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10 Years of Illusions

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A decade ago, S. Aglioti, J. F. X. DeSouza, and M. A. Goodale (1995) published an experiment that has had a big influence on the way that visual information is thought to control human behavior. Their findings have often been simplified as suggesting that action is immune to perceptual illusions. The current authors critically analyze the 4 steps involved in this simplification and argue that research during the last 10 years has shown that the validity of 3 of the 4 steps is doubtful. They conclude that this experiment cannot be regarded as firm support for the 2-visual-systems hypothesis (i.e., that the ventral stream is for perception and the dorsal stream is for visually guided actions).

Keywords: visual illusion, selection, action, grasping, dorsal pathway

A decade ago, Aglioti, DeSouza, and Goodale (1995) published an experiment that has had a big influence on the way that visual information is thought to control human behavior. They presented subjects with two disks on an Ebbinghaus figure: one surrounded by large flankers and the other by small flankers. By asking the subjects to pick up the largest (or smallest) disk, the authors showed that the flankers had a larger effect on the choice of the disk that was grasped than on the peak grip aperture of the reach-to-grasp movement. This result has often been simplified as indicating that action is immune to perceptual illusions, supporting the two-visual-systems hypothesis that the ventral stream is for perception and the dorsal stream for visually guided actions (Goodale & Milner, 1992). This simplification involves four steps of interpretation:

1. Choosing the target position is a perceptual (ventral) process.
2. This process is clearly influenced by the illusion.
3. Peak grip aperture is a good measure of how size is processed for action.
4. This measure is not affected by the illusion.

We argue that research during the last 10 years has shown that the validity of three of these steps is doubtful.

Although frequently cited as showing that “the maximal opening of a grasping hand is insensitive to the robust perceptual illusion” (Goodale & Westwood, 2004, p. 205) or “grip aperture completely resisted the illusion” (Goodale & Milner, 2004, p. 88), Aglioti et al.’s (1995) study showed a clear effect on peak grip aperture (see their Figure 5). All subsequent grasping experiments

that have used the Ebbinghaus illusion have also shown a larger grip aperture for disks that look larger but are not (reviewed in Table 1 of de Grave, Biegstraaten, Smeets, & Brenner, 2005). In some cases, the effect was not significant (Amazeen & DaSilva, 2005; Haffenden & Goodale, 1998), whereas in others the effect on peak grip aperture was equal to the perceptual effect (Franz, Gegenfurtner, Bühlhoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999). The last step is therefore not valid for the original experiment and also not generally valid for later replications.

The finding that in some situations the Ebbinghaus figure influences peak grip aperture as much as it does perception has been used to argue that peak grip aperture and perception are based on the same size information (Franz, 2001). Others claim that the lack of correlation between peak grip aperture and perception shows that these are based on two different size estimates (Amazeen & DaSilva, 2005). However, such claims can be made only if one agrees with the third step mentioned above: that peak grip aperture is a good measure of how size is processed for grasping. Unfortunately, there are good reasons to question this assumption. Information about object size may not even be used to control grasping at all (Smeets & Brenner, 1999). However, even if one assumes that object size is used to control grip formation in grasping, peak grip aperture can be considered to be a direct measure for the effects of the Ebbinghaus illusion on action only if the figure does not influence peak grip aperture in other ways. If the flankers surrounding the center circle are, for instance, regarded as obstacles, they will influence peak grip aperture (Biegstraaten, Smeets, & Brenner, 2003; Mon-Williams, Tresilian, Coppard, & Carson, 2001), which would explain why the separation between flankers and target has a different effect on grasping than on size estimation (Haffenden, Schiff, & Goodale, 2001; but see Franz, Bühlhoff, & Fahle, 2003). The fact that the larger peak grip aperture occurs earlier when grasping an object that appears to be larger due to the Ebbinghaus illusion can be regarded as support for the obstacle interpretation, because a larger peak grip aperture occurs later for larger objects but earlier for objects that are more difficult to grasp (Smeets, Glover, & Brenner, 2003). The finding that rotating the positions of the flankers influences the orientation of the hand when grasping also suggests that the flankers are

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regarded as obstacles (de Grave et al., 2005). The possibility that flankers act as obstacles can be used to defend the claim of Aglioti et al. (1995) from the direct criticism of Franz and colleagues (Franz et al., 2000). However, this possibility leads to the unfortunate conclusion that peak grip aperture is not a reliable measure for determining how visual information is processed for grasping. Thus, it cannot be used to support the claim that grip aperture is based either on the perceived size (Franz et al., 2000) or on another judgment of size (Aglioti et al., 1995) or on no judgment of size at all (Brenner & Smeets, 1996). The third step in the interpretation is therefore also not well founded.

