Attentional remapping inside and outside the visual field

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Abstract

Despite the fact that eye movements cause large-scale translations of the image falling on the retina, we perceive the visual world as stable and continuous. This paradoxical visual constancy has been explained by the discovery of frontoparietal neurons that shows a predictive response to stimuli that will fall into their receptive field only after the saccade. These neurons anticipate what the world looks like after a saccade and remapped the future locations of attended target. We have conducted two experiments that linked behaviorally the role of spatial attention with this remapping mechanism. We use an attention-based motion procedure to track this attentional remapping and to reveal the spatial accuracy of this mechanism. In a first experiment, we asked participants to make horizontal saccades of 10° while they attentionally monitored the displacement of two probes. Each probe was presented for 400 msec, the first was turned off 100ms before the saccade while the second was turned on about 100 msec after the saccade. These probes are displaced vertically but because of the eye movement they fell on the retina with a 10° horizontal shift. Under these conditions participants reported that the probes appeared to be in motion almost vertically, i.e. the spatiotopic direction, with a noticeable deviation from the true vertical. We measured this misalignment and devised maps of remapping errors for different spatial locations near the fovea. Small misalignments were obtained suggesting that the hard computation of spatial updating at the time of the saccade is managed with accuracy. Then in a second experiment, using the same spatiotopic apparent motion procedure, we wondered now what happen to stimulus presented at the limit of the visual field. Interestingly remapping of such stimulus implies the shift of remapped attention pointer outside the visual field, i.e. in location that does not have any retinal input. Participants made 20° leftward saccade on a front monitor and drew their attention to two probes that moved of 20° in the same direction on a side monitor set to right of the participants. Because of the saccade the probes were always presented in a position determined to be the rightmost edge of the participant’s visual field and there was little or no shift between the target’s two positions on the retina. Participant reported a leftward motion corresponding to the spatiotopic displacement (20°) not the retinotopic displacement (near 0°). This last result require that the representation of this stimulus may even be remapped outside the visual field and that retinotopic cortices may register locations that fall outside the limit of the retina.

Keywords

Remapping, visual attention, apparent motion, eye movements.
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Introduction

We perceive the world through a multiplicity of photoreceptors concentrated most densely at the fovea near the middle of the retina. As a consequence, we move our eyes typically three to five times per second in order for the regions of interest of the visual scene to land on this central region of high resolution. These eye movements or “saccades” separate the intervening periods of fairly steady fixation (Figure 1).

However, despite the fact that eye movements cause large-scale translations of the image falling on the retina interleaved with high-resolution snapshots centered on the fovea, we perceive the visual world as stable and continuous. How does our perception of the world remain stable, when the retinal images continually shift with each eye movement?

There is currently a growing consensus that this constancy of vision is achieved through a process called “remapping” which is carried out in the eye movement centers of the brain and the first section below gives a brief outline of this process. We developed an apparent motion stimulus that shifts location at the same time as the participant makes a saccade and we show that this stimulus can probe the nature and accuracy of the remapping process. We find that apparent motion, the perception of motion between two sequentially flashed stimuli, is based in spatial coordinates, independently of where the stimuli land on the retina. Results indicate small horizontal errors of remapping with a large variability between different positions tested and different participants.

In a second experiment, using the same apparent motion procedure, we demonstrate that remapping can shift the representation of a stimulus to a location outside the visual field, a location that does not have any retinal input. This last result requires that retinotopic cortices may register locations in extraretinal space.

Figure 1. Results of a study by A.L. Yarbus of eye movements recording during perception of complex visual scene. (A) The painting is titled “Morning in the Pine Forest” by the Russian landscape painter Ivan I. Shishkin. (B) The right panel is a record of the eye movement made during 2 minutes of free examination of the picture with both eyes. Black lines represent saccadic eye movements, and black dots represent steady fixation periods. Adapted from Yarbus (1967).

1. History of visual constancy

The puzzle of “visual constancy” has been the subject of speculation since the seventeenth century, but behavioral investigations emerged mainly during the last hundred years. Most interpretations of this perceptual stability focus on extra-retinal signals from signals sent to the eye muscles and from eye muscle stretch signals that can indicate the direction of the eye’s gaze.
a. Efference copy theory

The extra retinal signal that has received most attention is efference copy, a copy of the signals sent to the eye muscles that can predict where the eyes will go, in advance of the eye movement. The efference copy theory, first phrased in this term in a paper by von Holst & Mittelstaedt (1950), came from an empirical work on the continually circling flight of the *Eristalis* blowfly following a surgically imposed 180 degrees head rotation. The same year, similar observations were made by Sperry (1950) who surgically inverted the eyes of a fish. Sperry used the term “corollary discharge.”

Both researchers found the misguided behavior in their rewired specimens could be explained by a cancellation signal. Since the time of Helmholtz, efference copy was thought to be a displacement vector predicting the upcoming translation due to the saccade. This vector would be subtracted from the location of objects in retinal coordinates in order to cancel their displacement and recover their location in the world. To the extent that the efference copy was an accurate predictor of the eye movement, objects would not appear to move as the eyes moved. It was thought that the result of this subtraction of the efference copy would be placed in a stable spatiotopic map of objects. Over the years, however, there has been little evidence for such a spatiotopic map in the physiological studies of the visual system (Andersen et al., 1985; Galletti & Battaglini, 1989). The maps of the world seemed to remain resolutely in retinotopic coordinates as physiologists explored higher and higher areas of the visual system (Ben Hamed et al., 2001; Sommer & Wurtz, 2000). This means that the activations in response to objects in the scene are shifted across these retinotopic representations with every eye movement. How then would a stable world emerge?

b. Electrophysiological studies:

The generation of saccades is one of the most thoroughly studied motion processes of the primate brain. As a result, the exploration of the efference copy and its different pathways to sensory areas has been focused on saccades (Sommer & Wurtz, 2008). Indeed, several groups started to examine the physiological activity during saccades in a number of primate visual areas, such as SC (superior colliculus of midbrain), FEF (frontal eye field of frontal cortex) and LIP (lateral intraparietal area of parietal cortex). These studies led to the discovery of neurons in parietal and frontal areas of the monkey brain that show, often before the saccade, a predictive response to stimuli that will fall into the neuron’s receptive field after the saccade lands (Goldberg & Bruce, 1990; Duhamel et al., 1992).

