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REVIEW

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Illusions in action: consequences of inconsistent processing of spatial attributes

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Abstract Many authors have performed experiments in which subjects grasp objects in illusory surroundings. The vast majority of these studies report that illusions affect the maximum grip aperture less than they affect the perceived size. This observation has frequently been regarded as experimental evidence for separate visual systems for perception and action. In order to make this conclusion, one assumes that the grip aperture is based on a visual estimate of the object's size. We believe that it is not, and that this is why size illusions fail to influence grip aperture. Illusions generally do not affect all aspects of space perception in a consistent way, but mainly affect the perception of specific spatial attributes. This applies not only to object size, but also to other spatial attributes such as position, orientation, displacement, speed, and direction of motion. 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. To evaluate whether illusions affect actions when they influence the relevant spatial attributes we review experimental results on various tasks with inconsistent spatial processing in mind. Doing so shows that many actions are susceptible to visual illusions. We argue that the frequently reported differential effect of illusions on perceptual judgements and goal-directed action is caused by failures to ensure that the same spatial attributes are used in the two tasks. Illusions only affect those aspects of a task that are based on the spatial attributes that are affected by the illusion.

Keywords Human · Perception · Visuomotor · Saccades · Arm movement

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Introduction

Following the elegant experiment of Aglioti et al. (1995), many authors have performed experiments involving grasping objects in illusory surroundings (reviewed by Carey 2001). The vast majority of these studies (but not all, see Franz et al. 2000, 2001; Pavani et al. 1999; Vishton et al. 1999) report that illusions affect the perception of size more than they affect the maximum grip aperture during grasping. This observation has frequently been regarded as experimental evidence for the two-visual-systems model of Goodale and Milner (1992). However, there is another explanation for this phenomenon. We will start this review by presenting this explanation.

Our perception is based on various attributes of objects, such as colour, shape, size, orientation, location, and speed. Many of these attributes are physically related. For instance the physical orientation of a bar is determined by the physical locations of its end-points. As the brain uses different information processing to obtain such physically related spatial attributes (Zeki 1993), however, the obtained attributes are not necessarily consistent with each other (for a review see Gillam 1998). For instance the perceived orientation of a bar might be inconsistent with the perceived locations of its end-points. Many illusions induce such inconsistencies, affecting one spatial attribute (e.g. object orientation) without affecting physically related ones (e.g. the locations of distinct features on the object).

Such inconsistencies can be found between various attributes of spatial perception, and are often present in visual illusions. For instance, the Müller-Lyer illusion changes the perception of extent, without causing a corresponding change in the perceived positions of the end-points (Gillam and Chambers 1985; Mack et al. 1985; see Fig. 1A). A tilted framework around two dots can change the perceived alignment of the dots relative to vertical, without changing the perceived alignment with a third dot outside the frame (Wenderoth 1983). Induced motion changes the perceived motion of an object,

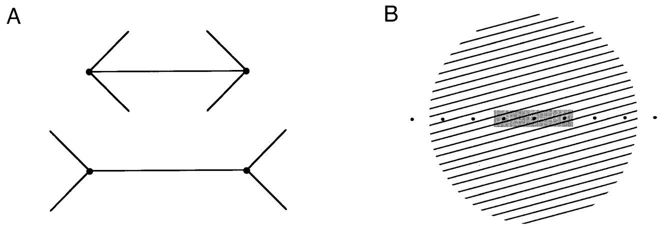

Fig. 1A, B Examples of inconsistencies between the perception of spatial attributes. **A** The Müller-Lyer illusion leads to inconsistent perception of length and positions. The *upper horizontal line* seems shorter than the *lower horizontal line* (which it is not). However, the *dots* at the end-points of both lines seem perfectly aligned (which they are). **B** Inconsistency between the perception of spatial attributes in the tilt illusion. The *grey bar* seems to be tilted clockwise, and seems oriented differently than the *long dotted line*. However, both the bar and the dotted line are exactly horizontal. The line of dots indeed seems to pass through the middle of the grey bar. The perception of the position of the dots relative to the bar is thus inconsistent with the perception of the orientation of the long dotted line relative to the bar

without causing a corresponding change in its perceived position (Smeets and Brenner 1995a). Despite the overwhelming evidence for such inconsistencies, the subjective sensation of consistency has led some to question the design of various experiments. For instance, Franz (2001) attributes all differences in the effect of size illusions to experimental artefacts, neglecting the possibility that size might be inconsistent with positions. Bridgeman et al. (1997a) argued that the apparent inconsistency between position and motion reported by Smeets and Brenner (1995a) was caused by their letting the background continue to move after the target disappeared in their position perception experiment. This criticism might apply to a preliminary publication of these results (Brenner and Smeets 1994), but the final paper shows that the perception of position did not depend on the time the background stops moving (compare experiments 2a and 2b in Smeets and Brenner 1995a).

Vishton et al. (1999) noted that absolute judgements are inconsistent with relative judgements. The tilt illusion used by Glover and Dixon (2001a, 2001b) shows that two relative judgements can reveal an inconsistency in spatial perception. In Fig. 1B, the line of dots appears to have a different orientation than the bar. Nevertheless, each dot within the bar appears to be at the same distance from both sides. The background of lines influences the perceived orientation of the line of dots relative to the bar, without influencing the perceived positions of the dots relative to that same bar. The two inconsistent attributes in this example (position and orientation) are both relative (allocentric) measures. Our argument is therefore more general than the distinction between "absolute" and "relative" made by Vishton et al. (1999).

Which of the physically related attributes is used in a task depends on which attribute gives the most direct (and thus reliable) information for performing that task, independently of whether the task can be classified as an action or not. Analogously, within a single task, each aspect of that task will be based on the attribute that gives the most direct (and thus reliable) information for performing that aspect. Thus even within a single movement, some aspects may be affected, while others are not. In the example of Fig. 1B, all aspects of tasks that are based on positions (such as pointing to a position) will be unaffected. On the other hand, aspects of tasks that are based on the orientation of the bar (such as orienting one's hand to grasp it) will be affected. For instance when a digit is approaching a point on a bar's surface, the direction of approach may be affected by a misperceived orientation, while the final position is not.

