Adaptation to multiple radial optic flows.

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ABSTRACT

There is long-standing evidence suggesting that our visual system can adapt to new visual environments, like a single radial optic flow generated when driving (Brown, 1931; Denton, 1966). In fact, as we move through the environment multiple optic flows can be generated. For example, when driving, we are often exposed to more than one radial optic flow at the same time. In this thesis I investigate whether the visual system can simultaneously adapt to two radial motion optic flows. More specifically, I explored this issue in three ways. First, I investigated whether the visual system could – through a fast low-level process – adapt to two optic flows present at two specific locations in space. Second, I probed whether the visual system could – through a perceptual learning process – learn to associate two radial optic flows with their locations in space. Third, I examined whether the visual system could – through a perceptual learning process – learn to associate each of two radial optic flows with preceding eye-movements.

With regard to the first issue, the results from Experiments 1 – 6 suggested following exposure to two radial motion stimuli, a fast low-level process in the visual system could adapt to a radial flow pattern at one location in space: the radial flow pattern generated by the most recently presented radial motion stimulus. With respect to the second issue, the results from Experiments 7 – 10 indicated that the visual system could not learn to associate specific locations with two different radial motion stimuli. Finally, regarding the third issue, the results from Experiment 11 suggest that the visual system can associate specific eye-movements with two different radial motion stimuli.

Taken together, these results suggest constraints on the way in which the visual system can adapt to radial motion, and emphasize the importance of self-movement in generating adaption to new visual environments.

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Chapter 1

GENERAL INTRODUCTION

You are driving at 65mph on the inside lane of the motorway on an early summer morning. The road is almost empty. After several hours of driving you take the exit road. Your approach to the roundabout ahead feels very slow, but a glance at the speedometer reveals you are still doing 60mph with the roundabout approaching fast. Such misperceptions of speed are common (Brown, 1931; Denton, 1966; Recarte & Nunes, 1996; Schmidt & Tiffin, 1969), and indeed traffic engineers attempt to compensate for them with lines across the road that prompt a braking action (Denton, 1980). The false perception of speed is explained through the brain adapting to the continual radial optic flow (Denton, 1966). It has been suggested that such adaptation could help people better discriminate speeds encountered while driving (Wallach, 1987).

Later the same day you are back on the motorway driving at 65mph. The motorway is now full and traffic is moving fast on both sides of the road. Cars on the opposite side of the motorway are moving very fast toward you, whereas most cars on your side of the motorway are travelling faster than you and pulling away. What happens now? Can your brain adapt to this situation? There is a strongly expanding radial flow field generated by the cars on the opposite side of the motorway, and a weakly contracting one generated by the cars that are overtaking you on your side of the motorway. Can your brain adapt to two different flow fields simultaneously?

Until now, only the example developed in the first paragraph has received attention from researchers (Brown, 1931; Denton, 1966; Recarte & Nunes, 1996; Schmidt & Tiffin, 1969). And yet the example developed in the second paragraph – where motion differs in two locations – is more common, and addressing this problem could possibly have implications on road safety policy. An examination of the literature reveals three ways in which our visual system could adapt to the two different radial optic flows.

First, the motion processing system could adapt to different patterns of motion that are located in different places relative to you (or relative to the windscreen of the car or the edges of the motorway). This would be simultaneous body-centric or allocentric adaptation[1] (i.e. the world-based coordinate of the pattern would be adapted to). The literature suggests that it is possible to adapt to pattern of motion presented at two locations on the retina[2] (i.e. the location of the pattern on the retina would be adapted to; Cameron, Baker Jr., & Boulton, 1992; Wade & Salvano-pardieu, 1998), or a single spatiotopic/allocentric location (Melcher, 2005; Turi & Burr, 2012). Based on this fast and low-level process of the visual system, a dual motion adaptation should take place if the two different patterns of motion induce a motion adaptation at different spatiotopic/allocentric locations.

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Second, we could adapt to the two different radial optic flows by learning that each side of the motorway or body corresponds to a specific optic flow. In this situation, we would need to be able to associate each optic flow to a spatiotopic location (e.g. learn that an expanding optic flow is always present on the opposite side of the motorway). Once these associations occur, our visual system would have associated the strongly contracting optic flow with the opposite side of the motorway and the weakly contracting optic flow with the same side of the motorway. The literature indicates that one rotating visual percept can be associated with a spatiotopic location (Haijiang, Saunders, Stone, & Backus, 2006). Based on this perceptual learning process of the visual system, a dual motion adaptation should occur if the two different radial optic flows are associated to their respective spatiotopic/allocentric locations.

Third, we could adapt to the two different radial optic flows by learning that when we look to the left toward the opposite side of the motorway we see a strongly contracting optic flow, and that when we look to the right toward the same side of the motorway we see a weakly contracting optic flow. In short, this third type of adaptation requires the visual system to learn to anticipate a specific optic flow after a specific eye-movement. The literature reveals that a new motion stimulus can be associated with a head-movement (Wallach, Frey, & Romney, 1969), and that two

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[1] Spatiotopic adaptation

[2] Retinotopic adaptation

colour stimuli can be associated to two different eye-movements (Bompas & O'Regan, 2006b). Based on this perceptual learning process of the visual system, a dual motion adaptation should occur if the two different radial optic flows are associated to two different eye-movements.

In this thesis I will address the question of whether we can simultaneously adapt to two radial flow fields (i.e. radial stimuli) in the ways described in the three preceding paragraphs. More precisely, I will first investigate whether we can adapt two radial stimuli at two different spatiotopic locations using the consequence of the presentation of radial stimulus: a radial percept moving in the opposite direction to that of the radial stimuli (i.e. a radial motion after effect, or MAE). Then, I will test whether we can adapt to the two radial optic flows by learning that each one is associated to a specific spatiotopic location. Finally, I will probe whether we can adapt to the two radial optic flows by learning that each optic flow is always preceded by a specific self-movement.

1 DUAL ADAPTATION: SPATIOTOPIC MAEs

Can we simultaneously adapt to two different radial motion stimuli present at two locations in the environment? The first way to approach this question is to ask if the visual system can generate two MAEs at the spatiotopic locations of the two radial motion stimuli. Whether MAEs can be observed at the spatiotopic locations of the initial motion stimuli (or adapting motion stimulus) is highly contentious: some research groups argue that a MAE can only be observed at the retinotopic location of the adapting motion stimulus (Gardner, Merriam, Movshon, & Heeger, 2008; Golomb & Kanwisher, 2012b; Knapen, Rolfs, Wexler, & Cavanagh, 2010; Wenderoth & Wiese, 2008), and others argue that the MAE can be observed both at the retinotopic and at the spatiotopic location of the adapting motion stimulus (d'Avossa et al., 2007; Ong, Hooshvar, Zhang, & Bisley, 2009; Yoshimoto, Uchida-Ota, & Takeuchi, 2014; Zimmermann, Burr, & Morrone, 2011).

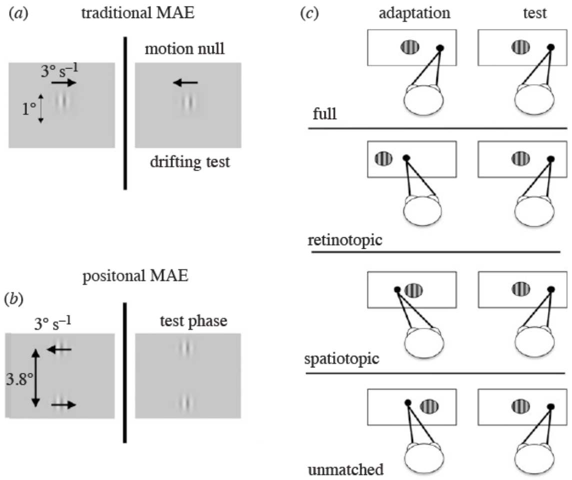

Figure 1.1: Illustration of the design of Turi and Burr (2012). (a) Adapting and test stimulus configuration for the traditional MAE. (b) Adapting and test stimulus configuration for the Positional MAE. (c) Adapting and test stimulus configuration in the four experimental conditions. In the full condition, the adapting and the test stimulus are at the same retinal and spatial location. In the retinotopic condition, the adapting and the test stimulus are the same retinal location but not the same spatial location. In the spatiotopic condition, the adapting and the test stimulus are the same spatial location but not at the same retinal location. In the unmatched condition, the adapting and the test are neither at the same spatial location nor at the same retinal location. Figure taken from page 3 of Turi and Burr (2012) with the courtesy of M. Turi.

This contradictory evidence is thought to reflect the fact that the reference frame of the MAE (e.g. spatiotopic, retinotopic) depends on the complexity of the adapting stimulus (Melcher, 2005; Turi & Burr, 2012). In Turi and Burr two types of motion stimuli were presented to observers, a simple one and a complex one. The simple one was a grating composed of black and white lines drifting from left-to-right within a Gaussian envelope (see Figure 1.1). When the lines stop drifting, observers had the impression that they drift in the opposite direction within the envelope (i.e. the MAE). The complex motion stimulus (see Figure 1.1) is composed of two of these gratings drifting in opposite direction (e.g. the top one drifting from left-to-right and the bottom one from right-to-left). The two gratings are vertically aligned but horizontally separated by 3.8º, and when they stop drifting, observers did not view two MAEs in opposite direction, instead they perceive the gratings at different locations in space (e.g. the top patch is perceived to be left of its previous position and the bottom one is perceived to be right of its previous position).

Both the simple and the complex adapting stimuli used by Turi and Burr (2012) induce an aftereffect that can be measured by a test stimulus. By presenting the test stimulus at different locations, it becomes possible to separate the adaptation that occurs in different reference frames (i.e. retinotopic and spatiotopic). In their experiment, the adapting motion stimulus and test stimulus were presented in four different configurations (see Figure 1.1): they could be at the same retinal and spatial location (i.e. full configuration); they could be at the same retinal location but not at the same spatial location (i.e. retinotopic configuration); they could be at the same spatial location but not at the same retinal location (i.e. spatiotopic configuration); or they could be at two different locations on both the spatiotopic and retinotopic reference frame (i.e. unmatched configuration).

The results showed that the aftereffect induced by the simple motion stimulus (i.e. a MAE) was only measured in the full and in the retinotopic configurations, whereas the one induced by the complex motion stimulus (i.e. the PMAE) was measured in the full, in the retinotopic, and in the spatiotopic configurations. Turi and Burr (2012) argue that because complex motion stimuli are processed at a higher level than simple motion stimuli (Burr, Badcock, & Ross, 2001; Morrone, Burr, & Vaina, 1995), they are encoded onto a more complex reference frame (i.e. a reference frame that determines the location of an object in space despite an observer's self-movement), the spatiotopic one (Melcher, 2005; Turi & Burr, 2012). Since Turi and Burr's findings suggests that an adapting stimulus will generate a spatiotopic MAE if it is a complex motion stimulus, then two adapting stimuli presented at two different location in space and containing complex motion should induce two spatiotopic MAEs. Since the flow fields encountered on a motorway (i.e. radial motion stimuli) are a case of complex motion (Burr, Badcock, & Ross, 2001; Morrone, Burr, & Vaina, 1995), can they induce two spatiotopic MAEs? This first question will be investigated in Chapters 3 and 4.

2 DUAL ADAPTATION: THE ASSOCIATION BETWEEN RADIAL OPTIC FLOWS AND SPATIOTOPIC LOCATIONS

In the motorway example given at the beginning of the introduction, two flow fields are present on each side of the road, and I posed the question: Can we adapt to both of them? The second way to approach this question is to ask whether we can learn that each side of the motorway corresponds to a different flow field. More precisely, can the visual system learn to associate each radial flow field with its spatiotopic location?

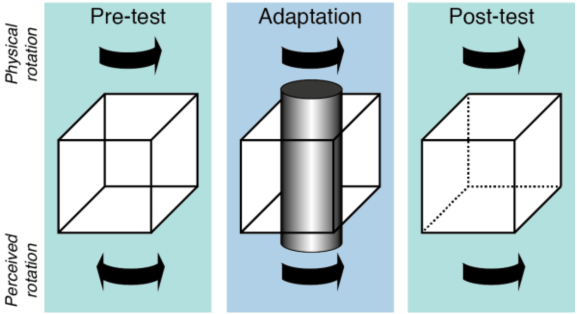

Figure 1.2: Illustration of the perceived stimulus during the different phases of Haijang et al's experiment. The two green areas correspond to the test phases of the experiment where observers have to indicate the cube's rotation. ***In the pre-test****, the cube's rotation depends on which face of the cube is perceived to be in front and therefore alternates between left and right.* ***In the adaptation phase****, the cylinder occludes one face of the cube and forces one face to be seen in front and the cube to rotate in one direction.* ***In the post-test phase****, when the stimulus is presented at the same location in the adaptation phase, the face of the cube that was seen in front during the adaptation phase is seen to be in front, despite the occlusion cue not being presented. Consequently, the cube's rotation is the same as the one seen during the adaptation phase.*

Evidence suggesting that motion stimulus could become associated with specific location was provided by Haijiang and colleagues (2006). To demonstrate this, a rotating Necker Cube, a three-dimensional (3D) wire-frame cube (*Figure 1.2*), was used the perceived direction of rotation direction was ambiguous. Because there are no visual cues separating the cube's front from its back, an observer can see two different cubes: a cube where the front face is the lower-left one, and a cube where the front face is the upper-right one (see left panel of *Figure 1.2*). These two interpretations alternate at a fixed rate. Because the cube is rotating, this alternation renders the cube's direction of rotation ambiguous. If the lower-left face of the cube is perceived to be in front, then the cube is perceived to be rotating in a counter-clockwise direction, and if the upper-right face of the cube is perceived to be in front, then the cube is perceived to be rotating in a clockwise direction.

To investigate the influence of experience on the percept of the rotating cube, Haijiang et al. (2006) added a disambiguating cue – an opaque cylinder – to the Necker Cube's centre that obscured one face of the cube, but not the other (*Figure 1.2*). As can be seen from the central panel of figure 0.3, the addition of the cylinder removes the ambiguity. The lower-left face is now seen at the front and consequently observers only see the cube rotating in one direction. The disambiguating cue was only presented when the stimulus was in the upper part of the screen, so observers only had an unambiguous percept when it was presented at that location. Under these experimental conditions, the location of the cube should become associated with a single, unambiguous, percept of the Necker cube. Consequently the presentation of the cube in the upper part of the screen should trigger that associated percept (i.e. the cube's direction of rotation imposed by the disambiguating cue).

To test whether the disambiguated percept of the Necker cube had become associated with the cube's location, the Necker cube was presented every eleventh trial without the occluder cue in the upper part of the screen (*Figure 1.2*), and observers indicated whether the cube rotated in a clockwise or counter clockwise direction. If the disambiguated percept is associated with the location at which it is constantly presented (i.e. the upper part of the screen) then the presentation of a bistable stimulus at this same location should trigger the associated percept (i.e. the cube's direction of rotation perceived when the Necker cube is presented with the occluder cue), the one seen with the disambiguated stimulus. Observers reported that they consistently saw the cube rotating in the direction of the disambiguated percept when it was presented in the upper part of the screen. In conclusion, these results suggest that the perception of an ambiguous object can be biased depending on its location (i.e. the upper part of the screen) through a process of training.

In Haijiang and colleague's experiment, eye-movements were not monitored, as "the logic of the experiment does not require that fixation was accurate". Given the fact that the stimulus did not have a precise location on the retinotopic reference frame, an association with the retinotopic location of the stimulus was unlikely to have formed due to the unreliability of the retinotopic location of the stimulus. However, the actual location in space of the stimulus was constant, so it seems reasonable to conclude that the association may have involved the spatiotopic location.

Based on Haijiang and colleagues (2006), it is possible to associate the direction of rotation of a stimulus (i.e. a complex motion stimulus (Burr, Badcock, & Ross, 2001; Morrone, Burr, & Vaina, 1995)) with a spatiotopic location. So, is it possible for the visual system to form not one but two associations based on the spatiotopic location of complex motion stimuli? This second question will be investigated in Chapters 5 and 6.

3 DUAL ADAPTATION: ASSOCIATING SELF-MOVEMENTS WITH RADIAL OPTIC FLOWS

Returning again to the motorway example, a third way to approach the question of whether we can adapt to two flow fields is by associating each flow field with a specific eye-movement. Will this process of association result in eye-movement specific adaptation?

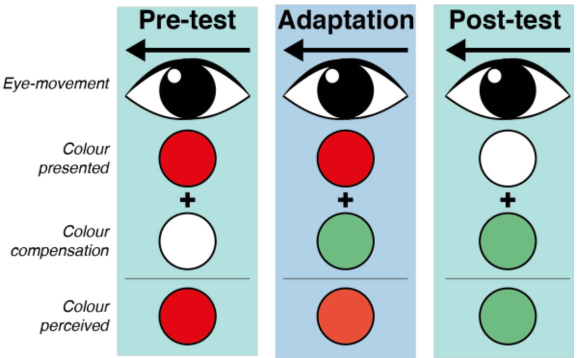

Figure 1.3: Illustration of the Bompas et O'Regan paradigm and its consequences on adapted and perceived colour. The two green areas indicate the test phase of the experiment whereas the blue area indicates the adaptation phase of the experiment. ***In the pre-test****, the colour presented following an eye-movement is the same as the colour perceived. For instance, if a red patch is presented after an eye-movement, the patch is perceived to be red, as illustrated in the left panel.* ***In the adaptation phase****, the contingency that arises between the colours presented after the eye-movement and the eye-movement is adapted for by the visual system. In the middle panel, the constant presentation of a red patch after a leftward eye-movement induces an adaptation for the colour red – green – which should diminish the intensity of the red colour perceived.* ***In the post-test****, the eye-movement triggers the adaptation mechanism and as no physical colour is presented, only the colour adapted for is perceived. In the right panel, following a leftward eye-movement, the visual system expects to see red and triggers the adaptation mechanism for red and as no physical stimulus is presented, only the colour adapted for is perceived – green.*

It has been reported that a change in perception can be brought about through associating a motor action with the presentation of a colour stimulus. Recently, Bompas & O'Regan (2006) combined eye-movements with colour patches: with a left eye-movement, for example, being associated with a red patch and a right eye-movement with a green patch (*Figure 1.3*). After maintaining this contingency for forty minutes (the adaptation phase), the same procedure was repeated but with two yellow patches in place of the red and green patches (the post-test phase), and participants saw the yellow patch presented after the left eye-movement as a shade of green and the patch presented after the right eye-movement as a shade of red (*Figure 1.3*). In this case, the effect of training was to imbue actions with the tendency to evoke the opponent colour percept rather than that directly given by the colour stimulus (cf. Haijiang et al., 2006). Thus the yellow patch of the post-test phase presented at the location of the red patch of the adaptation phase was seen in a shade of green, whereas the yellow patch of the post-test phase presented at the location of the green patch of the adaptation phase was seen in a shade of red.

The observations reported by Bompas & O'Regan (2006) suggest an interaction between learning and a colour adaptation mechanism in which the brain has adapted to a specific colour following a specific eye-movement command. More precisely, the eye-movement paired with red is adapted to red and will generate a green percept, and the eye-movement paired with green is adapted to green will generate a red percept. These learnt effects are fully evident during the test with yellow patches as the presence of the colour opponents after the left and right eye-movements.

In the previous example, the associations were between an eye-movement and a colour stimulus, but could they also occur between an eye-movement and a motion stimulus? There is evidence suggesting that a radial motion stimulus can be associated to a preceding self-movement (Durgin, Gigone, & Scott, 2005; Pelah & Barlow, 1996), and that the motion stimulus associated to a preceding self-movement can be changed for a new motion stimulus (Wallach & Kravitz, 1965; Wallach, Frey, & Romney, 1969). Consequently, it should be possible to form an association between a new motion stimulus and a preceding self-movement.

To sum-up, there is evidence that we can associate different colours with different eye-movements (Bompas & O'Regan, 2006b) and that we can associate a new motion stimulus to a self-movement (Wallach & Kravitz, 1965). So, is it possible for the visual system to form associations between preceding self-movements and two radial motion stimuli? This third question will be investigated in Chapter 7.

4 OVERVIEW OF THE THESIS

The overarching objective of this thesis is to investigate whether we can simultaneously adapt to two radial motion stimuli. In the previous section, I described three mechanisms that could support such dual motion adaptation. In this thesis, I will first investigate whether we can perceive to two MAEs occurring simultaneously at two spatiotopic locations through a fast adaptive low-level process, then I will probe whether we can perceptually learn to adapt to radial motion stimuli at two spatiotopic locations in the environment, and finally I will test whether we can perceptually learn to adapt to radial motion stimuli that each precede a self-movement.