The perceptual part of Aglioti et al.'s (1995) experiment has received very little attention. Choosing a perceptual measure to compare with grasping is not a simple issue (Franz, 2003). A very clever feature of Aglioti et al.'s study was to incorporate the perceptual judgment in the grasping task by letting the subjects choose which of two possible targets to grasp, on the basis of their size. Aglioti et al. thus implicitly claimed that selecting the target is a perceptual (i.e., ventral) process. The question is whether this claim (i.e., the first step of Aglioti et al.'s interpretation) is valid.

Some authors suggest that there might be independent selection mechanisms for perception and action. For instance, Bonfiglioli, Duncan, Rorden, and Kennett (2002) found that objects are not more easily recognized at the location of the auditorily indicated target for a goal-directed movement than at another location. Furthermore, subjects who have to respond under time pressure make more purely visual (nonsemantic) errors when choosing a gesture (an action task) to indicate the object's identity than when making a conscious "perceptually based" response, such as object naming (Rumiati & Humphreys, 1998). These differences between choosing an action and preparing a perceptual response have been explained by proposing that the dorsal pathway is responsible for choosing an action but not for choosing a perceptual response. If so, then choosing a target to grasp is not necessarily a (ventral) perceptual process. However, other experimental evidence suggests that the same mechanism is responsible for choosing a target for action and for perception (Deubel, Schneider, & Paprotta, 1998; Schiegg, Deubel, & Schneider, 2003). Irrespective of whether there is a single or more than one selection mechanism, the important question for the two-visual-systems hypothesis is whether the selection of a target for a goal-directed action is indeed part of the ventral stream. If the selection occurs in the dorsal stream or before the split of the two streams, the choice of the target in the experiment by Aglioti et al. cannot be regarded as a measure of the ventral processing of visual information for perception.

Recent behavioral research not involving any visual illusions provides compelling evidence for the involvement of the dorsal stream in target selection. Desmurget and colleagues have provided a tool to determine behaviorally whether the dorsal stream is critically involved in specific aspects of a task (Desmurget et al., 1999; Pisella et al., 2000). Using transcranial magnetic stimulation and a patient study, they showed that part of the dorsal route (the posterior parietal cortex) is necessary for fast (less than 150-ms latency) corrections of ongoing pointing movements to perturbations of object locations. If the fast dorsal route is also responsible for the selection of a target, subjects should be able to respond fast to changes in target identity in an experiment in which the subject has to choose the "correct" target location from two alternatives

(as in Aglioti et al., 1995). An experiment that we performed for another purpose addressed this issue (Brenner & Smeets, 2004). In the second session of that experiment, two squares appeared: a red one and a green one. Subjects had to point to the red one as fast as possible. As soon as the subject started to move, the luminance of the two squares changed considerably. In some trials the red square also became green at the same time (and vice versa). In these trials, the other target became the correct one. Subjects were able to adjust their choice to this change at a short (120-ms) latency. Because such fast responses rely on the dorsal pathway, as mentioned above, selecting the correct target must take place in the dorsal pathway, too, and is therefore presumably an integral part of motor control and not a separate perceptual process. This even holds for a choice based on color, an attribute that is irrelevant for executing the pointing action. In the grasping experiment of Aglioti et al. (1995), target selection was based on size, according to some a relevant attribute for grasping. It is therefore not at all evident that target selection cannot be considered to be an integral part of the action. Therefore, the first step of the interpretation is also questionable.

Four steps are needed to interpret the results of Aglioti et al. (1995) as showing that visual information is processed separately for perception and action. From the discussion above, we can conclude that 10 years of research have revealed that three of these four steps are at least questionable. So, the results of the original study do not warrant its conclusion. This does not necessarily lead to the conclusion that we should reject the two-visual-systems hypothesis. It is even questionable whether such a rejection is possible. If two tasks (one classified as perceptual and the other as an action) are equally influenced by an illusion, one can argue that this is because the illusion influences the visual processing before the two streams are separated (Dyde & Milner, 2002). Another frequently used argument that makes the hypothesis immune to rejection is that the analyzed measure is not a real motor measure but is influenced by perceptual contributions (Carey, 2001). The effect of the Ebbinghaus illusion on movement time in a fast pointing movement (van Donkelaar, 1999) and the effects of many other illusions on various other aspects of motor tasks (reviewed in Smeets, Brenner, de Grave, & Cuijpers, 2002) have therefore not been regarded as enough evidence to reject the hypothesis.