Inconsistent processing and grasping

A similar reasoning can explain the absence of an effect of size illusions on grip aperture: the processing of visual information does not necessarily lead to a judgement of size that is consistent with the judgement of the locations of the grasping positions. Accepting this premise, one realises that the observed linear relation between object size and grip aperture (known since the pioneering work of Jeannerod (1986) and reviewed in Smeets and Brenner (1999) does not necessarily signify that a visual estimate of object *size* is used to control hand aperture in grasping. We have argued that object size is not a very suitable source of information for controlling grasping (Smeets and Brenner 1999). In our view, only information about two *positions* at the object's surface, and the local surface properties at those positions, is needed to control the movements of the digits for grasping. There is therefore no reason to expect that an illusion that affects an irrelevant spatial attribute such as size will affect grasping. Although the size of the object is physically equivalent to the difference between the two positions at which it is grasped, a size illusion might only influence the perception of size. This distinction between size and the difference between two positions is the key for understanding the reported lack of effect of size illusions on grasping (Smeets and Brenner 2001a).

According to our view on grasping, only illusions that affect the perception of *positions* will affect grip aperture. Various illusions influence the perceived position of a target, either relative to the subject or relative to the environment (discussed in a later section). This might explain why in some cases illusions have a clear effect on grip aperture (reviewed by Franz 2001). To our knowledge, nobody has investigated how the stimuli used in grasping studies affect the perception of positions. On the other hand, illusory changes in size should influence aspects of grasping that have been shown to use *size*, such as the initial forces used when lifting the object that is grasped (Gordon et al. 1991). In line with our expectations, the Ponzo illusion does affect the forces used to grip (Jackson and Shaw 2000) and lift (Brenner and Smeets 1996) an object, without affecting grip aperture.

Considering this argument, we will not discuss the details of the numerous grasping studies (reviewed by

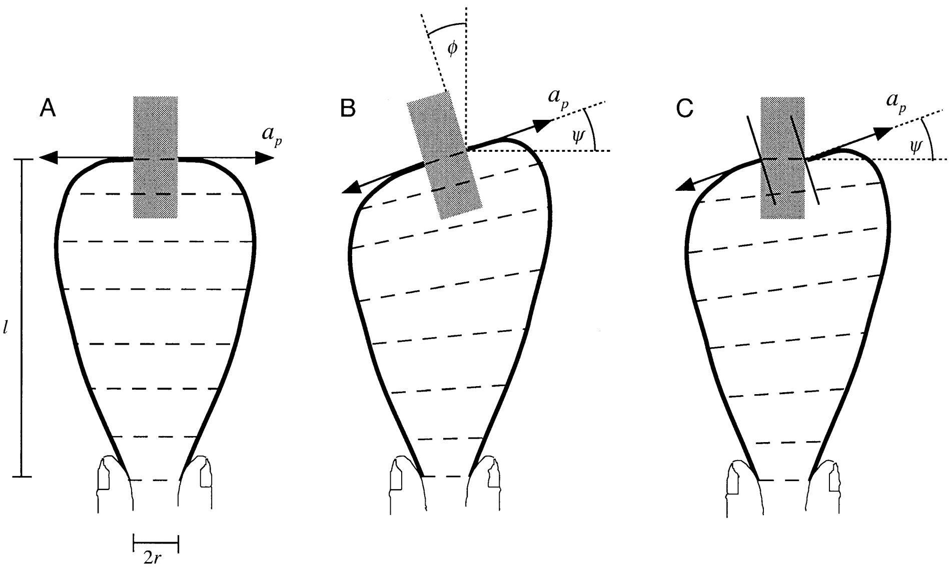

Fig. 2A–C Schematic representation of how inconsistent spatial attributes determine the orientation of the grip during a reach-to-grasp movement. The *dashed lines* indicate the grip orientation at various instances during the movement. **A** Grasping a vertically oriented object (width $2r$) at distance l. **B** Grasping the same object as in **A**, but now rotated. The apparent orientation ψ is the same as the actual orientation ϕ. During the movement, the grip is gradually reoriented in the direction of the object. **C** Grasping the same object, but now only the apparent orientation of its surfaces is rotated over an angle ψ. To ensure a perpendicular approach, the orientation of the grip gradually turns in the direction of the illusion. Although the digit movements approach the surface perpendicular to the illusory orientation, the orientation of the grip returns to zero near contact in order to end at the right positions

Carey 2001; Franz 2001; Plodowski and Jackson 2001). Neither will we discuss which (aspects of) tasks can be classified as actions, a major issue in many papers on illusions in action (e.g. Gentilucci et al. 1996; Rossetti 1998; Bridgeman et al. 1998, 2000; Smeets and Brenner 2001b). Instead, we will start the review of effects of inconsistent processing of physically related spatial attributes by discussing how position and orientation (Fig. 1B) will influence grasping. In the rest of this paper we will discuss how other inconsistencies can explain the effects of various illusions on performance in tasks other than grasping.

Positions and orientation

In order to link inconsistent processing of spatial attributes to the effects of illusions on a task, one needs to know which information is used for each aspect of that task. It is rather difficult to experimentally determine whether a variable is actually used in an action, as illustrated by the debate about whether 'tau' is used to time actions (Michaels et al. 2001; Tresilian 1999). Moreover, one should not only know what information is used, but also how it is used in the task. This is even less well known for most tasks, but it is essential for understanding the effect of illusions on a task.

As an example we will discuss the interpretation by Glover and Dixon (2001a, 2001b) of the effects of the tilt illusion on a reach to grasp movement. We will do so on the basis of a model of how such movements are based on spatial information (Smeets and Brenner 1999, 2001c; see Appendix A). For each digit, the model determines the maximally smooth movement that stops at a *position* on the bar's surface with the final approach perpendicular to the apparent *orientation* of the bar. In line with the discussion in the previous section, the object's *size* is not used. We will use this model to predict the effect of the tilt illusion such as the one presented in Fig. 1B.

To do so, we assume that the illusion has inconsistent effects on the two spatial attributes involved in grasping. It changes the perceived *orientation* of an object, without changing the perceived *positions* of the intended contact positions (Wenderoth 1983). Since each digit is to approach the object's surface perpendicularly, the hand will automatically orient itself towards the illusory perceived orientation of the bar as soon as it starts to move. As the locations of the intended contact positions are not affected, the illusion does not affect the final grip orientation. Therefore, the grip rotation due to the illusion must have vanished by the time the object is contacted (Fig. 2). The quantitative predictions (Fig. 3A) follow the qualitative argument made in Fig. 2B, C.

