



Review

Converging evidence for diverging pathways: Neuropsychology and psychophysics tell the same story

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ABSTRACT

In 1992, Goodale and Milner proposed the existence of a dedicated visuomotor control system that allows for the control of action without the need for conscious perception of the target object's form. The 'action and perception hypothesis' was motivated in large part by the surprising observation of spared visuomotor abilities in D.F., a patient with a severe deficit in visual form perception attributable to a lesion concentrated in the lateral occipital complex of the ventral stream. When D.F. reaches out to grasp an object, her hand posture in flight reflects the size, shape, and orientation of the object, despite the fact that she is unable to report those same object features. Nevertheless, there are systematic limits to her spared ability to grasp objects: her performance sharply deteriorates for objects defined by second-order contrast, objects whose principal axis of orientation is ambiguous, objects removed from view before the onset of the action, and objects seen without cues to absolute distance. At the same time, a considerable body of psychophysical evidence from healthy observers has accumulated that is consistent with the idea of a dedicated visuomotor control system that is independent of perceptual influence. Although some of this evidence is controversial, we will argue that, on balance, there is good agreement between the psychophysical and neuropsychological data – and that the action and perception hypothesis is still alive and well.

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1. Introduction

In 1992, Goodale and Milner proposed that the visual control of action is distinct from visual perception. Drawing primarily on evidence from neuroanatomy, neurophysiology, and neuropsychology, they suggested that this distinction between vision-for-action and vision-for-perception could be mapped onto the two prominent visual pathways arising from primary visual cortex: a dorsal 'action' pathway projecting to the posterior parietal cortex and a ventral 'perception' pathway projecting to the inferotemporal cortex. In the almost 20 years since the first exposition of what we will refer to here as the 'action and perception hypothesis', a considerable body of literature has built up around the basic idea that vision-for-action and vision-for-perception operate with some degree of independence. In some cases, the new data are consistent with the original hypothesis, and in other cases the data have challenged the idea and have led to refinements. Here we will discuss the specific issue of whether or not the data obtained from psychophysical studies of action and perception in 'healthy observers' (i.e., without any neurological, visual, or motor disturbances) are consistent with the original neuropsychological evidence from

the visual form agnostic patient D.F., whose case was so influential in the original formulation of the action and perception hypothesis. In order to place some reasonable boundaries on the scope of this commentary, we will focus primarily on studies of grasping. We have chosen this focus because D.F.'s ability to grasp objects despite a frank deficit in visual form perception was one of the most compelling observations that led to the formulation of the action and perception hypothesis. Moreover, the distinction between the processing of object features for action and perception distinguishes Goodale and Milner's interpretation of the division of labor between the dorsal and ventral streams from the ideas put forward by Ungerleider and Mishkin (1981), which focused on differences between spatial and object vision. We acknowledge that a comprehensive review comparing the neuropsychological and psychophysical evidence from a broader range of perceptual and motor tasks would be useful, but such a review is beyond the scope of this paper.

2. D.F.'s grasping behavior

2.1. Action without perception

A number of studies have investigated the grasping abilities of D.F., a patient with profound visual form agnosia resulting from

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brain damage concentrated primarily in the lateral occipital complex of the ventral visual stream (James, Culham, Humphrey, Milner, & Goodale, 2003). When she posted a wooden card into a series of slots placed a different orientations (Goodale, Milner, Jakobson, & Carey, 1991; Milner et al., 1991), D.F. rotated her hand to the orientation of the slot very early in the movement – well before she could have used visual or tactile feedback to monitor the accuracy of her action. This observation was particularly striking because D.F. could not report the orientation of the slot verbally or even manually (by adjusting the orientation of her hand or the hand-held card to match the orientation of the slot without posting it), a result that suggests that she could not perceive the slot's orientation at a conscious perceptual level. This finding provided the motivation for a broad exploration of her preserved visuomotor abilities. In one of the early studies, Goodale and colleagues (1991) showed that D.F.'s grip aperture in flight (i.e., the separation between her index finger and thumb) reflected the width of rectangular objects when she reached to grasp them, even though she could not report the objects' widths by opening her index finger and thumb a matching amount, a kind of magnitude estimation of their widths. The shapes used in the study were Efron (1969) blocks, which have a negative correlation between length and width, ensuring that all the blocks in the stimulus set have the same surface areas and thus the same amount of reflected light; therefore, D.F.'s ability to scale her grasp to the width of the target object could not be explained by a simple servomechanism linking grip size and the total luminance coming from the object's surface. In a subsequent paper, Goodale et al. (1994) showed that D.F. chose appropriate grasping postures when she picked up irregularly shaped objects. That is to say, that the opposition axis formed by the vector between the contact points for her index finger and thumb tended to pass through the object's center of mass, which is necessary to prevent the object from rotating out of the grasp during lifting and manipulation. Moreover, the initial points of contact for her finger and thumb also tended to coincide with points of maximum convexity, a strategy that minimizes the likelihood that the digits will slip from the object's surface. D.F.'s performance in this grasping task implies that her intact visuomotor system can process the entire form of the target object and not just the locations of high-contrast edges.