One might think that a meta-analysis of all perception-action studies involving illusions is a way to test the two-visual-systems hypothesis. Although there are a few studies showing a larger illusion effect on action than on perception (e.g., Yamagishi, Anderson, & Ashida, 2001), the vast majority show a smaller effect on action than on perception (reviewed by, for instance, Carey, 2001; Goodale & Westwood, 2004; Smeets et al., 2002). However, such a meta-analysis is biased for several reasons. The strongest bias is caused by the fact that no one will regard a stimulus that does not show any perceptual effect (but only a motor effect) as an illusion. Elements of such a stimulus are regarded as distractors (e.g., Fischer & Adam, 2001). The perceptual effect of distractors is generally not formally tested but is considered to be absent (otherwise it would have been an illusion). Second, when setting up experiments to study the effect of illusions, one ensures that the perceptual effect is as strong as possible (in order to be able to get significant effects). For instance, because making the central disk more similar to the flankers increases the strength of the Ebbinghaus illusion, experimenters generally use thin chips in

illusion experiments instead of the cylinders that are normally used in grasping experiments (Franz et al., 2000). It is easy to design perceptual experiments that are only marginally influenced by the illusion (Vishton, Rea, Cutting, & Nunez, 1999), but experimenters generally choose the task with the largest effect. This is reasonable if one believes that there is a single common representation underlying all tasks. But if one assumes that each task uses its own combination of (inconsistent) spatial attributes (Smeets et al., 2002), this selection creates a bias.

In this article, we have concentrated on one paradigm used to study a possible dissociation between perception and action: grasping the Ebbinghaus illusion. Although not reproduced as often, other paradigms have also been used to test this dissociation. We discuss two of them in the remainder of this article. Pointing (or jabbing) at targets surrounded by an eccentric frame is a task that was developed even before the use of the Ebbinghaus illusion in grasping (Bridgeman, 1991; Bridgeman, Gemmer, Forsman, & Huemer, 2000). The results for this illusion seemed unambiguous: Despite the clear perceptual mislocalization of the target (the induced Roelofs effect), the frame did not affect the endpoints of fast goal-directed movements (jabbing). However, 10 years after the initial publication, we questioned this interpretation (de Grave, Brenner, & Smeets, 2002), because the effect of the illusion on perceptual judgments of target location were not robust. In an experiment designed to investigate whether all effects are caused by the same shift in perceived "straight ahead," we found that the perceptual mislocalization disappeared in a session in which the subjects could be asked to judge the frame location. Without explicitly asking about the frame location, Bridgeman and colleagues concluded that both perceptual and motor effects could be explained by the same shift in perceived straight ahead (Dassonville, Bridgeman, Bala, Thiem, & Sampanes, 2004). Although there is still some controversy about the correct interpretation in terms of perceived straight ahead (Dassonville & Bala, 2004; de Grave, Brenner, & Smeets, 2004), all recent articles on the induced Roelofs effect agree that the results obtained with this paradigm are fully compatible with a common processing for perception and action.

Another interesting paradigm is the study of forces when lifting an object. For lifting, you need a judgment of the object's weight. Such a judgment can be obtained visually by combining the perceived size with an estimate of the object's density. A well-known illusion in which this judgment is fooled is the size-weight illusion: When comparing the weights of two objects of identical mass but different size, subjects perceive the larger one as being lighter. Of course, the difference in size influences the forces applied when lifting the object for the first time (as no veridical information is available until the object is lifted). Of interest, the size no longer affects the forces after the object has been lifted repeatedly, although the perceptual illusion is not reduced by such repetitions (Flanagan & Beltzner, 2000). This shows that the lifting force is not based on the same information as the perceptual judgment of the object's weight. The authors interpreted this as support for separate processing of information for perception and action.

Lifting forces have also been studied in combination with a visual size illusion: the Ponzo illusion (Brenner & Smeets, 1996; Jackson & Shaw, 2000). In these experiments, the illusion made subjects lift an object with larger grip and lift forces when it

appeared larger. It has been argued that the effect of the illusion on lifting does not eliminate the argument that visual processing for action is immune to illusions because the forces during grasping are "based on expectation" (Danckert, Sharif, Haffenden, Schiff, & Goodale, 2002, p. 279) or because "inferred object properties such as weight are vulnerable to perceptual illusions" (Dyde & Milner, 2002, p. 518). However, Flanagan and Beltzner's (2000) study on the size-weight illusion indicated that the forces that one applies to lift an object are not inferred on the basis of conscious inferences or expectations but are based on a direct sensorimotor prediction. So it is very likely also that the effects of the Ponzo illusion on the exerted forces are caused by a direct visuomotor prediction, rather than indirectly through properties that are inferred from the perceived size. If so, then the fact that the visual illusion affects lifting forces is a clear violation of one aspect of the two-visual-systems hypothesis: the presumed existence of a direct pathway for action that is immune to illusions.