Glover and Dixon (2001a, 2001b) examined how subjects grasp an object embedded in such an illusion. They compared the effect of ±10° background tilt with that of ±10° object tilt on grip orientation. They found that the effect of the background tilt was about 50% of that for a real orientation change in the initial part of the movement, but disappeared completely near the end of the movement (Glover and Dixon 2001b; symbols in Fig. 3B). In another study using the same illusion they

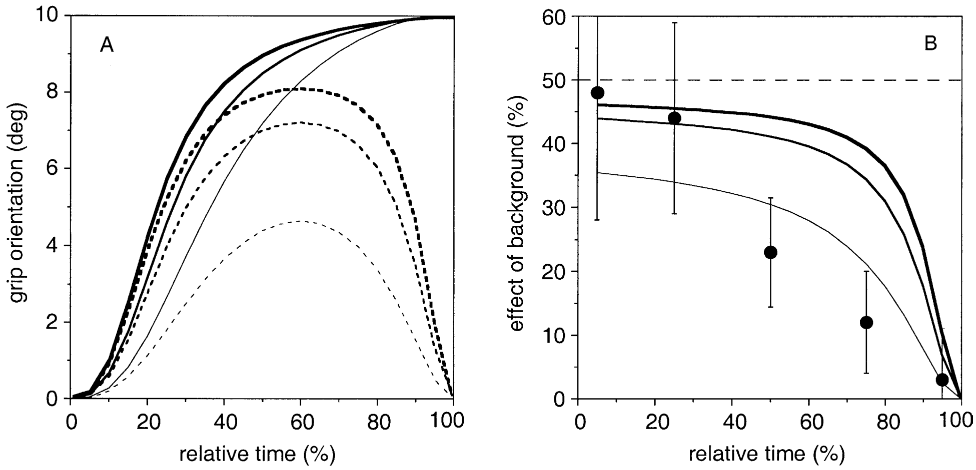

Fig. 3A, B Model predictions for the orientation of the hand when grasping a 2-cm-wide bar as in Fig. 2. Predictions (see Appendix A) are given for three values of the approach parameter (thick curves: 2.5 m; medium curves: 1.5 m; thin curves: 0.5 m). **A** Predicted grip orientations. *Continuous curves* indicate the predictions for grasping an object that is rotated over an angle ϕ=10° (see Fig. 2B). *Dashed curves* indicate the predictions for grasping an object while only the apparent orientation ψ is rotated by 10° (see Fig. 2C). **B** The effect of the illusion is determined by comparing two conditions: grasping an object with a 10° background tilt and grasping an object rotated over ϕ=10°. We assume that the background induces a 5° change in perceived surface orientation ψ (50% illusion). The *continuous curves* give the ratio between the predicted orientation of the hand in the two conditions. Because the grip is based on both *positions* and *orientation*, the effect of the background on grip orientation is always smaller than the illusory effect that was the input to the model. *Symbols* data from an experiment of Glover and Dixon (2001b), converted to our measure

found a similar pattern (Glover and Dixon 2001a). For our model predictions (curves in Fig. 3B) we assumed that the surface orientation at the contact points was judged to be rotated by 50% of the background tilt. Considering the confidence limits, the experimental data of Glover and Dixon (2001b, symbols in Fig. 3B) follow the predictions of our model. Note that we get this performance without assuming that the effect of the illusion changed during the movement. There is therefore no need to make any additional assumptions (for instance a different effect of the illusion on planning and execution) to explain the data of Glover and Dixon (2001a, 2001b).

We assumed in the above reasoning that the effect of the background tilt on the perceived line orientation is 50%. Glover and Dixon (2001b) report that in a perceptual experiment, in which subjects had to align the bar with their sagittal plane, the effect of the background tilt was considerably smaller (10%). A possible explanation for this difference is that aligning the bar with the sagittal plane may not be the same as judging the surface orientation. Differences between the results of two perceptual judgements that seem to be essentially orientation judgements are not uncommon. For instance, it has been shown that setting bars to be collinear and setting bars to be parallel yield different systematic deviations from veridical orientation matching (Cuijpers et al. 2002). Alignment, parallelity, and orientation have to be considered as physically related but independently processed spatial attributes.

Position, displacement and motion

Detecting a change in position (displacement) is based on different information than detecting motion (Smeets and Brenner 1994). One can experience this by performing a simple experiment on a sunny beach. Put a long stick in the sand, mark the end of the shadow, and watch carefully for a few minutes. You will not notice any motion of the shadow, because the speed is below the threshold of motion detectors. However, after a few minutes of looking at a stationary shadow, its end is clearly not at the marked position any more. Although no motion was visible, the representation of the motion integrated over time (position) has been updated. Various illusions (such as the motion aftereffect) can induce the opposite inconsistency: seeing motion without a change in perceived position. Whether such illusions affect aspects of an action depends on which of these physically related variables is used to control those aspects.

Induced motion (Duncker 1929) has frequently been used to study information processing for goal-directed actions. Motion of a background induces changes in perceived target speed (Brenner 1991) without equivalent changes in perceived target position (Bacon et al. 1982). When subjects are asked to track the motion of a target with their (invisible) hand, they tend to match the speed of the hand to that of the target, allowing large positional errors. We therefore expect motion of the background to affect tracking, inducing faster arm movements when the background moves in a direction opposite to the target and vice versa. This has indeed been reported for both sinusoidally moving targets (Farber 1979) and targets