To probe the existence of a dual spatiotopic MAE resulting from a dual motion adaptation, I conducted a series of preliminary experiments (Experiment 1 to 5 reported in Chapter 3) based on the method of Turi and Burr. The main objective of these experiments was to assess whether two MAEs can be observed at two spatiotopic locations. To ensure the feasibility of the dual spatiotopic MAE experiment, there were three intervening steps. I probed whether or not the adopted paradigm could measure (i) a single MAE following the presentation of a complex motion stimulus; (ii) two MAEs by presenting the two motion stimuli at two locations on their main frame of reference – the retinotopic frame; (iii), a single-stimulus spatiotopic MAE. Once these steps were completed, I assessed whether or not two radial motion stimuli could induce two spatiotopic MAEs.

In Experiment 5, two radial motion stimuli did not induce two spatiotopic MAEs. However, this experiment only required a limited number of eye-movements, and a recent hypothesis pointed out the importance of eye-movements in the construction of the spatiotopic representation (Zimmermann, Morrone, Fink, & Burr, 2013). As a result, a further study was conducted with more frequent eye-movements as to ensure that MAEs are encoded on a fully developed spatiotopic representation (Experiment 6 in Chapter 4). However, in this case too there was no evidence of the development of two MAEs encoded at their spatiotopic locations. Therefore, since two spatiotopic MAEs could not be observed in either Experiment 5 or Experiment 6, I rejected the idea a dual adaptation based on two flow fields located at two different locations in space could be generated by spatiotopic MAE.

Next, the capacity of the visual system to associate two events with two complex motion stimuli was assessed. At the beginning of the introduction, I described two other ways beside a fast adaptive low-level process in which the visual system could adapt for a complex motion stimulus: to associate the location of a stimulus with one of its visual motion properties, or to associate a proceeding self-movement with its consequence on the upcoming motion stimulus. The first study assessed whether the location of a stimulus could be associated with one of its visual motion properties (Haijiang et al., 2006), and the nature of location (retinotopic or spatiotopic) was considered. I then conducted two experiments (see Experiment 7 and 8 reported in Chapter 5) to determine directly whether complex motion stimuli could be associated with their respective spatiotopic locations. If they can be associated with their spatiotopic locations, then the visual system should have adapted to the complex motion stimuli at their spatiotopic locations (Haijiang et al., 2006).

The results of the Experiment 7 and 8 reported in Chapter 5 indicated that a motion stimulus could not be associated to its spatiotopic location. However, in the studies reported by both Haijiang and colleagues (2006) and by Bompas and O’Regan (2006) there was an attentional task during the adaptation phase. Attention is thought to drive the association process between two events (Mackintosh, 1975; Pearce & Hall, 1980), and it is possible that the motion stimulus could not be associated to its spatiotopic location because of the absence of attention task in the first two experiments of Chapter 5. To further investigate this matter, Chapter 5 describes two additional experiments (Experiment 9 and 10) that assessed whether an attentional task during the adaptation stage induced an association between a radial motion stimulus and its spatiotopic location. Even with the additional attentional task during the adaptation stage, the visual system did not appear to associate a radial motion stimulus to its spatiotopic location. The second failure to find dual adaptation based on the association between a complex motion stimulus and its location (Haijiang et al., 2006) led me to adapt the paradigm described by Bompas & O’Regan (2006) that used self-movement.

In the motorway example given at the beginning of the introduction, I described a third way in which the visual system could adapt for a complex motion stimulus: to associate a proceeding self-movement with its consequence on the incoming motion stimulus. In Chapter 6, I examined whether an eye-movement could be associated with a radial motion stimulus (Experiment 11). More precisely, the experiment aimed to associate two eye-movements with two radial motion stimuli. If an increase in motion adaptation is measured for both motion stimuli after the adaptation phase, then the visual adaptation mechanism is capable of associating each radial optic flow with a specific eye-movement. The question of interest was whether or not eye-movements could be linked to complex motion stimuli and if so, then what form will this learning take. I noted in the introduction that in Bompas and O’Regan, after adaptation the eye-movements generated an opponent response to the yellow test patches. Will this be the case in my final study?

A schematic of the development of the thesis is summarized in the form of a roadmap below.

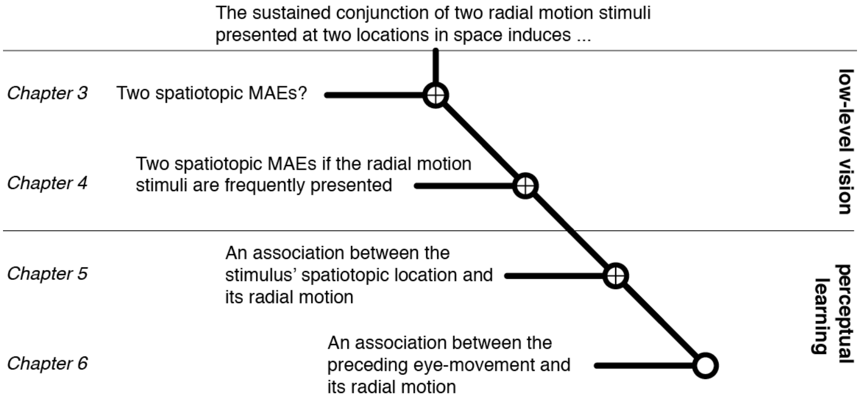

Figure 1.4: Schematic representation of the question addressed in the chapters of the thesis. The first two chapters address the low-level vision issue of the development of two spatiotopic MAEs, whereas the next two chapters test whether perceptual learning phenomena can occur with motion stimuli.

Chapter 2
GENERAL METHOD SECTION

1.1 Stimuli

1.1.1 *The stimulus*

The visual stimuli were presented in a dark room, on 22-inch, Viewsonic, P225f, CRT monitor at a refresh rate of 100Hz with medium-short persistence B22 phosphors. The visual stimuli were generated by a program written using Lazarus, a public domain Pascal compiler, and rendered using OpenGL. Antialising was set to high. Stimuli were rendered in red to minimise phosphor persistence and viewed through a red filter to maximise contrast.

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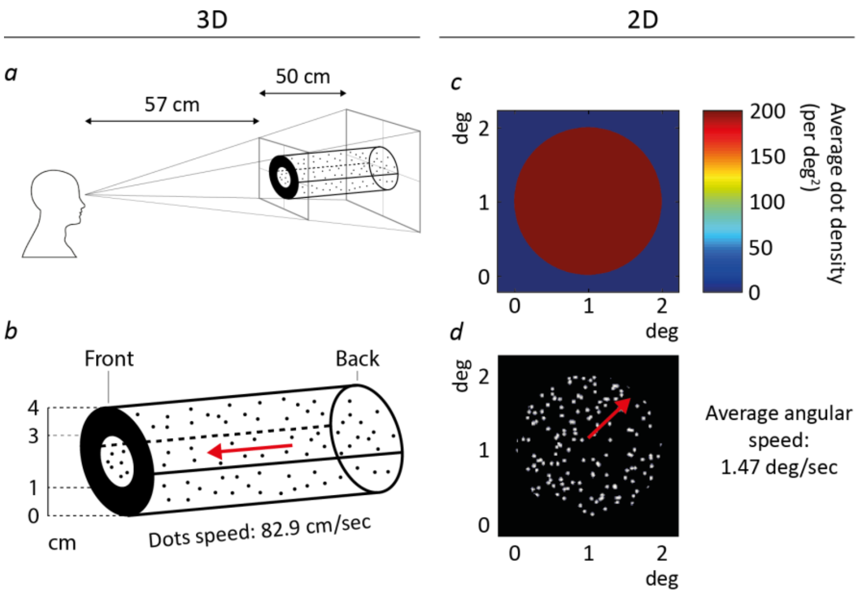

*Figure 2.1: Illustration of the radial motion stimulus **a**: Representation of the three dimensional space in which the stimulus was created. The scene was rendered with a perspective. **b**: 3D Representation of the stimulus: a 50 by 4 by 4 cm cylinder on top of which is apposed a 2cm black radius annulus with a 1cm radius aperture. Within the cylinder, 400 randomly distributed dots are moving forward at a speed of 82.9 cm/sec. **c**: 2D map of the average dot density: the average number of dot seen through annulus' aperture is constant. **d**: 2D screen capture of the stimulus: an expanding flow field where the average speed of the dot is 1.47 deg/sec.*

400 dots of 0.1 by 0.1 cm were located in a cylindrical volume of 50cm deep and a 4cm diameter, at a distance of 57 cm in front of the observer. On the topside of the cylinder, the side closer to the observer, was apposed a 2cm radius black annulus with a 1cm radius aperture from which the dots could be seen. The dots were assigned random locations within the cylindrical volume. They were rendered in perspective view on a monitor of 43 (W) by 32 (H) cm, 1200 pixels (W) by 1024 (H), at a distance of 57 cm ahead of the observer, see Figure 2.1 *a*. Under these two dimensional viewing conditions, an average of 215 dots equally spread within the 1cm radius aperture were seen moving at an average speed of 1.47 degree of visual angle per sec (ranging from 0.07 deg/sec at the inner edge to 2.83deg/sec at the outer edge for the case of an expanding stimulus, values are reversed for a contracting stimulus), see Figure 2.1 *c & d*.

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Commented [DBSDE&S4]: Comment 2.2: about the decceleration/acceleration of the dots in the stimulus.

1.1.2 *The adapting stimulus*

Complex motion stimuli are processed by different cortical areas than their simple motion counterparts (Morrone et al., 1995). It has been suggested that because of this difference, more complex stimuli are more likely to be encoded onto a spatiotopic representation (Melcher, 2005) and this hypothesis has been consistently verified with complex stimuli such as radial flow and recently the PMAE (Melcher, 2005; Meng, Mazzoni, & Qian, 2006; Turi & Burr, 2012).

The aim of Chapter 3 was to replicate Turi & Burr combined with the more global aim of the document to recalibrate the motion adaptation mechanism involved locomotion led us to chose the radial flow. It presents the advantage to be the most used, and the less controversial, stimulus to demonstrate spatiotopic coding and, as it is important to see if results generalise, the radial flow allows for a conceptual replication rather than a straight replication of Turi & Burr.

Within the simulated motion-in-depth, see Figure 2.1 *b*, the dots were moving inside the cylinder, from its bottom to its top or vice-versa, at a speed of 82.9 cm/sec. When dots reached one end of the cylinder, they were replaced at a random location on the other end of the cylinder but kept moving in the same direction. Rendered on the screen in a perspective view, see Figure 2.1 *d*, the dots were moving at an average speed of 1.47°/sec and forming a clear expanding or contracting pattern.

1.1.3 *The test stimulus*

We opted for a testing method to probe the motion aftereffect that had been previously used to demonstrate a spatiotopic encoding of spatiotopic MAE (Turi & Burr, 2012). With this method, the velocity of all dots was varied from trial to trial, and subjects had to indicate the direction in which they saw the test stimulus moving. Additionally, the test stimulus is a dynamic noise test pattern composed of the dots, which had a randomly distributed lifespan ranging from 10 ms (1 frame) to 300 ms (30 frames). Once a dot's lifespan elapsed, it was assigned a new random location within the simulated motion-in-depth cylinder, see Figure 2.1 *b*, and a new random distributed lifespan. This was implemented to mimic a dynamic test stimulus (DMAE), which is thought to measure the changes occurring at the integration-stage in MT (Kohn & Movshon, 2003), as opposed to a static test stimulus (SAME) that probes the changes occurring at the initial-stage in V1 (Morgan, Chubb, & Solomon, 2006).

Commented [DBSDE&S5]: Comment 2.3 about a better definition of the test stimulus

1.1.4 *The nulling method*

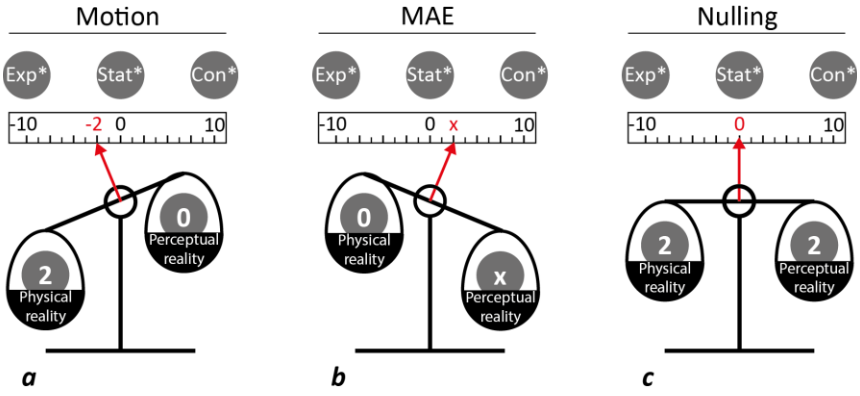

Figure 2.2: Illustration of the nulling method. ***a)*** *Upon presentation of an expanding stimulus of intensity 2, an expanding stimulus of intensity 2 is perceived.* ***b)*** *Following the presentation of the expanding stimulus intensity 2, a motion aftereffect is perceived in the opposite direction with an intensity x.* ***c)*** *To measure that intensity x, we aimed at presenting the physical motion that gives rise to a static percept. By finding this intensity, we have implicitly found the intensity of the MAE. Exp*: Expansion, Stat*: Static, Con*: contraction.*

To measure the intensity of the motion adaptation induced by the adapting stimulus, see Figure 2.2 *a* & *b*, we used a nulling method. With this method, instead of measuring directly the intensity of the illusory motion by asking the observers to match the perceived motion to physical motion, we reverse the process: the intensity of the perceived motion is indirectly measured by finding the physical motion that, when presented during the MAE, give to the observer the impression that the dots are not moving. When that point is found – the nulling point – the MAE intensity is indirectly gauged, see Figure 2.2 *c*. The combination of a nulling method with a dynamic testing method, see section Chapter 21.1.3, has been demonstrated to measure effectively the MAE induced by radial adapting stimulus (Blake & Hiris, 1993).

1.1.5 *The two alternative forced choice (2AFC) method*

Two general methods have been devised to relate a psychological intensity, e.g. the strength of the motion aftereffect, to a physical intensity, e.g. the dots' speed on the screen. In the first, the "Yes-no" method, observers are indicating whether they saw a signal, i.e. dot were moving, by pressing the "Yes" button or not, by pressing the "No" button (Macmillan & Creelman, 1991). In the second, the "two-alternative force-choice (2AFC) method, observer are indicating whether a signal was in one interval, e.g. dots were expanding, by pressing the "Interval 1" button or in the other interval, e.g. dots were contracting, by pressing the "Interval 2" button (Macmillan & Creelman, 1991).

The problem with the first method is that the question that the observer is asked is ambiguous. For instance, following the presentation of an expanding stimulus, the question "Are the dots contracting?" creates a dividing line between where observers thought the dots were contracting and where they thought they weren't. Experimental evidence suggests that under these circumstances, observers reduce the percept to a magnitude, e.g. a number, that they compare to an internal criterion (Nachmias, 1981). The result is therefore highly subjective and leads to different estimates from one observer to the other. This problem is circumvented by the 2AFC method as the two choices of stimulus are displayed, either successively or spatially, on the screen, which, in a detection task, forces the observer to press the key corresponding to the higher magnitude stimulus, without have to refer to an internal criterion (Macmillan & Creelman, 1991).

The method employed by Turi & Burr can be considered as a 2AFC method though only one stimulus is presented per trial (Pelli & Farell, 1991). In this hybrid case, the problem is really to know whether the task is unbiased, i.e. are the alternative stimuli symmetric for the observer? Because the question asked changes the paradigm from a detection task (i.e. whether the grating is moving) to a discrimination task (i.e. whether the grating is moving to the left or the right), the task is rendered less ambiguous. Thus the referral to an internal criterion seems less likely and as a consequence, the measured performance will be more reliable across observer.

The 2AFC method used in these experiment is not exempt of drawbacks and it is possible for the results to have included a response bias. Since subjects were aware of the motion direction of the adapting stimulus, they could have responded based on the direction of motion of the adapting stimulus. Yet, since the direction of motion of the adapting stimulus was randomised across subjects and throughout a single experiment, this bias is unlikely to affect the overall results of an experiment in the same direction. Therefore, I argue that this directional response bias is unlikely to play a major role on the obtained results.

Commented [DBSDE&S6]: Comment 3 about the caveat of the 2AFC method

Because the replication of Turi & Burr is at the heart of Chapter 3 and because their 2AFC method seems relatively unbiased, we adapted the method to our paradigm and used it throughout this document.

1.1.6 *The staircase method*

To locate the nulling point, the point where the speed of the physical motion nulls the strength of the after effect, see section 1.1.4, different speed have to be tested. For this task, within our experimental framework, three general methods exist: the method of adjustment, where observers manipulate themselves the intensity of the physical stimulus until they judge that it nulls the motion aftereffect; the method of constant stimuli, where multiple intensities are presented for the same number of trials in a random order and where, for each trial, a hybrid 2AFC is given to the observers, see section 1.1.5; and the sequential method estimation, the staircase method, where the response given by a observer, through a hybrid 2AFC method, see section 1.1.5, about a physical intensity directs the physical intensity of the stimulus in the next trial (Pelli & Farell, 1991).

One of the experimental aims of the first chapter was to probe whether, as suggested in the literature (Zimmermann et al., 2013), the encoding onto the different representations follow a different timeframe. Consequently, the experiments were designed to probe the motion aftereffect strength every ten seconds for fifty seconds. This experimental setting divided into two phases: first, building up and probing the motion adaptation; and second, destroying the motion adaptation accumulated during the first phase. Under these conditions, the time needed for the observer to find the nulling point, in the method of adjustment, could be detrimental to the build-up of motion adaptation: a motion stimulus presented for a sustained duration would change, if not overwrite, the motion adaptation from the adapting stimulus accumulated until that point. Additionally, because that method fully relies on the observer's individual criterion for when the signal is present and when it is not, it has the same response bias as the "Yes-no" method, see section 1.1.5.

The staircase method presents two advantages compared to the remaining candidate, the method of constant stimuli. First, experiments take less time with this method, where only stimulus intensities near the perceptual threshold are repeated than with the method of constant stimuli, where stimulus intensities is equally repeated. Consequently, with the staircase method, the risk that fatigue will contaminate the data is diminished. Second, Turi & Burr's experiment used a staircase method and given our objective to replicate their observation, the closer we are to their original paradigm, the more likely we are to replicate their findings.

The staircase method used in this thesis is based on an accelerated stochastic approximation method (Kesten, 1958), which has similar performances than the QUEST algorithm used Turi & Burr's, whilst having the advantage to be a non-parametric test and, as such, less sensitive to a mismatch between the assumed parametric model and the observer's "true" parameters (Treutwein, 1995).

The staircase had three starting parameters: a starting value, identical to the adapting stimulus intensity; a starting step value, set at sixty per-cent of the adapting stimulus intensity; and an ending step value, set at two per-cent of the adapting stimulus intensity. These three values were empirically chosen for their effectiveness in allowing the staircase to converge. Moreover, a maximum of thirty iterations was allowed per staircase. This threshold was implemented to ensure a reasonable duration for the experiment. During the actual experiment, the thirty-iteration threshold was never reached and, on average, a staircase converged after twenty-three iterations.

