Separate visual representations for perception and action revealed by saccadic eye movements

David C. Burr*†, M. Concetta Morrone*‡ and John Ross§

Some 30 years ago, Trevarthen [1] introduced the idea of two separate visual systems, a focal system for fine motor acts and an ambient system for gross body movements such as ambulation. More recent developments indicating anatomically and physiologically separate pathways in primate vision [2] have led to a different idea of separate visual systems, one for conscious perception and one for action [3]. It has received empirical support from several studies showing that pointing, reaching, and grasping can remain accurate while the perceived position or size of objects is subject to illusory distortion [4–6]. However, much of this evidence has been challenged on the grounds of methodological flaws, particularly failure to match perfectly the conditions for verbal and motor tasks and failure to replicate results [7–10]. Here we take advantage of the strong compression of perceived position that occurs around the time of saccadic eye movements [11, 12]. Under normal lighting conditions, stimuli flashed briefly over a wide range of spatial positions just before saccadic onset are neither seen nor reached for in their veridical positions, but are compressed toward the saccadic target. We validate the idea of separate systems by showing that, in the dark, subjects are able to point accurately to the correct target position, even though their verbal reports are still subject to compression.

Addresses: *Isitituto di Neurofisiologia del Consiglio Nazionale di Ricerca, Via G. Moruzzi 1, Pisa, Italy. †Dipartimento di Psicologia, Università di Firenze, Via S. Nicolò 89, Florence, Italy. ‡Facoltà di psicologia, Università Vita-Salute San Raffaele, Via Olgettina 58, Milan, Italy. §Department of Psychology, University of Western Australia, Nedlands, Western Australia 6009, Australia.

Correspondence: David C. Burr
E-mail: dave@in.pi.cnr.it

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Results and discussion

Figure 1 illustrates the experimental situation, described in the methods section. Figure 2 shows results for the verbal report of perceived positions of bars briefly displayed over a 40° range of positions within the 50 ms interval immediately preceding saccades, the period when perceptual errors have been found to be maximal (see Figure 4 and [11, 12]). The averaged verbal reports show the characteristic compression of perceived position toward the saccadic target (7.5°) and confirm previous reports under similar conditions [11, 12]. There was one interesting difference in experimental conditions; in this study, we removed all visual referents at the time of judgment by closing a liquid crystal shutter 75 ms after stimulus presentation, so observers had to *remember* the ruler (that they could see from time to time, but never during a trial). Nevertheless, both the pattern and the amplitude of the results are similar to conditions in which the ruler is physically present and the screen is always visible, with large errors of localization occurring over a wide stretch of space.

Figure 3 shows results for blind reaching, either with the eyes shut as rapidly as possible after the saccade (red squares) or with vision obscured by a shutter that closed 75 ms after the display of the bar (blue squares). There was a slight uniform shift in the condition in which vision was attenuated by the shutter (possibly because the attenuation was not perfect). However, there was none whatsoever when all visual input was removed by eye closure. With the eyes closed, there were no localization errors in the direction of the saccade, as are normally observed in the dark [13–16], and in neither case was there any compression toward the fixation and target that is typically observed under these conditions [11, 12, 16]. These results show that despite gross perceptual distortions around the time of saccades, veridical positional information is available to guide reaching.

Intriguingly, compression can be demonstrated with a reaching response when visual information is available. The right-hand curves of Figure 3 show results for the situation where subjects touched the fully visible screen (with their hands hidden from view). Under these conditions, the pattern of errors for reaching was virtually identical to that for verbal reports, and these results suggest that visual information overrides other sources of information, which thus leads to the characteristic compression errors we observe.