Indeed, while monkeys fixate and when a stimulus appears into the receptive field of a recorded neuron, an initial activity is observed with a certain latency relative to the onset of the stimulus (Figure 2A). The same neuron fires earlier when the stimulus appears in a position where the receptive field will be after a saccade (Figure 2B). This predictive activity emerges before any classical response to the stimulus when it does appear in the receptive field after the saccade lands, and even begins in some cells before the saccade onset. Duhamel and colleagues (1992) called this process “remapping” and assume that “it may contribute to the integration of visual information across eye movements and to the construction of a continuously accurate, retinocentric representation of visual space” (p. 92). Thus, this predictive mechanism, measured now in single-unit recording studies of awake monkeys, corresponds closely to the compensation theory described forty-two years ago by von Holst, Mittelstaedt and Sperry and predicted by Helmholtz. The efference copy leads to a predictive shift of target locations of the retinotopic map. So the locations shift, but the visual system knows beforehand where the target representations will move to. Given that, this
shift is attributed to the eye movement and not the object’s movement and the perception of the targets remains stable in the world.

In a series of studies, Sommer and Wurtz have linked the efference copy to these remapping shifts. They identified a pathway from SC to FEF through a thalamic relay (Sommer & Wurtz, 1998) and demonstrated that the SC is a potential source of efference copy (Sommer & Wurtz, 2002, 2004) and that drives the predictive activity registered in FEF neurons (Sommer & Wurtz, 2006). Specifically, when they blocked this pathway, the typical remapping activity of FEF was degraded.

Finally, neurons with predictive activity have been studied and identified in the principal brain areas associated with saccade programming such as LIP (Duhamel et al., 1992; Kusunoki & Goldberg, 2003; Heiser & Colby, 2006), FEF (Sommer & Wurtz, 2006; Umeno & Goldberg, 1997, 2001), CS (Walker, FitzGibbon & Goldberg, 1994), and even in earlier extrastriate visual areas V3A, V3 and V2 (Nakamura & Colby, 2002).

Altogether these studies support a retinotopic hypothesis of visual constancy (Wurtz, 2008; Duhamel et al., 1992) with a predictive remapping process of the visual scene implement on a retinotopic reference frame and based on efference copy vector.

When we move our eyes, the world remain stable because on retinotopic maps, (i.e. maps that treats the retinal inputs in a way that adjacent receptive fields correspond to adjacent parts of the visual field) a same spatial location is track and update to counteract its drift on the retina due to the eye movement.
2. Remapping and salience maps for attention

In the attention literature, the spatial layout of items of behavioral relevance is often called a salience map and it shares important features with the oculomotor network described above (Itti & Koch, 2001). This salience map indicates the attentional value of different locations in the scene. The spatial layout of eye movement targets, seen in areas of the visual system concerned with saccades, has been proposed to serve as the layout of attention (Rizzolatti et al., 1987). Specifically, when there is activity on these maps, it projects downwards to earlier visual cortices and enhances processing at the corresponding locations of these earlier maps. Microstimulation studies of Moore and Armstrong (2003) in FEF and Muller and colleagues (2005) in CS show that stimulating a cell in these eye movement regions (FEF) lowers the threshold for response in earlier visual cortices of cells having receptive fields with the same retinotopic location as the stimulated cell. This is evidence that these activity peaks in these eye movement areas are causally linked to the deployment of attention.

Furthermore, Gottlieb and colleagues demonstrate that attention play a crucial role on the predictive activity of LIP neurons (Gottlieb et al., 1998; Kusunoki et al., 2000).

They demonstrate that, even if a LIP neuron had a brisk response to the appearance of a stimulus in its receptive field during a fixation task (Figure 3A), little or no response was obtained for the same stimulus when it was later brought into the receptive field by a saccade (Figure 3B). On the other hand, when the saccade brought the same stimulus into the receptive field briefly after having been flashed, the neuron responds almost as briskly as it did to the abrupt appearance of the stimulus (Figure 3C).

**Figure 3.** Effect of recent onset flash on remapping activity of a single neuron in LIP. Diagrams in each panel show the fixation point and target for the saccade (red squares), receptive field before (circle) and after the saccade (dashed circle). Raster and spike density histogram are the same of those in Figure 2 and are aligned on the event indicated by the long vertical line. (A) Stimulus flashes in receptive field during fixation. The neuron has a brisk response with a classical visual latency. (B) Stable stimulus. An array of symbols remains on the screen unchanging throughout the task. Monkey makes a saccade (arrow) to the fixation point in the center of the array. The neuron has a minimal response in this condition even if the saccade brings a visual stimulus in its receptive field. (C) Recent onset stimulus. The eight stimuli appear while monkey fixates at the initial position. Monkey makes saccade that brings the stimulus into the receptive field. The neuron responds almost as briskly as it did to the abrupt appearance of the stimulus. Adapted from Gottlieb et al. (1998).
Similar results were observed by presenting a cue that drew task-relevant attention to a stimulus. When a saccade brought the now attended stimulus into the receptive field, a brisk response was seen. Only cued stimuli lead to a predictive activity of LIP neurons (Kusunoki et al. 2000). In both cases the neuron begin to fire at or before the end of the saccade, supporting the idea that remapping process only occurs for attended stimuli.