1.1.7 *The "thousand staircase" method*

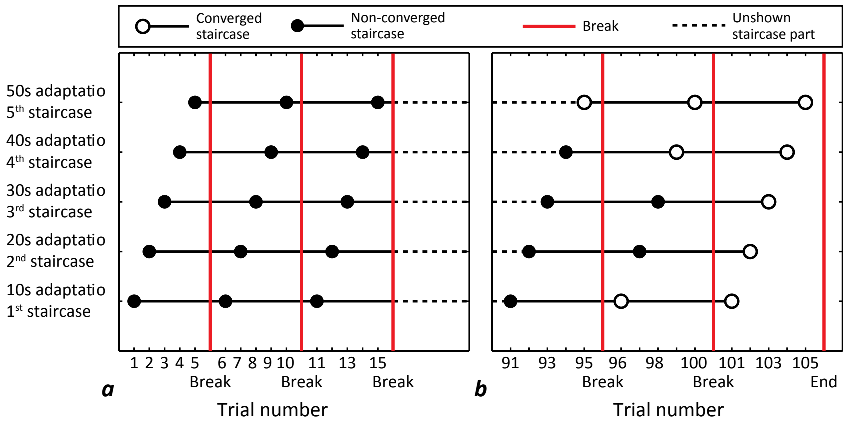

Figure 2.3: Illustration of the "Thousand staircase" method. ***a:*** *Illustration of the 50s cumulative adaptation method over the course of the first 3 blocks. The 5 trials of 10s of motion adaptation and break procedure allow us to probe the MAE at 5 time stages: 10s, 20s, 30s, 40s and 50s. Each new trial builds up the motion adaption by 10s and after 5 trials; the break sets the motion adaptation back to zero. As a consequence, the 1st trial after the break measures always the same level of motion adaptation, as does the 2nd trial after the break, the 3rd trial, the 4th trial and the 5th trial. To each period of cumulative adaptation is associated a staircase procedure. The response given on a trial, at a level of motion adaptation, will predict the test stimulus intensity at the same level of motion adaptation next trial (e.g. the response given on the 1st trial predict the intensity displayed on the 6th trial).* ***b:*** *Illustration of the 50s cumulative adaptation method over the course of the last 3 blocks. If a staircase had converged, but the others had not, the PSE obtain for that level of motion adaptation will be presented at that level until all the 5 staircases converged (e.g. at the 10s of motion adaption level, the staircase had converged at the 96th trial, therefore, the PSE it had converged to was displayed again on the 101th trial).*

As mentioned earlier, see section 1.1.6, one of the objectives of the first chapter was to measure the impact of time spatiotopic encoding. This requirement lead to a two-tier experiment, where, during a first phase, motion adaptation was accumulated then, during a second phase, erased. Therefore, during the first phase, a motion adaptation probed at a time "t" will be inferior to one probed at a time "t+1". Yet, one of the requirements of the staircase method is that the perceptual threshold to be qualified has to remain constant as the response in one trial predicts the signal's intensity in the next.

To circumvent the problem of the staircase method's requirement for sequential dependency, we employed a "thousand staircase" procedure, where each staircase is assigned to a single level of motion adaptation (Cornsweet & Teller, 1965). After experimental trials on the researchers, it was decided that five moments of motion adaptation were going to be tested: after ten, twenty, thirty, forty and fifty seconds of motion adaptation. With this method, proved to accurately measure the evolution of motion adaptation with time (P. Bex & Bedingham, 1999), each staircase probes a different but constant time-point of motion adaptation: the first staircase probed the MAE after ten seconds of motion adaptation, the second staircase probed the MAE after twenty seconds of motion adaptation and so on, see the y-axis of Figure 2.3.

The fifth staircase marked the end of the first phase of the experiment and the beginning of the second phase, where the motion adaptation accumulated had to be erased. In order to fulfil this objective, the laboratory lights, maximally dimmed during the first phase, as in Turi & Burr's experiment, were fully turned on. Researcher observed during preliminary trials that a period of eighty seconds was necessary for any accumulated MAE over fifty seconds to be eradicated.

This two-tier method allowed for a sequential dependency to be established: the MAE induced by a ten seconds motion adaptation at the beginning of the experiment should be equal to the one induced by a ten seconds motion adaptation after the end of the first break, which should be itself equal to the one induced by a ten seconds motion adaptation after the end of the second break, etc. Thus, a single staircase could be implemented at those three time-points without violating the sequential dependency requirement.

In the experiments of Chapter 3 five staircases were fitted to the paradigm, each probing a different level of motion adaptation. As to ensure that they always probed the same period of motion adaptation, the five staircases were presented in the same order after each break. For the first staircase, which probes the MAE after ten seconds of motion adaptation, the response to the motion intensity presented at the first trial predicts the intensity presented at the sixth trial, which itself predicts the intensity presented at the eleventh trial, etc. This example is described for each of the five staircases by the Figure 2.3 *a*, where each line corresponds to a staircase.

Since different staircases probed the different levels of motion adaptation, and since a staircase were set to converge when they reach a certain threshold not after a certain number of iteration (see section 1.1.6), the number of iteration in each staircase could differ across the five staircases.

To maintain a constant level of precision for each threshold acquired via a staircase, when a staircase had converged before the others, the intensity displayed for that staircase at its next iteration was the intensity the staircase had converged to. This is illustrated by the Figure 2.3 *b*, where, because the first staircase converged at the ninety-first trial, the intensity presented at trials ninety-sixth and a hundred-and-one is the converged value from the ninety-first trial.

Due to the upper-boundary on the number of possible iterations per staircase, the experiment could hypothetically take up to one hour and forty-five minutes. Yet, on average, its duration was of one hour and fifteen minutes.

1.1.8 *The "top-up" procedure*

The top-up procedure used in Chapter 4 is similar to the thousand-staircase procedure in the sense that a staircase is assigned to a single level of motion adaptation. The difference between the two methods is that the "top-up" method only probes one level of motion adaptation when the "thousand staircase method" probes for multiple ones. The advantage of this method compared to the when the "thousand staircase method" resides in its duration, and because only one level of motion adaptation is probed, the overall length of the experiment is significantly reduced.

Practically, the top-up method is composed of two parts. First, an initial adaptation period where motion adaptation is accumulated until a desired threshold. During an experiment, that part corresponds to trials where only the adapting motion stimulus is presented. Second, the "top-up" procedure itself, where only the motion adaptation accumulated at the desired threshold is probed. During an experiment, that part corresponds to trials where both the adapting motion stimulus and the test stimulus are presented.

1.2 Procedure

1.2.1 *Observers*

Through this thesis, informed consent was obtained from all observers and the experiment was approved by the local ethics committee and performed in accordance with the Declaration of Helsinki.

The number of subject per experiment depended on the relative importance of their conclusion. For experiments 1 to 4, 7 and 9 we used six subjects as in Turi and Burr 2012. For Experiments 6, 8, 10 and 11, aimed at bringing a final answer to the problem raised by each chapter, we used 10 subjects to increase the power of the statistical test. Finally, in Experiment 5, we used 24 subjects as based on the previous experiments, we were expecting one of effect to be relatively small: a larger sample would have allowed us to detect such a small effect.

Commented [DBSDE&S7]: Comment 7 about the difference in subject's number throughout the experiments.

1.2.2 *Laboratory settings*

Observers viewed the stimuli binocularly, from a distance of 57 cm from the screen, with their chins resting on a chin-rest to reduce head movements. The intensity of illumination in the laboratory was modified depending on the experiment phase observes were in. During the first phase of the experiment, the motion-adaptation-accumulation phase, see section 1.1.7, the lights were turned to their dimmest intensity. During the second phase of the experiment, the motion-adaptation-break-down phase, see section 1.1.7, the lights were turned to their brightest intensity.

Commented [DBSDE&S8]: Comment 2.4 about luminane (luminance value removed because I'm not able to do any measurement of the lab as I don't live in Cardiff anymore).

1.2.3 *Instructions*

The observers were instructed to maintain fixation on the fixation point throughout the experiment and when the fixation point turned into a fixation cross to press the right arrow if the stimulus was perceived as expanding or the left arrow if it was perceived as contracting.

1.2.4 *The ten seconds blank period in single motion adaptation experiments*

In single motion adaptation experiments (see Experiment 1 and 3), the test stimulus was presented after a 10sec delay. This delay was implemented to match the MAE testing conditions of dual adaptation experiments. In these experiments, the first adapting stimulus was followed by the second adapting stimulus, so the MAE induced by the first adapting stimulus could only be probed once the second adapting stimulus had been displayed. Given that each adapting stimulus was presented for 10sec, a MAE induced by the first adapting stimulus could only be probed after 10sec. Therefore, to make sure that we could measure a MAE 10sec after the adapting stimulus had been displayed, we added a 10sec blank period in single adaptation experiment to mimic the conditions encountered in dual adaptation experiments.

1.2.5 *The break period*

At the end of block of five trials, observers were given a break; the observers were instructed to get up from seat and turn the laboratory lights on. The purpose of the break period was twofold, to provide a rest, and to extinguish any motion adaptation accumulated during the preceding five trials, see section 1.1.7. An eighty-second break was chosen so as to be longer than the time required to extinguish any motion adaptation but not too long as to induce boredom. Ten seconds before the end of the break, the observers were instructed to dim the laboratory lights to their minimum and to press a key, which triggered the start of a new block of five trials.

1.3 **Data analysis**

To facilitate comparison across experiments, the motion intensity of the test stimulus was always analysed as a function of the motion intensity of the adapting stimulus: a dots' speed of the test stimulus that equalled the adapting stimulus dots' speed was labelled "100%". A test stimulus with static dots has a value of "0%" and a value below 0% signifies that the test and the adapting stimulus have opposite directions of radial motion, see Figure 2.4.

1.3.1 *The composite observer*

For the purpose of illustration, a composite observer method for the data analysis was used. To this end and for every experimental condition, individual data sets were combined, see Figure 2.4 *b*. The advantage of this method lies in its capacity to minimize the influence of individual differences and therefore to allow for typical patterns to be seen more clearly.

1.3.2 *The fitting analysis*

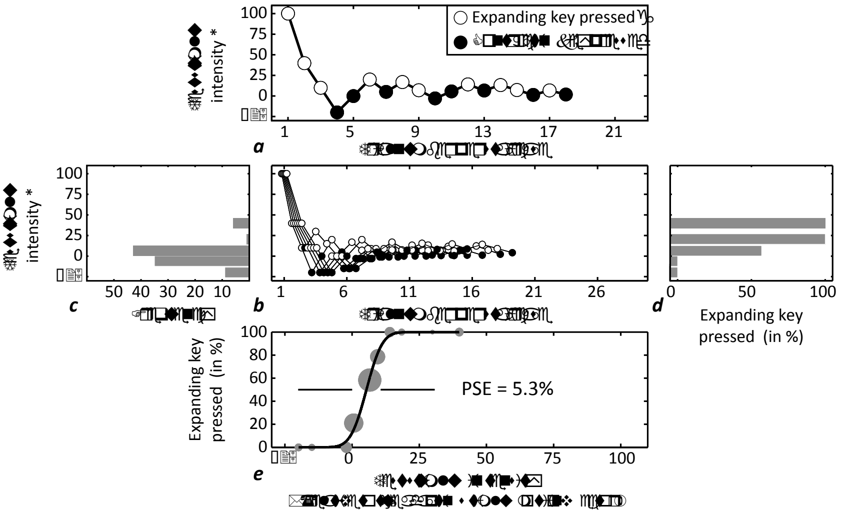

Figure 2.4:Analysis conducted to estimate the strength of a MAE ***a:*** *Test stimulus motion intensity oscillation within a single staircase for one observer. The staircase converged after 18 iterations.* ***b:*** *Test stimulus motion intensity oscillation within a single staircase for the 6 observers representing the composite data set. Individual staircase trajectories are slightly separated to ease the figure's comprehension.* ***c:*** *Histogram of the test stimulus intensity displayed in the composite data set.* ***d: "****Expanding" key pressed as a function of the intensity displayed based histogram bins from Figure 2.4 c.* ***e:*** *Figure 2.4 d re-plotted with an axis inversion (i.e. the abscissa is now the ordinate and vice versa) and fitted with a cumulative Gaussian algorithm based on maximum likelihood estimates. The grey circle of different size corresponding to the data bins from Figure 2.4 d are plotted to ease the figure's reading.*

The data for each staircase of each observer was analysed through a fitting analysis, see the panel *a* of Figure 2.4. To this end, two pieces of information were extracted from each staircase: the intensity presented and the response given for each intensity, respectively panel *c* & *d* of Figure 2.4. A cumulative Gaussian curve was then fitted to these two pieces of information using a Maximum Likelihood Estimation (MLE) – an algorithm widely used in psychophysics (e.g. de la Malla & López-Moliner, 2010), see the panel *e* of Figure 2.4. From each fit was obtained two parameters, the mean, which gave an indirect indication of the MAE strength, see section 1.1.4, and the standard deviation, which gave an indication of the measurement 's precision.

In addition, the same analysis was performed onto the composite observer's data as to obtain a clear illustration of the MAE's strength.

1.3.3 *The Matlab analysis*

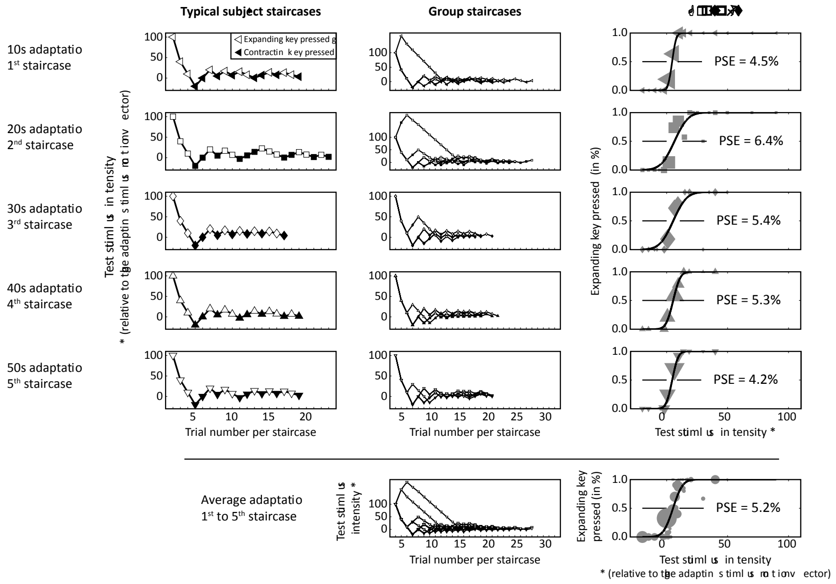

Figure 2.5: Matlab analysis description for one experiment. A observer's data, the group staircases and the group fits are presented, respectively, on the left column, middle column and right column of the figure. The transition from the first column to the third is explained in detail in the previous paragraph. The top five rows illustrate the process of measuring the MAE's intensity produced by each level of motion adaptation. The final bottom row illustrate the process of measuring the average MAE's intensity produced across each level of motion adaptation.

A mean MAE's strength was obtained for each time-point based on the composite observer's data, see row one to five of Figure 2.5. Also, the composite observer's data from each time-point were pulled together into an overall composite observer's data from which was obtained an average MAE's strength across the fifty second of motion adaptation, see row six of Figure 2.5.

1.3.4 *Non parametrical statistical analysis*

To statistically compare the experimental conditions, we followed Turi & Burr, 2012 in using two-tailed bootstrap sign tests. For this technique, using the composite observer's data, responses at given intensity are randomly reshuffled with replacement across intensities. The new distribution of responses is fitted and a mean estimate of the distribution is obtained. This operation is repeated two thousand times to obtain a distribution of mean estimates from which the 2.5% and 97.5% percentile are extracted, the two-tailed 95% confidence interval. A problem with this method is that it produces rather large confidence intervals. To compensate for this flaw, we used a bias-corrected and accelerated correction (BCa), which adjusts the bias and the skewness of the bootstrap distribution and produces narrower confidence interval (Efron & Tibshirani, 1994). This BCa bootstrap was done using MATLAB's "bootci" function, which provides the adjusted BCa intervals based on the test stimulus' intensity presented and the subject's response for each. If the lower bound of the BCa confidence interval was above zero, the distribution was considered to be significantly different from zero.

Commented [DBSDE&S9]: Comment 10.8: I used a matlab function from their Statistical toolbox to use the BCA bootstrap.

1.3.5 *The parametric analysis*

One-way ANOVAs were conducted to test whether the five stages of cumulative adaptation were significantly different from each other. The ANOVA's assumptions were probed by three tests: a Shapiro-Wilk test to probe the normality distribution of the individual PSE, a Levene's test to probe the homogeneity of variance for each group combination of my two variables, and a Mauchly's test to probe the assumption of sphericity. If the sphericity assumption was violated, the number of the degrees of freedom was adjusted using the Greenhouse-Geisser method. If a variable of the ANOVA had more than two levels, we conducted post-hoc tests that were corrected for the inflation of type II error that is the increased possibility to not reject when the null hypothesis is false.

Additionally, and to follow Turi & Burr's method, the MAE's estimate obtain on each time-point for each observer were clustered together and, when possible, a *t*-test was performed on these values as to corroborate the confidence interval obtained via the non-parametric BCa boostrap method.

Chapter 3

DUAL SPATIOTOPIC AND LOW-LEVEL ADAPTATION OF THE VISUAL SYSTEM

1 ABSTRACT

Space can be represented in a number of different coordinate frames. Current research on this matter has focused on two in particular: the retinotopic map where objects are encoded based on their location on the retina, and the spatiotopic map where objects are encoded based on their actual location in the outside world. Motion after-effects have been used to probe for the presence of both maps in the brain, and some of the results point toward the existence of a spatiotopic map. New evidence suggests that is possible to produce a single spatiotopic motion after-effect (Turi & Burr, 2012). Here I extend this result by investigating whether two different spatiotopic locations can be simultaneously adapted. If there is a spatiotopic map, then it should be possible to measure a dual spatiotopic motion adaptation.

2 INTRODUCTION

In the motorway example described in the general introduction, we imagined that there is fast moving traffic on both sides of the road: the cars on opposite side of the motorway going toward you very fast, and the cars on your side are travelling faster than you. Translated in terms of optic flow, the opposite side of the motorway contains an expanding radial flow, and the same side of the motorway contains a contracting radial flow. Could we adapt to these different optic flows? In this case, each optic flows should induce a different after-effects, and these after-effects should be spatially restricted to the location in the visual field were the optic flows occurred (i.e. spatiotopic location).

Commented [DBSDE&S10]: Comment 10.2 about the reptition of the motorway exemple

In the literature the issue of whether or not aftereffects can occur at spatiotopic location is debated; some researchers argue against a spatiotopic aftereffect (Knapen, 2009), whilst others argue in favour of this idea (Melcher, 2005). However, amongst the contradictory results, one axiom seems to hold: the more complex a motion stimulus is, the more likely it is to be encoded onto a spatiotopic map (Melcher, 2005). For instance, a translational motion stimulus will only induce an illusory percept moving in the opposite direction to that of the motion stimulus – a motion aftereffect (MAE) – at the retinotopic location of the motion stimulus (Knapen, 2009), but a complex rotational motion stimulus will induce a spatiotopic MAE (Melcher, 2005).

Recently, Turi & Burr, 2012, in an further attempt to reconcile the conflicting evidence, adapted a single location using either a simple motion – a MAE – or a complex motion – inducing a PMAE. For each stimulus, three conditions were devised to probe the adaptation at three different locations: at a same retinal location, at a same spatial location or at an irrelevant location corresponding to neither of the previous two. They demonstrated that a simple motion stimulus was encoded solely onto a retinotopic map, whereas a complex motion stimulus was encoded onto both retinotopic and spatiotopic maps. They concluded that the spatiotopic encoding of a stimulus depended on its complexity.

If Turi & Burr are correct, and a spatiotopic MAE can be observed when induced by a complex motion stimulus, then as long as the optic flow encountered whilst driving on a motorway is complex, then it should be possible to obtain two spatiotopic MAE at two locations. In fact, the optic flow encountered on a motorway whilst driving is a radial optic flow, and this optic flow belongs to the category of complex motion stimulus (Bex, Metha, & Makous, 1999; Burr, Badcock, & Ross, 2001; Burr & Santoro, 2001; Meng, Mazzoni, & Qian, 2006; Morrone et al., 2000). Here, I attempted to adapt two different locations simultaneously onto a spatiotopic map, using Turi & Burr's paradigm.

The two notable departures from Turi & Burr are as follows: first, my choice to use another complex stimulus – a radial motion pattern (Bex, Metha, & Makous, 1999; Burr, Badcock, & Ross, 2001; Burr & Santoro, 2001; Morrone et al., 2000) – in order to generalise their claim that complex motion stimulus, not just a PMAE stimulus (Turi & Burr, 2012) is encoded spatiotopically. Second, I assessed the time-course of the effect. Spatiotopic MAE have been recently reported to grow stronger with time, so by probing the MAE after different duration of motion adaption, I can verify the accuracy of this claim (Zimmermann et al., 2011). Consequently, I measured the motion adaptation at multiple consecutive time points: every 10s for 50 cumulative seconds (i.e. Turi and Burr measured motion adaptation at a duration similar to the 50s time point), as to assess the development of the motion adaption.