The studies cited thus far would appear to suggest that D.F.'s visuomotor abilities are perfectly preserved, but this is not the case. Goodale and colleagues (1994) conducted a series of experiments designed to probe the limits of D.F.'s visually guided abilities to match the orientation of her hand to the orientation of a target stimulus defined by different features. They first did this by varying the type of visual information that was used to define the target in relation to the background. In these experiments, D.F. was required to reach out with a handheld rectangular card and 'stamp' its inked edge onto an oriented bar presented on a sheet of paper so that the edge of the card was aligned with the principal axis of the stimulus. The data from these studies showed that D.F. could perform well only when the target stimulus was defined by first-order contrast (i.e., edges defined by luminance contrast). For example, her performance deteriorated when the target was defined by a difference in the textural elements from its background or by a vernier offset, suggesting that the 'stripped-down' visuomotor system, i.e. one working without input from an intact perceptual network works, relies largely on luminance-defined edges. In another test, D.F. was asked to post a T-shaped object into a T-shaped slot. Interestingly, in this case, the final position that D.F. adopted with the stem of the T-shaped object was aligned with one of the two principal axes of the T-shaped slot. In other words, she either succeeded in putting the T-shaped card into the slot, or she completely failed, choosing a position that was orthogonal to the correct orientation. This suggests that her visuomotor system

was capable of processing only one axis of elongation at a time – and that the task of matching one pattern with another, a requirement for successful insertion of a T-shaped card into a T-shaped slot, requires an intact perceptual system. It is useful to point out that this conclusion does not contradict the observation noted earlier that D.F.'s actions can take into consideration the entire shape of a target object, as in the case of grasping the irregular shaped objects in Goodale et al. (1994). D.F.'s difficulty with the T-shaped object matching task emerges not because she is unable to process the entire shape of the T-shaped target slot, but because she is required to compare (and ultimately align) the shapes of two different objects.

2.2. Memory-linked impairments in action

Most actions are directed at visible objects, but sometimes we work 'off-line', responding to objects that are no longer in view or mimicking a target-directed action but in another part of the workspace. Goodale, Jakobson, and Keillor (1994) compared D.F.'s ability to reach out and grasp objects in a natural condition, in which the target objects were visible, with her ability to pantomime those actions after the target had been removed from view for 2 s. They also looked at actions made to a location displaced from the actual position of the target, another kind of pantomimed grasp. D.F. was able to scale her peak grip aperture to the width of the target stimuli only in the natural condition. Indeed, the shape of D.F.'s grip aperture profile across the entire action was qualitatively different for the natural condition as compared to the delayed or displaced pantomimed conditions, in which her grip scaling was either very poor or entirely absent. On the basis of these results, Goodale et al. (1994) proposed that D.F.'s visuomotor system can operate only in 'real time', and only when the action is directed towards the target object. When memory for the target object is required to guide her action or when an action is directed towards a displaced location, D.F.'s performance collapses, implying that a representation of the target object derived from perceptual processing is required to guide action in these unusual circumstances.

2.3. Monocular impairments in action

Dijkerman, Milner, and Carey (1996) studied D.F.'s ability to grasp flat objects that were rotated within the depth plane, and found that her posture of her fingers in flight reflected the orientation of the object when she carried out her movement with binocular vision, but her performance deteriorated when one eye was covered. Similar decrements in performance under monocular viewing were not observed in the control participants, which suggest that D.F.'s preserved visuomotor abilities depend critically on the availability of binocular visual information about the target object. Presumably, the good performance of the control participants in the monocular grasping task can be attributed to a contribution from form perception, which is damaged in D.F. This idea seems plausible because the square objects used in the study would have cast quite different trapezoidal images on the retina depending on their orientation in depth. Dijkerman et al. argued that this observation is consistent with neurophysiological studies that show a number of areas in the dorsal stream have a preponderance of neurons with binocular receptive fields. In other words, the dedicated visuomotor modules that reside in the dorsal stream might require binocular cues about object form and distance to carry out their computations (Sakata et al., 1999). Building upon these ideas in a follow-up study, Dijkerman, Milner, and Carey (1999) found that D.F.'s ability to grasp objects rotated in the depth plane was improved in monocular conditions when she was allowed to move her head from side to side, which presumably allowed her

visuomotor system to utilize self-generated retinal motion – a useful source of information about absolute distance. This suggests that the visuomotor systems in D.F.'s intact dorsal stream can make use of either binocular or retinal-motion cues about the absolute distance of the target object, but not pictorial cues based on form. In a related study, Marotta, Behrmann, and Goodale (1997) explored the role of binocular vision in the grasping abilities in D.F. and another patient with visual form agnosia, focusing on the scaling of grip aperture to the size of the target object presented at various viewing distances. Both patients calibrated their grasp to the size of the target object regardless of distance in the binocular conditions, but showed impairments in the monocular condition, failing to calibrate image size for viewing distance. Taken together, these findings further support the notion that absolute distance information is critical to the ability of the visuomotor system in the dorsal stream to guide action – and that basic optical cues such as binocular vision and self-generated motion cues play a central role in the underlying computations.