Figure 4 shows how reported position varies with time of

Figure 1

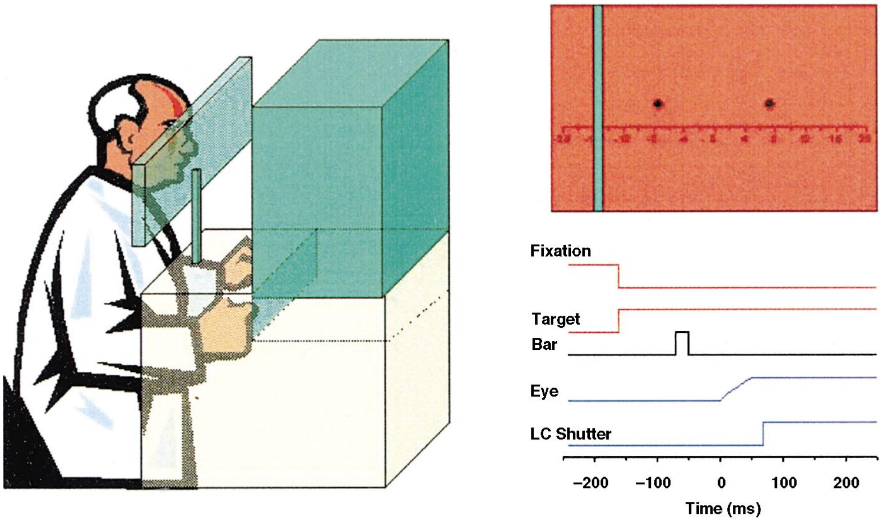
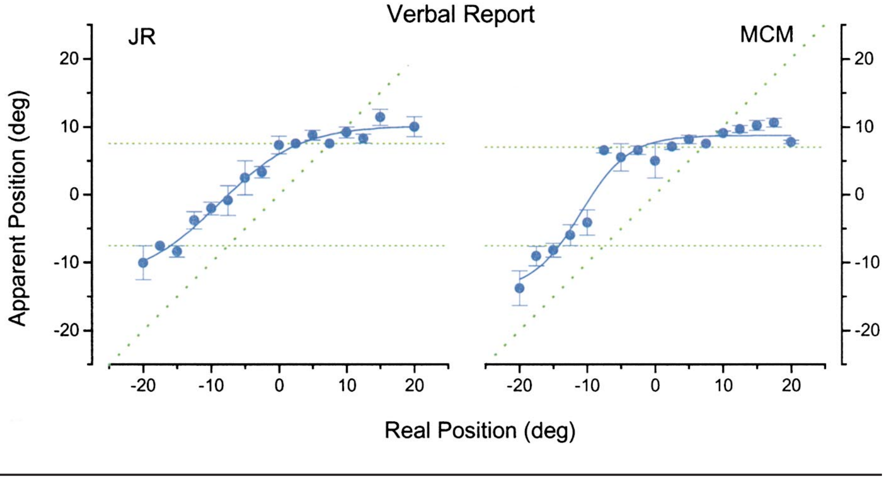


Illustration of experimental setup. Observers viewed an NEC MultiSynch XE21 monitor equipped with a MicroTouch touch screen from a distance of 40 cm through a liquid crystal shutter, with hands obscured from view by an opaque board (left figure). The screen (50° × 34°) was lit to a uniform red of 20 cd/m^2 (top right). The graduated ruler was not normally present, but observers could call it up on demand. Before each trial, observers fixed the black *fixation* dot 7.5° to the left of center (with the other dot extinguished). After a warning signal, the fixation dot was extinguished, and the *target* dot appeared 7.5° to the right of center. After a characteristic latency (around 140 ms, depending on the observer), observers saccaded to the target. At a specific time (usually just prior to saccade initiation), a bright (60 cd/m^2) green bar (2° × 34°) was flashed for one frame (8.3 ms). Under most conditions, the shutter then closed, and the screen darkened 75 ms after bar display. Observers indicated the position of the bar, either verbally or by touching the screen with the index finger of the right hand.

stimulus presentation for three different stimulus positions with two different response conditions. The subject responded by pointing, either to a visible screen (left curves) or with the eyes closed (right curves). When vision was available to guide responses, the characteristic compressive errors (mislocalization toward saccadic target) commenced 100 ms before saccades and rose to a maximum around saccadic onset. However, when the subject pointed with the eyes closed, there was no evidence for compression in response, only a slight uniform shift of the perceived position of the centrally displayed bar.