2.1 Radial motion stimuli and the spatiotopic MAE

If the assessment of the MAE time-course is unlikely to deter my chances at observing a single spatiotopic MAE (in the worst case scenario the spatiotopic MAE grows weaker with time, and I measure the spatiotopic MAE only once), the choice of a complex motion stimulus can be seen, at first, as a riskier gamble.

Complex motion stimuli, such as radial motion stimuli, adapt larger areas than simple motion stimuli because they are processed by different cortical structures. Simple motion stimuli are processed by V1 neurons that have small receptive field, whereas complex motion stimuli are processed by MSTd neurons that have very large receptive fields (Duffy & Wurtz, 1991). Because of this difference, the sustained presentation of a complex motion stimulus adapts an area larger than the stimulus' size (i.e. the size of a MSTd receptive field). This adaptation of the entire receptive field of a MSTd neuron gives rise to a Phantom MAE, where a MAE observed is at locations nearby the adapting stimulus' location (see Price, Greenwood, & Ibbotson, 2004 and Meng et al., 2006 for a phantom MAE with a radial motion stimulus; and Snowden & Milne, 1997 for a phantom MAE with a PMAE stimulus). Because of this Phantom MAE, the MAE thought to reflect the spatiotopic encoding of a stimulus could actually correspond to a general adaptation of the visual field; thus thwarting any meaningful conclusions on the existence of a spatiotopic MAE.

The issue of the separation between the spatiotopic MAE and the phantom MAE can be resolved by testing the MAE at a location that is neither the spatiotopic nor the retinotopic location of the stimulus. In this condition, the MAE is tested at the same distance from the adapting stimulus as in the spatiotopic or the retinotopic condition but at a different location. The MAE probed at this "unmatched" location indicates the spread of the adaptation induced by the motion stimulus; therefore estimating the phantom MAE at the spatiotopic and retinotopic locations. If the MAE at the unmatched location – the phantom MAE – is equal to the one observed at the spatiotopic location – the spatiotopic MAE – then the spatiotopic MAE is likely to actually correspond to a general adaptation of the visual system. If the MAE at the unmatched location is weaker than the one observed at the spatiotopic location, then a general adaptation of the visual system is not sufficient to explain the spatiotopic MAE, and it suggests that the spatiotopic location of the adapting stimulus has been encoded. Using this technic Turi and Burr (2012) and Melcher (2005) have shown that complex motion stimuli and notably radial motion stimuli induce a MAE that is specific to the stimulus' spatiotopic location; therefore disentangling an adaptation of MSTd neurons from one induced by the spatiotopic encoding of the stimulus.

In Chapter 3, the very nature of the experimental question – an adaptation to different optic flows at different location in space – should be sufficient to separate the phantom MAE from the spatiotopic MAE. The presentation of two radial optic flows should induce two phantom MAEs, but given that these optic flow are in opposite direction (i.e. an expanding radial flow and a contracting radial flow), the induced phantom MAEs should be in opposite direction. Because of this difference, I argue that the phantom MAE should cancel each other out. Consequently, the only remaining MAEs left to observe would be the ones related to the referential encoding of the adapting stimuli (i.e. retinotopic and spatiotopic reference frame).

Taken together, the evidence that radial motion stimuli induce specific spatiotopic MAEs (Melcher, 2005), and that two motion stimuli with opposite radiation are unlikely to give rise to a phantom MAE suggest that any effect reported in Chapter 3 is likely to be the result of a spatiotopic encoding of the adapting stimulus rather than a general adaptation of the visual system.

Commented [DBSDE&S11]: Comment 1 about the implication of the phantom MAE in the retinotopic vs. spatiotopic debate

2.2 Preliminary experiments: Experiment 1 to 3

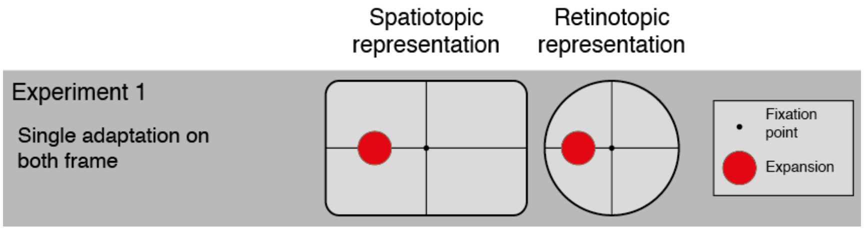

Figure 3.1: Illustration of the experimental design of Experiment 1, and in particular of the adapted location(s) on both the spatiotopic and the retinotopic map. The red patch is only given as an illustration of the three possible stimuli configuration, during the actual experiments, the locations containing the expanding and contracting stimuli were counterbalanced across observers.

To investigate the nature of a possible spatiotopic map required four intermediary steps. Because of the added parameters (i.e. the radial nature of the adapting stimulus, and the multiple time-points assessment of the MAE), I first decided to probe whether I could measure a basic MAE with an extension of Turi and Burr's method. As a first preliminary step, I simply measured whether the radial motion stimulus could induce a MAE. To this end, I presented the adapting and the test stimulus at the same location (see Experiment 1 in Figure 3.1). I assessed the evolution of the MAE induced by the adapting stimulus at five consecutive 10 seconds window.

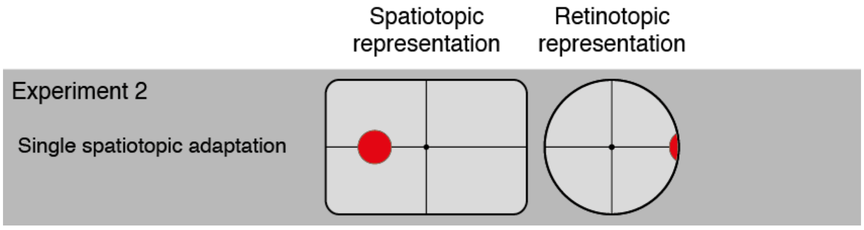

Figure 3.2: Illustration of the experimental design of Experiment 2, and in particular of the adapted location(s) on both the spatiotopic and the retinotopic map.

The second step was to replicate Turi & Burr’s findings by measuring a single spatiotopic adaptation with the modified method (see Experiment 2 in Figure 3.2).

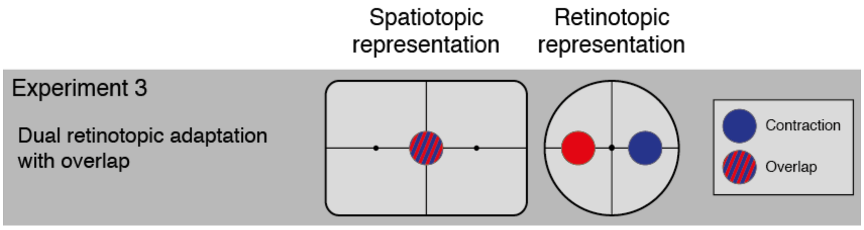

Figure 3.3: Illustration of the experimental design of Experiment 3, and in particular of the adapted location(s) on both the spatiotopic and the retinotopic map. The red, blue, and red-blue patches are only given as an illustration of the three possible stimuli configuration, during the actual experiments, the locations containing the expanding and contracting stimuli were counterbalanced across observers.

The third step involved attempting to demonstrate whether my procedures were sufficiently sensitive to detect dual adaption of stimuli on the retinotopic map (Experiment 3 in Figure 3.3). In Experiment 3, one adapting stimulus was expanding while the other was contracting and the adapting stimuli were presented at different locations on the retinotopic map. Since adapting stimuli had different locations on the retinotopic map, they should induce MAE at their respective retinotopic locations.

2.3 **Main experiments: Experiment 4 to 5**

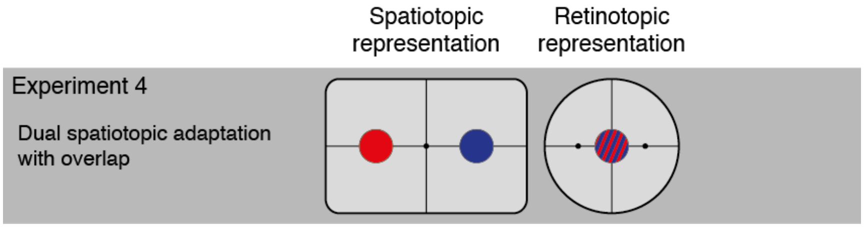

Figure 3.4: Illustration of the experimental design of Experiment 4, and in particular of the adapted location(s) on both the spatiotopic and the retinotopic map. The red, blue, and red-blue patches are only given as an illustration of the three possible stimuli configuration, during the actual experiments, the locations containing the expanding and contracting stimuli were counterbalanced across observers.

In Experiment 4, see Figure 3.4, I examined dual spatiotopic adaptation by reversing Experiment 3’s paradigm: the two opposite radial motion stimuli were adapted at two locations on the spatiotopic map, but at one on the retinotopic map. Since the adapting stimuli had different locations on the spatiotopic map, they should induce MAE at their respective spatiotopic locations. As it transpired, the adapting stimuli did not induce two spatiotopic MAEs: the two motion adaptations induced on the retinotopic map did not cancel each other.

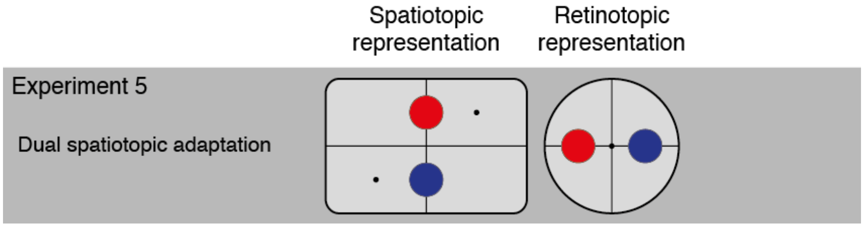

Figure 3.5: Illustration of the experimental design of Experiment 5, and in particular of the adapted location(s) on both the spatiotopic and the retinotopic map. The red, blue, and red-blue patches are only given as an illustration of the three possible stimuli configuration, during the actual experiments, the locations containing the expanding and contracting stimuli were counterbalanced across observers.

To further test whether dual motion adaptation was possible on the putative spatiotopic map, Experiment 5 circumvented the issue of the adapting stimuli overlapping with one another on the retinotopic map. To this end, the paradigm was slightly modified, and I examined the dual spatiotopic adaptation with two opposite radial motion stimuli at two locations on the spatiotopic map but also at two different locations on the retinotopic map (Experiment 5 in Figure 3.5). As a result, the locations adapted on the spatiotopic map did not correspond to adapted locations on the retinotopic map, and so the adapting stimuli should be able to induce MAEs only at their spatiotopic locations.

3 EXPERIMENT 1

3.1 Introduction

The role of the first experiment is to establish that I can generate a MAE as well as to characterise its evolution over time. To this end, each trial contained a radial motion stimulus presented for 10 sec and was repeated five times, as to measure the induced MAE at five consecutive intervals. After the fifth trial, observers had a mandatory break designed to break down the motion adaptation accumulated, see section 1.2.5 of the general method for a precise description of the adapting stimulus and the rationale behind the 10 sec adaptation period. The experiment measured MAEs at five consecutive intervals, after 10 sec, 20 sec, 30 sec, 40 sec and 50 sec of cumulative motion adaptation; see section 1.1.7 of the general method for a description of the cumulative motion adaptation. Since both the adapting stimulus and the fixation were held constant in the adapting phase and in the testing phase, the adapting stimulus' location coincided on both spatiotopic and retinotopic maps.

3.2 Method

3.2.1 *Observers and stimuli*

Five naive observers and the experimenter participated in the experiment. Their ages ranged from 24 to 25 with an average at 24.7 years. There were 2 females and 4 males observers. All had normal or corrected-to-normal vision.

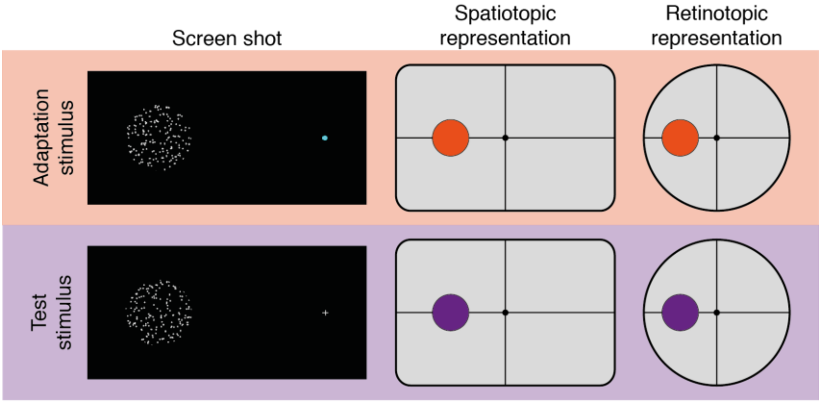

Figure 3.6: Stimulus location as a screenshot, together with and illustration of its location in the spatiotopic and retinotopic maps. Rows indicate the experiment phase whereas columns describe three ways to understand the stimulus location. The screen shot is at the $^{1}/_{15}$ *scale.*

The adapting stimulus was composed of 400 dots of a fixed size, 0.008 cm^{2}, and moving radially inwards (contracting) or radially outwards (expanding) at an average speed of 1.47 cm/sec (see section 1.1.2 for further details). The test stimulus was similar to the adapting stimulus with the two exceptions: the speed was dictated by a psychometric staircase based on observers' response (i.e. observers' previous responses on the dots' speed of the test stimulus decided the dots' speed of the next test stimulus), and dots that composed the test stimulus gave observers the impression of sparkling (see general method section 1.1.3 for more detail).

The fixation point was displayed at the centre of the screen and was separated from the adapting stimulus by 7° of visual angle. Adapting stimulus and test stimulus were at the same location. In this spatial configuration, the motion adaptation tested is at the same location on both the spatiotopic and retinotopic maps, see Figure 3.6.

3.2.2 *Procedure*

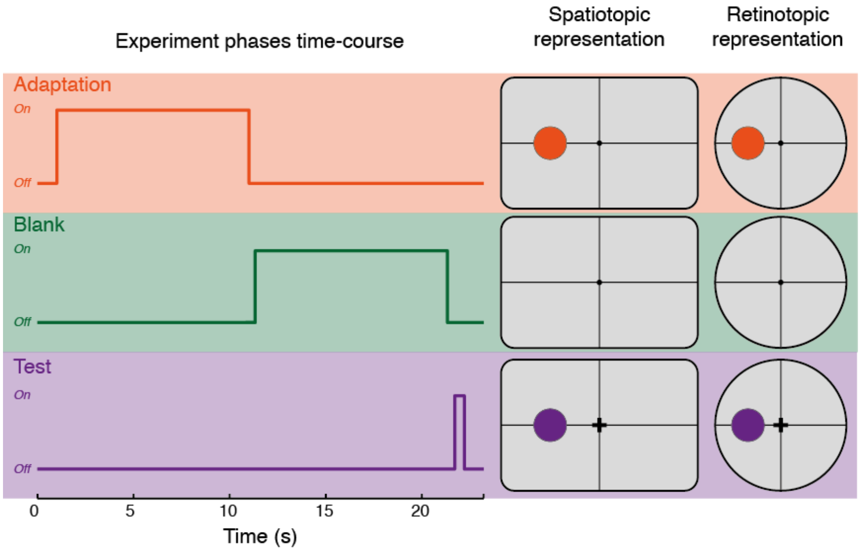

Figure 3.7: Time-course illustration of the main experiment phases of one trial. The illustration describes the time-course of the main experiment phases and their spatial configurations on the spatiotopic and retinotopic representations.

Figure 3.7 illustrates the main phases of a single trial in Experiment 1, and the exact time-course of a trial is as follow. A fixation point was displayed in the centre of the screen for the entire duration of a trial. After 0.66s, the adapting stimulus was displayed for 10s as illustrated in “Adaptation” panel of Figure 3.7. Once 10s had elapsed, a fixation point remained on the screen for 10s (“Blank” panel of Figure 3.7). At the end of this period, the fixation point turned into a fixation cross and the test stimulus appeared for 0.5s (“Test” panel of Figure 3.7). When 0.5s had elapsed, the fixation-cross remained on the screen for 1s or until a key was pressed.

When the fixation-cross appeared, the observer was instructed to press a key indicating the direction of radial motion (see section 1.2.3). If no key was pressed within the allocated time (indicated by the fixation cross disappearing), the staircase’s step was not incremented and stayed the same (see section 1.2.3).

A block consisted of five consecutive presentations of a single adapting stimulus, and it accumulated 50 sec of motion adaptation at one location (see section 1.1.7). At the end of this block of five trials, observers were given an 80 sec break to erase any accumulated motion adaptation (see section 1.2.5). The direction of radial motion of the adapting stimulus, i.e. contraction and expansion, was randomized across blocks.

3.2.3 *Data analysis (see section 1.3)*

To establish the strength of the perceived MAE for the different durations of motion adaptations, I analysed the data collected during the experiment. To this end, I related the different velocities presented by the test stimulus to the observers' responses for each by fitting a sigmoid curve between the two; see section 1.3.2 for a precise explanation. From this curve, I obtained the point of subjective equality (PSE), which corresponds to the point where an observer is unable to say whether the physical stimulus is expanding or contracting, it is the point where the physical intensity presented cancels the perceived one. By finding the physical intensity needed to cancels the perceived one, I have indirectly measured the intensity of the MAE, so once the PSE obtained, I have established the strength of the perceived MAE. From the fitted sigmoid curve I bootstrapped an estimate of the variability of the PSE, i.e. a confidence interval (see definition in method section 1.3.4).

First, I ran a *t*-test based on the average cumulative motion adaption of each observer; see section 1.3.5 of the general method for a precise description of the statistical analysis. Then I conducted an ANOVA with one independent variable, the time after which the after-effect was tested (i.e. 10s, 20s, 30s, 40 and 50s of cumulative adaptation).

3.3 Results

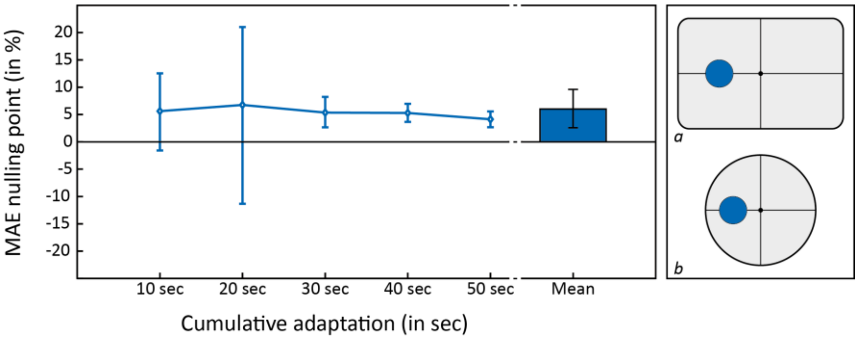

Figure 3.8: Overall and cumulative motion after effect adaptation over 50 sec of adaptation. The motion after effect intensity is indicated relative to the adapting motion stimulus (in %). Error bars represent confidence intervals. The cumulative motion after effect (blue line) reaches significance from 30s of cumulative adaption (95% CI [1.01 7.50]) and the average motion after effect (blue bar) is significant (95% CI [1.41 8.85]). b: Illustration of the adapting stimulus locus on both the spatiotopic and retinotopic representation. The motion after effect was tested 10s after the adapting stimulus was removed: the Remote adaptation condition (blue colour).

Figure 3.8 shows the magnitude of the MAE as a function of cumulative duration of adaptation. A first glance at the figure suggests that the MAE did not change with the duration of exposure to the motion stimulus. This first observation is supported by the statistical analysis: the MAE's intensity is not affected by the duration of the adapting motion stimulus, one-way within subject ANOVA [F(1, 5) = 0.269, p = 0.626]. At second glance, we see that the first two time points (i.e. 10s and 20s of motion adaptation) vary more relative to the three others (i.e. 30s, 40s and 50s of motion adaptation). This increased variability is the consequence of the erroneous responses given by two observers on the first two trials of the experiments. On average, the MAE is approximately 5% of the adapting speed (blue bar of Figure 3.8), and this average shift in the magnitude of the MAE is found to be significant (95% CI [1.01 7.50])[3].