To summarize, studies of D.F.'s grasping abilities suggest the existence of a visuomotor system – presumably located in the dorsal visual stream – that is capable of guiding grasping actions but neither requires nor generates conscious perceptual awareness of the target object's form. This specialized system is able to operate within a limited range of circumstances in which the target: (1) is separated from the background by luminance-contrast edges, (2) is visible, (3) is viewed in conditions that provide absolute distance cues, and (4) is the direct target of the action. Given the conditions in which humans tend to operate, one would suspect that these constraints would rarely come into play. Nevertheless, control participants remain able to produce relatively accurate grasping movements in conditions like these, conditions that produce devastating effects on D.F.'s performance. From this, we conclude that in these cases the control of action may depend on the visual systems that support conscious object perception – the systems located in the ventral visual stream that are at the center of D.F.'s lesion and at the root of her visual form agnosia.

3. Data from psychophysical studies of action and perception

3.1. What could psychophysics contribute to the action and perception hypothesis?

It is obvious that patient D.F. is a special case – although a number of other similar cases with similar dissociations have occasionally been reported both in the older literature (e.g., Campion, 1987) and more recently (e.g., Karnath, Rüter, Mandler, & Himmelbach, 2009). Nevertheless, if the ideas that derive from analyses of her perceptual and visuomotor abilities in any way reflect the general functional architecture of the human brain, it might be possible to demonstrate patterns of performance in healthy observers that are consistent with the existence of a specialized visuomotor control system that can operate separately from conscious form perception. It is not a foregone conclusion that such demonstrations will be possible, given the extensive connections that exist between the visual areas of the dorsal and ventral visual streams (for review, see Milner & Goodale, 2006). Indeed, it would be extraordinary if the control of action were completely divorced from conscious visual perception. For the same reason, the failure to demonstrate a clear distinction between action and perception in a particular task or situation can never be taken as strong evidence against the action and perception hypothesis. By saying this, we do not mean to imply that the action and perception hypothesis is irrefutable. But it is important to point out that studies that fail to find a difference between action and perception are difficult to interpret for all

the same reasons that make it difficult to argue in favor of a statistical null hypothesis. In a similar vein, viable alternatives to the action and perception hypothesis would have to account for the results of not only one study or experiment, but also the neuropsychological data discussed earlier (as well as a host of neuroimaging and neurophysiological studies); in other words, one cannot simply claim that action and perception are guided by a common representation of the visual world since the data from patient D.F. (and other neurological cases) have already disconfirmed that possibility. If we are to advance farther in this field, it is critical that testable alternative hypotheses be presented as part of any study reporting data that are incompatible with the action and perception hypothesis.

Since the initial formulation of Goodale and Milner's (1992) hypothesis there have been a number of psychophysical studies in healthy observers whose results appear broadly consistent with the basic tenets of the action-perception distinction. Some of these studies have been carefully scrutinized and challenged on a variety of grounds ranging from methodology to interpretation. Our goal here is not to take a defensive posture about the studies in question, but rather to offer some reflection and counterpoint to the criticisms that have been raised, while acknowledging that certain findings might not be as compelling as once thought. Indeed, some important lessons have been learned along the way about the need to use careful psychophysical approaches when studying the relation between action and perception in healthy observers. Despite these words of caution, we remain convinced that there is good evidence from the psychophysical literature to support the idea that the visual control of action can operate independently from conscious visual perception, and that the conditions under which this independence is observed tend to mirror the conditions under which D.F.'s visuomotor abilities deteriorate. For reasons outlined earlier, we will attempt to restrict our discussion to those studies of grasping that speak most directly to the action and perception hypothesis.

3.2. Is there dissociation between action and perception for visual illusions?

In their seminal study, Aglioti, DeSouza, and Goodale (1995) reported that an Ebbinghaus size-contrast illusion did not produce a significant effect on the preshaping of grip aperture despite the fact that the illusion led participants to reliably misjudge the sizes of the target objects in the display. This surprising finding was followed up by Haffenden and Goodale (1998) in a study that addressed some methodological concerns with the original Aglioti et al. paper. Taken together, these studies appeared to provide evidence in favor of the independence of action and perception in the intact nervous system, consistent with the action and perception hypothesis.

