than a few seconds.

Motor systems might resist visual illusions

The second suggestion for non-clinical research on the two-visual-systems theory has received more attention. In 1995, Aglioti, DeSouza and Goodale⁴ argued that a size-contrast illusion was resisted by the sensorimotor systems that control grasping. When participants grasped a disc that they acknowledged looked smaller than a second disc in a different visual context (the Titchener illusion), their maximum grip aperture was relatively unaffected (see Fig. 1). In spite of the existence of earlier studies showing similar dissociations (e.g. Ref. 5) the Aglioti *et al.* paper has captured most of the limelight.

Reviewing some of the numerous follow-up papers for academic journals has been a fascinating experience. Some replicate, some don't, and some 'sort of replicate. As I have said elsewhere⁶, I am

somewhat concerned about how many of the second category (those that don't) are not submitted for publication in the first place.

The 'critiques and caveats' phase

The papers of the third category interest me most, because, if you are a believer in the Milner-and-Goodale viewpoint, they are interpreted as evidence for intercommunication between the two streams. If you are not (because motor responses are usually affected in some way by the illusion in question), experimental conditions, rather than a 'real' dissociation between perception and action, accounts for the 'illusory impenetrability' of the action.

Attending to one or two stimuli?

For example, for Titchener and Müller-Lyer illusions at least, participants may look at/attend to only one of two stimulus configurations while grasping. Both Pavani et al.7 and Franz et al.8 have advanced this sort of argument, by showing that perceptual responses drop to effect levels seen in grasping conditions, if only one stimulus configuration is shown at a time. Franz et al. go so far as to claim that their result 'removes one critical piece of evidence that is usually counted in favour of this [Milner and Goodale] theory' (p. 24). This recent criticism has already been praised⁹ as well as questioned: Jacob and Jeannerod have argued that 'if a stimulus does not give rise to a perceptual illusion, it does not provide an adequate basis for drawing any conclusion upon Goodale and Milner's hypothesis' (Ref. 10, p. 9). I interpret this argument as something like: 'if you had a circular target with no annuli and no illusion, and perceptual and motor responses were equivalent, what could you conclude from that?' Nevertheless, I think Franz et al. are suggesting the mechanism of motor-system resistance, even when both stimuli are present: processing resources are concentrated on a single target in grasping while both arrays are looked at and attended to in perceptual tasks.

Although the 'one versus two stimuli' argument has some merit, in many experiments participants have been asked to make perceptual judgments with both arrays present, immediately before making a motor response to one of the two stimuli. In this way, chances for perceptual processes to affect the grasp seem to be maximized (c.f. Expt 4 in Ref. 11). In these cases if the argument is that *immediately* before or during the actual grasp the target is processed preferentially over the surround, then the criticism has converged with the theoretical position of Aglioti and colleagues regarding what the dorsal stream does (and hence becomes a restatement of the original position). Of course, in certain instances motor systems have to process information about the surround near to a target, in order to avoid obstacles.

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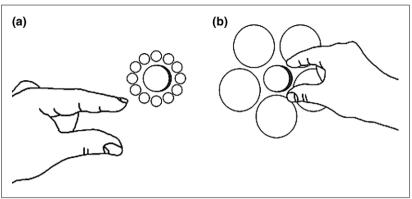


Fig. 1. Perceiving and grasping the Titchener illusion. A schematic view of a matching response is depicted at left. In such trials the size of the gap between index figure and thumb is used by participants to show how large or small the target appears to be. The terminal phase of a grasping response is shown at right. The maximum grip size on such trials occurs quite early in the movement and is relatively insensitive to the illusory effects of the surrounds

Does the reaching hand occlude part of the illusory array?

Another critique of the Aglioti et al. and related findings, also of the 'task conditions and constraints' type, was recently published by Mon-Williams and Bull12. They argued that the view of the reaching hand could occlude a portion of the stimulus configuration (in their case the Judd illusion figure, also used by Ellis et al. in a similar experiment¹³), thus reducing the illusory consequences of the full array. This argument also has its merits as a critique of task differences when the hand is visible during the motor task. However it says little about action versus perception differences in tasks where the hand can't be seen relative to a target (as the authors acknowledge). Additionally, in some of the hand-visible experiments, occlusion of any part of the stimulus array by the hand would happen well after maximum grip aperture (the dependent measure of choice in the initial studies; see Fig. 2).

