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Influence of Visual Motion on Object Localisation in Perception and Action

Hiroshi Ashida

1 Introduction

The topic of this chapter is visual localisation of objects. Object recognition normally refers to the ability to identify *what* it is without concerned for *where* it is. In other words, the question is how we obtain a location-invariant representation of object. There is also a rationale derived from physiological findings indicating two separate pathways for *what* and *where* information (Ungerleider and Mishkin 1982). However, it is often equally important in real life to know where the object lies. We cannot eat an apple if we can not reach it with our hand and grasp it. To do this, we need to know its precise location together with its identity as a fresh apple that can be eaten. Object localisation is therefore closely related to object recognition in an ecological sense, and it would make sense to take a short break from the intense discussion on recognition in this book to consider localisation.

More specifically, recent findings on the role of visual motion on spatial localisation will be discussed. We sometimes need to interact with objects that move across the visual field. This happens daily when you walk on a busy street or play with your cat, but it is more typical in sports such as baseball, cricket, and soccer in which the players need to interact with fast moving balls. Of course, we need to develop our motor skill to achieve good performance, but it is also expected that the visual system has been evolved to cope with dynamic interaction with objects.

A problem then is that neural signal processing is rather slow. For example, the latency typically measured in macaque striate cortex is about 30 to 50 ms (Maunsell and Gibson 1992). A ball coming at a speed of 150 km/h travels more than one meter during this delay, leaving no chance of hitting it. Obviously, we need to have some methods of anticipating the target path. Given that the delay in physical action is large and effector-dependent, it is likely that most of the adjustment should be accomplished through motor planning and its execution. However, the visual system seems to have its own process for delay

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Graduate School of Letters, Kyoto University, Kyoto 606-8501, Japan

compensation, as suggested by several motion-related illusions. Also, such compensation might work specifically for visuomotor action without always being consciously perceived. Here, I review such illusions after brief summary of separate systems of vision for perception and action (Milner and Goodale 1995), and describe results from our group that indicated action-specific visual motion extrapolation.

2 Vision for Perception and Action

2.1 Separate Visual Pathways for Perception and Action

Milner and Goodale (1995) proposed that the brain has separate visual pathways for conscious perception and direct visuomotor control, and this proposal has been followed by intensive discussion over the past decade. They extended the idea of two visual pathways for *what* and *where* information (Ungerleider and Mishkin 1982) and argued that the ventral pathway is dedicated to the detailed conscious perception, while the dorsal pathway is dedicated to direct control of action (Fig. 1). It was radically assumed that the two pathways are independent and information through the dorsal pathway is not always accessible to conscious perception.

Supporting evidence for their theory has mainly come from case studies of human brain damage patients and lesion studies of monkeys. A patient with visual form agnosia was able to perform precise action like grasping or mailing without being able to perceive the detail (Goodale et al. 1991; Milner et al. 1991). There are also cases of "blindsight" patients who can point to the target without conscious perception (Weiskranz 1986). These patients generally have damage in the occipital lobe, and somtimes in the primary visual cortex (V1), that causes an overall dysfunction of the ventral stream. The dorsal pathway is relatively intact with possible support from the subcortical path through the superior col-

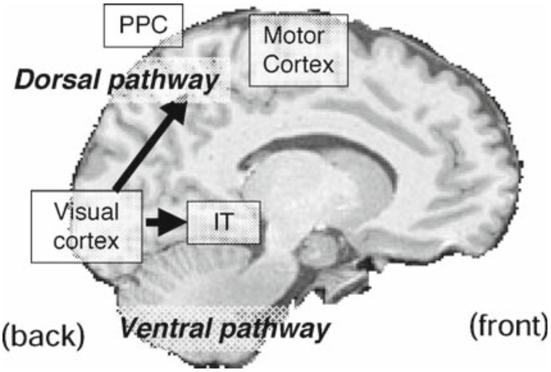

FIG. 1. The two major visual pathways in a human brain. From the visual cortex in the occipital lobe, the dorsal pathway extends into the posterior parietal cortex (*PPC*) through V5, while the ventral pathway goes into the inferotemporal (*IT*) cortex

liculus, which is considered to enable visuomotor coordination. On the other hand, patients with optic ataxia (Bálint syndrome) tend to show difficulties in visually-guided actions like reaching, while conscious perception is relatively unaffected (Bálint 1909). This syndrome generally involves damage in the parietal lobe. Recently, it has been suggested that the damage is more specific to direct or on-line visuomotor control in a specific area within the dorsal pathway (Glover 2003; Rossetti et al. 2003). Interestingly, the accuracy of pointing action was improved if the patient waited for 5s before initiating the action (Milner et al. 1999), which supports this recent view. There is insufficient space to describe the details here, but the results of monkey studies basically parallel these findings; lesion in the posterior parietal areas causes disorder in visuomotor action while lesion in the infero-temporal areas disrupts perceptual judgements (see Milner and Goodale 1995).