Franz, Gegenfurtner, Bulthoff, and Fahle (2000) replicated some of the effects reported by Aglioti et al. (1995) but argued that the larger effect of the Ebbinghaus illusion on perception compared to action could be attributed to the fact that size judgments involved a comparison of two objects presented inside different configurations of the illusion, whereas grasping movements were directed toward a single object inside a single illusion configuration. After correcting this confound, Franz et al. reported that the effects of the illusion on action and perception were basically equivalent; similar results have been reported by Pavani, Boscagli, Benvenuti, Rabuffetti, and Farne (1999) and Vishton, Rea, Cutting, and Nunez (1999). The single- versus dual-illusion argument could not account for the effects of the illusion on grasping and manual size estimation reported in Haffenden and Goodale (1998)'s study, but Franz et al. suggested that the 'non-conventional' manual estimation procedure used to gauge the perceptual effects of the

illusion in that experiment is problematic because it produces a much larger perceptual illusion than has been reported using more conventional psychophysical techniques.

Franz (2003) went on to compare manual size estimation and a traditional psychophysical technique (i.e., the method of adjustment), confirming that the effect of the Ebbinghaus pictorial illusion is much larger for manual size estimation. Moreover, Franz found that manual size estimation showed a larger response to changes in the veridical size of the target stimulus than either the method of adjustment or the peak grip aperture of grasping. It is worth mentioning that not all studies show different size-scaling functions for grasping and manual size estimation: whereas the data presented in Haffenden and Goodale's (1998) Fig. 5 (C and D; small and large objects shown against a blank background) appear to show a slightly larger size-scaling function for manual estimation as compared to maximum grip aperture, the data from Ganel, Chajut, and Algom (2008) and Westwood, Danckert, Servos, and Goodale (2002) show relatively similar size-scaling functions for grasping and manual size estimation (see Fig. 1). Franz argued that the difference in the underlying size-scaling functions for various response types must be considered when comparing the effects of illusions, and he recommended correcting the absolute effect of the illusion measured for a particular response by dividing it by the slope of the size-scaling function for that response. When this correction is done, Franz showed that the effect of the Ebbinghaus illusion reported by Haffenden and Goodale (1998) is virtually identical for grasping and manual size estimation (see also Franz & Gegenfurtner, 2008).

Franz's analyses and interpretation could be particularly challenging for the relevance of the action and perception model to the behavior of healthy observers, given that the visual illusion paradigm has been held up as a bridge that crosses the gap between neuropsychology and psychophysics. Without diminishing the importance of Franz's work, which is substantial, we would like to point out a few issues that require further consideration before concluding that visual illusions produce equivalent effects on action and perception.

Franz's conclusions depend heavily on the claim that it is necessary to correct the effect of a visual illusion measured in a particular type of response (e.g., peak grip aperture in grasping) by normalizing it to the size-scaling function for that response type. This correction is likened to the standard scientific laboratory procedure of instrument calibration, in the sense that a signal observed in a response (i.e., an absolute effect of an illusion) cannot be interpreted without knowing the sensitivity of the response to a standard set of inputs (i.e., a true change in the size of the object).

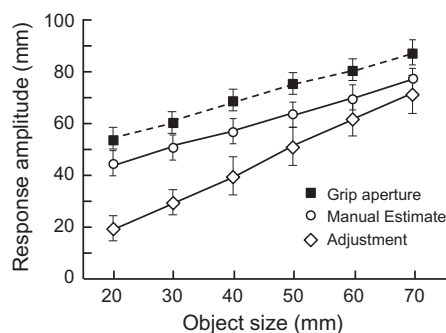


Fig. 1. The effect of object size on peak grip aperture, explicit manual estimates, and adjustment of a comparison stimulus (on a computer screen) extracted from the experiment on Weber's law carried out by Ganel et al. (2008). Note that the slopes of these three functions are remarkably similar. Indeed, there is virtually no difference in slope between grip aperture and manual estimates. Error bars reflect the standard error between subjects, and are unrelated to the within-subject variance used to calculate Weber fractions. Data kindly provided by Ganel.

Although this logic seems appealing, it is not beyond challenge. In fact, the instrument calibration analogy is useful for illustrating our point. Instruments detect a specific type of signal (e.g., intensity of light) and generate an output response (e.g., a digital output). There is a non-arbitrary relationship between the input and output signals that can be mapped by regressing the instrument's output responses against a set of known input signals. After calibration, it becomes possible to interpret the instrument's response when an unknown signal of the same type (i.e., light intensity) is fed into the system. The instrument calibration analogy breaks down when considering the issue of absolute illusion effects and size-scaling functions, however, because there is an imperfect relationship between the standard signal used to generate the calibration curve (veridical object size) and the signal that is later fed into the system (the effects on object size – or not – of the contextual elements of the particular illusion). Although one could argue that illusions operate on an internal representation of object size, and can therefore be considered as an equivalent signal to the veridical size of the object, we suggest that this assumption is flawed in at least one regard.