Are some aspects of actions influenced by the illusion? This leads us to a related issue: why use maximum grip aperture and not some other motor-dependent measure as the index of visuomotor processes? A critique of the Aglioti et al. study by Brenner and Smeets14 and more recently by Jackson and Shaw15 raises several questions of this sort. Both groups looked at perceptual and action based responses to Ponzo illusion configurations. The results of both studies are consistent: grip scaling was not affected by the illusory stimulus but the velocity of object pick-up14 and grip force¹⁵ were. The authors conclude that perceived mass of the targets was influenced by the illusory context prior to object contact. Thus, participants gripped and lifted objects that they perceived as larger more forcefully than objects they perceived as smaller.

What is contentious is the interpretation of this finding? Because the grip force and lifting velocity were influenced in the appropriate directions by the illusions, and are obviously parts of a motor act, illusions can affect motor acts, which the Milner and Goodale account² would classify as dorsal. A similar argument (that not all types of hand-invisible pointing movements are insensitive to visual illusions), based on quite different tasks, has been advanced in an

excellent paper by Post and Welch¹⁶. Other studies along the same lines are too numerous to describe in detail. but the best of them include^{17–20}.

Are all actions 'dorsal'?

The demonstration that perceptual information can influence actions is not necessarily a damning critique of the Milner and Goodale account. For example, most of the contributors to this literature would surely agree that using the gap between the finger and thumb to show how large a target 'looks' would not be considered as a 'pure motor' (dorsal) response. The Milner and Goodale model acknowledges that stored information can be used to shape motor responses in many circumstances.

"... a patient scales her grip size to familiar, recognized targets... but fails to do so to unfamiliar targets that vary in size."

For example, a patient (AT) with a parietal lesion (thought to be in the human equivalent of the dorsal stream) scales her grip size to familiar, recognized targets, such as lipsticks and pint glasses, but fails to do so to unfamiliar targets that vary in size 21 . How did she manage the former and not the latter? Presumably she used the same neural machinery that would let anyone *mimic* picking up a pint glass of beer versus a stick of carrot.

Other ways in which perceptual processes or memory can influence actions are too numerous to list. I think Jackson and Shaw¹⁵ and Brenner and Smeets¹⁴ might contemplate the familiar experience of picking up an object that was less heavy than expected (an empty glass of beer when a near full one was expected is a disappointingly familiar example for myself). My own opinion regarding which visuomotor processes should be considered exclusively dorsal are outlined more fully elsewhere²² but suffice it to say that my best guess is that the dorsal stream grasping systems are even 'dumber' than Goodale thinks they are (c.f. Ref. 23). These circuits process egocentric coordinates, size (or aspect ratio²²) and three-dimensional orientation of a selected target, and on the basis of these attributes extract appropriate grasp points and the necessary innervatory patterns (and feedback monitors) to get the hand there quickly, efficiently and effortlessly (the latter in cognitive and perceptual terms, that is). Like an earlier attack by Ettlinger²⁴ on the Ungerleider and Mishkin two-visual-systems theory, I have no doubt that dorsal stream mechanisms (and their partners in crime in the frontal lobe) also play several non-visual roles in motor control (monitoring efference copy and/or proprioceptive feedback about limbs and eyes, controlling orienting responses to auditory targets, etc.).

Fig. 2. The stimulus display used by Otto-de Haart et al.6 and a participant late in a reaching movement. Participants were required to look at both stimuli before the left or right arrow shaft was specified as a target. A right-handed movement to the targets in the picture plane would minimize any occlusion of the illusory enducers until very late in the movement (what might appear to be occlusion is in fact an artefact of the viewpoint of this figure). From the participant's viewpoint, any occlusion was unlikely, even at the late phase of the movement depicted here.



I do have doubts about exclusively dorsal roles for movements made in response to targets on a computer screen, where proprioceptive feedback about hand (or, worse, mouse) movements are distant and in a different plane from their visual consequences. I also have some concerns about movements that are directed at targets in which a 'standard sensorimotor mapping' (Ref. 25; what Bridgeman calls an 'isomorphic response' 11,26) does not necessarily apply. Examples include moving to targets that are defined by other targets, such as bisecting a 2-D Judd figure with a pointing movement (Ref. 16 but see also Ref. 13), moving towards 2-D drawn targets (e.g. 'as if reaching to pick up a very thin object'; Ref. 27, p. 1662) or moving towards a 3-D target from a plane further from the participant than that plane on which the target lies (e.g. pointing from underneath a table towards its surface, which lies between the participant and their moving limb¹²).