We can thus hypothesize that an efference copy of an impending eye movement trigger a remapping of activity for attended items in areas such as LIP and FEF. This mechanism displaces, before an impending saccade, the attention pointers to salient stimuli in the direction opposite to the saccade (Figure 4A, 4B). These remapped pointers will lie exactly where the attended target will land after the saccade, maintaining spatial constancy despite drastic change in retinal input (Figure 4C).

3. Spatiotopic apparent motion

We have developed a probe of remapping that depends on the link between attention and apparent motion. When a stimulus is flashed briefly at one location and followed immediately by a second stimulus flashed at a nearby location, a strong impression of motion is seen. This apparent motion can be seen even if the two flashes are so widely separated that their presentation cannot stimulate any directionally selective neurons. These directionally selective neurons have receptive fields fixed in retinotopic coordinates and their responses are considered to be the basis of a low-level motion system, one that responds reflexively to any movement as long as it falls in their receptive field, and that responses in a strictly retinotopic manner.

When the displacement between two stimuli is too large to be picked up by any directionally selective
receptive fields, motion may still be seen, and this motion is considered processed by the high-level motion system, a system that is attention-based (Anstis, 1970; Ramachandran & Anstis, 1983; Mather & Cavanagh, 1989; Cavanagh, 1991; Dick et al., 1991; Verstraten et al., 2000). Specifically in this model of high-level motion (Verstraten et al., 2000), the displacement of attention from the first stimulus to the second is the source of the motion percept. Using this, we can ascertain whether apparent motion is based in spatiotopic coordinates and, if so, use it to measure the accuracy of remapping.

To do so, we present a first flash just before the beginning of a saccade and follow it after the saccade by a second flash at a different location (see Method & Figure 5B). The blank between the two stimuli compels the visual system to maintain a representation (Duhamel et al., 1992) of the pre-saccadic location of the first flash. After the saccade, the attention pointer to this first flash should be remapped to point in space to where the first flash had been. When the second flash appears, this attention pointer will be dragged to the location of the second flash and the participant should experience an apparent motion between the two locations in space, despite the very different direction of displacement of the two flashes on the retina. This apparent motion should therefore be seen in spatiotopic, not retinotopic coordinates. In fact, Rock and Ebenholtz (1962) originally reported a spatiotopic apparent motion but for displacement along the direction of the saccade.

**Questions**

In a first experiment using this procedure, we ask whether spatiotopic apparent motion is seen in spatiotopic coordinates and then we examine the spatial accuracy of remapping.

Then, in a second experiment we focus on the particular case of target presented at the limit of the visual field. Interestingly, a saccade away from a stimulus near the edge of the visual field should shift the remapped attention pointer outside the visual field. Because remapping has been observed for different saccadic amplitudes and different directions (Heiser & Colby, 2006), we examine whether the visual system can represent stimuli in this extraretinal space in a way that contributes to apparent motion.

**Experiment 1**

1. **Method**
   a. **Participants**

   Four volunteers from the Université Paris Descartes took part in the first experiment (2 authors and 2 participants naive as to the purpose of the experiment, age 24-60 years; 1 female). All had normal or corrected-to-normal vision and gave their informed consent. The experiments were carried out according to the ethical standards specified in the Declaration of Helsinki.

   b. **Apparatus and stimuli**

   Participants were seated in a silent and dimly lit room with the head positioned on a chin rest, 63 cm in front of a computer screen. Stimuli were presented on a gamma linearized 22” Formac ProNitron 22800 screen with a spatial resolution of 1440 by 1050 pixels (36.7 by 27.6°) and a vertical refresh rate of 100 Hz. The experiment was controlled by an Apple MacPro Dual Intel-Core Xeon computer. Manual responses were recorded via a standard keyboard and mouse. The experimental software controlling stimulus display
and response collection was implemented in Matlab (MathWorks, Natick, Massachusetts, USA), using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997).

c. Procedure

Two fixation targets, one red and one green, each 0.7° in diameter, were presented at 5° to the right and 5° to the left of screen center. The red and green targets swapped position each 600 msec. Participants were instructed to always fixate the green target and follow it as accurately as possible as it moved back and forth. The green target could equiprobably start at the left or at the right side of the screen. After a few back and forth cycles, participants were able to synchronize their saccades with the exchange of the two targets (“synchronizing cycles”: Figure 5A). Once they were moving their eyes in synchrony with the green target, they were instructed to press a button on the keyboard to start a trial. As they pressed the button, two circular black probes (0.7° in diameter) were presented sequentially, one before and one after the saccade (“adjustment cycles”: Figure 5B). Each probe was presented for 400 msec, the first was turned off about 100 msec before the saccade and the second turned on about 100 msec after the saccade. These probes could appear at nine equiprobable locations on the screen equally spaced by 10° horizontally and 5° vertically from center of the screen (Figure 5C). They were originally displaced perfectly vertically on the screen by 3° of amplitude, but this displacement could randomly be one of four others combinations of horizontal drift of the two probes by ±1° or ±2°, producing a left or right physical tilt (Figure 5D) in the displacement. The order of appearance of these two dots was equiprobably upward or downward.