Most pictorial illusions employ contextual features that convey a sense of depth or distance, such that their effects on size perception are typically attributed to inappropriate size-constancy mechanisms (Gregory, 1997). If this is correct, then one could argue that the effect of a pictorial illusion on judgments of object size is mediated by quite a different mechanism (i.e., inappropriate size-constancy scaling) than the effect of a veridical change in the size of the target object on judgments of object size (i.e., increasing the size of the object's retinal image). Because each mechanism could affect the response via a different scaling function, it might not be appropriate to 'calibrate' one effect (the illusion) based on the scaling function for another effect (veridical size). The rationale for the size-scaling correction is even less compelling for responses like peak grip aperture in grasping because it is well established that peak grip aperture is affected by many factors other than the veridical size of the target object; for example, peak grip aperture can be affected by eliminating visual feedback (Franz, Hesse, & Kollath, 2009), switching from binocular to monocular viewing (Servos, Goodale, & Jakobson, 1992), or placing obstacles in the path of the grasping movement (Tresilian, 1998). Thus, it is unclear that knowledge of the relationship between true object size and peak grip aperture is of any value in interpreting, let alone correcting, any of the other effects that can be detected for grasping movements. Before scientists in this field move to adopt the correction procedure recommended by Franz, we propose that one ought to first provide some compelling evidence that the effect of the illusion in question is mediated by the same mechanism responsible for the effect of a change in veridical target size. Of course, this would be necessary for any of the response types (i.e., peak grip aperture in grasping, manual size estimation, and other conventional measures of size perception) for which the correction procedure is recommended. One way to do this would be to demonstrate a strong, positive, within-subjects correlation between the effect of a particular illusion and the effect of a parametric variation in the size of the target object. Such a correlation would provide some reassurance that the two effects are mediated by a common mechanism, and that it might be appropriate or even necessary to correct the measured effects of illusions in the calibration-like way advocated by Franz.

In our opinion, it is premature and possibly even inappropriate to use the illusion correction procedure recommended by Franz (2003), although we appreciate that some type of correction may be necessary to account for potential differences between responses in their sensitivity to sources of information that are relevant to the effect of the illusion. A more appropriate way to do this might be to 'calibrate' the effect of an illusion using the sensitivity

of the particular response to some intrinsic feature or property of the illusion itself. For example, one could assess the sensitivity of grasping, manual size estimation, or some other more conventional measure of size perception, to a parametric variation in the sizes of the circles in the annular rings of the Ebbinghaus illusion, the angle or length of the fins that form the ends of the Muller-Lyer illusion, or perhaps even the luminance contrast of the illusion's inducing elements.

Even if one accepts the logic of the illusion correction procedure recommended by Franz (2003), there are several studies whose findings cannot be explained by differences in the size-scaling functions for action and perception. One particularly compelling example is the study of Ganel, Tanzer, and Goodale (2008) who constructed a stimulus display in which two objects with different sizes were displayed within a Ponzo-type figure that created the perceptual illusion that the small object was actually larger than the large object. This creates an interesting scenario in which the veridical sizes of the objects are exactly opposite to their perceived sizes. [A similar approach was used by Grandy and Westwood (2006) to explore the effect of a size-weight illusion on heaviness judgments and lifting dynamics.] Consistent with the action and perception hypothesis, Ganel, Tanzer et al. (2008) found that peak grip aperture was scaled to the veridical sizes of the target objects, whereas perceptual judgments of object size reflected the illusory sizes of the target objects; in other words, the direction of difference between the two target stimuli was opposite for action and perception. Whether or not there are different underlying size-scaling functions for grasping and perceptual judgment, the conclusions of this study would not change since an illusion correction procedure could not reverse the sign of the observed differences; presumably, both action and perception would show a positive size-scaling function.

3.3. Beyond illusions: different psychophysical principles for action and perception

Beyond the illusion paradigm, Ganel, Chajut, and Algom (2008) have demonstrated a fundamental difference between the psychophysical laws that govern grasping and size perception, which suggests that the two functions are distinct. According to the results of this study, grasping movements do not conform to Weber's law in the sense that the sensitivity of grip aperture to changes in the size of the target object is stable across a range of object sizes.¹ Of course, perceptual judgments of object size readily conform to Weber's law, such that the sensitivity to changes in object size was proportional to the overall size of the target object. In a similar vein, Ganel and Goodale (2003) showed that speed with which perceptual judgments of object shape were made were affected by the requirement to filter an irrelevant stimulus dimension (e.g., the width of the object, when the task was to respond only the length), whereas no such slowing occurred when the task was to grasp the target object. This observation further supports the idea that the visual control of grasping is guided by fundamentally different

psychophysical principles than the visual perception of object features, consistent with the basic idea behind the action and perception hypothesis.

3.4. Memory-linked changes for action

Earlier we discussed evidence showing that D.F.'s good visuomotor abilities deteriorate when the target object is removed from view prior to the action. Control participants can grasp remembered objects with relative ease, which implies that the control of action depends upon the form perception system when memory is required. There is now considerable support from the psychophysical literature for the idea that visually guided and memory-guided actions are distinct, and that perceptual representations of the target object are required for the latter but not the former.