2.2 Psychophysics on Dissociation of Perception and Action

There are psychophysical results that suggest similar dissociation in normal human observers. Displacement of a target near the time of saccade is not noticed but pointing action can be accurately performed (Bridgeman et al. 1979). A stationary target appears to move when the surrounding frame moves back and forth, but reaching action is not affected (Bridgeman et al. 1981). Controversies have arose after Aglioti et al. (1995) reported that grasping action is not markedly affected by the size illusion of Titchener-Ebbinghaus circles (Fig. 2a). The "maximum aperture size" between the thumb and the index finger varied in relation to the actual object size, but it was relatively unaffected by the size contrast illusion induced by surrounding larger and smaller disks. They argued that the hand is not deceived by the illusion in conscious perception.

There have been criticisms of this experiment by Aglioti et al. (Franz 2001; see also Carey 2001). The most controversial point was the different task requirements. The perceptual task inherently involved comparison of two central disks, but the grasping task did not require this once the participant decided which target to pick. When the figure was shown one by one in both cases, there was no difference between perception and action (Franz et al. 2000). It has also been pointed out that the use of reference frames might cause different results (Bruno

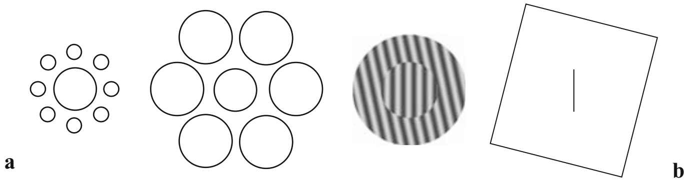

Fig. 2. **a** The size contrast illusion (Tichener-Ebbinghaus circles). The left central disk appears larger than the right one because of the surrounds, although they are of the same size. **b** The orientation contrast effect used by Dyde and Milner (2002). The central grating on the left appears tilted clockwise due to the adjacent tilted grating. The central vertical line in the right panel appears tilted counter-clockwise due to the tilted frame

2001). It seems that we have not come to a final conclusion, but the criticisms also have problems. As Milner and Goodale (1995) originally pointed out, different use of reference frames could be inherent in perception and action. The conclusion of Aglioti et al. seems to make sense even with the difficulties in the task differences. Findings of Bridgeman et al. regarding manual pointing seem less controversial because the task requirement of target localisation is equal in perception or action.

But why is action necessarily more accurate than perception? A case where action is more erroneous would complete double dissociation. Dyde and Milner (2002) conducted a clever experiment in which the illusion is cancelled for perception but not for action, leading to apparent larger errors in action. First, they showed that orientation contrast between adjacent gratings (as seen in Fig. 2b, left) affected both perception and action (mailing: to orient a card as if putting it between bars) while a far frame induces orientation contrast only in perception (Fig. 2b, right). Then, when the left pattern is surrounded by an oppositely-tilted frame, the perceptual effects are cancelled out, but the visuomotor effect is not. The measured illusion was actually larger in action than in perception. This result demonstrated double dissociation between perception and action when coupled with the case where perceptual errors were larger with the far frames alone. They reasoned that the contrast between adjacent gratings occurs at an early level where the two pathways have not branched, while the frame effect occurs later in the vision-for-perception pathway. Their results, however, do not provide sufficient evidence for separate visual pathways. Action might ignore visual processing at a later stage, but this does not necessarily mean that the visual information is separately elaborated for visuomotor control. A critical case is missing where vision for action is directly more susceptible to an illusion, which is fulfilled by our results on motion-related illusions.

3 Motion Extrapolation Revealed by Visual Illusions

3.1 Flash Lag

When a visual object is briefly presented near a continuously moving visual object, the moving one is perceived ahead of the flashed one (Fig. 3a), which has been called “flash lag” (FL). This effect had been already reported by MacKay (1958), but Nijhawan (1994) reinterpreted it as evidence for extrapolation of target motion to compensate for the neural delay, which has triggered numbers of follow-up studies. Nijhawan considered that compensation is particularly important for catching action, although it was just speculative.