3.4 Discussion

The first experiment established that I could obtain a robust MAE with the experimental stimulus, even if a 10 sec gap is introduced between the motion adaptation and the testing of the MAE. In this simple experiment, a plateau in

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[3] [t(5) = 0.00002, $p < 0.05$]

adaptation appears to be reached within the first ten seconds. This first experiment confirms that the validity of the stimulus for generating MAEs and it provides a baseline for subsequent experiments.

4 EXPERIMENT 2

4.1 Introduction

The previous experiment demonstrates that the radial motion stimulus could induce a MAE measurable at five consecutive time-points. The aim of the second experiment is to conceptually replicate, with the method developed in the previous experiment, Turi & Burr's findings that a complex motion stimulus can induce MAE at its spatiotopic location. The main departure from Turi & Burr's paradigm is the consecutive MAE's measurement method, where the MAE's intensity is probed after five consecutive adaptation times. This difference means that the resulting MAE is generated by motion stimulus whose overall duration increases with each adaptation time. The relationship between stimulus duration and spatiotopic encoding suggests that the likelihood to observe a MAE encoded at its spatiotopic location should increase with each period of adaptation (Zimmermann et al., 2013; Zimmermann, 2013).

The experiment aimed to measure the spatiotopic encoding of a radial motion stimulus via its induced MAE. It was hypothesised that, as the duration of the adapting motion stimulus increases, the chance to observe a spatiotopic MAE increases as well.

4.2 Method

4.2.1 *Observers and stimuli*

Nine naive observers and the experimenter participated in the experiment. Their ages ranged from 24 to 28 with an average at 25.2 years. There were 4 females and 6 males observers. All had normal or corrected-to-normal vision.

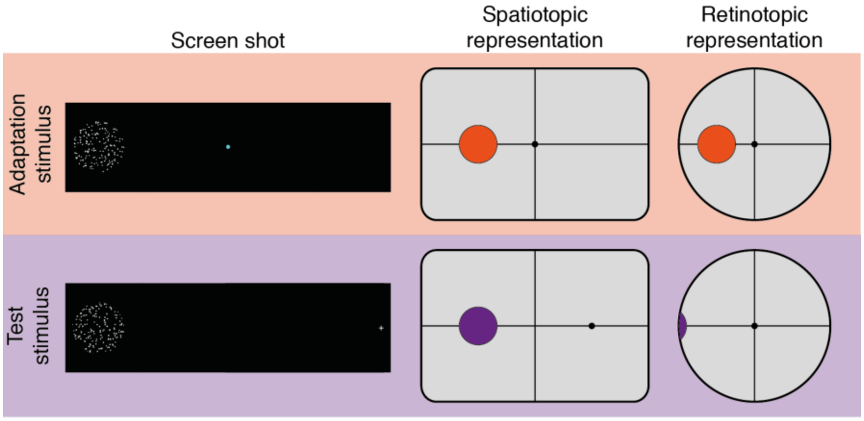

Figure 3.9: Stimulus location's screen capture and illustration of its location in the spatiotopic and retinotopic maps. Rows indicate the experiment main phase whereas columns give, from left to right, a screen capture of the stimulus, an illustration of its spatiotopic location and one of its retinotopic location. The screen shot is at the $^{1}/_{15}$ *scale.*

During the adaptation phase, the fixation point was located at the centre of the screen whilst the adapting stimulus was located 7° to the left of fixation. During the test phase, the test stimulus was displayed at the adapting stimulus location whilst the fixation point was presented 14° to the left of the test stimulus. On the retinotopic representation, the adapted and tested sites were at two different locations as illustrated in the "Retinotopic representation" column of Figure 3.9. On the spatiotopic representation, the adapted and tested sites were at the same location as illustrated in the "Spatiotopic representation" column of Figure 3.9.

4.2.2 *Procedure*

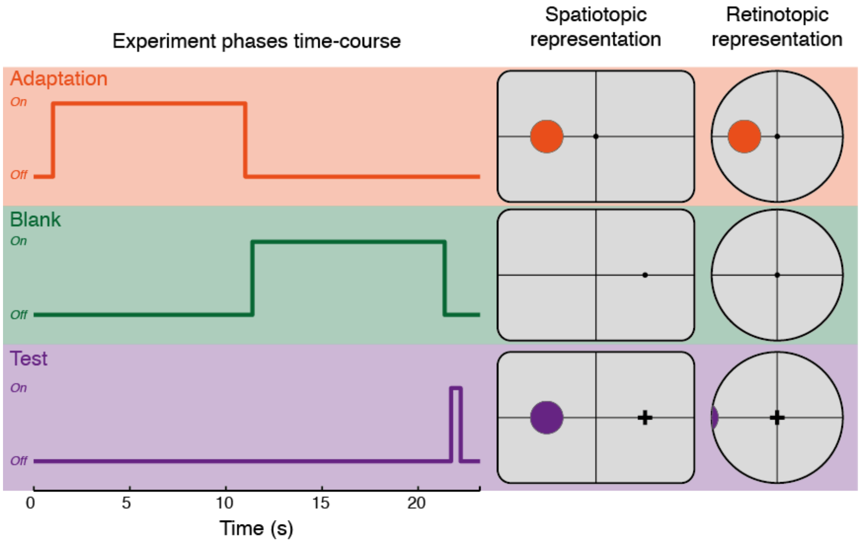

Figure 3.10: Time-course illustration of the main experiment phases. The illustration describes the time-course of the main experiment phases and their spatial configurations on the spatiotopic and retinotopic representations.

The main components of a single trial are illustrated in Figure 3.10, and details of a single trial follow. A fixation point was displayed at the centre of the screen for the 0.35s and was followed by a 0.35s arrow indicating the next fixation point's location. Once the arrow disappeared, a fixation point was solely drawn on screen for 0.35s and was then drawn in conjunction with the first adapting stimulus for an extra 10s as illustrated in the "Adaptation 1" orange row in Figure 3.10. At the end of the "Adaptation 1" period, a solitary fixation point was displayed for 10.7s at a new location. Subsequently, the fixation point turned into a fixation cross and a test stimulus appeared on the screen for 0.5s as illustrated in the "Test" purple row in Figure 3.10. When the 0.5s had elapsed, the fixation-cross remained on the screen for 1s or until a key was pressed.

4.3 Results

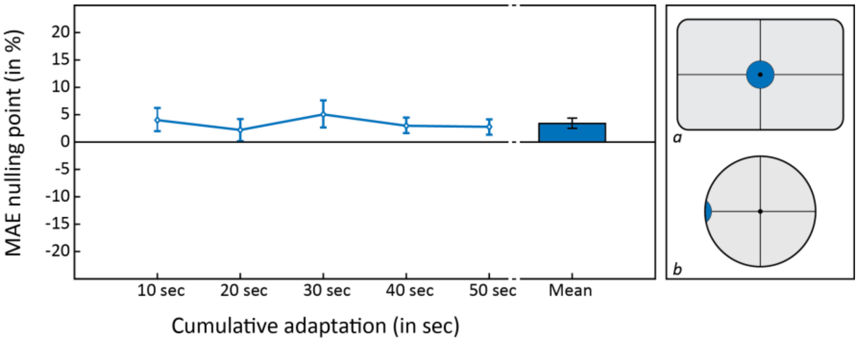

Figure 3.11: a: Overall and cumulative motion after effect adaptation over 50 sec of adaptation. The motion after effect intensity is indicated relative to the adapting motion stimulus (in %). Error bars represent confidence intervals. The cumulative motion after effect (blue line) reaches significance from 10s of cumulative adaption (95% CI [1.98 6.22]) and the average MAE (blue bar) is significant (95% CI [0.51 5.76]).

Figure 3.11 shows the magnitude of the MAE as a function of cumulative duration of adaptation. The average MAE is, approximately, 3% of the adapting speed. When the magnitude of the MAE collapsed over time is significantly different from zero (95% CI [0.514 5.763])[4]. Statistical significance is reached by the first time point (95% CI [1.98 6.22]) and remains significant through to the final time point. In fact, the duration of exposure does not affect its intensity, ANOVA [$F(1, 9) = 0.575$, $p = 0.683$].

4.4 Discussion

The aim of Experiment 2 was to demonstrate a spatiotopic encoding of a stimulus location (Turi & Burr, 2012). As in Experiment 1, duration did not have an impact on the magnitude of the MAE, consistent with the idea that a plateau in adaptation is reached within the first ten seconds. The main conclusion of the experiment is that it was possible to replicate a spatiotopic encoding at a single stimulus location with a MAE (cf. Biber & Ilg, 2011; Ezzati et al., 2008; Melcher, 2005; Nishida, 1995; Turi & Burr, 2012; Zimmermann et al., 2013).

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[4] [t(9) = 0.00001, p<0.05]

5 EXPERIMENT 3

5.1 Introduction

Before I can proceed to examine whether a dual spatiotopic MAE can be observed, it was first necessary to establish that with the current stimuli and training procedures I can observe a dual retinotopic MAE.

The use of a successive, dual motion adaptation is the main difference with previous experimental procedures. In Experiment 3, one retinal location was adapted for 10s with, for example, an expanding pattern, and then a second location was adapted for 10sec, with a contracting pattern. The test assessed the induced MAE at either the first retinal location or the second. In the spatiotopic map, the two adapting stimuli with opposing radial pattern were presented at the same location, which should prevent motion adaptation from occurring on this map.

Before proceeding it is worth considering the stimuli. A hierarchically organised pathway of cortical areas processes radial motion. The output of directionally selective cells in V1 feeds into MT which in turn feeds to MST and a range of parietal areas (Mineault & Khawaja, 2012). Some neurons in a region of MST, MSTd are known to have particularly large receptive fields, between 30° to 40° (Duffy & Wurtz, 1991; Lagae, Maes, & Raiguel, 1994; Raiguel et al., 1997). On the retinal map, 14 only separated the adapting stimuli° (see section 5.2.1). Because both adapting stimuli could fall within the same MSTd receptive field, and because they have opposite radial motions, the adaptation induced by the second motion stimulus might cancel by the one induced by the first motion stimulus; however, since MSTd MSTd neurons respond to either expanding motion pattern or to contracting one, expanding and contracting motion stimuli should target different neurons (Tanaka, Fukada, & Saito, 1989).

Could two adapting stimuli with opposing radial motion falling in overlapping receptive field of MSTd neurons cancel their induced motion adaptation? Since the retinotopic MAE is thought to occur in MT (Kohn & Movshon, 2003), where receptive fields are smaller than in MSTd (Duffy & Wurtz, 1991; Lagae et al., 1994; Raiguel et al., 1997), then the adapting stimuli should only adapt the MT neurons whose receptive fields are comprised between 5º to 10º. So the retinotopic MAEs should be able to occur at two retinal locations separated by 14º despite the two adapting stimuli falling within overlapping receptive field of MSTd neurons.

Experiment 3 assessed whether two radial motion stimuli could be encoded at two different retinal locations by assessing their respective MAEs at five consecutive time-points. It was hypothesised that two opposite retinotopic MAEs would be measured.

5.2 **Method**

5.2.1 *Observers and stimuli*

Five naive observers and the experimenter participated in the experiment. Their ages ranged from 24 to 26 with an average at 24.7 years. There were 2 females and 4 males observers. All had normal or corrected-to-normal vision.

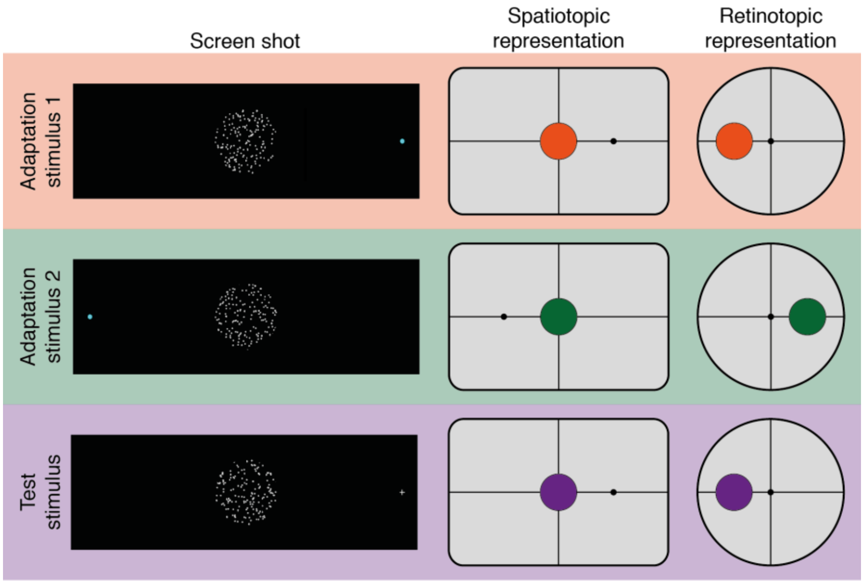

Figure 3.12: A schematic of the stimuli and procedure in relation to potential spatiotopic and retinotopic representations for Experiment 3. The rows depict experimental phases and the columns represent the stimuli (left column) and the two types of representations (spatiotopic and retinotopic). The screen shot of the stimuli is at the $^{1}/_{15}$ *scale.*

During both adaptation phases, the adapting stimuli were located at the centre of the screen but had opposite directions of motion (e.g. the first adapting stimulus was contracting whereas the second adapting stimulus was expanding). The fixation points were located 7° of visual angle away from the adapting stimulus and 14° of visual angle away from each other (e.g. the first fixation point was 7° to the right from the centre of the screen whereas the second fixation point was 7° to the left). During the test phase, the fixation point could be displayed at either of its two previous locations. The test stimulus appeared at the centre of the screen.

With respect to a spatiotopic representation, the procedure adapts the same location being adapted twice with opposite motion stimuli, which should cancel any motion adaptation on this representation (see Figure 3.12). In contrast, this procedure should result in adaptation at two different locations and allow the MAE at two different retinotopic locations to be assessed during the test.

5.2.2 *Procedure*

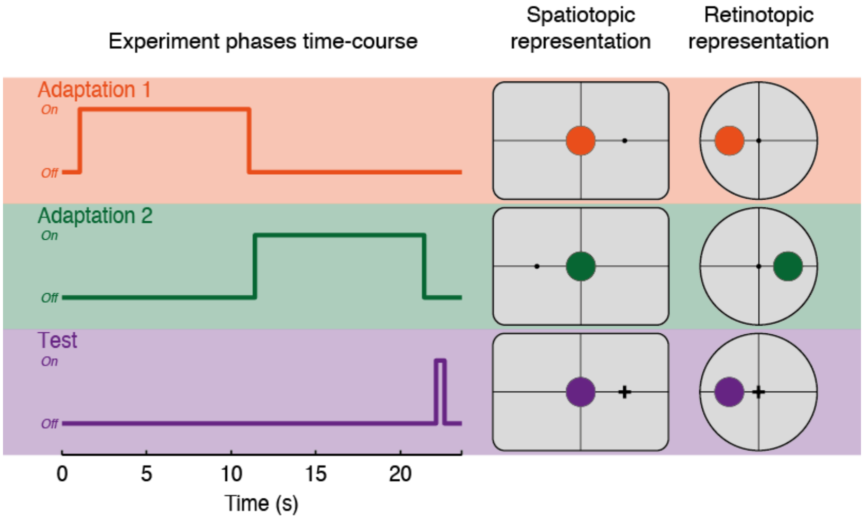

Figure 3.13: A schematic of the main phases of Experiment 3. The illustration describes the time-course of the main experiment phases and their spatial configurations on the spatiotopic and retinotopic representations.

A schematic showing the time course of a single trial is shown in Figure 3.13. A fixation point is displayed at the centre of the screen for the 0.35s and is followed by a 0.35s arrow indicating the next fixation point’s location. Once the arrow disappears, a fixation point is solely drawn on screen for 0.35s and is then drawn in conjunction with the first adapting stimulus for an extra 10s as illustrated in the “Adaptation 1” orange row in Figure 3.13. At the end of the “Adaptation 1” period, a 0.35s fixation point is solely displayed at a new location. During the next 10s, the fixation point and the second adapting stimulus are displayed together on the screen as illustrated in the “Adaptation 2” green row in Figure 3.13. At the end the “Adaptation 2” period, a 0.35s arrow is displayed indicating the next fixation point’s location and is followed by a 0.35s fixation point. Subsequently, the fixation point turned into a fixation cross and a test stimulus appears on the screen for 0.5s as illustrated in the “Test” purple row in Figure 3.13. When the 0.5s have elapsed, the fixation-cross remains on the screen for 1s or until a key is pressed.

Per block of five trials, the test stimulus is probing the same adaptation stimulus, for instance, the “Adaptation 1” stimulus. The adaptation stimulus assessed by the test stimulus , i.e. “Adaptation 1” or “Adaptation 2”, was randomized across block.

5.2.3 *Data analysis (see section 1.3)*

To carry out a thorough investigation of the MAEs resulting from this novel procedure, I grouped the data by the adaptation phase tested (i.e. when the test stimulus was probing the “Adaption 1” phase as illustrated in Figure 3.13 or when the test stimulus was probing the “Adaption 2”). From this point onward, the former situation will be labelled “Remote adaptation” as the motion after effect was tested 10s “remote” from the adapting stimulus presentation and the latter situation will be labelled “Recent adaptation” as the motion after effect was tested immediately after the adapting stimulus presentation.

The data from each sub-group, i.e. remote and recent conditions, underwent the data analysis described in section 3.2.3.

5.3 Results

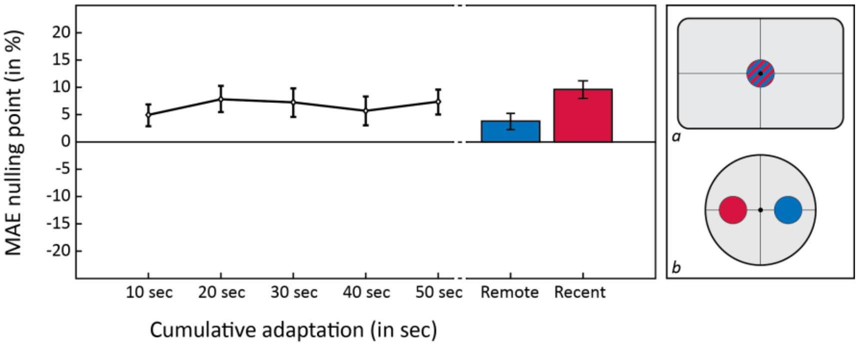

Figure 3.14: a: Cumulative motion after effect over 50 sec of adaptation and the mean remote and recent after effect. The motion after effect was either tested 10.7s after the adapting stimulus was removed (the remote adaptation condition; blue colour bar) or 0.7s after the adapting stimulus was removed (the recent adaptation condition; red colour). The motion after effect intensity is plotted relative to the adapting stimulus motion vector (in %). Error bars represent confidence intervals. The cumulative motion after effect (black line) reaches significance from 10s of cumulative adaption (95% CI [2.95 6.99]) and the motion after effect collapsed across time point for both remote and recent testing (respectively blue and red bars) are significant (95% CI [2.29 5.21], 95% CI [8.00 11.36]). b: Illustration of the adapting stimulus loci on both the spatiotopic and retinotopic representation.

Figure 3.14 shows the magnitude of the MAE as a function of cumulative duration of adaptation. The average MAE is, approximately, 6% of the adapting speed. A closer look at the MAE according to the time after which the MAE was tested (i.e. remote or recent) shows the same picture with both condition yielding significant results (remote: 95% CI [2.29 5.21]; and recent: 95% CI [8.00 11.36]). Statistical significance is reached by the first time point (95% CI [2.95 6.99]) and remains significant through to the final time point. The duration after which the motion after effect is measured does not affect its intensity, one-way within subject ANOVA [F(1, 5) = 0.403, p = 0.553]. However, the recent condition MAE is significantly more intense than the remote condition MAE (95% CI [3.68 8.01]).

5.4 Discussion

Experiment 3 assessed whether the stimuli and general procedures used in Experiments 1 and 2 can be employed to generate a dual retinotopic MAE. The significant MAEs observed at the five stages of cumulative motion adaption as well as the significant average of those five stages suggests that the procedures are effective. However, the definitive evidence comes from finding a significant MAE can be found in both the recent and remote conditions. This finding provides the basis for two main conclusions. The difference observed between the remote and recent condition can be again explained by the time-course of the MAE recovery function (Bex & Bedingham, 1999; Hammett, Thompson, & Bedingham, 2000; Hershenson, 1989; Hoffmann, Dorn, & Bach, 1999; Keck & Pentz, 1977): A MAE measured 10s after an adaptation is expected to be weaker than one measured immediately after an adaptation. Second and most importantly, both MAEs in the remote and recent conditions were statistically different from zero, which indicates that stimuli locations are encoded on a well defined retinotopic map of the world. The current results are, in this respect, consistent with both the psychophysical literature (Knapen, 2009; Turi & Burr, 2012) and the physiology which found a well defined retinotopic map of the visual world in the visual system (Gardner et al., 2008; Golomb & Kanwisher, 2012a; Wandell & Winawer, 2011).