Westwood and colleagues conducted a series of studies on visually guided and memory-guided grasping with the Muller-Lyer (ML) pictorial illusion, motivated by the dramatic difference in D.F.'s grasping abilities in such conditions. Westwood, Chapman, and Roy (2000) showed that peak grip aperture in natural grasping, in which vision of the target display was available before and during the action, was unaffected by the configuration of the surrounding ML illusion, whereas a robust effect of the illusion was seen in pantomimed grasping, where the target and display were physically removed 2 s before the response. The magnitude of the illusion effect was identical for manual size estimation in the two visual conditions. This observation is consistent with the dramatic deterioration of D.F.'s grasping abilities in pantomimed compared to natural conditions, suggesting that perceptual representations are required for the control of pantomimed actions. However, follow-up studies by Westwood, Heath, and Roy (2000) and Westwood, McEachern, and Roy (2001) found that the increased effect of the ML illusion in conditions that required memory for the target were more likely due to the confounding effect of eliminating on-line visual feedback in the memory-dependent conditions compared to the visually guided condition; in other words, the effect of the illusion was present for pure open-loop grasping movements, in which vision was removed at the onset of the action, and did not increase further when vision was removed at the time of response cueing, or 3 s prior to response cueing. This finding was replicated and extended recently by Franz and colleagues (2009). Westwood and colleagues (2001) argued that on-line visual feedback might be necessary for the visuomotor system to resist the 'non-illusory' effects of the ML stimulus, by which they meant the potential for the fins of the stimulus to be construed as potential obstacles to the placement of the fingers on the ends of the target object. Interestingly, a study by Heath, Rival, and Neely (2006) showed that the increase in effect of the ML figure in open-loop as compared to closed-loop grasping disappears when the two visual conditions are mixed in random compared to blocked order; in the random mixing condition, the effect of the ML stimulus increased for the closed-loop trials and came to match that seen in open-loop trials. This finding suggests that participant strategies can influence the effect of this particular stimulus on grasping behavior (for a discussion of this issue, see Whitwell & Goodale, 2009; Whitwell, Lambert, & Goodale, 2008), although the same may not be true for other types of illusion-inducing stimuli as discussed below. As suggested by an anonymous reviewer, an alternative interpretation of Heath et al.'s (2006) results is that the visuomotor system may be able to adapt to the errors induced by the ML figure in closed-loop trials when these are done in blocked order because visual feedback is available for a series of consecutive trials; the same may not be possible in randomly intermixed open-loop and closed-loop trials. In any case, if participant strategies can indeed alter the effect of an illusion-inducing stimulus on a particular response, this challenges the logic of correcting abso-

¹ Of course, this finding (as well as the fact actions are often resistant to size-contrast illusions) fits well with the 'double-pointing' hypothesis of Smeets and Brenner's (1999), Smeets and Brenner's (2001). According to their account, the visuomotor system does not compute the size of the target object but instead computes the two locations on the surface of object where the digits will be placed. Thus, size is irrelevant to the planning of these trajectories, and variation in size will not affect the accuracy with which the finger and thumb are placed on either side the 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 seems to be impervious to the effects of the illusion. Their view, of course is completely antithetical to Franz's claim that grasping is sensitive to the perceived size of target objects.

lute illusion effects by the underlying size-scaling function for the response since this procedure assumes that any change in the response occurs because of a change in an underlying representation of size. From the point of view of the Westwood and colleagues' (2001) arguments, the increased effect of the ML stimulus in Heath et al.'s randomly mixed closed- and open-loop trials is presumably due to a change in participant strategy (perhaps in dealing with the fins as obstacles) rather than a change in the underlying representation of the object's size or the perceptual illusion itself. This poses some real difficulty for Franz's correction procedure.

Hu and Goodale (2000) studied the effect of a relative-size illusion on peak grip aperture and manual size estimation in real time open-loop and 5-s delay conditions, ensuring that on-line was not available in either condition. The study showed no effect of the single flanking object on grasping in the open-loop condition, but a larger and significant effect in the 5-s delay condition. Manual size estimation was significantly affected by the flanker's size in both conditions. This study provides support for a memory-linked transition from a mode of control for grasping that is independent of a perceptual illusion to one that is dependent upon the illusion, consistent with the speculation derived from Goodale and colleague's (1994) study with D.F. It is worthwhile to note that Franz and Gegenfurtner (2008) have challenged the statistical analysis used by Hu and Goodale (2000) and carried out their own calculations based on the published data. According to their own calculations, Franz and Gegenfurtner conclude that the effects of the flanking object on grasping for the open-loop and 5-s delay conditions are not significantly different when the two conditions are compared to each other directly; however, this is not particularly surprising given the relatively low statistical power of the original dataset to detect such an interaction.