Unfortunately, this very intriguing idea of motion extrapolation has not been supported by later studies. A major objection was that no overshoot of target motion is perceived if the moving target turns back at the time of the flash (Whitney and Murakami 1998). Extrapolation should have resulted in shift in the direction of the target motion before the unexpected reversal, but the moving

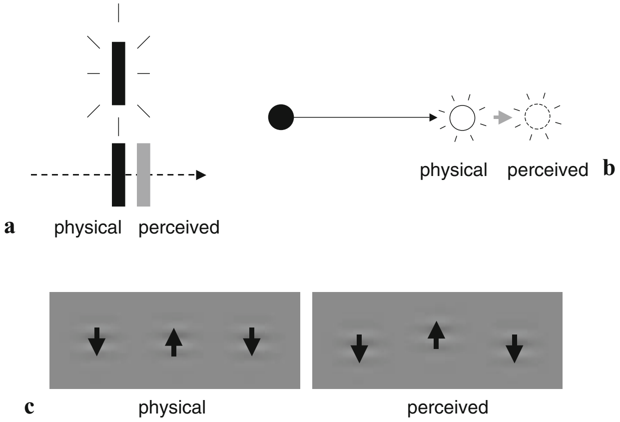

Fig. 3. **a** The flash lag illusion. A bar briefly flashes over a moving bar. When the two bars are physically aligned, we perceive that the flashed bar lags behind the moving one and they are not aligned. **b** The "representational momentum". The final location of a suddenly disappeared moving target is often perceived to be shifted ahead. **c** Motion related positional shift. When the three drifting Gabor patches with stationary windows are vertically aligned, the central patch looks misaligned, shifted in the direction of motion. These figures illustrate typical displays, but many variations have been demonstrated

target is actually perceived as shifted in the direction after the reversal (Eagleman and Sejnowski 2000; Whitney and Murakami 1998). Furthermore, while no offset is perceived when the moving target disappears with the flashed one (flash terminated cycle, FTC), clear offset is perceived when the flash appear together with the moving one (flash initiated cycle, FIC) although there is no prior motion for extrapolation (Eagleman and Sejnowski 2000). Moreover, the size of the FL depends on the motion speed after the flash (Brenner and Smeets 2000). All of these observations contradict the extrapolation hypothesis. It is rather suggested that the perceived spatial offset is caused by a delay in the processing of the flashed target. In other words, FL is caused by the latency difference between continuous and suddenly-appearing targets (Whitney and Murakami 1998; Whitney et al. 2000), as the term "flash lag" correctly implied. Reduction of latency for a moving target can be related to attention (but see also Khurana et al. 2000; Namba and Baldo 2004). But latency difference alone might not be sufficient (Arnold et al. 2003). Full explanation would include several factors like temporal averaging before and after the flash, and occasional release from it ("postdiction" by Eagleman and Sejnowski 2000).

The FL phenomenon therefore does not prove target extrapolation for "predicting the present" (Cavanagh 1997). However, a shorter latency for a moving object would at least partially compensate for the delay to facilitate action control. It is notable then that similar phenomenon has been reported cross-modally between vision and hand movement (Nijhawan and Kirschfeld 2003).

3.2 Representational Momentum

When a moving target suddenly disappears, its final position tends to be perceived ahead of the physical position (Fig. 3b). This phenomena has been called "representational momentum" (abbreviated as RM or sometimes "RepMo") since it is as if our internal representation of the target has a momentum that cannot stop immediately (Freyd and Finke 1984). Intuitively, RM is understood as a signature of visual motion extrapolation. Note that the terminology does not necessarily imply the underlying mechanism at least in this article.

RM is apparently related to the FL (flash lag), but these two are distinct with regard to whether it involves relative judgement of position. The situation of RM is similar to the FTC case of FL, but note that the general finding of no FL for FTC is therefore not contradictory with RM. Interestingly, FL can occur even in the FTC if the spatial uncertainty is increased (Kanai et al. 2004).

As the terminology suggests, RM has been considered a cognitive effect on a memorised representation of the target, as supported by the effects of gravity and surface friction (Hubbard 1995). However, the basic effect might occur at an early perceptual level. Pursuit eye movement is crucial especially for a linear motion path; when the observer maintained fixation, the effect nearly disappears (Ashida 2004; Kerzel 2000). Cognitive extrapolation could have been more stable when the visual motion is more accurately coded in the vicinity of eye movement, but it is not. Kerzel proposed that overshoot of pursuit eye movement should be the direct cause of the perceived RM, coupled with visible persistence and centrifugal bias (Kerzel 2000).