6 EXPERIMENT 4

6.1 Introduction

Experiment 3 demonstrated that it was possible to adapt simultaneously two locations on a retinotopic frame. Experiment 2 showed that a single MAE could be encoded on a spatiotopic map. If a true spatiotopic map exists, then it should be possible to adapt two locations on it using a modified version of the procedures employed in Experiment 3. In Mayhew's experiment, 1973, later replicated by Nishida et al., 2003, observers had to adapt to two opposite nearby rotational stimuli by alternating their fixation gaze every 10s to the centre of each stimulus. In Bompas & O’Regan's experiment, 2006, observers had to adapt to two opposite nearby colour stimuli by alternating their fixation gaze every 400ms to the centre of each stimulus. In both experiments, the two adapting stimuli have the same retinal location but different spatial ones and in both experiments gaze-contingent aftereffects were observed. Experiment 4 aimed to demonstrate a dual spatiotopic MAE with the same method as in the previous dual retinotopic experiment: by presenting the adapting stimuli with opposite radial motion at two locations on the spatiotopic map, but at only one on the retinotopic map, see Experiment 4. It was hypothesised that a dual spatiotopic MAE would be observed.

6.2 Method

Nine naive observers and the experimenter participated in the experiment. Their ages ranged from 24 to 28 with an average at 25.2 years. There were 5 females and 5 males observers. All had normal or corrected-to-normal vision.

The test and adapting stimuli parameters were the same as in Experiment 1 (see sections 1.1.2 and 1.1.3). The general features of the design and how those map onto the two types of frame (spatiotopic and retinotopic) are illustrated in Figure 3.15.

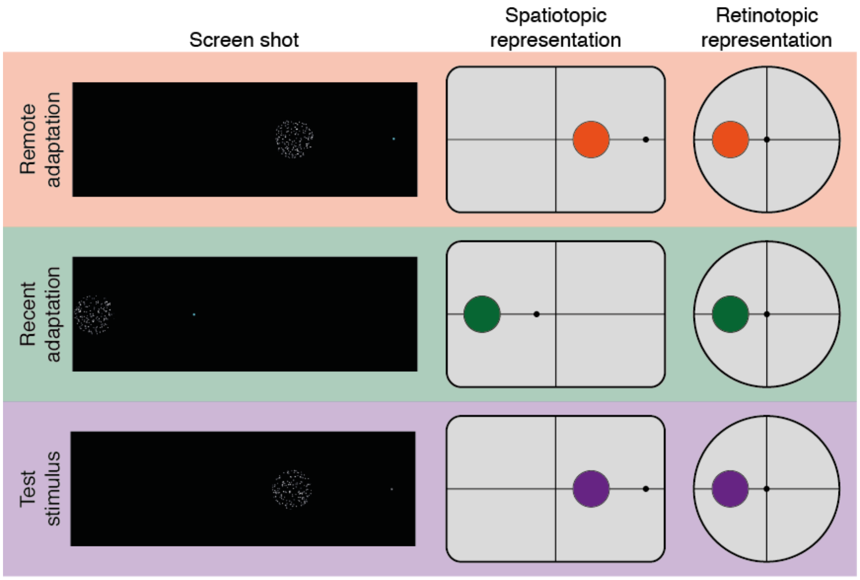

Figure 3.15: Stimulus location's screen capture and illustration of its location in the spatiotopic and retinotopic maps. Rows indicate the experiment phase whereas columns describe three ways to understand the stimulus location. The screen shot is at the $^{1}/_{15}$ *scale.*

During the adaptation phases, the adapting stimuli were separated by 14° of visual angle and had opposite directions of radial motion. For example, the first adapting stimulus was located 3.5° right of the screen centre and was contracting, whereas the second adapting stimulus was located 10.5° left of the screen centre and was expanding as illustrated in the "Screen shot" column of Figure 3.15. The fixation points were located 7° away from the adapting stimulus and 14° from each other. For example, the first fixation point was 7° to the right from the centre of the screen whereas the second fixation point was 7° to the left.

On the spatiotopic representation, the two adapting stimuli with opposing radial motion were successively presented at two different locations, as illustrated by the first two rows of the "spatiotopic representation" column of Figure 3.15). During the test phase, the fixation point and the test stimulus could probe the spatial position of either of the two adaptation phases (e.g., in the "Test stimulus" row of Figure 3.15, the test phase assesses the "Remote adaptation" spatial configuration).

On the retinotopic representation, the two adapting stimuli with opposing radial motion were successively presented at the same location, as illustrated by the first two rows of the "retinotopic representation" column of Figure 3.15). The presentation of the two adapting stimuli with opposing radial pattern at the same retinal location should prevent any motion adaptation from taking place on this map.

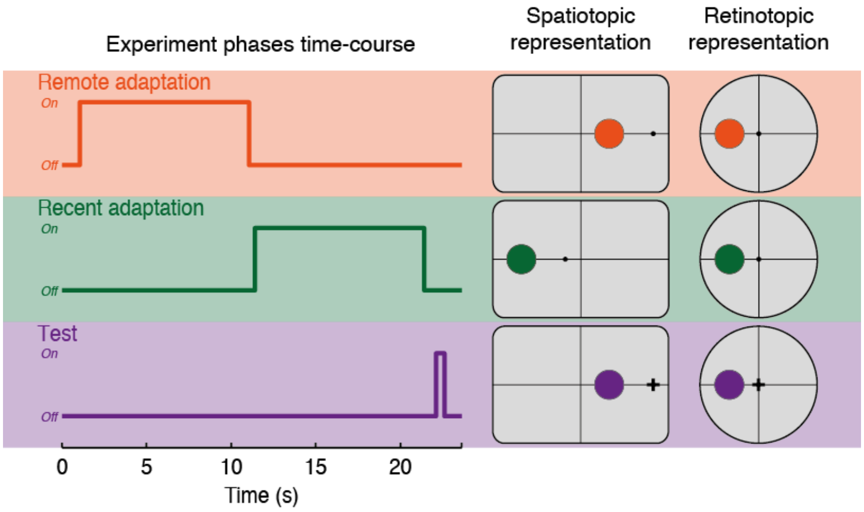

Figure 3.16: Time-course illustration of the main experiment phases. The illustration describes the time-course of the main experiment phases and their spatial configurations on the spatiotopic and retinotopic representations.

The exact time course of each experiment phase is identical to one described in section 5.2.2 of Experiment 3. The Figure 3.16 illustrates the main phase of the experiment where, the remote adaptation stimulus is presented for 10s ("Remote adaptation" orange row of Figure 3.16) followed by the recent adaptation stimulus for 10s ("Recent adaptation" green row of Figure 3.16). Finally, a test stimulus is presented for 0.5s ("test" purple row of Figure 3.16).

6.3 Results

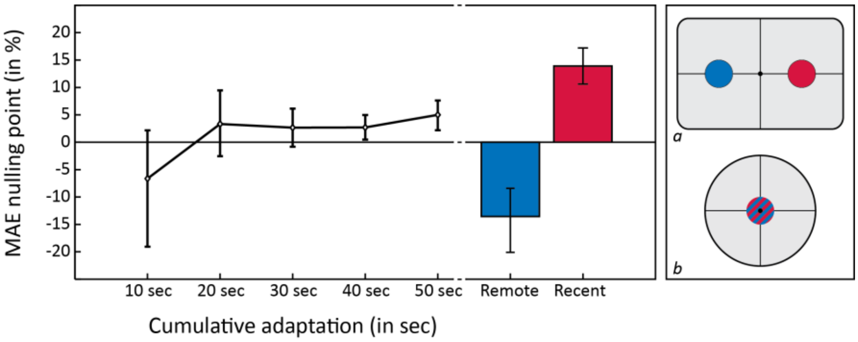

Figure 3.17: a: Cumulative motion after effect adaptation over 50 sec of adaptation and overall remote and recent testing motion after effect intensities. The motion after effect intensity is plotted relative to the adapting stimulus motion vector (in %). Error bars represent confidence intervals. The cumulative motion after effect (black line) reaches significance from 40s of cumulative adaption (95% CI [0.48 4.98]) and the motion after effect collapsed across time point for both remote and recent testing (respectively blue and red bars) are both significant (95% CI [-20.1 -8.41], 95% CI [10.63 17.21]).

Figure 3.17 shows the magnitude of the MAE as a function of cumulative duration of adaptation. On average, the MAE is approximately 1% of the adapting speed. Statistical significance is reached by the fourth time point (95% CI [0.48 4.98]) and remains significant through to the final time point. The duration after which the motion after effect is measured does not affect its intensity, one-way within-subject ANOVA [F(1, 9) = 2.142, p = 0.177].

A closer analysis reveals that the MAEs are actually in the same direction, not the opposite direction as expected. The MAEs are presented relative to the radial motion of the adapting stimulus, and we can clearly see that the MAE induced by remote adapting stimulus is reversed, it is in the same direction as the remote adapting stimulus (blue bar, -13.56% of the adapting stimulus). Furthermore, not only is the remote MAE reversed, it is also equal in magnitude to the recent MAE: they are both perceived to be moving in the same direction at the same intensity (13.56% for the remote MAE against 13.90% for the recent). These two observations suggest that I did not measure two MAEs induced by two different adapting stimulus but the same one induced by only one adapting stimulus.

6.4 **Discussion**

Experiment 4 was designed to measure two MAEs encoded at two locations on a spatiotopic map. The negative MAE observed in the remote condition challenges the view that a dual adaptation took place during the current experiment. When the presentation of two adapting stimuli with opposite radial motion occurred at the same spatial location but two retinal locations (i.e. Experiment 3), a dual retinotopic adaptation was observed. Yet, when the two adapting stimuli with opposite radial motion were presented at the same retinal location but two spatial locations (i.e. Experiment 4), the same MAE was measured twice.

The sub-analysis dividing data between remotely and recently tested MAE indicated that whilst the recent condition yields a conventional motion after effect, the remote condition yields a reversed motion after effect: e.g. after an expanding adapting stimulus, an expanding motion after-effect is measured. An explanation for the measured reversed MAE is that when the test stimulus was probing the motion adaptation induced by the remote adapting stimulus, it was actually probing the motion adaptation induced by the recent adapting stimulus because the test stimulus was probing the same retinal location twice. If the "recent" adapting stimulus had not only erased the adaptation from the "remote" one, but also adapted that retinal location, the test stimulus in the retinal coordinate would have measured the MAE induced by the "recent" adaptation in both remote and recent condition, see "test stimulus" purple row in the "retinotopic representation" column of Figure 3.15. Consequently, as the same outcome is measured twice and each condition is coded with reference to its adapting stimulus, the MAE measured in the "remote" condition is inverted.

Given the fact that the result can be explained by a simple retinotopic MAE measured at two occasions, because the adapting stimuli were presented at the same retinal location, the experiment will address this issue by not only presenting the two adapting stimuli at different spatiotopic locations but also at different retinotopic locations.

7 EXPERIMENT 5

7.1 Introduction

Experiment 4 might have failed to demonstrate a dual spatiotopic encoding because the two adapting stimuli were sharing the same retinal location. Since they were presented at the same location, the motion adaptation induced by the second adapting stimulus erased the one induced by the first adapting stimulus on the retinotopic map. So, when I probed the motion adaptation induced by the first stimulus it seems like I probed the motion adaptation induced by the second stimulus. Experiment 5 was designed to circumvent this issue by separating the two locations adapted on the retinotopic map from the two adapted on the spatiotopic map. Consequently, the two locations adapted on the retinotopic map, 7º left and right to the map's centre differed from the two locations adapted on the spatiotopic map, 7º above and below the centre of the screen, see experiment 5. It was hypothesised that the contracting adapting stimulus would induce an expanding MAE at one spatiotopic location, and that that the expanding adapting stimulus would induce a contracting spatiotopic MAE at another spatiotopic location.

7.2 Method

7.2.1 *Observer & stimuli*

23 naive observers and the experimenter participated in the experiment. All had normal or corrected-to-normal vision. Their ages ranged from 23 to 29 with an average at 24.7 years. There were 12 females and 12 males observers.

The test and adapting stimuli parameters were the same as in Experiment 1 (see sections 1.1.2 and 1.1.3). Spatial configuration of the stimuli; more precisely how they map onto the two types of frame (spatiotopic and retinotopic) is illustrated in Figure 3.18.

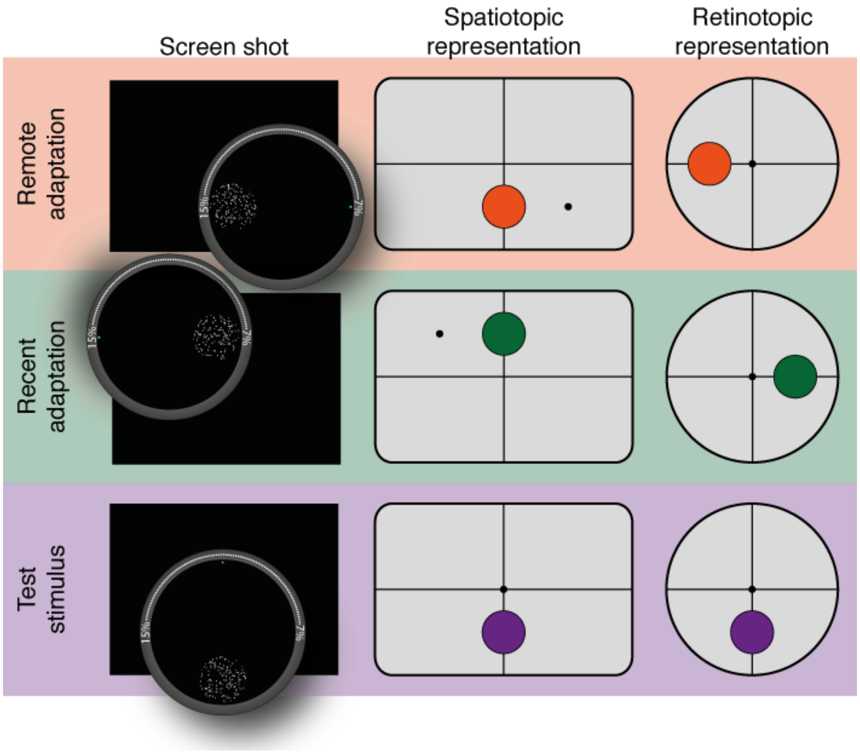

Figure 3.18: Stimulus location as a screenshot, together with an illustration of the location of the stimulus in the spatiotopic and retinotopic maps. Rows indicate the experiment phase whereas columns describe three ways to understand the stimulus location. The screen shot is at the scale of 1:15 outside the zooming lens and at the scale of 1:6 inside the zooming lens.

During the adaptation phases, the adapting stimuli were separated vertically by 14° of visual angle and had opposite radial motion (e.g. the remote stimulus was located 7° down from the screen centre and was contracting, whereas the recent stimulus located 7° up from the screen centre and was expanding as illustrated in the “Screen shot” column of Figure 3.18). The fixation points were located 7° of visual angle away from the adapting stimulus horizontally and 14° of visual angle from each other (e.g. the first fixation point was 7° right of the first adapting stimulus in the lower part of the screen whereas the second fixation point was 7° left of the first adapting stimulus in the upper part of the screen).

On the spatiotopic representation, the two adapting stimuli with opposing radial motion were successively presented at two different vertical locations, 7º above or below the centre of the screen, as illustrated by the first two rows of the “spatiotopic representation” column of Figure 3.18. During the test phase, the fixation point and the test stimulus could be presented at same location of either of the two adaptation phases (e.g., in the “Test stimulus” row of Figure 3.18, the test phase assesses the “Remote adaptation” spatial configuration).

On the retinotopic representation, the two adapting stimuli with opposing radial motion were successively presented at two different horizontal locations, 7º to the left or to the right, as illustrated by the first two rows of the “retinotopic representation” column of Figure 3.18). The location probed by the test stimulus did not correspond to either the first or the second retinal location of the adapting stimuli, as illustrated by the “retinotopic representation” column of Figure 3.18).

7.2.2 *Procedure*

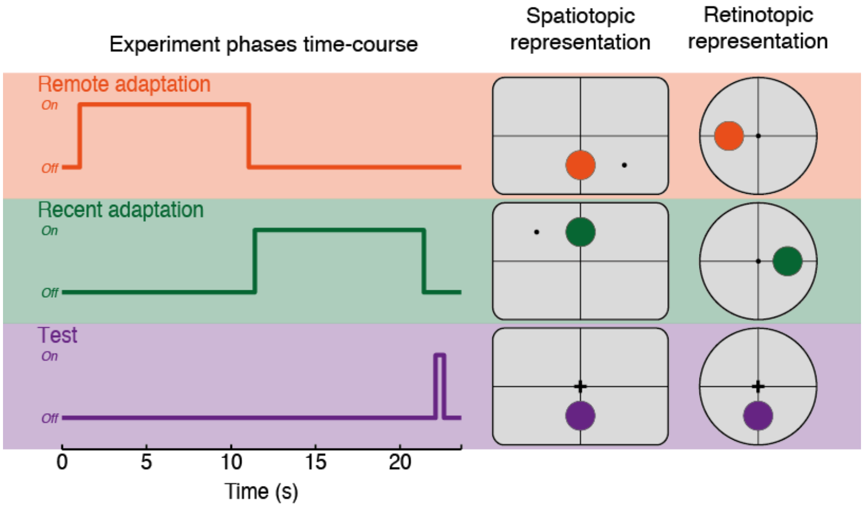

Figure 3.19: A schematic of the main phases of Experiment 5. The illustration describes the time-course of the main experiment phases and their spatial configurations on the spatiotopic and retinotopic representations.

The exact time course of each experiment phase is identical to one presented in section Chapter 35.2.2 of Experiment 5. The Figure 3.19 illustrates the three main phases of the experiment: first the remote adaptation stimulus presented for 10s (“Remote adaptation” orange row of Figure 3.19), second the recent adaptation stimulus presented for 10s (“Recent adaptation” green row of Figure 3.19), and third the test stimulus is presented for 0.5s (“test” purple row of Figure 3.19).

During the previous experiments, the time after which the MAE is probed and the radial motion of the test stimuli were randomized across blocks of five trials. For each observer, both the adapting stimuli's radial motion and the adapting stimulus probed are constant. For instance, during an experiment an observer would see the remote adapting stimulus as expanding, and the recent adapting stimulus as contracting, and the test stimulus would probe the MAE induced by the remote stimulus. The radial motion of the adapting stimuli is counterbalanced across observers.

For the location probed by the test stimulus, the observers took the experiment twice: once for each testing condition (i.e. the recent and remote conditions). The order with which the two conditions were tested was counterbalanced across observers.

7.2.3 *Data analysis*

To establish the MAE's strength for the different durations of motion adaptations and for the different testing condition, I analysed the data collected during the experiment based on the analysed described in section 3.2.3. Briefly, for each observer I obtained an indirect estimate of the MAE's strength for each testing condition and for each duration of motion adaptation.

An ANOVA was conducted to test whether the five stages of cumulative adaptation interacted with recent and remote testing. Three different tests checked that the ANOVA's requirements (i.e. the normality of data distribution, the homogeneity of variance, and the sphericity assumption) were met (see section 1.3.5).