Most other illusion experiments that are claimed to support the two-visual-systems hypothesis can also be interpreted as opposing the hypothesis (reviewed by Smeets et al., 2002). The fact that the results of some paradigms cannot be regarded as evidence for a dissociation between visual processing for perception and action in healthy subjects does not mean that there are not two visual streams with different roles (Mishkin, Ungerleider, & Macko, 1983; Trevarthen, 1968) or that lesions to one of these streams will not affect some perceptual tasks differently than some motor tasks (Goodale, Milner, Jakobson, & Carey, 1991). However, even the behavioral deficits of the patient on whom the two-visual-systems hypothesis is based (D.F.) do not completely follow a dissociation between perception and action but depend on whether egocentric or allocentric information is required (Schenk, 2005). This recent experimental result is in line with Smeets et al.'s (2002) earlier claim that "whether an illusion influences the execution of a task will therefore depend on which spatial attributes are used rather than on whether the task is perceptual or motor" (p. 135).

References

- Aglioti, S., DeSouza, J. F. X., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*, 679–685.
- Amazeen, E. L., & DaSilva, F. (2005). Psychophysical test for the independence of perception and action. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 170–182.
- Biegstraaten, M., Smeets, J. B. J., & Brenner, E. (2003). The influence of obstacles on the speed of grasping. *Experimental Brain Research*, *149*, 530–534.
- Bonfiglioli, C., Duncan, J., Rorden, C., & Kennett, S. (2002). Action and perception: Evidence against converging selection processes. *Visual Cognition*, *9*, 458–476.
- Brenner, E., & Smeets, J. B. J. (1996). Size illusion influences how we lift but not how we grasp an object. *Experimental Brain Research*, *111*, 473–476.
- Brenner, E., & Smeets, J. B. J. (2004). Colour vision can contribute to fast corrections of arm movements. *Experimental Brain Research*, *158*, 302–307.
- Bridgeman, B. (1991). Complementary cognitive and motor image processing. In G. Abrecht & L. W. Stark (Eds.), *Presbiopia research: From molecular biology to visual adaptation* (pp. 189–198). New York: Plenum Press.
- Bridgeman, B., Gemmer, A., Forsman, T., & Huemer, V. (2000). Process-