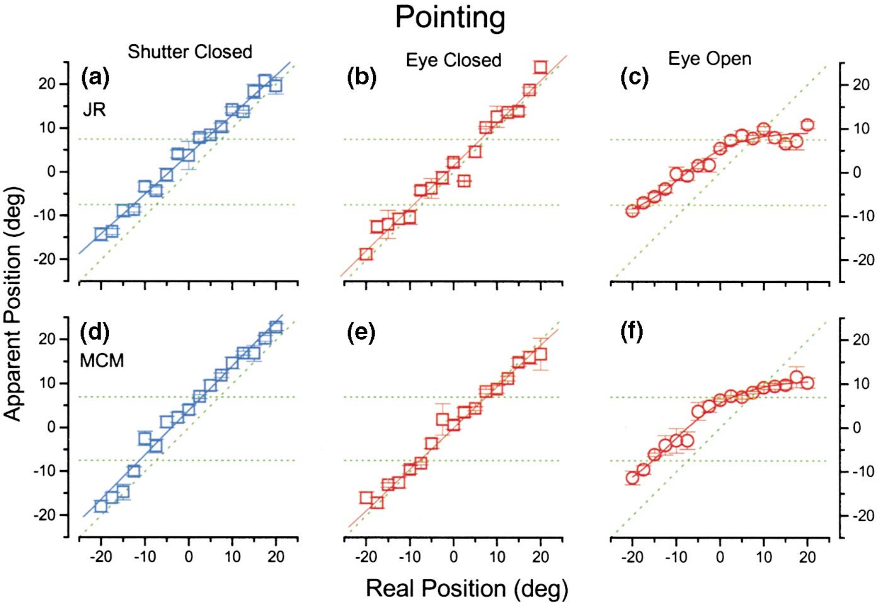
It should be pointed out that not all experimental conditions lead to the compression of perceptual space. Other studies have shown a uniform displacement in the direction of the saccade [13–15], with no compression for objects presented beyond the end point of the saccade. Lappe et al. [16] have suggested —with supporting evidence — that compression occurs only when visual references are present immediately after a saccade has ended. While this may be part of the explanation, the fact that we find strong compression for verbal reports with a closed shutter (thereby removing all physical references) suggests that other factors may be involved. Under these conditions observers must recall a visual scale from memory, which perhaps provides some form of reference. Or

Figure 2



Verbal reports of the perceived position (relative to a memorized ruler) of a bar flashed briefly to various positions over a 40° range while an observer made a 15° saccade (from −7.5° to +7.5°). Seventy-five milliseconds after bar presentation, the liquid crystal shutter closed, and the screen darkened and obscured visual referents. Results are reported only for stimuli falling within the 50 ms interval immediately preceding saccades. At this time the eyes are stationary, so there is a perfect correspondence between external and retinal coordinates. Each point is the average of 4–6 presentations. Bars presented to a wide range of positions straddling the right side of the screen tended to be seen near the site of the saccadic target.

Figure 3

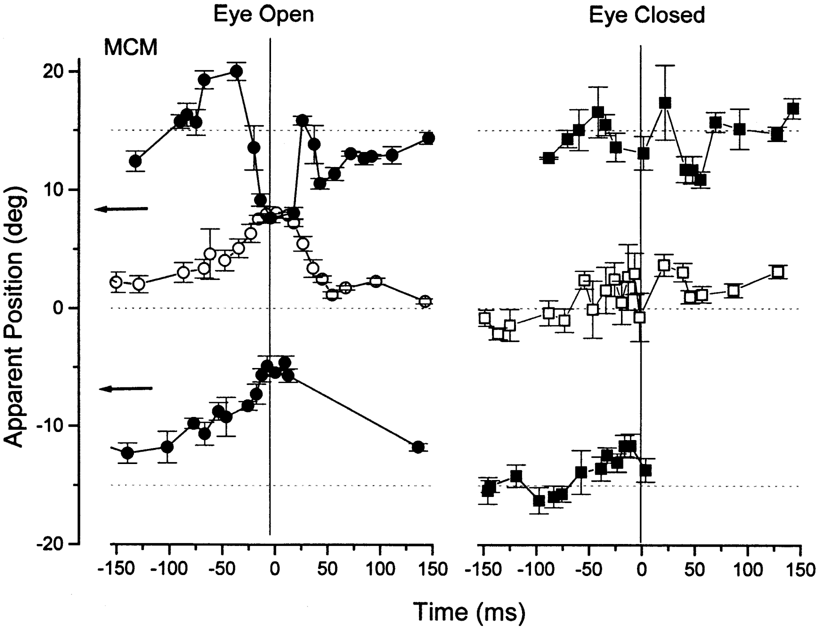


Subjects were asked to point to the position of a bar briefly flashed to a range of positions during the 50 ms preceding a 15° saccade. **(a,d)** For the left-hand curves, the liquid crystal shutter closed, and the screen darkened 75 ms after bar presentation. **(b,e)** For the middle curves, subjects closed their eyes as soon as possible after the saccade (always within 150 ms). **(c,f)** For the right-hand curves, the screen remained fully visible during the response (although the hand was hidden from view). When visual information was unavailable, the manual pointing was near veridical or slightly shifted uniformly in the direction of the saccade. When visual information was available, the illusory perceptual distortion dominated.

perhaps the level of light adaptation is important, as vision is of little help in the dark (the experiments of Lappe et al. were performed at very low light levels). Whatever the reason for compression not occurring under other conditions, the current experiment produced strong and reliable compression when subjects made verbal reports, even when the screen was obscured; under these very same conditions, subjects point accurately to the target, with no evidence of compression.