7.3 Results

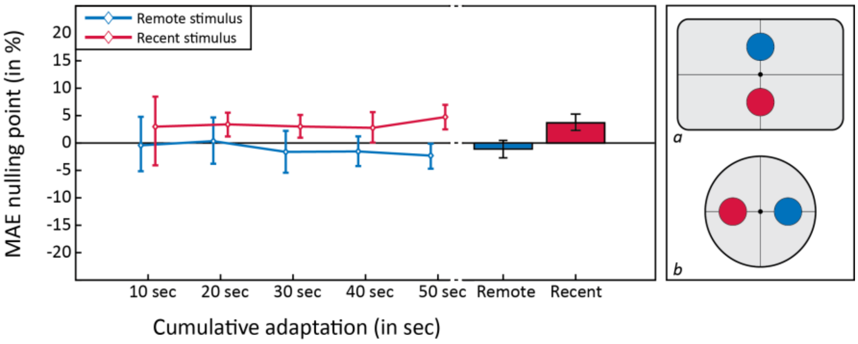

Figure 3.20: a: Cumulative and overall motion after effect adaptation over 50 sec of adaptation for the remote and recent testing motion after effect intensities. The motion after effect intensity is plotted relative to the adapting stimulus motion vector (in %). Error bars represent confidence intervals. The remote cumulative motion after effect (blue line) reaches significance from 50s of cumulative adaption (95% CI [-4.68 -0.12]) and its collapsed motion after effect across time point is not significant (95% CI [-2.70 0.48]). The recent cumulative motion after effect (red line) reaches significance from 20s of cumulative adaption (95% CI [1.22 7.74]) and its collapsed motion after effect across time point is significant (95% CI [2.31 5.27]).

Figure 3.20 shows the magnitude of the MAE as a function of cumulative duration of adaptation for both of the remote and recent testing condition. On average the remote MAE is approximately -1% of the adapting speed, whereas the recent MAE is approximately 4% of the adapting speed. ANOVA confirmed that the duration after which the MAE was measured (10-50s) did not affect its intensity [$F(1, 22) = 0.108$, $p = 0.745$], and there was no significant effect of trial type (recent or remote) [$F(1, 22) = 4.210$, $p = 0.052$], and no interaction between these factors [$F(1, 22) = 2.679$, $p = 0.116$]. However, the trend for a difference between remote and recent conditions is observed in the collapsed over time-points analysis, where the shift is not significant (95% CI [-2.70 0.48]) for the remote, but is significant for the recent (95% CI [2.31 5.27]).

Post-hoc tests revealed that for the last time-point, 50 sec of motion adaptation, the effect observed in the remote condition is significant (95% CI [-4.68 -0.12]). However, the direction of the effect is not consistent with the remote adapting stimulus. As in Experiment 4 (see section 6.3), the MAE measured in the remote condition is in the same direction as the adapting stimulus instead of being in the opposite direction. The MAE measured in the remote condition is consistent with a motion adaptation induced by recent adapting stimulus.

7.4 Discussion

Experiment 5 was designed to measure whether MAEs could be encoded at two different locations on a spatiotopic map. When the testing stimulus probes the motion adaptation induced by the second motion stimulus, a MAE is measured at the spatiotopic location. When the testing stimulus probes the motion adaptation induced by the first motion stimulus (i.e. the remote condition), no MAE is observed at the spatiotopic location, except at 50s of motion adaptation. However, this MAE measured at 50s of motion adaptation is not consistent with the adaptation induced by first motion stimulus.

As in Experiment 4, the motion adaptation induced by the remote adapting stimulus is in the direction of the recent adapting stimulus. To understand the MAE observed at 50s of motion adaptation in the remote condition, it has to be seen as a consequence of the recent adapting stimulus. In Experiment 3 (see section 5.1), I described a possible mechanism which could account for two retinotopic MAEs despite their inducing adapting stimuli being relatively close, because retinotopic MAEs are processed by MT neurons whose receptive field are relatively small (Duffy & Wurtz, 1991; Lagae et al., 1994; Raiguel et al., 1997). However, the MAE in the direction of the second adapting stimulus when I measure the first adapting stimulus seems to indicate that at least some part of the motion adaptation is transferred on MSTd neurons (i.e. the area where radial motion is processed). In this case, the motion adaptation transferred to MSTd would spread across the large receptive field of an MSTd neuron (Duffy & Wurtz, 1991), and would adapt a large span of the visual field. If the adapting stimuli adapt MSTd neurons with very large receptive field, then the adaptation induced by the second adapting stimulus could have erased the one induced by the first adapting stimulus; therefore a MAE in the direction of the second adapting stimulus is observed even when the adaptation induced by the first adapting stimulus is probed.

Overall, the failure of two motion stimuli, with opposite radial motions, to be simultaneously adapted at different locations on a spatiotopic map suggests that the existence of such a representation cannot be revealed by motion adaptation.

8 GENERAL DISCUSSION

The aim of Experiments 1-5 was to establish whether two MAEs could occur on in a spatiotopic map. Experiment 1 demonstrated the sensitivity of the measure as five motion aftereffects were measured at five consecutive time points. The second experiment replicated Turi & Burr, 2012, where a single location was adapted on the spatiotopic map. Experiment 3 investigated the retinotopic map by adapting two stimuli with opposite directions of radial motion at two different locations on the retinotopic map and demonstrated that it is possible to adapt a single frame at two locations. Experiments 4 and 5 failed to find evidence of dual spatiotopic adaptation using a procedure based on Experiment 3.

The importance of the retinotopic map is further demonstrated by the measurement of two MAEs encoded at two retinotopic locations. Physiological studies on the cat visual cortex, imaging ones on the organisation of the human visual cortex, and psychophysical ones on the MAE have all demonstrated the prevalence of the retinotopic frame in encoding stimuli' locations (Gardner et al., 2008; Gaze, Jacobson, & Szekely, 1963; Golomb & Kanwisher, 2012a; Knapen, 2009; Wandell & Winawer, 2011). In line with these results, Experiment 3 indicates that this representation is sufficiently precise for two stimuli with opposite direction of radial motion to be encoded at two different locations. However, the results of Experiment 5 suggest that this degree of specificity does not extent to spatiotopic map.

The single MAE at the spatiotopic location of its adapting stimulus does not seem to reflect an actual capacity of the visual system to encode one location in space. There is – at least, for complex motion stimuli – a consistent body of literature (Melcher, 2005; Nishida et al., 2003; Turi & Burr, 2012), as well as the results of Experiment 2 that demonstrate the possibility to measure a single spatiotopic MAE; however the results of Experiment 5 contradict this hypothesis.

The measurement of a MAE induced by the second adapting stimulus at the location of the first adapting stimulus suggests that the motion adaptation induced by the second adapting stimulus has spread to a large area of the visual field. This phenomenon, the Phantom MAE, could be due to the MT neurons feeding their activity to MSTd neurons whose receptive field are very large (Duffy & Wurtz, 1991), and which are known to process radial motion stimulus (Tanaka et al., 1989). Moreover, there is already evidence indicating that following the presentation of a motion stimulus, a large part of the visual system is adapted to motion (Knapen, 2009). In brief, following the presentation of a motion stimulus, the visual system could be in a general state of adaptation that could induce a phantom MAE.

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Regarding the first main question concerning dual spatiotopic adaptation resulting from a temporary motion adaptation, the results seem to indicate that in a paradigm inspired by Mayhew (1973), two adapting stimuli could not have induced a dual spatiotopic adaptation. A possible explanation could be that Mayhew's findings were not the simple result of a dual adaptation of the visual system following the presentation of motion stimuli at two locations. Instead they can be understood in light of the next two main questions of the thesis: the visual system could have learned that each motion stimulus is presented at a location, or learned the each motion stimulus is always preceded by the same eye-movement.

However, before ruling out the possibility that two MAEs can be encoded at their spatiotopic locations, I need to double check whether a third factor could influence the spatiotopic encoding of MAEs during a dual adaptation experiment. In fact, a difference between the current design and the one used by most spatiotopic paradigms lies in the frequency of the adapting stimulus: relatively low in Experiment 5 and much higher in other experiments (Burr, Tozzi, & Morrone, 2007; Melcher, 2005; Turi & Burr, 2012; Zimmermann et al., 2013). Because of this difference, I hypothesised that a more frequent adapting stimulus could induce a stronger, more defined motion adaptation in the spatiotopic map, which could allow for two spatiotopic MAEs to be measured. The next chapter addresses this issue and aims to circumvent it by demonstrating that a higher frequency of adapting stimulus does not generate spatiotopic MAEs at two different locations.

Chapter 4

DUAL SPATIOTOPIC ADAPTATION IS NOT AFFECTED BY THE FREQUENCY OF THE ADAPTING STIMULUS

1 EXPERIMENT 6

1.1 Abstract

There is long-standing evidence that the visual system is capable of adapting to one optic flow (Brown, 1931; Denton, 1966). Here we ask whether the visual system is capable of adapting to more than one: can we adapt to two optic flows located at two different locations in space? If we understand the adaptation of the visual system as an aftereffect of the prolonged exposure to the optic flow, then the question becomes: can we experience two aftereffects at two locations in space (i.e. at two spatiotopic locations)? The results of Experiment 5 suggest, perhaps surprisingly, that when two motion stimuli are presented, only one is found to be encoded on a spatiotopic map. Here, we investigate whether the training schedule frequency is critical for two motion stimuli to be spatiotopically encoded. In Experiment 6, I used two frequencies of adapting stimulus: a high frequency condition, where both adapting stimuli are presented very frequently, and a low frequency condition, where both adapting stimuli are presented at the same frequency as during Experiment 5. I measured the spatiotopic MAEs induced by two radial motion stimuli in both conditions and found no difference. I concluded that the frequency of the adapting stimulus does not impact their encodings on the spatiotopic reference frame, and that encoding the location of the most recent optic flow could serve as a spatiotopic pointer.

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1.2 Introduction

The world we see is constantly moving, and yet we perceive a relatively stable external world. A solution to this conundrum is to generate an internalized representation of the outside world (i.e. a spatiotopic reference frame) that is anchored in external or body-centric coordinates rather than retinal coordinates. In Experiment 5, we presented a radial motion stimulus at two locations and measured the induced spatiotopic MAE at each location. A spatiotopic MAE was only found at one location. This result suggests that the brain can encode the location of one stimulus but not the locations of two stimuli in a spatiotopic reference frame. Is this really the case? Could it be that the paradigm I used did not allow for the creation of two spatiotopic MAEs.

Time is a critical parameter when generating spatiotopic aftereffects (Zimmermann, Morrone, Fink, & Burr, 2013; Zimmermann, Burr, & Morrone, 2011). Experiment 5 departs from the standard paradigms used to generate spatiotopic adaptation effects in two ways (D. Burr et al., 2007; Melcher, 2005; Turi & Burr, 2012; Zimmermann et al., 2013). First, the adapting stimulus duration that was presented for 10s (see Mayhew, 1973) as opposed to between 3s and 8s in the literature (D. Burr et al., 2007; Melcher, 2005; Turi & Burr, 2012; Zimmermann et al., 2013). Given that longer periods of adaption result in stronger aftereffects (Zimmermann, Morrone, Fink, & Burr, 2013; Zimmermann, Burr, & Morrone, 2011), and that in Experiment 5 the stimuli were presented for 10s at a time (i.e. longer than duration used in the literature), then this duration should have been sufficient for the spatiotopic encoding of the motion stimulus to fully develop.

The second departure of Experiment 5 from the standard paradigms that are used to generate spatiotopic adaptation effects was the overall duration of a single trial (D. Burr et al., 2007; Melcher, 2005; Turi & Burr, 2012; Zimmermann et al., 2013). In Experiment 5, a single trial that lasted for 25s (i.e. the presentation of the fixation points, of the two adapting stimuli and of the test stimuli, see section 3.2.2) instead of 4s to 10s in the literature (D. Burr et al., 2007; Melcher, 2005; Turi & Burr, 2012; Zimmermann et al., 2013). This increase in the duration of a single trial is due to the consecutive presentation of the two adapting stimuli, and it means that the motion adaptation induced by the first adapting stimulus could only be interrogated after the presentation of the second adapting stimulus.

It is possible that the motion adaptation induced by the first adapting stimulus did not survive the presentation of the second adapting stimulus. However, Experiment 3 showed that a 10-s break (i.e. equivalent to the duration of the second adapting stimulus) between a single adapting stimulus and a test stimulus leaves a robust spatiotopic MAE. Thus, the argument that a dual adaptation effect cannot be measured because the first spatiotopic adaptation does not survive the duration of the second adapting stimulus is implausible.

A third factor that might limit the strength of the MAE could be the ratio of the two previous departures: the duration of the adapting stimulus relative to the overall duration of a single trial. The adapting stimuli were only presented once every 25s

(0.04Hz), as opposed to once every 4s to 10s (0.25Hz to 0.1Hz) in other experiments that have examined spatiotopic adaptation (D. Burr et al., 2007; Melcher, 2005; Turi & Burr, 2012; Zimmermann et al., 2013). Consequently, it is possible that the relatively low number of presentation of the adapting stimulus did not allow for the spatiotopic adaptations to fully develop on the spatiotopic reference frame.

Experiment 6 investigated whether increasing the frequency with which the adapting stimulus is presented would increase the likelihood of observing dual spatiotopic adaptation. To this end, I adapted the design of Experiment 5 to accommodate two adapting conditions: the Control condition, 0.04 Hz, identical to the frequency with which the adapting stimuli were presented in Experiment 5; and the rapid condition, 0.4Hz, was ten times faster than the control condition and was similar to the study by Zimmerman and colleagues (2013), which reported a spatiotopic aftereffect with the highest frequency of adapting stimulus in the literature.

The experimental design was simplified relative to that used in Experiment 5. More precisely, I removed the “thousand staircase” paradigm that probed the time course of the MAE. The repeated absence of change in the MAE as the adapting stimulus duration increased means that the time-consuming “thousand staircase” paradigm (i.e. an 80s break has to be included every five trial to measure the time-course of the MAE, see section 1.2.5) is not bringing any additional information about the MAE. Consequently, I rationalised the design and adopted a “top-up” method where the experiment is divided in two main phases: a build-up phase and a “top-up” phase. During the build-up phase, each adapting stimulus was presented for 50s (in 0.5s intervals in the high-frequency condition and 10s intervals in the low-frequency condition). Once the adapting stimuli had disappeared, a test stimulus probed the spatiotopic MAE induced by one of the adapting stimuli. A “top up” followed each test stimulus, a 0.5s period of the adapting stimuli. Both adapting stimulus locations were probed during the testing period.

A larger MAE in high frequency condition would indicate that the motion adaptation induced by both adapting stimuli had been successfully encoded on the spatiotopic reference frame, see Figure 4.1.

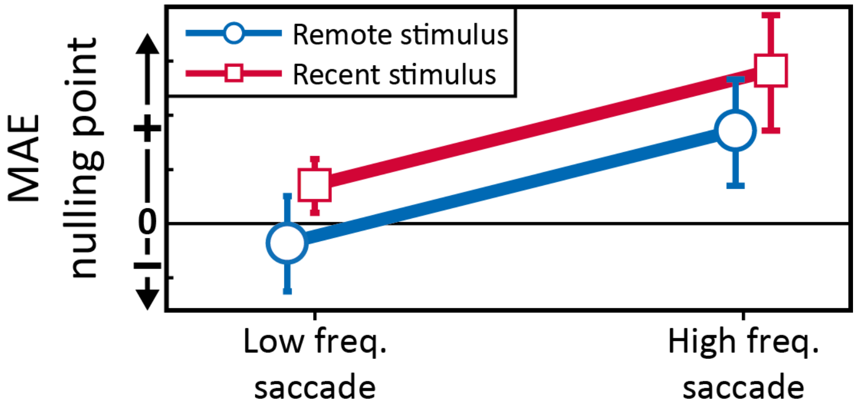

Figure 4.1: Illustration of the experimental hypotheses on the MAE induced by the adapting stimuli in the low and in the high saccade frequency. The values from the low saccade frequency are taken from the experiment 5 (see section 7.3), and they correspond to the average MAEs reported in the remote condition (i.e. the MAE induced by the first adapting stimulus) and recent condition (i.e. the MAE induced by the second adapting stimulus). Error bars represent confidence intervals. I expect the MAE levels reported in both remote and recent conditions to increase when the adapting stimuli are presented at a higher frequency.

1.3 **Method**

1.3.1 *Observers & stimuli*

Nine naive observers and the experimenter participated in the experiment. Their ages ranged from 24 to 26 with an average at 25.2 years. There were 4 females and 6 males observers. All had normal or corrected-to-normal vision.

The adapting stimulus is identical to the one used in the previous experiment and was composed of 400 dots that formed an expanding or contracting radial pattern of motion. The average dot speed was 1.47cm/s (see the general methods section 1.1.2 for further information). The initial test stimulus speed was 1.47cm/s with subsequent test speeds being determined by the psychometric staircase. Individual dots of the test stimulus were presented for a random duration and then replaced at another location in the test stimulus (see general method section 1.1.3 for more detail).

An illustration of the spatial configuration of the stimuli and their mapping onto the retinotopic and spatiotopic location is given by Figure 4.2.

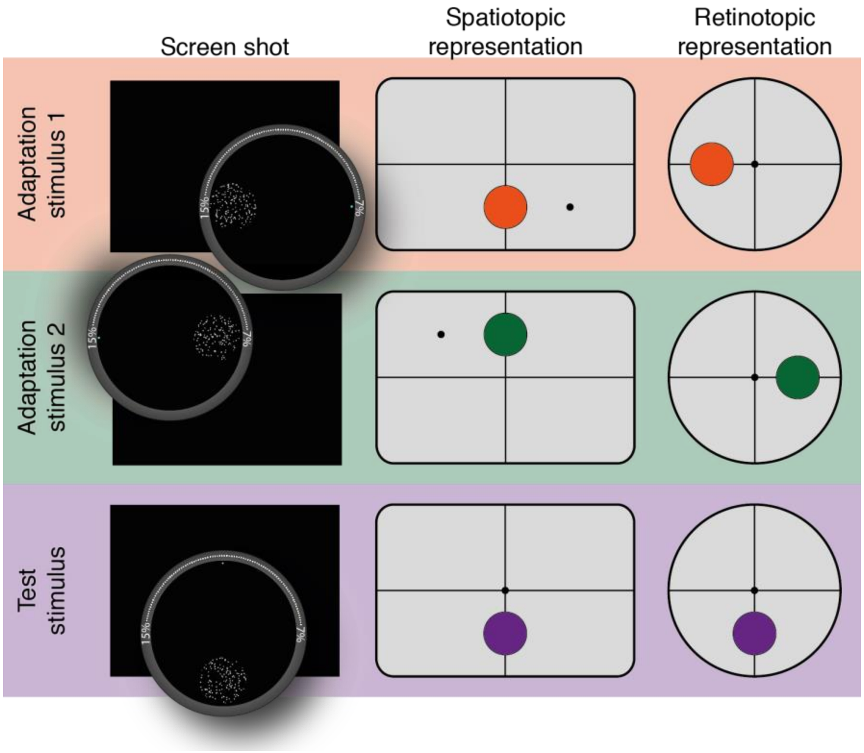

Figure 4.2: Stimulus location as a screenshot, together with an illustration of the location of the stimulus in the spatiotopic and retinotopic reference frames. Rows indicate the experimental phases and columns describe three ways to code the location of the stimulus from each phase. The screen shot is at the scale of 1:15 outside the zooming lens and at the scale of 1:6 inside the zooming lens.

Retinotopic and spatiotopic locations of the two adapting stimuli were identical to the ones described in Experiment 5 (see section 7.2.1). In brief, the spatiotopic locations were located 7º above or below the centre of the screen and the retinotopic locations were 7º to the left or right of fixation

1.3.2 *Procedure*

I chose 50s of initial motion adaptation, as that was the longest duration of motion adaptation in the previous experiments.

In the control condition (i.e. the low frequency condition), the build-up phase consisted of five adapting trials, where in each trial the motion stimuli were presented for 10s, and where each stimulus was presented at a frequency of 0.05Hz.

In the rapid condition (i.e. the high frequency condition), the build-up phase consisted of one hundred adapting trials, where in each trial the motion stimuli were presented for 0.5s, and where each stimulus was presented at a frequency of 0.41Hz.

After the build-up phase, we probed the motion adaptation while keeping adaptation topped up at the two locations. The content of a single test trial of the top-up phase is described in Figure 4.3 below.