- ing spatial information in the sensorimotor branch of the visual system. *Vision Research*, 40, 3539–3552.
- Carey, D. P. (2001). Do action systems resist visual illusions? *Trends in Cognitive Sciences*, 5, 109–113.
- Danckert, J. A., Sharif, N., Haffenden, A. M., Schiff, K. C., & Goodale, M. A. (2002). A temporal analysis of grasping in the Ebbinghaus illusion: Planning versus online control. *Experimental Brain Research*, 144, 275–280.
- Dassonville, P., & Bala, J. K. (2004). Are the original Roelofs effect and the induced Roelofs effect confounded by the same expansion of remembered space? *Vision Research*, 44, 1025–1029.
- Dassonville, P., Bridgeman, B., Bala, J. K., Thieme, P., & Sampanes, A. (2004). The induced Roelofs effect: Two visual systems or the shift of a single reference frame? *Vision Research*, 44, 603–611.
- de Grave, D. D. J., Biegstraaten, M., Smeets, J. B. J., & Brenner, E. (2005). Effects of the Ebbinghaus figure on grasping are not only due to misjudged size. *Experimental Brain Research*, 163, 58–64.
- de Grave, D. D. J., Brenner, E., & Smeets, J. B. J. (2002). Are the original Roelofs effect and the induced Roelofs effect caused by the same shift in straight ahead? *Vision Research*, 42, 2279–2285.
- de Grave, D. D. J., Brenner, E., & Smeets, J. B. J. (2004). An apparent compression cannot explain the difference between the original and the induced Roelofs effect: Reply. *Vision Research*, 44, 1031–1032.
- Desmurget, M., Epstein, C. M., Turner, R. S., Prablanc, C., Alexander, G. E., & Grafton, S. T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience*, 2, 563–567.
- Deubel, H., Schneider, W. X., & Paprotta, I. (1998). Selective dorsal and ventral processing: Evidence for a common attentional mechanism in reaching and perception. *Visual Cognition*, 5, 81–107.
- Dyde, R. T., & Milner, A. D. (2002). Two illusions of perceived orientation: One fools all of the people some of the time; the other fools all of the people all of the time. *Experimental Brain Research*, 144, 518–527.
- Fischer, M. H., & Adam, J. J. (2001). Distractor effects on pointing: The role of spatial layout. *Experimental Brain Research*, 136, 507–513.
- Flanagan, J. R., & Beltzner, M. A. (2000). Independence of perceptual and sensorimotor predictions in the size–weight illusion. *Nature Neuroscience*, 3, 737–741.
- Franz, V. H. (2001). Action does not resist visual illusions. *Trends in Cognitive Sciences*, 5, 457–459.
- Franz, V. H. (2003). Manual size estimation: A neuropsychological measure of perception? *Experimental Brain Research*, 151, 471–477.
- Franz, V. H., Bühlhoff, H. H., & Fahle, M. (2003). Grasp effects of the Ebbinghaus illusion: Obstacle avoidance is not the explanation. *Experimental Brain Research*, 149, 470–477.
- Franz, V. H., Gegenfurtner, K. R., Bühlhoff, H. H., & Fahle, M. (2000). Grasping visual illusions: No evidence for a dissociation between perception and action. *Psychological Science*, 11, 20–25.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15, 20–25.
- Goodale, M. A., & Milner, A. D. (2004). *Sight unseen: An exploration of conscious and unconscious vision*. New York: Oxford University Press.
- Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991, January 10). A neurological dissociation between perceiving objects and grasping them. *Nature*, 349, 154–156.
- Goodale, M. A., & Westwood, D. A. (2004). An evolving view of duplex vision: Separate but interacting cortical pathways for perception and action. *Current Opinion in Neurobiology*, 14, 203–211.
- Haffenden, A. M., & Goodale, M. A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience*, 10, 122–136.
- Haffenden, A. M., Schiff, K. C., & Goodale, M. A. (2001). The dissociation between perception and action in the Ebbinghaus illusion: Nonillusory effects of pictorial cues on grasp. *Current Biology*, 11, 177–181.
- Jackson, S. R., & Shaw, A. (2000). The Ponzo illusion affects grip-force but not grip-aperture scaling during prehension movements. *Journal of Experimental Psychology: Human Perception and Performance*, 26, 418–423.
- Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences*, 6, 414–417.
- Mon-Williams, M., Tresilian, J. R., Coppard, V. L., & Carson, R. G. (2001). The effect of obstacle position on reach-to-grasp movements. *Experimental Brain Research*, 137, 497–501.
- Pavani, F., Boscagli, I., Benvenuti, F., Rabuffetti, M., & Farnè, A. (1999). Are perception and action affected differently by the Titchener circles illusion? *Experimental Brain Research*, 127, 95–101.
- Pisella, L., Grea, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., et al. (2000). An “automatic pilot” for the hand in human posterior parietal cortex: Toward reinterpreting optic ataxia. *Nature Neuroscience*, 3, 729–736.
- Rumiati, R. I., & Humphreys, G. W. (1998). Recognition by action: Dissociating visual and semantic routes to action in normal observers. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 631–647.
- Schenk, T. (2005). *Is the dissociation between perception and action in the visual system based on a dissociation between allocentric and egocentric vision?* (Abstract Viewer/Itinerary Planner Program No. 363.4). Washington, DC: Society for Neuroscience.
- Schiegg, A., Deubel, H., & Schneider, W. X. (2003). Attentional selection during preparation of prehension movements. *Visual Cognition*, 10, 409–431.
- Smeets, J. B. J., & Brenner, E. (1999). A new view on grasping. *Motor Control*, 3, 237–271.
- Smeets, J. B. J., Brenner, E., de Grave, D. D. J., & Cuijpers, R. H. (2002). Illusions in action: Consequences of inconsistent processing of spatial attributes. *Experimental Brain Research*, 147, 135–144.
- Smeets, J. B. J., Glover, S., & Brenner, E. (2003). Modeling the time-dependent effect of the Ebbinghaus illusion on grasping. *Spatial Vision*, 16, 311–324.
- Trevarthen, C. B. (1968). Two mechanisms of vision in primates. *Psychologische Forschung*, 31, 299–348.
- van Donkelaar, P. (1999). Pointing movements are affected by size-contrast illusions. *Experimental Brain Research*, 125, 517–520.
- Vishton, P. M., Rea, J. G., Cutting, J. E., & Nunez, L. N. (1999). Comparing effects of the horizontal-vertical illusion on grip scaling and judgment: Relative versus absolute, not perception versus action. *Journal of Experimental Psychology: Human Perception and Performance*, 25, 1659–1672.
- Yamagishi, N., Anderson, S. J., & Ashida, H. (2001). Evidence for dissociation between the perceptual and visuomotor systems in humans. *Proceedings of the Royal Society London, Series B*, 268, 973–977.

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