Figure 5. Experimental procedure. (A) Synchronization cycle. Two fixation targets, one red and one green swapped position each 600 msec. Participants fixated the green target and synchronized their saccades with the exchange of the two targets. The green target could start equiprobably at the right or at the left side of the screen. Here only a rightward saccade is shown. (B) Adjustment cycle. Two probes were presented sequentially, one before and one after the saccade for 400 msec each. The order of appearance of the probes was equiprobably upward or downward. Here only a downward trial is shown. (C) Probes could appear at 9 equiprobable locations on the screen, enumerate on this panel. (D) The two probes were originally displaced vertically by 3° of amplitude (black circles) but this displacement could randomly be one of the four others combinations of horizontal drift of the two probes by ±1° or ±2° producing a left or right physical tilt (dashed lines). Participants adjusted with the mouse the relative horizontal position of the probes until they were perceived to move vertically. Leftward movement of the mouse (red arrow) led to a displacement of the bottom probe to the left and of the top probe to the right. A rightward displacement (blue arrow) led to the opposite effect.
As they moved their eyes back and forth, participants were instructed to adjust with the mouse the relative horizontal position of the two probes until they were perceived to move vertically. A leftward movement of the mouse led to a displacement of the bottom probe to the left and of the top probe to the right. A rightward movement led to the opposite effect (Figure 5D).

Each adjustment cycle was alternated with a synchronization cycle leaving participants the time after each appearance of the black targets to adjust the mouse to change the subsequent appearance. Once the participant was satisfied with the adjustment, usually after a few cycles, he or she pressed a button to indicate their final setting. Three participants ran 5 sessions of 36 trials each (180 trials) and one participant ran 6 sessions (216 trials).

2. Results

All trials were included in these analyses giving for each participant, 4 sets of 9 mean apparent horizontal misalignment arising from the combination of the two directions of saccade (rightward vs. leftward) with the two directions of the probes (upward vs. downward) for the nine different spatial locations tested.

We were interested in measuring the apparent misalignment of the vertical apparent motion, which we interpret as an error in remapping the location of the first black probe. To do so, we measured the horizontal distance “Δm” between the two probes (Figure 6D).

For the four participants, the presentation of a downward or upward displacement of the probes led to roughly the same pattern of results (Annex 1, Figure 1). We compared the mean values the two directions of probe displacement for each participant and observed for the 72 comparisons tested only 2 significant differences (Annex 1, Table 1). Because there was no overall significant difference for results in the two probe directions, we collapsed the data across this variable and investigate only the effect of saccade direction and spatial location of probes.

To perceive an apparent motion between the two probes, the first probe (that appears before the saccade) needs to be remapped in the direction opposite to the saccade. If this remapping is accurate, participants should perceive a vertical apparent motion between the two probes. But if this remapping is too long (hypermetric) or too short (hypometric) participants should perceive a deviation in the direction of motion away from vertical.

For example, for a rightward saccade, with downward presentation of probes in the middle of the screen (#5 of Figure 5C), the first probe is presented on the horizontal axis at 0° relative to the screen or at +5° relative to the fovea (Figure 6A). Because participants prepare a 10° rightward saccade, the accurate remapped position of this first probe is now on the horizontal axis at -5° relative to the fovea. But if the remapping is hypermetric (Figure 6B1), the first probe location should be remapped farther and should lead to a misalignment of the vertical apparent motion tilt to the left (Figure 6C1). However, if the remapping mechanism is hypometric (Figure 6B2), misalignment of the vertical apparent motion should be tilted to the right (Figure 6C2).

Individual data for the four participants are shown in Figure 7. For the main analysis, results are plotted for each participant on a map of apparent misalignment as a function of saccade direction. The data are presented in retinal coordinates (i.e. in coordinate relative to the fovea). These maps show, for each of
Figure 6. Hypermetric and hypometric remapping. (A) Rightward saccade. The first probe was presented on the horizontal axis at +5° relative to the fovea (black line circle), because participants prepare a 10° rightward saccade, the accurate remapped attention pointer of this first probe (light-orange circle) is remapped of 10° to the left (orange arrow). (B1) Hypermetric remapping. The first probe attention pointer is remapped farther than the accurate remapped location (C1) and led to a misalignment of the vertical apparent motion tilt to the left (orange arrow), even if physically the second probe (black circle) appeared perfectly below the first one. Participants moved the mouse to the left (red arrows). (D1) They perceived now a vertical apparent motion of the two probes. We measured the horizontal distance between the two probes "Δm". (B2-C2-D2) Hypometric remapping. Same reasoning but this time remapping is too short and lead to a misalignment of the vertical apparent motion tilted to the right. Participant moved the mouse to the right (blue arrow). (E1-E2) Maps of apparent misalignment. These maps show the accurate remapped location (grey circles) and the horizontal distances between the two probes (red circles). The apparent misalignment is interpreted as remapping errors and the x-axis represents the horizontal component of these errors. We plot hypermetric remapping as positive values and hypometric as negative values relative to the accurate remapped location.

The nine spatial locations tested, the accurate remapped location of the first probe (grey circle) and the horizontal components of the apparent misalignment perceived (red of blue circle) derived from the horizontal distance between the two probes (Δm) after the participant’s adjustment.

We interpret the apparent misalignments of the vertical apparent motion as remapping error of the first probe position and we plot hypermetric remapping as positive values, and hypometric as negative values relative to the accurate remapped location.

This first result suggests that the direction of apparent motion between the two probes is perceived quite close to vertical, with only a small deviation (Figure 7). This demonstrates that participants perceived the spatiotopic (not retinotopic) displacement of the probes. Indeed, on the retina the two probes appeared with a horizontal displacement of about 10° (the saccade amplitude).

In order to estimate the magnitude of the deviation perceived, we calculated for each participant the mean value of perceived misalignment (independently of the sign of the effect) divided by the accurate remapping amplitude (the saccade amplitude). We interpreted these values as the percentage of remapping errors during a 10° saccade. Results are summarized in Figure 8 and indicate that across participants, a 10° saccade lead to less than 5% (4.18%) of remapping errors for targets presented near the fovea.