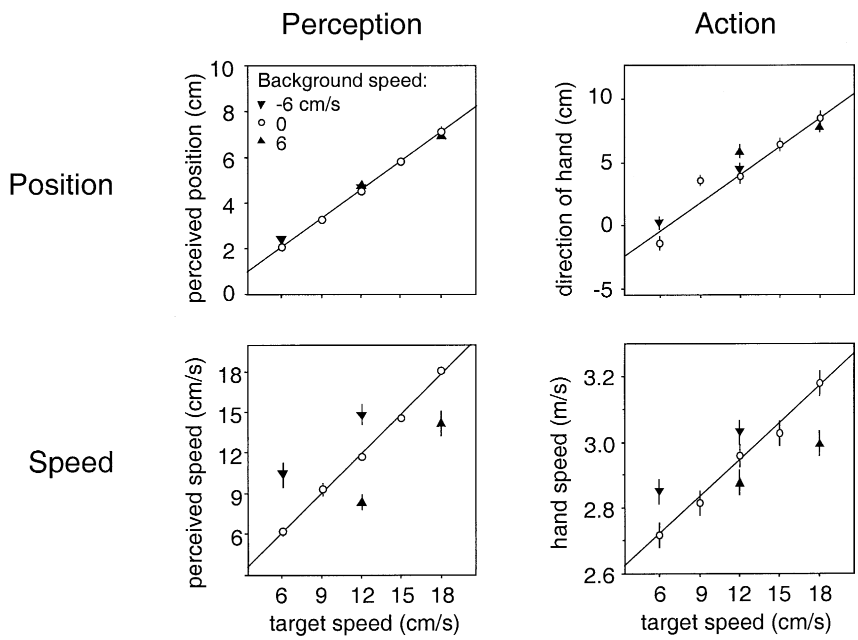

Fig. 4 The independent effect of background motion on position and speed is observable in both perception and action (data from Figs. 4, 5A, 12, and 13 in Smeets and Brenner 1995a). The *different symbols* indicate the direction of motion of the background relative to that of the target. The *error bars* indicate the between subjects standard error of the mean, the *continuous line* indicates the effect of real target speed. *Upper row* Motion of the background neither leads to a change in the perception of a target's position, nor to a change in the initial direction of a fast goal-directed hand movement towards it. *Lower row* The same motion of the background leads to a change in the perceived speed of that target, and to a similar change in the peak speed of a fast goal-directed hand movement towards that target

moving at constant speed (Masson et al. 1995). When one asks subjects to point at the position at which a moving target disappears, there is no need to consider information about its prior motion. Background motion therefore has little effect on the end position of pointing movements (Bridgeman et al. 1981).

When one tries to follow a target with the eyes, the eyes will not only correct retinal errors, but also anticipate the movement of a target (anticipatory saccades). The accompanying head movements when performing such experiments with the head free are also thought to be directed towards future positions of interest (Smeets et al. 1996). To pursue a moving target, the retinal error and retinal slip of the target are more relevant than its actual motion. As soon as retinal slip is removed as source of information (by stabilising the target on the retina), pursuit eye movements make the same errors as perception (Holtzman et al. 1978). When making anticipatory saccades or head movements towards a moving target, its motion is useful information to predict the target's future position. We therefore expect that induced motion will affect both anticipatory saccades and head movements towards moving targets, but not pursuit eye movements, which is indeed the case (Zivotofsky et al. 1995). When retinal error and retinal slip give incomplete information (for instance when the target moves behind an occluder), the brain will use information on the target's actual motion. As this information source is affected by the illusion, the pursuit eye movements will be too. Stone et al. (2000) indeed showed that visual illusions affect the tracking of partially occluded objects.

If one asks subjects to intercept such a moving target as fast as possible, one might have expected a prediction of the interception position based on the misperceived speed. This is not what is found: the hand's path is not influenced by the illusion (Smeets and Brenner 1995a), probably because the speed information of previous trials is used (de Lussanet et al. 2001). However, this does not mean that interception is insensitive to the illusion: the speed of the movement depended on the speed of the target, and was influenced in the same way by the illusion as was the perceived speed (see Fig. 4). Motion of a background perpendicular to the direction in which a target is moving changes the perceived direction of the target's movement (Bacon et al. 1982; Smeets and Brenner 1995b). When asked to track such a target with their invisible hand, subjects tracked the perceived direction of motion, not the actual direction (Bacon et al. 1982). When asked to hit the target, subjects start their movement in a direction which is influenced by the background motion in a similar way as is the percept (Smeets and Brenner 1995b).

Motion of the background not only leads to misperception of target motion, but also to misperception of the accompanying displacement. We therefore predict that if information about a target's displacement can be directly used to perform the task, a moving background will have a clear effect on performance. This is indeed what

Abrams and Landgraf (1990) found in a series of experiments. In one of their experiments, they investigated goal-directed hand movements towards the final position of a moving target. While the target was moving, the background could move in either the same or the opposite direction. In a first condition, the hand started at the same position as the target. In a second condition, the initial positions of hand and target differed. Thus, the displacement of the target corresponded directly to the required hand movement in the first condition, but not in the second. The result was according to our predictions: the background motion had more effect in the first condition than in the second.

A similar distinction between position and displacement helps to understand why one can point correctly to a target despite not having noticed its displacement in a saccadic suppression paradigm (Bridgeman et al. 1979; Pélisson et al. 1986). In this paradigm, subjects are asked to point to a target. Before the actual pointing movement starts, subjects make a saccade towards the target. During this saccade, the location of the target is changed. This displacement is not perceived. However, there is no reason to assume that the new location itself is not perceived correctly. To point accurately, information on the current target position is needed, probably combined with information on the present hand location. Information about target displacements only gives very indirect information about the present target position. There is therefore no need to consider information about target displacements in this task.

Motion information seems irrelevant for localising a stationary target. However, motion of a texture around or inside a stationary target can change the perceived position of this target in the direction of the texture motion (Brenner and Smeets 1997; Yamagishi et al. 2001). Motion of a target's background therefore has opposite effects on two physically related attributes: the target's position is shifted in the direction of the background motion, but the target's motion is perceived in the opposite direction. If one makes a fast goal-directed movement towards such a target, this movement follows the illusory position (which is relevant), and not the (irrelevant) speed. This following occurs at a very short latency (about 150 ms; Brenner and Smeets 1997). This last result is especially interesting, because these short latency adjustments have been reported to depend on processing within the dorsal visual pathway of the brain (Desmurget et al. 1999).

A last example of the dissociation between position and motion is from another sensory modality: proprioception. A commonly used way to elicit proprioceptive illusions is to vibrate a muscle tendon. This changes the output of muscle spindles, so that the perception of the limb's *position* is changed. What is interesting with respect to our view is that the vibration has a separate effect on the perception of the *speed* of the arm (Sittig et al. 1985). The effect of vibrating a muscle tendon of a stationary (and invisible) arm is thus that one feels the arm continuously moving, while the (erroneously) felt position does not change. These two effects depend in a different way on the frequency of vibration. The largest speed illusion is found for a higher vibration frequency than the largest position illusion. There is experimental evidence that for fast goal-directed movements speed is the main controlled variable (Smeets et al. 1990), whereas for slow movements position is a more likely controlled variable. Our view predicts therefore that the distinct effects of vibration on position and speed should be visible when comparing the end-points of fast and slow goal-directed arm movements. Indeed, the largest errors in end-point position of slow movements were found for the vibration frequency that had the largest effect on position perception, whereas for fast movements the largest errors were found for the frequency that had the largest effect on speed perception (Sittig et al. 1987).