Other related examples of so-called exclusively 'motor' responses include manipulations for hand-invisible reaching that require participants to close their eyes (I, Subbiah, J.M. Loomis and J.W. Philbeck, pers. commun.). The accomodative/vergence changes that accompany eye closure alone are sufficient grounds to question a 'pure motor' category for such a behaviour. That is, when 'open-loop' conditions are created by extinguishing room lights as (or just before) a hand-movement begins, an eye-position signal can still play a significant role in successful reaching²⁸. Such signals might be interfered with during 'eyes-closed' movements.

I would argue that all of the movement tasks described above can, in one way or another, engage perceptual mechanisms in neurologically-intact participants. I seriously doubt that a 'blindsight' patient or a severe visual agnosic could perform such tasks with the same ease as they solve standard sensorimotor puzzles like picking up plastic rectangles or pointing towards a just-extinguished target (has anyone ever looked at the effects of delay on localization in blindsight patients?).

Properties of the dorsal stream

This reasoning might seem a little circular for the critics of the Aglioti *et al.* story. Nevertheless there are some empirical predictions that a strong two-systems view makes about movements that are 'dorsal' versus movements that require participation of perceptual mechanisms and/or enduring representations (e.g. how much beer is left in my glass?) of target attributes^{29,30}.

First, task performance should be particularly sensitive to delay, given the theoretical and empirical reasons to think that dorsal stream systems operate in real time. Second, the theory proposes that dorsal systems use viewer-centred, egocentric codes that are metric. Movements that require processing information about coordinates of the target relative to other non-targets (that aren't obstacles, that is) are probably not exclusively dorsal³¹. Third, targets have to be real objects, and not 2-D or virtual stimuli. I appreciate why some authors believe that virtual objects defined stereoscopically might, to some extent, interest dorsal mechanisms, but the lack of haptic feedback after a few 'grasps' at such targets would probably result in actions that are more pantomimed than not.

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I also suspect that holes aren't appropriate stimuli as targets for grasping³² although they must be navigated by dorsal stream mechanisms in reaching (and thus would influence dorsal stream control of wrist orientation). Fourth, at least some of the circuitry of the dorsal stream should process targets preferentially in peripheral rather than central vision (or show small differences relative to central vision at least³³).

Some remaining questions

Even taking into account the above caveats, it is not so easy to see any obvious 'perceptual' component in two recent demonstrations of illusory effects on action. First, van Donkelaar has found that response times and durations of pointing movements are biased by Titchener dispays³⁴, such that perceptually larger targets are reached for more quickly (presumably owing to a speed–accuracy trade off similar to that seen when real target size is increased or decreased). Second, Glover and Dixon have used an orientation illusion to examine posting and matching responses (S.R. Glover and P. Dixon,

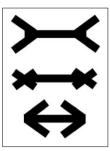


Fig. 3. Stimuli used in the Westwood et al. experiment²⁰. Three-dimensional versions of these stimuli would be grasped very differently depending on which configuration was reached towards. (Reproduced, with permission, from Ref. 20.)

pers. commun.). Although posting movements achieved orientations that seem unaffected by illusory context towards the end of the movement, early phases were indeed biased by the illusions. They concluded that the distinction should not be between visuomotor and visuoperceptual processes *per se*, but instead might be better fit by a preplanning versus on-line feedback dichotomy, which cuts across both perception and action.

This critique is interesting and I look forward to seeing it in a fuller form. However, I wonder about its distinctiveness from sensorimotor conceptualizations of dorsal stream function. They argue that the feedback module doesn't need to see the reaching limb against the visual target, because error corrections in movements can happen in the absence of visual feedback (which strongly implicates a feedforward signal like an 'efference copy' of the motor commands to move the eyes and limb and a feedback signal from the moving limb on its current position and trajectory). This signal sounds remarkably like a function that I would attribute to the dorsal stream. Nevertheless, illusion effects early in movements rather than later are worth examining in more detail, as are illusions which occur at different levels of the visual pathways, which are shared or not shared contributors to both dorsal and ventral streams³⁵.

Are small effects on motor responses dependent on the illusion itself?