3.3 Motion-Related Positional Shift

Perception of object position is more directly affected by visual motion signals. A typical example is a drifting grating seen through a stationary window, when the edges are blurred as in Gabor patches. The whole window is perceived as shifted in the direction of the carrier motion (De Valois and De Valois 1991) so that aligned patches of oppositely drifting carriers do not appear aligned (Fig. 3c).

This illusion has been considered to reflect spatial extrapolation for compensation of neural delays (Anstis and Ramachandran 1995). Technically speaking, however, there is no need to extrapolate the position of the stationary window. This suggests that the spatial shift is caused by a simple automatic process at a relatively early level. It even does not require real retinal motion signals, because adaptation to motion causes opposite spatial shifts (Nishida and Johnston 1999; Snowden 1998) with perceived motion aftereffect (MAE) in the stationary pattern. Even visible MAE does not seem a necessary condition for positional shifts. While MAEs are selective to spatial frequency (see Mather et al. 1998 for general reviews), the positional shift was immune to it; when the carrier orientation in the test pattern was orthogonal to that of the adapting one, we see little or no MAE but still see positional shifts (McGraw et al. 2002). Conscious perception of adapting motion is not necessary, either; positional shift occurs when the adapting motion is not identifiable due to crowding (Whitney 2005). Underlying mechanisms for the positional shift are still open for further studies, but these results suggest that positional shifts reflect early internal motion signals regardless of final perception of motion.

Visual motion in the background area also affects target localisation. The position of a briefly presented target is shifted in the direction of a drifting grating even when the target is spatially separated from the grating (Whitney and Cavanagh 2000). It is as if motion stimuli distort the whole visual field, but an important difference is that the target must be presented only for a short period. The background motion probably helps to compensate for our body or eye movement in order to point to the target accurately (Whitney et al. 2003b).

3.4 Visual Motion and Reaching: Evidence of Extrapolation for Action?

Visual illusions should be related to ecological roles of specific visual functions, if they may not have obvious ecological merits themselves. In this respect, the motion-related illusions described above should be more closely related to direct action if they reflect some operations for delay compensation. Flash lag involves a relative judgement of positions that is not easily tested by action in an unbiased way, but the other two illusions have been tested in similar conditions for perception and action.

We have reported that motion-related positional shift is more prominent in open-loop reaching action than in perceptual judgement (Yamagishi et al. 2001). A Gabor patch with a drifting vertical sinusoidal carrier was presented briefly to the right of fixation. The observers then judged the horizontal location of the target and responded either by touching the location using a rubber pen (*visuomotor* task) or by reading a visual ruler that was presented on the screen (*perceptual* task). Note that the task requirement was similar and there is no task-dependent bias for different reference frames. In the visuomotor task, the observers made ballistic movement of their hand without seeing their arm and hand (open-loop action). The stimuli were observed through a mirror for this purpose. The absolute locations of responses were not always veridical without feedback, and we computed the averaged difference in responses to leftward and rightward stimuli as an index of the effect of carrier motion on localisation. The left panel of Figure 4 shows a typical result from one observer. Obviously, localisation error in the visuomotor task was larger than that in the perceptual task, increasing more rapidly with carrier speed. This difference cannot be attributed to the intrinsic open-loop gain of the motor system, because the difference in the two response modes almost disappeared when the response was delayed by 4 s (Fig. 4, right panel). Delayed responses had to rely on the stored perceptual representation (Hu and Goodale 2000; Milner et al. 1999). We also suggested that visuomotor responses are less asymmetric than perceptual ones with regard

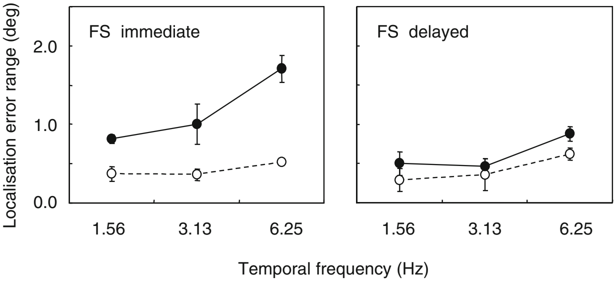

FIG. 4. Localisation errors for a drifting Gabor patch in perception and action for one observer. Differences in the mean responses for leftward and rightward stimuli are shown as a function of temporal frequency (speed). Immediate responses (*left*) and delayed (by 4s) responses (*right*). Adapted from Yamagishi et al. (2001)

to the motion direction. The result supports separate visual mechanisms, demonstrating a case where action is more prone to illusion.