In an extension of Hu and Goodale's (2000) basic paradigm, Westwood and Goodale (2003) introduced some methodological changes that included randomly interleaving open-loop and memory-guided trials to equate the attentional demands and participant strategies of the two visual conditions. The study included a very short (i.e., visual occlusion at the time of response cueing) and a longer memory condition (i.e., visual occlusion 3 s prior to response cueing). Like in Hu and Goodale's study, a single-flanker relative-size illusion was used to study the influence of perceived object size on the control of grasping. The results (Fig. 2) showed a significantly greater effect of the flanker in the short-delay condition compared to the open-loop condition, even though the only difference between the two types of trials was that vision was occluded at movement onset in the open-loop trials (enabling participants to use vision to program the movement) but at the time of response cueing in the short-delay trials (forcing participants to rely on a memory of the target that had been in view only a moment before). Importantly, the magnitude of the flanker's effect did not increase in the 3-s delay condition compared to the short-delay condition. Given the brevity of the brief delay period, we proposed that a very rapid transition in movement control occurs when the target is removed from view, from a mode of control that does not require form perception to one that does. This led us to suggest that the visually guided mode of control, which is not influenced by the perceptual system, operates in real time; that is, it does not begin the transformation of visual information from the target into a motor program until the time the action is required. If the target is not visible when the action is required, the motor control system accesses a stored perceptual representation of the target object that presumably was initially processed by form perception mechanisms in the ventral stream.

Moving away from visual illusions, two of the studies cited earlier by Ganel and colleagues (2008) and Ganel and Goodale (2003), included visually guided and memory-guided grasping conditions. In Ganel, Chajut et al. (2008), visually guided grasping violated We-

ber's law, but memory-guided grasping did not.² In the Ganel and Goodale (2003) study, visually guided grasping was not affected by the need to filter an irrelevant stimulus dimension, but memory-guided grasping was. In a study of visuomotor priming, in which congruent or incongruent target objects were seen before responding to a visible or a remembered target object, Cant, Westwood, Valyear, and Goodale (2005) found no evidence of priming for visually guided grasping movements but significant effects for memory-guided grasping. Hesse, de Grave, Franz, Brenner, and Smeets (2008) carried out a somewhat similar study but report results suggesting that priming can occur in visually guided grasping; however, this study did not include a memory-guided grasping condition, so it is not clear whether the reported effect of priming would be larger in such a condition. Consistent with the evidence from the relative-size illusion studies discussed earlier, these studies provide some support for the role of perceptual information in the control of memory-guided but not visually guided grasping.

Overall, there appears to be considerable agreement between the psychophysical and neuropsychological literatures about the role of perceptual information in the control of memory-guided but not visually guided grasping. There remains some concern that several studies of memory-guided grasping did not include appropriate open-loop conditions for comparison, but concerns about the role of on-line visual feedback in the memory-linked effects on action do not apply to many of the key studies cited above. Interestingly, strong data showing that D.F. is able to grasp objects without on-line visual control are not available. There are anecdotal reports that D.F.'s grasping abilities are not impaired when vision is removed at movement onset, and there is some evidence to this effect in a paper by Schenk and Milner (2006). Moreover, the original studies of D.F.'s visuomotor posting abilities (Milner et al., 1991) showed evidence of very early scaling of grasping to the orientation of the target slot (300 ms into the action, which was the earliest time point reported), which decreases the likelihood that her motor performance can be attributed wholly to on-line visual guidance.

3.5. Monocular-linked changes for action

In contrast to the robust evidence in favor of a role for perception in the control of memory-guided action, which mirrors the neuropsychological evidence from patient D.F., there are surprisingly few studies showing the same for monocular grasping, even though this visual manipulation has a substantial negative effect on D.F.'s grasping performance as discussed earlier. Certainly a large number of studies have shown that grasping performance is less accurate and more variable in monocular as compared to binocular conditions (e.g., Bradshaw & Elliott, 2003; Bradshaw et al., 2004; Melmoth & Grant, 2006; Servos & Goodale, 1994; Servos et al., 1992; Watt & Bradshaw, 2003), but these studies did not directly address the possibility that this difference is specifically related to an increased role for perception in the monocular conditions.

Marotta, DeSouza, Haffenden, and Goodale (1998) explored the effect of the Ebbinghaus size-contrast illusion on grasping in mon-

² The fact that Weber's law is obeyed in delayed grasping cannot be easily explained by Smeets and Brenner's (1999), Smeets and Brenner's (2001) double-pointing 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 it explain the fact that grip aperture is sensitive to relative size differences in delay (Hu & Goodale, 2000; Westwood & Goodale, 2003) without making a similar concession. 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 grasping, which is mediated by the ventral stream, uses object size.