We were then interested in the direction of the remapping error. As we explained above, remapping mechanism could be hypermetric or hypometric resulting in the perception of motion of the probes with a tilt to the right or to the left for exactly the same configuration of stimuli (Figure 6). The patterns of remapping errors for each participant are shown in Figure 7. These maps give us the opportunity to appreciate the large variability in the amount and the direction of remapping errors. In fact, for two
Figure 7. Maps of apparent misalignment. Each row corresponds to rightward and leftward saccade condition for each four participants. Data are presented in retinal coordinates, i.e. coordinates relative to the fovea. Scales at the top and at the right of each map reflect the horizontal and vertical distance from the fovea in visual degree. Grey circles reflect the accurate remapped location (see Figure 6 for an example at coordinates [-5°; 0°]). Red and blue circles reflect the horizontal component of apparent misalignment interpreted as remapping error. The mean value of remapping error for each spatial location tested is given by the scale below each map. Note that these scales are reversed for rightward and leftward saccade, and are multiplied by a factor of 4 compared to the retinal scales. Each horizontal error bar indicates SEM.
Figure 8. Magnitude of deviation perceived. Mean value of perceived misalignment (independently of the sign of the effect) for each subject divided by the accurate remapping amplitude. Each bar reflects one participant and each error bar indicates SEM.

different participants, the same spatial position with the same saccade direction, could lead to data totally reversed in magnitude and direction. Then, for the same experimental condition, two different participants could report that the probe appears in motion tilt in opposite directions.

This variability took different patterns for different participants. However, for probes remapped from one hemifield to the other, horizontal remapping errors were generally hypermetric (-5° on the rightward maps and +5° on leftward map of Figure 7). In other words, for probes presented in the middle vertical axis of the screen, remapped attention pointers are generally put farther than the accurate remapped pointer position. And it is always the case for probe exactly in the middle of the screen (0° on the vertical axis in Figure 7).

We did not observe the same tendency for probes presented and remapped in the same hemifield (-15° and +5 in rightward saccade; -5° and +15° for leftward saccade).

Although the remapping errors are idiosyncratic to each participant, the data demonstrated a large inter-trial reliability. In particular, one participant was tested two times with 3 months between the two sessions. The pattern of results (Figure 9) was very similar across this large interval, demonstrating the robustness of the effect.
3. Conclusion

Participants report the motion of the two probes as mostly vertical but with a noticeable and easily measured deviation. We attribute this deviation to the error of the mechanism, between eye movements, at remaps locations of interest in order to maintain visual constancy. Our quantitative method allows us to address the question of spatial accuracy of this mechanism. We observed the horizontal component of these remapping errors and found that they are generally small. As expected, the magnitude of these errors does not exceed 5%, explaining the perception of a stable and continuous visual world.

Finally, the study of the direction of the error does not lead to any clear pattern of errors that could identify how the oculomotor system computes the remapped locations based on efference copy information. In fact, we observed different pattern of results specific to each participant. These patterns didn’t change over time suggesting that our procedure is reliable and robust and also that, remapping errors are systematic and specific to each participant and positions of the visual space.
Experiment 2

1. Method

a. Participants

Six volunteers from the Université Paris Descartes took part in the second experiment (1 author and 4 participants naive as to the purpose of the experiment, age 24-34 years). All had normal or corrected-to-normal vision and gave their informed consent.

b. Apparatus and stimuli

Participants were seated in a silent and dimly lit room with the head positioned on a chin rest. Two computer screens were used in this experiment, one in front of the participant and the second was set to the right. Both were positioned on a circle of 40 cm of radius (Figure 10). Stimuli were presented on a Apple iMac Built-in 24" widescreen TFT active-matrix liquid crystal display, with a spatial resolution of 1920 by 1200 pixels (73.3° by 45.8°), refresh rate of 60 Hz and on a Apple 24" LED-backlit TFT active-matrix liquid crystal display, with a spatial resolution of 1920 by 1200 pixels (73.3° by 45.8°), refresh rate of 60 Hz. The second screen (set to the right) was positioned before the beginning of the experiment in such a way that when participants fixated at 10° to the left of the screen center, a black or white circular probe (6° in diameter) presented 3° to the right of the center of the second screen couldn't be report by the participants. The experiment was controlled by an Apple iMac Intel Core 2 Duo computer. Manual responses were recorded via a standard keyboard. The experimental software controlling stimulus display and response collection was implemented in Matlab (MathWorks, Natick, Massachusetts, USA), using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997).

![Figure 10](image_url)

**Figure 10.** Experimental apparatus: view from above. Two computer screens were positioned at 40 cm from the participants. The first was set in front (1st screen) and the second was set to the right (2nd screen) of the participants. The second screen is positioned before the experiment in a such a way that when participants fixate the first fixation target (FT 1), only the first probe (PROBE 1) fall inside their visual fields (green arc of a circle) but the second probe (PROBE 2) fall outside their visual field. Thus, when participants fixate the second fixation target (FT 2), positioned on the fist screen at 20° to the right of FT 1, PROBE 1 as well as PROBE 2 fall inside their visual fields (orange arc of a circle).
c. Procedure

On a gray background, two fixation targets, one red and one green each 0.7° in diameter were presented at 10° to the right (fixation target 1: ‘FT 1’) and 10° to the left (fixation target 2: ‘FT 2’) of the first screen center (Figure 10). Participants were instructed to always fixate the green target and follow it as accurately as possible as it moved back and forth. The green target could equiprobably start at the left or at the right side of the screen and swapped position each 600 msec. After two synchronizing cycles, participants were able to synchronize their 20° saccades with the exchange of the two targets. Then, moving their eyes in synchrony with the green target, they were instructed to draw their attention to two large circular black probes (6° in diameter) that were presented sequentially on the second screen (set to the right), one before and one after the saccade. Each probe was presented for 400 msec, and as in the previous experiment, the first probe was turned off about 100 msec before the saccade, and the second was turned on about 100 msec after the saccade (‘detection cycles’). These probes always appeared at the same spatial location, at 10° to the left (‘PROBE 1’), and at 10° to the right (‘PROBE 2’) of the second screen center. As explained above, we positioned the second screen in such a way that PROBE 2 was only visible when participants were fixating the right fixation target (i.e. FT 2) on the first screen and fall outside their visual field when they fixated the left fixation target (i.e. FT 1). Thus, PROBE 2 fell at the rightmost edge of participants’ visual field. The order of appearance of theses two probes was equiprobably leftward (PROBE 1 then PROBE 2) or rightward (PROBE 2 then PROBE 1).