Positions and size or extent

As opposed to the illusions of motion and displacement, the use of illusions of size has become popular only very recently. Most of these studies are based on the (in our view false; Smeets and Brenner 1999) notion that the maximum aperture of the hand during grasping is related to information about the size of the object. The results of these studies are discussed by Carey (2001) and Plodowski and Jackson (2001). We discuss here the results for two other movement characteristics that are related to object size or extent. The first is that the duration of a pointing movement increases as target size decreases (Fitts and Peterson 1964). An illusory decrease in size should have exactly the same effect, which has indeed been shown (van Donkelaar 1999). A recent failure to replicate this result (Fischer 2001) is probably due to the very weak (<0.3 mm) illusion that was used. As they reported that a millimeter increase in real object size resulted in about a 1-ms reduction of movement time, the expected effect of the illusion was only 0.3 ms. They found a non-significant effect of the illusion of less than 3 ms. We can therefore safely state that their result did not differ from the expected effect of the illusion.

The second movement characteristic (which we will discuss in the rest of this section) is the amplitude of the movement (or its physically related end position). The effects of illusions of extent on this movement characteristic can be predicted using a similar reasoning as for illusions of motion (discussed in the previous section). Our prediction is that the compatibility with the task determines whether extent or position is used, and thus whether or not an illusion of extent has an effect. The mechanisms for processing positions and extent are clearly distinct. For instance, if one fixates a target binocularly, its egocentric position can be determined fully on the basis of information about the eyes' orientations. In contrast, the determination of a line's extent also requires information about the extent of the retinal image.

The Müller-Lyer illusion affects the perceived extent of a line much more than it affects the perceived positions of its end-points (Gillam and Chambers 1985; Mack et al. 1985, Fig. 1A). Our claim is that the illusion will have an effect on pointing movements towards its end-points if the line's extent is reliable information for the task. Eye movements are a factor that influence this reliability. When making pointing movements between the end-points of the illusion, subjects could use either position or extent to plan their movement. If one fixates the target position, one has more direct information on the (egocentric) location of the target than if one fixates the position at which the hand starts. Therefore, we expect a larger contribution of extent information (and thus a larger effect of the illusion) in the latter condition, which indeed has been found (Gentilucci et al. 1997). When subjects make concurrent hand and eye movements to an end-point of a Müller-Lyer figure, they fixate the target position before the hand movement is completed, and can therefore use eye orientation as direct information to guide their hand to the target's position. If the stimulus is removed during the saccade, subjects can no longer reliably fixate the target position, and are forced to use extent information. As the illusion affects perceived extent, and not position, we expect a larger effect of the illusion on the final hand position in the latter situation, which is indeed the case (Binsted and Eliot 1999).

In the experiments of Gentilucci et al. (1996, 2001), subjects had to make pointing movements from one end of the Müller-Lyer illusion to the other end, using various delays between the vision of the display and the hand movement. The rapid decay of the reliability of egocentric information (Rossetti 1998) suggests that the use of extent, and thus the effect of the illusion, will increase when delaying the movement. Gentilucci et al. (1996, 2001) found clear effects of the illusion, which increased considerably by delaying the movement. For pointing movements which start outside the Müller-Lyer figure, information about extent is not directly related to the requirements of the task. According to our reasoning, such movements should be immune to the illusion, which is indeed what has been reported (Post and Welch 1996). When subjects are asked to walk the distance of a line in another direction, they have no other option than to use its extent. When walking to a line's end-point, they can use the more direct (egocentric) position information. Illusory changes in extent will therefore influence the first task, and not the latter, which has been experimentally confirmed (Wraga et al. 2000).

The Judd illusion shifts the perceived location of (the centre of) a line segment, so actions towards the centre of a Judd-figure should be affected by the illusion. In the same paper that reported no effect of pointing at end-points of an illusion, Post and Welch (1996) report that the Judd illusion affected pointing movements to the centre of the line. When subjects are asked to pick up a bar, they must try to grasp it at its centre in order to lift it in balance. When the bar is placed to form the main line of a Judd figure, subjects grasp systematically away from the centre, as one would expect on the basis of the illusion (Ellis et al. 1999; Mon-Williams and Bull 2000).

Egocentric and allocentric position cues

The last section of this review does not deal with two different (but physically related) attributes, but with two information sources for one attribute: position. The position of a target relative to oneself could be localised purely by egocentric information. However, allocentric cues can also give information about this position. It has been argued that the direction of locomotion is generally controlled on the basis of allocentric information ('optic flow') alone (reviewed by Lappe et al. 1999). On the other hand, Rushton et al. (1998) did an experiment that showed that in a real world setting the direction of locomotion is controlled on the basis of pure egocentric position information. Following our reasoning, one would expect that the reliability of the two information sources determines which one is used. In a richly structured virtual environment, optic flow is much more reliable than in an empty virtual field. In a recent experiment, Warren et al. (2001) showed that the structure of such a virtual environment indeed determines to what extent egocentric and allocentric information is used.

If one surrounds a visual target with a frame that is off-centre, the target seems to be shifted in a direction opposite to the eccentricity of the frame (the induced Roelofs effect). This effect has been shown not only in perceptual tasks, but also in motor tasks such as open-loop pointing (Bacon et al. 1982; Bautista and Korienek 1999). Bridgeman et al. (1997a), however, found no effect on motor tasks in half of their subjects. It is not clear why those subjects did not show the effect the others showed. Using a slightly modified motor task (jabbing instead of pointing), Bridgeman and Huemer (1998) did not find an effect of the frame in any of their subjects. Apparently, the choice between egocentric and allocentric position cues depends on very subtle differences between experiments and subjects. The choice between position cues has indeed been reported to depend on the aspect of a movement (Abrams et al. 1994), and on the instructions given to the subject (Heuer and Sangals 1998). Also in perceptual tasks, the choice between position cues (and thus the magnitude of the induced Roelofs effect) can be influenced by subtle experimental manipulations (de Grave et al. 2002).