We have also found that the enhanced visuomotor localisation error is specific to achromatic stimuli (Ashida et al. 2005). Equiluminant chromatic stimuli (red-green) did not yield a significant difference between perception and action. Given the weak response of V5 to chromatic stimuli (Gegenfurtner et al. 1994), it is tempting to conclude that the visuomotor-specific positional errors occur within the dorsal visual pathway, while perceptual errors reflect interaction of the two pathways where chromatic and achromatic motion signals are integrated.

A study of RM supported these findings (Ashida 2004). The final position of a horizontally moving disk on the screen was indicated using an on-screen cursor (perceptual) or by directly touching the screen (visuomotor). Visual feedback was controlled using a liquid crystal shutter goggle. The main result is shown in Figure 5, which demonstrates three major findings. First, open-loop action yielded larger forward shifts that increased with target speed more linearly than perception, which is very similar to the left panel of Figure 4. Second, closed-loop responses were almost identical to the perceptual ones. It seems that perceptual information was dominant in this case. Finally, and most interestingly, perceptual shifts were reduced to almost zero by eye fixation (Kerzel 2000), but open-loop responses remained nearly the same. This implies an intriguing possibility that extrapolation might occur within the egocentric coordinate that would be the default in visuomotor action. Perception might rely more on a retinotopic or possibly allocentric coordinate (not distinguishable under this condition). It is conjectured that perceptual RM occurs because perception uses egocentric signals when the retinotopic signals are unstable due to eye movements. In any case, further evidence was provided for separate visual processing for perception and visuomotor action in qualitative as well as quantitative ways.

While these results in general agree with the theory of Milner and Goodale (Milner and Goodale 1995), one problem arises regarding anatomical structures. They proposed that conscious perception arises only within the ventral brain

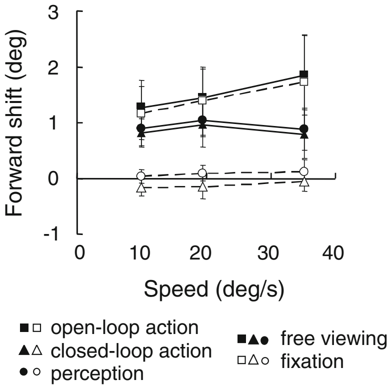

Fig. 5. The "representational momentum" for perception and action. Illusory forward shifts are plotted as a function of the target speed (n = 4, averaged). Adapted from Ashida (2004)

pathway. But if so, how can we understand conscious perception of visual motion that is believed to be based upon area V5 (MT/MST) within the dorsal pathway? The basic idea of two visual systems has been confirmed by the results, but the underlying anatomical structure should be reconsidered. It now seems more plausible to assume that some parts of the dorsal pathway are involved in conscious perception. According to Rizzolatti and Matelli (2003), there are two distinct pathways within the dorsal pathway, one from V6 to the superior parietal lobule and the other from V5 to the inferior parietal lobule. The former is considered to support on-line visuomotor control while the latter might underlie space perception (Ungerleider and Mishkin 1982). More studies would be required for further understanding of the two pathways.

4 Concluding Remarks

Effects of visual motion on spatial localisation have been extensively studied over the past several years. I have concentrated on manual action, but eye movements have also been studied for visuomotor coordination, as partly discussed in the chapter by Sogo and Osaka in this book.

However, we have not yet come to understand the underlying neural mechanism. We have been surprised by the fMRI (functional magnetic resonance imaging) results that the stimulus representation in V1 might be shifted in the opposite direction by visual motion (Whitney et al. 2003a). Although it has turned out that the effect is small and there is no overall opposite shifts (Ashida and Smith 2005; Liu et al. 2004), it is plausible that early visual areas are not responsible for motion-related shifts, which is also suggested by dissociation between perception and action in our studies. Activities in V1 would have affected both equally. Despite a positive result in cat's primary visual cortex (Fu et al.

2004), higher areas should be sought for humans as suggested by a TMS (transcranial magnetic stimulation) study (McGraw et al. 2004); giving TMS to V5 reduced the positional shifts after motion adaptation but TMS to V1 had no effect. Techniques have been developed to investigate higher and smaller cortical areas and new insights are expected to be provided in the near future.

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