A better example of confounds in some of the unsupportive experiments is illustrated in an experiment by Haffenden and Goodale³⁶. They

Outstanding questions

- Are sensorimotor systems sensitive to certain illusions but not others?
- Do illusions effect motor systems in early trials but then repeated exposure to the arrays decreases the illusion magnitude, or provides accurate haptic and proprioceptive feedback, which recalibrates visual grasping?
- Are there limitations on how 2-D information can be used by sensorimotor systems?
- What can be learned about perception and action if some movement parameters are influenced by visual illusions but others are not?
- Are similar dissociations between illusion and action seen in non-visual modalities like audition and touch?
- Can communication between two visual streams be visualized with fMRI, using illusory stimuli with and without delayed responses?

compared the effects of 'flankers' on size judgments and grasping of disks. They found that flankers at a certain distance above and below the target disk tended to decrease the size of the maximum grip aperture, as if the motor system was concerned with avoiding collision with the flankers during the approach. In certain circumstances (e.g. as with Titchener annuli larger than the central disk) such an effect on maximum grip is in the appropriate direction for the illusion, but in other conditions Haffenden and Goodale produced effects on perception and action in the opposite directions. The effects obtained were small and need to be replicated, but certainly suggest the importance of undertstanding how all components of the task effect grasping as well as perceiving, particularly any effects which are independent of those responsible for the illusion in question.

I was puzzled by the Haffenden and Goodale results because (as with most stimulus surrounds used in this genre) the flankers were twodimensional but the target to be grasped was three-dimensional. The authors argue that 'visuomotor systems depend on rapid and reliable computations for which edges, even two dimensional edges, could form part of the input for programming and controlling the movement' (p. 1600). Surprisingly, grasping systems of the dorsal stream seemed unable to determine that the depth plane of the flankers was different from that of the targets, which doesn't sit well with Milner-and-Goodale-type accounts of pictorial cues as exclusively ventral (although see Ref. 37 for a later account). I am surprised that this has not been seen as an obvious critique against the idea of motor resistance to illusions in grasping (although see Ref. 6).

An analysis of the effects of the arrowheads in Müller-Lyer figures modelled on Haffenden and Goodale's analysis of the flankers in the Ebbinghaus illusion is also called for. Recently Westwood et al. have claimed that the velocity of finger-thumb opening is effected by illusory figures even in hand-invisible conditions where maximum grip aperture is relatively resistant to the illusion²⁰. Nevertheless, this study needs to be replicated using faster movements. The central portions of the figures to be grasped were relatively thin (as are all stimuli in such experiments, in order to minimize depth cues from shadows etc.) and were presented horizontally, which may have made them difficult to grasp. The long movement times in their sample support this interpretation. Grip-aperture profiles can contain small maximum apertures, seemingly fitted to the targets towards the end of a movement, if participants are particularly slow and the targets are hard to grasp. Nevertheless, if these data are replicated, such a study should examine the effects of different arrowheads on grip aperture formation in the absence of a Müller-Lyer illusion (see Fig. 3). In

fact, presenting the stimuli one-at-a-time rather than in pairs makes sense in this context: any effects of arrowhead type which occur *independently* of illusion magnitude could be identified and discounted.

Conclusions

I am not surprised that the initial enthusiasm for the findings of Aglioti *et al.* have been followed by some very strong reservations (and equally strong 'meta-reservations'). This isn't the first time that a scientific claim has captured the imagination of a number of other scientists, but inevitably the debate must move into a second phase, where the really hard thinking about control conditions, statistical analysis, and so on, comes to the fore. Even if the critics of Aglioti *et al.* win the day, in the long run, good experimental work will have to be done that examines how different types of visual information are used to control action. Flanker effects, 2-D versus 3-D cues, attentional biases and

the like are all potential variables which need to be understood in motor control with the same attention to detail as the excellent work done on visual perception.

Finally, I confess to some reservations about having just endorsed predictions about a construct ('the human dorsal stream'), which remains relatively theoretical in itself. The link between 'illusionimpervious' motor responses and areas of occipitoparietal cortex remains unproven, in spite of a few early attempts to provide evidence in neurologically-intact participants (Ref. 6, but see Ref. 38 for an alternate viewpoint). Nevertheless, I am confident that technologies for recording movements and for imaging brain activity in neurologically intact subjects will confirm some of these speculations and dismiss others (and no doubt add to the debate about the Milner and Goodale account in general, and not just with regard to illusions and the two-stream theory).

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