The organisation of cortical processing of sounds resembles that of vision, with a dorsal "where" system and a ventral "what" system (Rauschecker 1998). If one followed the reinterpretation of this distinction by Goodale and Milner (1992), one would expect different auditory processing for perception and action, with a larger effect of illusions on perception. Our hypothesis, on the other hand, predicts that such illusions should have similar effects on perception and action. One of the few studies on spatial illusions in the auditory domain has been performed by Bridgeman et al. (1997b). They found that if a sound source was surrounded with a frame of speakers with the same sound, the sound source was mislocalised in a direction opposite to the frame. As our view predicts, this mislocalisation was the same for perceptual and motor tasks.

Conclusion

When discussing the effect of illusions on various tasks, it has frequently been assumed that illusions work on processes in the ventral stream, whereas the processing in the dorsal stream is veridical. Our review showed that the effect of illusions is not confined to the ventral pathway, but also found in tasks for which the dorsal pathway is assumed to be responsible. The clearest example is the short-latency adjustment of an ongoing movement (Desmurget et al. 1999). Not only actual changes in target position, but also illusory changes induced by background motion lead to such fast adjustments (Brenner and Smeets 1997). Studying how illusions influence human performance in various tasks is therefore not a very good tool to study the functional distinction between the dorsal and ventral pathway.

We have discussed a wide range of studies on the effects of illusions on various tasks. This showed that if one realises that various attributes of space are not necessarily processed in a consistent way, perception and action are equally susceptible to visual illusions. The illusions affect some aspects of spatial perception. Whether this affects execution of a task does not depend on whether the task is perceptual or motor, but on which spatial attributes are used in the task. If this conclusion is true, one could ask why there are so many reports on differential effect of illusions on perceptual judgements and goal-directed action. A first reason is that the illusions investigated are a biased selection: they are chosen for their known (large) effect on certain perceptual tasks. A second reason is that it is very difficult (if not impossible) to equate visual information used in two tasks (Mon-Williams and Bull 2000). On the other hand, aspects of an action can be controlled on the basis of a single attribute, whereas in perceptual tasks subjects might give answers that reduce the inconsistency between related attributes. Therefore, it is not surprising that sometimes the effect on action is larger than on perception (Glover and Dixon 2001b; Mon-Williams and Bull 2000; Yamagishi et al. 2001).

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Appendix A

In this appendix, we apply the model for grasping as derived by Smeets and Brenner (1999, 2001c) to an experimental setup as discussed in the section "Positions and orientation". This model calculates for each digit the maximally smooth movement (minimum jerk, Flash and Hogan 1985) that ends more or less perpendicularly to the object's surface. In general, a minimum jerk movement in one dimension is given by:

$$x(t) = c_0 + c_1 t + c_2 t^2 + c_3 t^3 + c_4 t^4 + c_5 t^5 \tag{1}$$

With c_i determined by the boundary conditions for position, speed and acceleration:

$$c_0 = x(0)$$

$$c_1 = \dot{x}(0)$$

$$c_2 = \tfrac{1}{2}\ddot{x}(0)$$

$$c_3 = \tfrac{1}{2}\big(MT^2(x(MT) - 3\ddot{x}(0)) - 4MT(2\dot{x}(MT) + 3\dot{x}(0)) \\ +20(x(MT) - x(0))\big)/MT^3$$

$$c_4 = \tfrac{1}{2}\big(-MT^2(2\ddot{x}(MT) - 3\ddot{x}(0)) + 2MT(7\dot{x}(MT) \\ +8\dot{x}(0)) - 30(x(MT) - x(0))\big)/MT^4$$

$$c_5 = \tfrac{1}{2}\big(MT^2(\ddot{x}(MT) - \ddot{x}(0)) - 6MT(\dot{x}(MT) + \dot{x}(0)) \\ +12(x(MT) - x(0))\big)/MT^5$$

To describe a movement in more than one dimension, these equations hold for each dimension separately. In order to apply the model to the experimental condition in Glover and Dixon (2001b), we consider grasping a bar with half-width r starting with the same separation between digits (see Fig. 2). The distance to the bar is l. The positions at which the bar is grasped depend on the actual tilt (angle ϕ) of the bar. The final deceleration has a magnitude a_p/MT^2 and is perpendicular to the *apparent* surface orientation ψ. The magnitude of the approach parameter a_p determines the length of the path that is approaching the object's surface perpendicularly. For the finger, this yields the following boundary conditions for position, speed and acceleration:

$$x(0) = r;\ \ x(MT) = r\cos\phi;\ \ \dot{x}(0) = 0;\ \ \dot{x}(MT) = 0;$$
$$\ddot{x}(0) = 0;\ \ \ddot{x}(MT) = a_p\cos\psi/MT^2$$
$$y(0) = 0;\ \ y(MT) = l + r\sin\phi;\ \ \dot{y}(0) = 0;\ \ \dot{y}(MT) = 0;$$
$$\ddot{y}(0) = 0;\ \ \ddot{y}(MT) = a_p\sin\psi/MT^2$$

Substituting $-r$ for r and $-a_p$ for a_p yields the boundary conditions for the thumb. Given these constraints and introducing a normalised time $t_r=t/MT$ the minimum jerk trajectory for the finger is:

$$x(t_r) = r + \Big(\tfrac{1}{2}a_p\cos\psi(t_r - 1)^2 + r(\cos\phi - 1)\big(6t_r^2 - 15t_r + 10\big)\Big)t_r^3$$
$$y(t_r) = \Big(\tfrac{1}{2}a_p\sin\psi(t_r - 1)^2 + (l + r\sin\phi)\big(6t_r^2 - 15t_r + 10\big)\Big)t_r^3 \tag{2}$$

Substituting $-r$ for r and $-a_p$ for a_p in Eq. 2 yields the trajectory for the thumb. Taking the differences between the values for thumb and index finger yields for the components of the grip:

$$\Delta x(t) = 2r + (a_p\cos\psi(t_r - 1)^2 \\ +2r(\cos\phi - 1)(6t_r^2 - 15t_r + 10))t_r^3$$
$$\Delta y(t_r) = (a_p\sin\psi(t_r - 1)^2 + 2r\sin\phi\big(6t_r^2 - 15t_r + 10\big))t_r^3 \tag{3}$$

The grip aperture $\sqrt{\Delta x^2 + \Delta y^2}$ is thus independent of the distance l to the object. Using Eq. 3, one can easily compute the size and orientation of the grip for various situations. Unfortunately, the resulting formula for grip aperture is not as simple as for the situations in which the digits start in contact (Smeets and Brenner 1999) or when the orientation of the grip does not change (Smeets and Brenner 2002). To make the predictions in Fig. 3b, we used r=0.02 m, and three values for a_p (0.5, 1.5, and 2.5 m). The curves in Fig. 3b give the ratio between the amount of grip rotation for a 5° apparent object-tilt (ϕ=0°, ψ=5°) and the amount of grip rotation for a 10° real object-tilt (ϕ=ψ=10°).