Each trial was composed of two synchronizing cycles, followed by two detection cycles with a synchronizing cycle placed between them.

After each trial a tone indicated that participants had to report if they’ve seen or not an apparent motion of the two probes. The combination of the two saccade directions and the two probe directions led to 4 different conditions illustrated in Figure 11. This conditions were renamed “Intraretinal remapping” (rightward saccade, rightward probes: Figure 11A), “No vision” (rightward saccade, leftward probes: Figure 11B), “No motion” (leftward saccade, rightward probes: Figure 11C) and “Extraretinal remapping” (leftward saccade, leftward probes: Figure 11D). During “No vision” and “No motion” trials, one of the two probes fell outside participants’ visual field. We expected that they did not perceive motion. Thus the results obtained in these two conditions were considered and used as reference for the two others (i.e. Intraretinal and Extraretinal remapping, respectively).

During all the time of the experiment, participants were instructed to maintain the same position of their head. To control this, we tested participants with a forced-choice contrast detection task before and after the main task.

In this control task participants were first instructed to fixate a single green fixation target (0.7 in diameter) on the first screen and once they were fixating, draw their attention to the second screen and pressed a button on the keyboard. The fixation target could appear equiprobably at one of the two fixation targets of the main experiment (FT 1 or FT 2). As they pressed the button a circular probe (6° in diameter) was presented for 400 msec, positioned equiprobably at one of the two probes locations of the main experiment (PROBE 1 or PROBE 2). This probe could either be brighter or darker than the background. Participants were instructed to report the contrast of the probe detected: brighter or darker than the background. When participants didn’t see the probe they were instructed to answer randomly.
Figure 11. Experimental procedure. Diagrams show a view from above of the participants (represented by a single eye), the 1st and 2nd screen (gray rectangles), projection lines of the green fixation target (green line) and of the probes (black lines), participants' visual field when they fixated FT 1 (green arc of a circle) or FT 2 (orange arc of a circle). (A) Intraretinal remapping. The 1st probe appeared at 10° to the left of the 2nd screen center (PROBE 1). Participants prepared a 20° rightward saccade. The 1st probe's attention pointer is supposed to be remapped by 20° to the left (blue line) of the 1st probe's original location (gray line). After the rightward saccade, the 2nd probe appeared at the same position on the retina, but at 10° to the right side of the 2nd screen center (PROBE 2). (B) No vision. The 1st probe appeared outside participants' visual field when they fixated FT 1. After a rightward saccade, the 2nd probe appeared at PROBE 1. (C) No motion trial. The first probe appeared at PROBE 1. Because participants prepared a 20° leftward saccade, the 1st probe's attention pointer is supposed to be remapped by 20° to the right (blue line). After the saccade the second probe fell outside participants' visual field. (D) Extraretinal remapping. The 1st probe appeared at the rightmost edge of the retina (PROBE 2) when participants fixated FT 2. Because participants prepared a leftward saccade, the 1st probe's attention pointer is remapped at 20° to the right (blue line) of the 1st probe's original location, i.e. outside the participants' visual field. After the saccade, the 2nd probe appeared at the same position on the retina, but with a 20° displacement on the 2nd screen (PROBE1). In these four different conditions, participants had to report if they've seen or not an apparent motion of the two probes.

Six participants ran 20 sessions of 4 trials each (80 trials) during the main experiment and 20 sessions of 2 trials each (40 trials) during the control experiment.

2. Results

We first verified that before and after the main experiment, subject didn't perceive PROBE 2 when they fixated at FT 1. Thus, the mean responses obtained under this condition before and after the main experiment were compared to chance level 0.50 using a one sample Student’s t-test. Discrimination accuracies were consistently at chance level before (Figure 12; t(5)= 0.696 ; p = 0.259, one sample comparison with 0.5 chance level) and after (Figure 12; t(5)= 0.415; p = 0.348 , one sample comparison with 0.5 chance level) the main experiment, indicating that participant weren’t able to perceive PROBE 2 when they fixated at FT 1. However, when they fixated at FT 2, PROBE 1 and PROBE 2 was always perceived and discriminate correctly as well as PROBE 2 when they fixated at FT 1 (Figure 12).
We were then interested in measuring the detection of apparent motion in the four different experimental conditions. We then calculated the mean report of apparent motion for each individual participant (Figure 13A) and across all participants (Figure 13B). Using paired sample Student’s t-tests we compared results obtained in “intraretinal remapping” and “extraretinal remapping” conditions with their respective control conditions, “No vision” and “no motion”.

Apparent motion reports were significantly more frequent in “Intraretinal remapping” compared to “No vision” trials (Figure 13B; t(4)= 66.82; p < 0.0001 , paired t-test). And apparent motion reports were significantly more frequent in “Extraretinal remapping” compared to “No motion” trials (Figure 13B; t(4)= 75.25; p < 0.0001 , paired t-test). Thus, in both conditions (i.e. Extraretinal and intraretinal), participants experienced apparent motion in spatiotopic direction, even if on the retina the two probes fall roughly at the same location.