Several previous studies have reported accurate motor responses to targets flashed before and during saccades. Hansen and Skavenski [17] showed that subjects could accurately strike a target, and Lightstone and Hallett's [18] subjects performed accurate second saccades to targets presented during the onset of the primary saccade. However, these claims have been challenged by more recent work that reports no difference between verbal and motor responses. For example, Dassonville et al. [8,

Figure 4



Results of pointing to bars displayed at positions −15°, 0°, and 15° as a function of time (with respect to saccadic onset). The arrows indicate the fixation spot and saccadic target. In the left-hand plot, the screen (but not the hand) was visible at the time of the response. In the right-hand plot, the observer closed her eyes within 200 ms of saccadic onset. The visually guided pointing shows the characteristic distortion during the period near saccadic onset, while the blind pointing remains veridical throughout the timecourse. There are few data points after saccadic onset for the −15° presentation (lower curves) because the subject found difficulties in localizing these colored stimuli presented in the far periphery. Another observer (JR) produced near-identical results.

9] report large localization errors (in the order of 10°) for manual pointing and for second saccades, as well as for verbal reports. On the other hand, Bokisch and Miller [10] report very small displacement errors (less than 2° at saccadic onset) for pointing, eye movements, and verbal reports. Unfortunately, we cannot at this stage explain the gross inconsistencies in magnitude between these studies nor the discrepancy between their results and ours.

On the other hand, several experiments have provided indirect evidence for dissociation of perception and action under light-adapted conditions similar to ours [19]. When a saccadic target is displaced by up to 30% of saccadic size during a saccade, observers do not notice the displacement [20]; however, these large changes in target position often cause corrective saccades toward the new position of the target, and these saccades tend to be quite accurate [19] and show a veridical motor response to a shift in target that the subjects did not notice consciously. Further evidence that veridical information is indeed available but is overridden by perceptual references is provided by the fact that if the saccadic target is momentarily blanked, sensitivity to displacement is restored [21].

Possible neural substrates for two representations of space, one plastic and error prone, the other not, are to be found in the parietal visual cortex; neurons in some areas (such as LIP, VIP, MST, and superior colliculus) change their receptive fields immediately before saccades [22, 23]. Some shift their receptive fields in the direction of saccades in anticipation of saccadic image shifts; others continue to respond at the presaccadic image position, so the net population response effectively stretches to respond to stimuli in both pre- and postsaccadic retinal positions [24]. Input from LIP might thus indicate that stimuli are in false positions and that stimuli distributed over a large area are in the same position. Such a situation would result in compression. Neurons in other areas, such as 7a, VIP, and V6 have less labile world- or body-centered receptive fields; some of these neurons are involved in reaching [25–29]. Perhaps these neurons could contribute to the neural substrate of the spatial representation that seems to guide the motor system.

The compression of visual space by saccades is a recent discovery that opens a new window on the operations of the visual system. Why it occurs is still not clear, but it may be entailed in ensuring a seamless transition from one point of fixation to the next. Whatever the functional role of compression might be, we find that at the time at which the perceptual representation of space is most compressed, there is no distortion of the representation of space used to guide reaching. This occurs only when subjects are transiently deprived of visual information; when vision is available, observers use it and make mistakes in reaching. We conclude that there are separate representations of visual space, one plastic and subject to distortion, the other not. The plastic system, used for conscious visual perception, seems to dominate when both systems are available.

Materials and methods

Figure 1 illustrates the experimental situation. Observers fixated on a black dot 7.5° to the left of the center of a touch screen. After a warning signal, they made a saccade to a visual target 7.5°to the right of center and reported the position of a vertical green probe bar that was flashed briefly before, during, or after the saccade. Reports were made in two different ways: (1) observers called out a number corresponding to a position on a visible or memorized scale, or (2) they touched the screen with the index finger of the right hand (always hidden from view). For most experiments, we obscured the screen from view during the report, either by asking subjects to shut their eyes soon after the saccade or by closing the liquid crystal shutter and darkening the screen shortly after bar presentation. No feedback was provided to subjects under any conditions.

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