The experimental data of Glover and Dixon (2001b, symbols in Fig. 3b) follow (within the confidence of their data) the predictions for a small value of the approach parameter. A small approach parameter is characteristic for accurate movements. Such a value seems a reasonable choice to describe the experiment by Glover and Dixon (2001b), as their subjects were instructed to move accurately rather than quickly. The value of the approach parameter could be estimated independently from the maximum grip aperture. Unfortunately, Glover and Dixon (2001b) did not measure this parameter.

References

Abrams RA, Landgraf JZ (1990) Differential use of distance and location information for spatial localization. Percept Psychophys 47:349–359

Abrams RA, Van Dillen L, Stemmons V (1994) Multiple source of spatial information for aimed limb movements. In: Umilta C, Moscovitch M (eds) Attention and performance XV. MIT Press, Cambridge, MA, pp 267–290

Aglioti S, DeSouza JFX, Goodale MA (1995) Size-contrast illusions deceive the eye but not the hand. Curr Biol 5:679–685

Bacon JH, Gordon A, Schulman PH (1982) The effect of two types of induced-motion displays on perceived location of the induced target. Percept Psychophys 32:353–359

Bautista AB, Korienek GG (1999) Manual aiming in the presence of visual frames of reference. J Hum Mov Stud 36:153–166

Binsted G, Elliot D (1999) Ocular perturbations and retinal/extraretinal information: the coordination of saccadic and manual movements. Exp Brain Res 127:193–206

Brenner E (1991) Judging object motion during smooth pursuit eye movements: the role of optic flow. Vision Res 31:1893–1902

Brenner E, Smeets JBJ (1994) Different frames of reference for position and motion. Naturwissenschaften 81:30–32

Brenner E, Smeets JBJ (1996) Size illusion influences how we lift but not how we grasp an object. Exp Brain Res 111:473–476

Brenner E, Smeets JBJ (1997) Fast responses of the human hand to changes in target position. J Mot Behav 29:297–310

Bridgeman B, Huemer V (1998) A spatially oriented decision does not induce consciousness in a motor task. Conscious Cogn 7:454–464

Bridgeman B, Lewis S, Heit G, Nagle M (1979) Relation between cognitive and motor-oriented systems of visual position perception. J Exp Psychol Hum Percept Perform 5:692–700

Bridgeman B, Kirch M, Sperling A (1981) Segregation of cognitive and motor aspects of visual function using induced motion. Percept Psychophys 29:336–342

Bridgeman B, Peery S, Anand S (1997a) Interaction of cognitive and sensorimotor maps of visual space. Percept Psychophys 59:456–459

Bridgeman B, Aiken W, Allen J, Maresh TC (1997b) Influence of acoustic context on sound localization: an auditory Roelofs effect. Psychol Res 60:238–243

Bridgeman B, Gemmer A, Forsman T, Huemer V (2000) Processing spatial information in the sensorimotor branch of the visual system. Vision Res 40:3539–3552

Carey DP (2001) Do action systems resist visual illusions? Trends Cogn Sci 5:109–113

Cuijpers RH, Kappers AML, Koenderink JJ (2002) Visual perception of collinearity. Percept Psychophys 64:392–404

de Grave DDJ, Brenner E, Smeets JBJ (2002) Are the original Roelofs effect and the induced Roelofs effect caused by the same shift in straight ahead? Vision Res 42:2277–2283

de Lussanet MHE, Smeets JBJ, Brenner E (2001) The effect of expectations on hitting moving targets: influence of the preceding target's speed. Exp Brain Res 137:246–248

Desmurget M, Epstein CM, Turner RS, Prablanc C, Alexander GE, Grafton ST (1999) Role of the posterior parietal cortex in updating reaching movements to a visual target. Nature Neurosci 2:563–567

Duncker K (1929) Über induzierte Bewegung (ein Beitrag zur Theorie optisch wahrgenommener Bewegung). Psychol Forsch 12:180–259

Ellis RR, Flanagan JR, Lederman SJ (1999) The influence of visual illusions on grasp position. Exp Brain Res 125:109–114

Farber JM (1979) Manual tracking of induced object motion (abstract). Invest Ophthalmol Vis Sci 18:3

Fischer MH (2001) How sensitive is hand transport to illusory context effects? Exp Brain Res 136:224–230

Fitts PM, Peterson JR (1964) Information capacity of discrete motor responses. J Exp Psychol 67:103–112

Flash T, Hogan N (1985) The coordination of arm movements: an experimentally confirmed mathematical model. J Neurosci 5:1688–1703

Franz VH (2001) Action does not resist visual illusions. Trends Cogn Sci 5:457–459

Franz VH, Gegenfurtner KR, Bülthoff HH, Fahle M (2000) Grasping visual illusions: no evidence for a dissociation between perception and action. Psychol Sci 11:20–25

Franz VH, Fahle M, Bülthoff HH, Gegenfurtner KR (2001) Effects of visual illusions on grasping. J Exp Psychol Hum Percept Perform 27:1124–1144

Gentilucci M, Chieffi S, Daprati E, Saetti MC, Toni I (1996) Visual illusion and action. Neuropsychologia 34:369–376

Gentilucci M, Daprati E, Gangitano M, Toni I (1997) Eye position tunes the contribution of allocentric and egocentric information to target localization in human goal-directed arm movements. Neurosci Lett 222:123–126

Gentilucci M, Benuzzi F, Bertolani L, Gangitano M (2001) Visual illusions and the control of children arm movements. Neuropsychologia 39:132–139

Gillam B (1998) Illusions at century's end. In: Hochberg J (ed) Perception and cognition at century's end. Academic Press, San Diego, pp 95–136