3. Conclusion

During intraretinal remapping trials (Figure 11A), just before the saccade, the first probe attention pointer was supposed to be remapped by 20° (the saccade amplitude) to the left (opposite direction of the saccade). Thus after the saccade landed, the position of the remapped attention pointer should correspond to the probe’s original spatial location. After the saccade, even though the second probe appeared roughly at the same location on the retina, participants reported an apparent motion from the spatial position of the first probe to the second probe. We interpreted this result as the displacement of the remapped attention pointer from its position corresponding to the first probe to the position of second probe leading to a spatiotopic apparent motion.

This early result implies that an attended target at the edge of the visual field can be remapped and participate in motion perception despite the poor visual resolution in the far periphery.
Figure 13. Results of the main experiment. The mean report of apparent motion is plotted for each four different experimental conditions (see Figure 10). (A) Results for the six individual participants. (B) Average across participants. In both intraretinal and extraretinal remapping conditions, participants experienced apparent motion more frequently than in their respective control conditions (i.e. no vision and no motion). Each error bar indicates SEM.

For extraretinal remapping trials (Figure 11D), just before the saccade, because participant prepares a leftward saccade, the first probe attention pointer should be remapped by 20° in the opposite direction. Given that the first probe is presented at the edge of the visual field, the remapped attention pointer therefore should be remapped outside the participant's visual field. Again, even though the second probe appear nearly at the same position on the retina as the first, participants reported an apparent motion in the same direction of the saccade. Thus if the remapping explanation of the spatiotopic apparent motion is correct, this result implies that a target's representation may even be remapped outside the visual field and that this extraretinal representation can participate in motion perception.

Finally we expected that participants would rarely report apparent motion when one probe appear outside the visual field (“No vision” and “No motion”), and this is grossly the case for four of our six participants, nevertheless two participants report seeing apparent motion in about one third of these trials. Both were naïve subjects that had never done any experiment involving eye movements. Even though they didn’t report having trouble following the green fixation target during the experiment, we assumed that they executed their saccades too early or too late during these trials and so saw the probes that would have been outside the visual field if they had timed their saccades accurately.
Following the original report of Rock and Ebenholtz (1962), we have conducted two experiments that demonstrate that an apparent motion of two single dots presented before and after an eye movement can be perceived in spatiotopic direction, including spatiotopic apparent motion from location that fell, following the saccade, outside the visual field.

Apparent motion is considered processed by a high-level attention-based motion system and can be used as a probe for locating and tracking displacement of attention. Using this high-level motion, we can thus examine recent model of visual constancy such as “remapping” (Duhamel et al., 1992). Remapping is a mechanism that allows the visual system to anticipate what the world looks like after an eye movement by predicting the future locations on the retina of different attended targets. This mechanism implies the spatial updating of attended targets locations on retinotopic maps. Thus, we used apparent motion to track this attentional spatial updating and to reveal remapping processes.

We have conducted two experiments that linked behaviorally the role of attention with the process of remapping both inside and outside the visual field. The main goal of the first experiment was to examine the possibility that attention pointer could be remapped to its expected spatiotopic location across saccade and participate in visual function such as motion perception. The results indicate that a perfectly vertical apparent motion across eye movements is report in spatiotopic direction with an interesting small misalignment. We interpreted that apparent misalignment as error of the oculomotor remapping and measured its horizontal component for attended targets near the fovea. These errors were generally small suggesting that the hard computation of spatial updating at the time of the saccade is managed with accuracy.

In a second experiment, using a similar procedure we examined the particular case of attended target at the limit of the visual field. Our results indicate that spatiotopic apparent motion is detected, suggesting that remapping of attention pointer could happen in peripheral vision. Moreover our results indicate that an impending saccade could lead to a remapping of an attention pointer to a location outside of the visual field, suggesting that visual cortices may even register extraretinal locations.

We will discuss these findings in relation with spatial attention and its role in visual constancy, to a reference frame supposed to deal with this attentional remapping, to previous behavioral procedures that assessed inter-saccadic perception and to human imaging studies of remapping.

Change blindness studies, in which large modification of content in visual scene can go unnoticed (O’Regan et al., 1999) support the idea that we don’t form a detailed representation of our surrounding. However, they also suggest that attention is required to perceive the change (Rensink et al., 1997) and that changes across saccades are detected better for attended than unattended items (Cavanaugh & Wurtz, 2004). Thus, there is no visual constancy problem for unattended items, and remapping would be required only those few attended ones. Indeed, evidence for remapping responses in single cells of LIP show that only attended salient stimuli (not all visual details) are remapped. (Gottlieb et al., 1998; Kusunoki et al., 2000). Moreover, visual attention seems to be directly linked with those eye movement control areas that governed remapping mechanism. The same neuronal activity that prepares for generation of saccade (CS) also contributes to the shift of visual attention (Cavanaugh & Wurtz, 2004). And human imaging studies
indicate that frontoparietal system including FEF is even more extensively activated with covert than overt attention task (Nobre et al., 2000). Altogether these results support the idea of the remapping of attention pointer allow a spatial continuity for attended targets. Therefore, based on the efference copy, neurons whose activity initially represent the location of the attended target transfer their activity to another population of neurons that represents the target’s location after the saccade (Berman & Colby, in press), whatever the distance from the fovea or the saccade amplitude (Heiser & Colby, 2005). In that sense our results of spatiotopic apparent motion near the fovea or in peripheral vision imply that attended targets before an impending saccade are remapped in eye movement centers and then participate in spatiotopic attention-based motion perception.