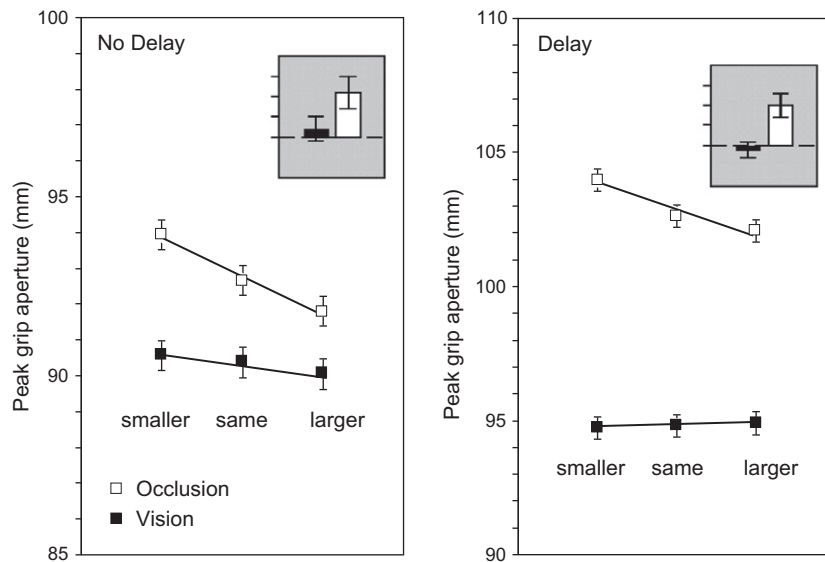


Fig. 2. Effect of relative flanker size (small, same, large) on the scaling of peak grip aperture on vision and occlusion trials for no-delay and delay groups. In the no-delay group, all participants had a 500-ms view of the target object and flanker at the beginning of a trial before the auditory cue to grasp the object was presented. Vision of the target was available between movement cueing and movement onset for the vision trials, whereas vision was occluded between movement cueing and movement onset for the occlusion trials. For the delay group, all participants were given a 500-ms preview followed by a 3-s period with no vision. On vision trials, vision was re-introduced when the cue to grasp was presented and was removed when the movement began. On occlusion trials, vision remained unavailable for the rest of the trial. Vision and occlusion trials were randomly interleaved for both the no-delay and the delay groups. Although the presence of flankers of different sizes did not affect peak grip aperture on vision trials for either the no-delay or the delay group, it did affect grip aperture on occlusion trials. Thus, on occlusion trials, grip aperture was larger when the target object was accompanied by a smaller flanker and was smaller when the target object was accompanied by a larger flanker. Inset: peak grip aperture difference scores for small flanker trials minus large flanker trials. Reprinted with permission from Westwood and Goodale (2003).

ocular and binocular viewing conditions, and discovered that the effect was greater in the monocular condition. This observation was true only for a condition in which the height of the stimulus array in the visual scene was varied on a trial by trial basis, which prevents participants from using vertical gaze angle (a monocular cue to object distance) to help calibrate their grasping actions. Although this finding is consistent with the data from D.F., a related study by Otto-de Haart, Carey, and Milne (1999) using the ML illusion found equivalent, significant effects for monocular and binocular grasping. These authors did not vary the distance of the target stimulus across trials, so it is possible that binocular vision was not needed to properly calibrate the grasping actions in the experiment. This would mean that grasping in both conditions ought to show significant effects of the illusion, given that other studies tend to find small but significant effects of the ML illusion on grasping in binocular conditions (e.g., Franz et al., 2009; Westwood et al., 2001). It seems that further studies on this topic are warranted.

4. Conclusions

Goodale and Milner's (1992) proposal that there is a dedicated system for the control of visually guided action that neither depends upon, nor produces, conscious form perception has generated a tremendous amount of research. The action and perception hypothesis was driven in large part by surprising observations from a specific individual, D.F., who had a rather rare lesion that was concentrated largely within the lateral occipital complex in the ventral visual stream. D.F.'s case provided an opportunity to study the capacity for control of action in the absence of conscious perception of object form. Data from a number of studies with D.F. suggested that the visuomotor networks that underlie her residual capacity for action have clear constraints. These networks appeared to break down when: (1) the target object was defined by second-order contrast (i.e., not by luminance contrast), (2) the

primary axis of the target object was ambiguous (i.e., multiple salient cues to orientation were included), (3) the object was removed from view prior to the action, and (4) visual cues to absolute distance were unavailable (i.e., in monocular viewing, without head movements). Psychophysical studies of 'healthy observers' have produced some results that are consistent with D.F.'s visuomotor performance constraints. The studies that have used pictorial illusions have generated considerable controversy, but we have some outstanding concerns with the methodological criticisms raised by those who claim the effects of illusions on action and perception are equivalent. Nevertheless, as discussed above, there are several reports that show dissociations between action and perception that do not employ visual illusions and that are therefore immune to the controversies that exist in that domain. There is broad support from psychophysical studies for the notion that conscious form perception is required for the control of memory-guided but not visually guided grasping, and some limited evidence suggesting that perception is required more for monocular than binocular grasping. To reiterate the conclusion foreshadowed in the title of this article, we believe that the neuropsychological and psychophysical data converge in support of Goodale and Milner's (1992) action and perception hypothesis.

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