Gillam B, Chambers D (1985) Size and position are incongruous: measurements on the Müller-Lyer figure. Percept Psychophys 37:549–556

Glover S, Dixon P (2001a) Motor adaptation to an optical illusion. Exp Brain Res 137:254–258

Glover S, Dixon P (2001b) Dynamic illusion effects in a reaching task: evidence for separate visual representations in the planning and control of reaching. J Exp Psychol Hum Percept Perform 27:560–572

Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. Trends Neurosci 15:20–25

Gordon AM, Forssberg H, Johansson RS, Westling G (1991) Visual size cues in the programming of manipulative forces during precision grip. Exp Brain Res 83:477–482

Heuer H, Sangals J (1998) Task-dependent mixtures of coordinate systems in visuomotor transformations. Exp Brain Res 119:224–236

Holtzman JD, Sedgwick HA, Festinger L (1978) Interaction of perceptually monitored and unmonitored efferent commands for smooth pursuit eye movements. Vision Res 18:1545–1555

Jackson SR, Shaw A (2000) The Ponzo illusion affects grip-force but not grip-aperture scaling during prehension movements. J Exp Psychol Hum Percept Perform 26:410–423

Jeannerod M (1986) The formation of finger grip during prehension. A cortically mediated visuomotor pattern. Behav Brain Res 19:99–161

Lappe M, Bremmer F, van den Berg AV (1999) Perception of self-motion from visual flow. Trends Cogn Sci 3:329–336

Mack A, Heuer F, Villardi K, Chambers D (1985) The dissociation of position and extent in Müller-Lyer figures. Percept Psychophys 37:335–344

Masson G, Proteau L, Mestre DR (1995) Effects of stationary and moving textured backgrounds on the visuo-oculo-manual tracking in humans. Vision Res 35:837–852

Michaels CF, Zeinstra EB, Oudejans RD (2001) Information and action in punching a falling ball. Q J Exp Psychol A 54:69–93

Mon-Williams M, Bull R (2000) The Judd illusion: evidence for two visual streams or two experimental conditions? Exp Brain Res 130:273–276

Pavani F, Boscagli I, Benvenuti F, Rabuffetti M, Farnè A (1999) Are perception and action affected differently by the Titchener circles illusion? Exp Brain Res 127:95–101

Pélisson D, Prablanc C, Goodale MA, Jeannerod M (1986) Visual control of reaching movements without vision of the limb. II. Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of a double-step stimulus. Exp Brain Res 62:303–311

Plodowski A, Jackson SR (2001) Vision: getting to grips with the Ebbinghaus illusion. Curr Biol 11:R304–R306

Post RB, Welch RB (1996) Is there dissociation of perceptual and motor responses to figural illusions? Perception 25:569–581

Rauschecker JP (1998) Cortical processing of complex sounds. Curr Opin Neurobiol 8:516–521

Rossetti Y (1998) Implicit short-lived motor representations of space in brain damaged and healthy subjects. Conscious Cogn 7:520–558

Rushton SK, Harris JM, Lloyd MR, Wann JP (1998) Guidance of locomotion on foot uses perceived target location rather than optic flow. Curr Biol 8:1191–1194

Sittig AC, Denier van der Gon JJ, Gielen CCAM (1985) Separate control of arm position and velocity demonstrated by vibration of muscle tendon in man. Exp Brain Res 60:445–453

Sittig AC, Denier van der Gon JJ, Gielen CCAM (1987) The contribution of afferent information on position and velocity to the control of slow and fast human forearm movements. Exp Brain Res 67:33–40

Smeets JBJ, Brenner E (1994) The difference between the perception of absolute and relative motion: a reaction time study. Vision Res 34:191–195

Smeets JBJ, Brenner E (1995a) Perception and action are based on the same visual information: distinction between position and velocity. J Exp Psychol Hum Percept Perform 21:19–31

Smeets JBJ, Brenner E (1995b) Prediction of a moving target's position in fast goal-directed action. Biol Cybern 73:519–528

Smeets JBJ, Brenner E (1999) A new view on grasping. Motor Control 3:237–271

Smeets JBJ, Brenner E (2001a) Action beyond our grasp. Trends Cogn Sci 5:287

Smeets JBJ, Brenner E (2001b) Perception and action are inseparable. Ecol Psychol 13:163–166

Smeets JBJ, Brenner E (2001c) Independent movements of the digits in grasping. Exp Brain Res 139:92–100

Smeets JBJ, Brenner E (2002) Does a complex model help to understand grasping? Exp Brain Res 144:132–135

Smeets JBJ, Erkelens CJ, Denier van der Gon JJ (1990) Adjustments of fast goal-directed movements in response to an unexpected inertial load. Exp Brain Res 81:303–312

Smeets JBJ, Hayhoe MM, Ballard D (1996) Goal-directed arm movements change eye-head coordination. Exp Brain Res 109:434–440

Stone LS, Beutter BR, Lorenceau J (2000) Visual motion integration for perception and pursuit. Perception 29:771–787

Tresilian JR (1999) Visually timed action: time-out for 'tau'? Trends Cogn Sci 3:301–310

van Donkelaar P (1999) Pointing movements are affected by size-contrast illusions. Exp Brain Res 125:517–520

Vishton PM, Pea JG, Cutting JE, Nunez LN (1999) Comparing effects of the horizontal-vertical illusion on grip scaling and judgment: relative versus absolute, not perception versus action. J Exp Psychol Hum Percept Perform 25:1659–1672

Warren WH, Kay BA, Zosh WD, Duchon AP, Sahuc S (2001) Optic flow is used to control human walking. Nat Neurosci 4:213–216

Wenderoth P (1983) Identical stimuli are judged differently in the orientation and position domains. Percept Psychophys 33:399–402

Wraga M, Creem SH, Proffitt DR (2000) Perception-action dissociations of a walkable Müller-Lyer configuration. Psychol Sci 11:239–243

Yamagishi N, Anderson SJ, Ashida H (2001) Evidence for dissociation between the perceptual and visuomotor systems in humans. Proc R Soc Lond B 268:973–977

Zeki S (1993) A vision of the brain. Blackwell Scientific, Oxford

Zivotofsky AZ, Averbuch-Heller L, Thomas CW, Das VE, DiScenna AO, Leigh RJ (1995) Tracking of illusory target motion – differences between gaze and head responses. Vision Res 35:3029–3035