To compensate for large scale translations induced by saccades, eye movement centers are supposed to deal with retinal input of our eyes as well than with attention and salience map. These frontoparietal areas finally transfer all remapped activity to earlier visual areas using back projection (Nakamura & Colby, 2002). Eye movement centers (Sommer & Wurtz, 2000; Ben Hamed et al., 2001) as well as well as early visual areas are known to be retinotopically organized. It is then reasonable to consider that the remapping of attended target is more likely to be process in a retinotopic rather than in a spatiotopic reference frame (Wurtz, 2008). Some authors have proposed models for this retinotopic updating (Quaia et.al, 1998; Keith & Crawford, 2008). In particular they suggest that salience map (LIP, FEF) at the time of the saccade must be update using horizontal learned connections to represent the new coordinates of the attended spatiotopic location (Quaia et.al, 1998). Altogether, theses studies support the retinotopic hypothesis of visual constancy (Duhamel et al., 1992; Wurtz, 2008).

But this hypothesis doesn’t take in account the extraretinal spatiotopic apparent motion reported by our participants. In fact, retinotopic areas ought to be limited, logically to representation of retinal input. Even if we can orient to locations outside the visual field, to sounds, or something we saw briefly when we turn and glance behind us, our result is the first evidence that extraretinal locations may be represented in a way that allows them to participate in purely visual phenomena such as motion. If we assume that spatiotopic apparent motion is process by saccade-related cortical areas such as LIP and FEF, this result suggests that in these areas there may be cells at the margin of retinally supported locations that represent locations from outside the visual field.

We have thus developed a probe of remapping that depends on the link of attention and apparent motion and our results indicate that only small remapping errors occurred. This last point supports the idea that remapping of attention pointers is an accurate mechanism that can underlie visual constancy. Contrary to other behavioral studies of perisaccadic perception, our procedure employed long duration of probe presentation that disappeared before the onset of the saccade. This scenario corresponds to the case of remapping of memory trace described by Duhamel and colleagues (1992). They physiologically demonstrate that memory trace could be elicited by stimulus flashes less than 50 msec in duration presented even 1 sec before the saccade, and that predictive activation could be registered in LIP neurons even though the stimulus has been extinguished well before the saccade (Berman & Colby, in press). In our case the stimulus reappears about 100 msec after the saccade lands and the remapped attention pointer (memory trace) is dragged to another location. Participants showed idiosyncratic pattern of remapping errors that don't correspond to the results obtained in previous studies of perisaccadic mislocalisation (Honda, 1989; 1991; Dassonville et al., 1995) and studies of visual compression (Ross et al., 1997; Lappe et al., 2000).
In perisaccadic mislocalisation studies, targets flashed before the saccade were mislocalized in the direction of the saccade, whereas those flashed immediately after the saccade were mislocalized in the opposite direction. For mislocalisation studies target beyond the saccade goal are mislocalized in the direction opposite to the saccade, but targets proximal to the saccade goal are mislocalized in the saccade direction. In our case, attended target always appeared before the saccade, but could be mislocalized in the opposite direction (hypermetric) or in the direction (hypometric) of the impending saccade in function of different spatial locations tested and the different participants. However it is important to note that the stimuli used in these previous studies remained on the screen for less than 5 msec whereas our experiments employed duration of 400 msec. Indeed, an early results of Jeffries and colleagues (2007), underline the fact that longer probe durations in classical double-step task lead to mislocalisation always in the direction opposite to the saccade. This result can be linked with the hypermetric tendency that we observed for probes remapped from one hemisphere to the other.

Nevertheless, even if procedures differ largely between these studies, they all should bear on the same mechanism. We assume that the differences observed arose from procedural differences: we measured remapping errors with an online judgment (not a delayed report) and used long probe duration.

Our procedure is thus more likely to reflect the final result of oculomotor remapping rather than intermediate results.

In humans, neuroimaging experiments using functional MRI to investigate brain regions involved in remapping point out a role of dorsal parietal regions, certainly homologous to monkey area LIP (Medendorp et al, 2003; Merriam et al., 2003). These studies investigated the remapping of a highly salient flickering stimulus that was presented initially to the left of the fixation point. As expected, this presentation led to an activation of the right parietal cortex. But when observers made a large leftward saccade that shifted the location of the (no longer present) stimulus to the left, the right cortex was activated with a time course that suggested remapping. It is thus reasonable to consider that similar activations could be observed as in our case with covert attention drawn to single probe presented near fovea or at the limit of the visual field.

In summary, we have conducted two experiments in which we observed that attention pointers could be remapped at the time of the saccade and participate in attention-based motion perception. This procedure allowed us to investigate behaviorally the spatial accuracy of oculomotor remapping. Results suggest that this remapping is fairly accurate both for central and peripheral vision. This updating process occurs on the salience maps of the oculomotor system (such as LIP and FEF) which are retinotopic in nature. This updating therefore constructs effective spatiotopy on retinotopic maps. These retinotopic maps, according to our second experiment may even represent extraretinal locations when remapping places the pointer to an attended target outside the visual field. Extraretinal spatiotopic apparent motion suggests that salience map should contain visual neurons able to treat more than retinal inputs.

In these two experiments we address only spatial aspects of this mechanism, but the spatiotopic apparent motion gives us a large number of opportunities for future studies. For example we can start with the temporal properties of attentional remapping and assess their effects on apparent motion perception. Finally, additional studies of extraretinal remapping could clarify our assumption of an extraretinal representation in retinotopic maps.
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References


Annex 1

**Figure 1.** Maps of apparent misalignment in function of probes and saccade direction. For a description of this maps see Figure 6 and Figure 7. Columns correspond to rightward and leftward saccade and rows correspond to downward and upward probes directions. All maps reflect the result of the same participant. Upward and downward displacement of the probes led to roughly the same pattern of results.

**Table 1.** Effect of the direction of probes displacement. We compared the mean values the two directions of probe displacement for each participant and observed for the 72 comparisons tested (paired t-test with Bonferroni corrections) only 2 significant differences. We thus collapsed the data across this variable.