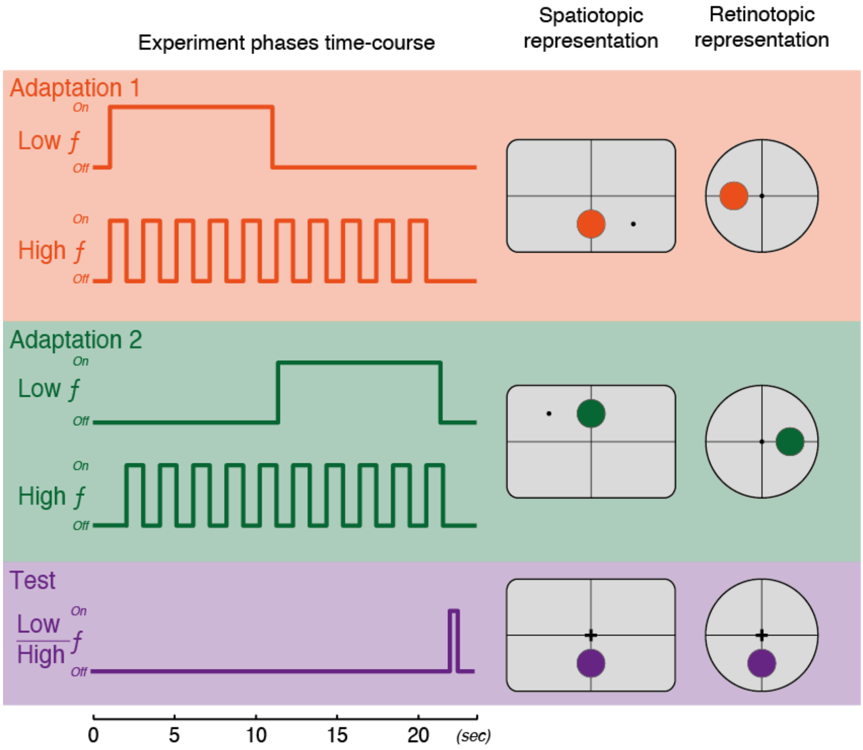

Figure 4.3: A schematic of the main phases of Experiment 6. The illustration describes the time-course of the main phases for each condition of adapting stimulus frequency (high and low frequency illustrated by High ƒ and Low ƒ symbols, respectively) and the spatial configurations of the stimuli on the spatiotopic and retinotopic reference frames.

Figure 4.3 illustrates the main stages of a test trial time-course for the two eye-movement frequency conditions. For the control condition, the time-course of a single trial is identical to the one described in Experiment 5 (see section 7.2.2). The time-course of the rapid condition is identical to one from the low-frequency saccade condition with one exception: because of the adapting stimuli's duration of only 0.5s, instead of the 10s of the control condition, the adapting stimuli were presented 20 times per test trial in the high frequency condition to match the adaptation duration of the low frequency trial.

Because of the added test stimulus during the test phase, the frequencies of the adapting stimulus conditions were slightly modified from their values in the initial adaptation phase. The added test stimulus, whose duration was identical in both low and high frequency condition, increased the total duration of the trial but the adapting stimuli were still presented for the same duration, so their presentation frequency decreased: from 0.05Hz to 0.04Hz in the low frequency condition and 0.41Hz from to 0.4Hz in the in the high-frequency one.

Experiment 6 included two within-subject variables: the frequency of adapting stimulus presentation (see section 1.2), and the test stimulus recency. We ran both conditions (control and rapid) on each observer. The second variable, the test recency is the same as in Experiment 5 and corresponded to the time after which the motion adaptation was interrogated, either immediately after (i.e. recent condition) or after a delay due to the presentation of the second adapting stimulus (i.e. remote condition), see section 1.3.2.

The order of the adapting stimulus frequency was counter-balanced: half of the observers were first probed on the rapid condition then the control condition, and the other half started with the control condition and then received the rapid condition. The test recency condition probed on each trial was randomized, and the MAEs induced at the remote and recent locations were probed by four independent staircases. Half were ascending staircases and half were descending ones. In the both conditions, to avoid fatigue effects, the experiment was split in two sessions.

The order of the locations in which the stimuli were presented and the order of their direction of radial motion was fully counterbalanced across the experiment. Each observer viewed the two motion stimuli in the same order and at a constant location throughout the experiment; however across observers, the order of location and the order of direction of motion was counter-balanced.

1.3.3 *Data analysis*

To estimate the value of a MAE for an observer in a given condition, a curve was fitted between the test stimulus motion velocities presented during the experiment in the condition and the observer's responses to these motion intensities. From this curve, an estimate of the Point of Subjective Equality (PSE) was determined that provides an index of the MAE's strength, and through use of bootstrapping (see section 1.3.4 for details) I also obtained the margin of error of this estimate: the PSE's confidence interval (see general method for precise description). The issues of central interest were whether the frequency of the adapting stimulus and test recency affected the MAE.

An ANOVA with two within-subject variables was conducted. The prediction was that that the high frequency of adapting stimulus would result in greater spatiotopic adaptation than the low frequency condition, and that there might also be some effect of the recency of the test stimulus (cf. Experiment 5). The ANOVA's assumptions (i.e. the normality of data distribution, the homogeneity of variance, and the sphericity assumption) were checked by three different tests (see section 1.3.5 of Chapter 2) and corrections were applied when appropriate.

1.4 **Results**

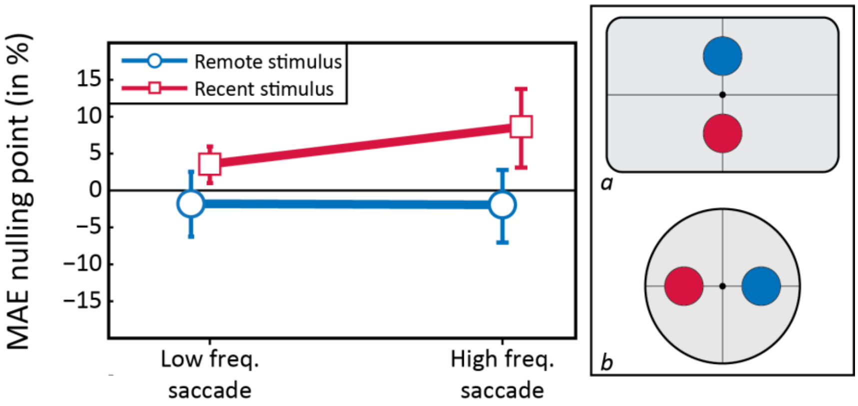

Figure 4.4: Motion after effect intensity after 50s of motion adaptation in the high and low adapting stimulus frequency conditions and for both the remote and the recent testing. The motion after effect intensity is indicated relative to the adapting motion stimulus (in %). Error bars represent ± SEM. ***b****: Illustration of the adapting stimulus locations on both the spatiotopic and retinotopic reference frames. The motion after effect of the remote condition was either tested 10.7s after the adapting stimulus was removed in the low frequency condition or 1.7s after the adapting stimulus was removed in the high frequency. The motion after effect of the recent condition was tested 0.7s after the adapting stimulus was removed in both frequency conditions.*

Figure 4.4 shows the MAE magnitude at 50s of cumulative adaptation for both of the remote and recent testing – corresponding to the two spatiotopic locations – in the high and low frequency conditions. Inspection of the figure suggests that spatiotopic MAEs in the remote condition do not seem to be affected by the adapting stimulus frequency but are slightly in the opposite direction compared to their adapting stimulus. Inspection of the figure also indicates that the MAE in the recent condition is more apparent in the high frequency condition compared to the low frequency condition. However, ANOVA showed that there was neither a main effect of the adapting stimulus frequency [F(1, 4) = 0. 47, p = 0.838], nor a main effect of the test recency [F(1, 4) = 0.47, p = 0.840], nor an interaction between the adapting stimulus frequency and the test recency [F(1, 4) = 2.294, p = 0.204]. Post-hoc tests revealed that the effect observed in the recent condition is significant in the low frequency condition (95% CI [0.5 2.98]) and in the high frequency condition (95% CI [1.55 6.88]).

1.5 Discussion

The aim of the experiment was to explore the effect of the frequency with which the adapting stimulus was presented on simultaneous motion adaptation (MAE) at two different spatiotopic locations. To this end, two conditions were compared: a high frequency condition (0.4Hz) and a low-frequency one (0.04Hz). I found that when the testing stimulus probes the motion adaptation induced by the second motion stimulus, a MAE is measured at the spatiotopic location in both frequency conditions; however I found that the frequency of the adapting stimulus did not significantly impact the spatiotopic MAEs perceived – dual adaptation was still not found. This result illustrates that the spatiotopic reference frame is unlikely to be affected by the frequency of the adapting stimulus under the experiment’s current design.

Commented [DBSDE&S14]: Comment 8 about inferring from the null result

1.5.1 *Concluding remarks on a possible dual spatiotopic MAE*

The experiments reported in Chapter 3 and Chapter 4 investigated whether the sustained presentation of two complex motion stimuli at two locations could generate spatiotopic MAEs. In Chapter 3, I observed that the sustained presentation of two complex motion stimuli generated two retinotopic MAEs. I also noticed that adaptation to one complex motion stimulus induced a spatiotopic MAE (Turi & Burr, 2012). However, I failed to demonstrate dual spatiotopic MAEs, but instead found a single spatiotopic MAE involving the most recent of stimuli that had been adapted. In Chapter 4, I failed to show that the frequency of adapting stimulus impacted the spatiotopic encoding of two complex motion stimuli. The similarity between the MAEs obtained in the low-frequency condition of Experiment 6 and the MAEs obtained in Experiment 5 constitutes further evidence that a dual spatiotopic motion adaptation is not possible with the present procedures. In conclusion, the results presented in both Chapter 3 and Chapter 4 consistently point toward the conclusion that only one location can be encoded onto a spatiotopic reference frame.

1.5.2 *Implications for the spatiotopic MAE findings*

If the findings do not reflect a methodological problem, then why is it not possible to generate two spatiotopic MAEs? There seem to be three possible explanations: either radial motion stimuli cannot generate two spatiotopic MAEs, or MAEs cannot reveal the existence of the spatiotopic reference frame, or the spatiotopic MAE induced by the lasted motion stimulus presented reflects another process. I will evaluate each of these possibilities in turn.

First, since complex motion stimuli such as radial motion stimuli are more likely to be encoded onto a spatiotopic reference frame than less complex types of motion stimulus (Melcher, 2005; Turi & Burr, 2012), the radial MAEs should be encoded onto a spatiotopic map. However, because radial motion stimuli are processed by neurons with receptive field as large as 40º (Duffy & Wurtz, 1991), there is a possibility that the adapting stimuli could adapt large areas of the visual field, the Phantom MAE. This explanation is consistent with the results of Experiments 5 and with the trend observed in experiment 6: in the remote condition of both experiments (i.e. when the test stimulus was probing the motion adaptation induced by the first

Commented [DBSDE&S15]: Comment 1 about the Phantom MAE adapting stimulus), the MAE was in the opposite direction compared to the first adapting stimulus (i.e. the MAE was in the same direction as the first adapting stimulus). If this explanation can apply to Experiment 5 and to the trend observed in Experiment 6 – the remote MAE was in the opposite direction compared to its adapting stimulus -, that MAE was not significantly different from 0 and can not be attributed to a Phantom MAE.

The observation reported in Experiment 5 can result from a Phantom MAE consequence of a general adaptation of the visual system: because both adapting stimuli are processed by MSTd neurons with overlapping receptive field, the motion adaptation induced by the first adapting stimulus is erased and replaced by the one from the second adapting stimulus. Evidence of a general adaptation of the visual field following the presentation of a motion stimulus already exist in the literature (Knapen, 2009; Price et al., 2004; Snowden & Milne, 1997); therefore, when probing the adaptation induced by the first adapting stimulus, there is a possibility that due to a general adaptation of the visual system, I actually probed the one induced by the second stimulus.

The general adaptation of the visual system possibly observed in Experiments 5 and 6 is not contradicting the results from Experiment 3, where two retinotopic MAEs are observed, because the retinotopic frame is the primary frame of spatial encoding. As mentioned in Chapter 3 §8, the visual cortex areas are organised retinotopically, which confers the retinotopic reference frame its default spatial organisation status (Gardner et al., 2008; Gaze et al., 1963; Golomb & Kanwisher, 2012a; Knapen, 2009; Wandell & Winawer, 2011). Like in Experiments 5 and 6, a general adaptation of the visual system probably occurs in Experiment 3, but since the adapting stimuli are strongly encoded onto the retinotopic reference frame, the effects of the general adaptation are not strong enough to override the retinotopic adaptation. The idea that the results from Experiment 5 and 6 are due to a general adaptation of the visual system is therefore still valid.

Second, since I could only observe a single spatiotopic adaptation, and a spatiotopic reference frame encoding only one location in space drastically limits the interaction we can have with surrounding objects (Land, 2014), I argue that MAEs did not reveal a spatiotopic reference frame in the form of a fully defined representation of the exterior world. Instead I argue that the spatiotopic reference frame can only encode one object based on its spatial location, and I reject the idea that there is spatiotopic map made available to the visual system (see Experiment 5 and 6). More specifically I hypothesise that the visual system has access to the retinotopic reference frame plus a spatiotopic pointer that points to the last object by taking into account eye-movements. There is already some evidence in the literature that a short-term visual memory might preserve location information (Curtis, 2006; Todd, Todd, Marois, & Marois, 2004; Umeno & Goldberg, 2001). With this explanation, the spatiotopic pointer could act as a compass that gives an indication to where “north” is with each new eye-movement. I will expand upon this analysis in my final chapter.

Commented [DBSDE&S16]: Comment 4 about the explanation of the failure of dual spatiotopic MAE experiments

Box 1. Thesis next question

- Chapters 3 and 4 investigated whether two MAEs could be measured, and they revealed that two radial motion stimuli could produce two retinotopic MAEs but not two spatiotopic MAEs.
- Dual motion adaptation is only observable in the reference frame where the MAE is mainly processed: the retinotopic reference frame.
- I now address the second experimental question on dual adaptation: can dual adaptation occur when the visual system has learned that the motion stimuli occur at specific spatiotopic locations.
- More precisely, in Chapter 5, I investigate whether two radial motion stimuli can be associated to two spatiotopic locations as is suggested by Haijiang and colleagues (2006).

Chapter 5

THE VISUAL SYSTEM CANNOT LEARN THAT RADIAL MOTION STIMULI ARE PRESENTED AT TWO SPATIOTOPIC LOCATIONS

1 ABSTRACT

It has recently been suggested that our visual system is able to learn the lasting relationship between a spatiotopic location (i.e. the location of an object in the real-world coordinates) and an attribute of the visual scene (Haijiang et al., 2006). However, whether the visual system can learn to form more than one association remains an open question. To answer this question, I investigate whether or not the radial motion properties of two stimuli can be associated with their spatiotopic locations, when each radial motion stimulus is constantly presented at a specific spatiotopic location. The results indicated that no association between the spatiotopic location of a stimulus and its direction of radial motion was formed.

2 INTRODUCTION

In the motorway example described in the general introduction, we set a situation where the driver is exposed to two different optic flows: one on our side of the road generated by the other cars overtaking us, a contracting optic flow, and one on the opposite side of the motorway induced by the cars driving in the other direction, an expanding optic flow. Can the driver adapt to these two different regions of optic flow?

Commented [DBSDE&S17]: Comment 10.2 about the repetition of the motorway exemple

The experimental work described in Chapters 3 and 4 investigated the role of aftereffects in the dual adaptation of the visual system following the presentation of two optic flows at two locations in space (i.e. one for each side of the motorway). The results suggested that different MAEs could not occur simultaneously at two different spatiotopic locations. However, other mechanisms could allow dual adaptation of the visual system to take place, and amongst those is the possibility that the visual system could implicitly learn that each side of the motorway corresponds to a specific optic flow. More specifically, the visual system could learn to associate each optic flow with a precise spatiotopic location, which could induce adaptation of the visual system at two different spatiotopic locations.

The literature on prism adaptation suggests that the visual system is capable of learning an association between two perceptual dimensions (i.e. perceptual learning), even if one is not explicitly told to learn this association (Stratton, 1896, 1897; Welch, 1974). In prism adaptation experiments, subjects wear prism-glasses that distort their visual environment by a certain angle and that impair their ability to make self-movement (e.g. they reach for objects at the wrong place, or stumble into walls). Yet, if the glasses are worn for a sufficient duration, the subjects stop making erroneous self-movement. The visual system has adapted to the new requirements imposed on the visual scene by the prism glasses: the self-movements have been recalibrated based on the new optical rearrangement without explicit instructions from the experimenter.

Arguably, the magnitude of the optical distortion induced by the prism-glasses, and their immediate effect on self-movements, could be considered as an instance of explicit learning where subjects are forced to consciously correct their movements; however cue-recruitment experiments suggests that visual adaptation occurs even when subjects are unaware of the new relationship between perceptual dimensions (Adams, Graf, & Ernst, 2004; Harrison & Backus, 2010; Jain & Backus, 2010; Jain & Backus, 2013; Seitz & Watanabe, 2003). In these experiments a cue is used to, without the subject’s awareness, create or modify a relationship between two variables. For instance, patches that are brighter at the top are generally seen as convex, whereas patches that are brighter at the bottom are generally seen as concave because we expect the light to come from above (Sun & Perona, 1998). This existing relationship between the brightness of a surface and its shape can be reversed by consistently presenting new haptic cues: a concave surface when a patch is brighter at the top, and a convex surface when a patch is brighter at the bottom (Adams et al., 2004). After several attempts, subjects unconsciously associate the brightness of a patch with the haptic cues, and this new relationship remains even when the haptic cues are not presented (e.g. a patch brighter at the top is seen as concave). In other word, visual adaptation can occur even when subjects are unaware of the new relationship between perceptual dimensions.

If the visual system can learn to associate perceptual dimensions without the subject's awareness, can this association occur when one of the perceptual dimensions is space? Indeed, there is evidence that the visual system can learn to associate a moving percept to a location in space (Haijiang et al., 2006). During the Haijiang and colleagues (2006) experiment, observers were constantly presented a unidirectional rotation stimulus at a one location in space (i.e. at a spatiotopic location). After maintaining this contingency for a sustained duration, observers were presented a bi-stable rotating stimulus (i.e. a stimulus whose direction of rotation is ambiguous) at the location of a unidirectional rotation stimulus. Observers consistently saw the bi-stable stimulus to rotate in the same direction of the unidirectional rotation stimulus when it was presented at the location of the unidirectional rotation stimulus. This result was interpreted as reflecting the formation on an association between the direction of the rotation of the stimulus and its location.

Commented [DBSDE&S18]: Comment 1 about Passive associative learning

In Haijiang and colleagues' experiment, the stimulus was presented at a fixed location on the screen. As eye movements were not controlled, the retinal location of the stimulus varied. Therefore it is likely the percept was associated with the spatiotopic location of the stimulus rather than its retinotopic location. This result suggests that we are able to associate a percept of motion with a location in space. If we extrapolate from the findings of Haijiang and colleagues (2006), then perceptual learning may provide a mechanism that allows a driver to simultaneously adapt to different patterns of motion on each side of the motorway. Consequently, the visual system might be able to learn to associate the two optic flows encountered whilst driving on a road to their respective spatiotopic locations.

3 EXPERIMENT 7: LEARNING THAT TWO RADIAL MOTION STIMULI ARE PRESENTED AT TWO SPATIOTOPIC LOCATIONS: PART 1

3.1 Introduction

Experiment 7 investigated whether or not the radial motion of two stimuli can be associated with two spatiotopic locations by measuring whether the visual system adapts to the different radial motion at two spatiotopic locations. To this end, I divided the experiment into three phases: a pre-test, an adaptation and a post-test phase. A difference observed between the pre-test and the post-test should be attributed to the 40 min adaptation phase, where observers had to alternate their gaze every 10sec from one motion stimulus to the other to implicitly learn the relationship between the stimuli's spatiotopic location and their radial motion. During the adaptation phase, subjects were continuously and consistently exposed to the relationship between the stimuli's spatiotopic location and their radial motion, and this was thought to induce an association between the two as had been suggested in the perceptual learning literature (Bompas & O'Regan, 2006b; Haijiang et al., 2006; Seitz & Watanabe, 2003; Watanabe, Náñez, & Sasaki, 2001).

Subjects also had to make eye-movements toward the adapting stimuli in the experiments of Chapters 3 and 4, but there are two reasons for which an associative process is unlikely to have taken place in these experiments. First, in Experiments 1 to 4, the type of radiation presented at one location was randomised from one block to the other, so the possibility that subject had learned the relationship between location and radiation is highly unlikely. Second, in Experiment 5 and 6, subjects were not continuously exposed to the relationship between a stimulus' location and its radiation: every five trials, they had a break that lasted the entire duration of the five trials. If it is not impossible that subjects had learned the relationship between a stimulus' location and its radiation during these blocks of five trials in Experiments 5 and 6, the increased exposure to this relationship in the adaptation phase of Experiment 7 should induce a much stronger association and yield much stronger MAEs (Bompas & O'Regan, 2006b; Haijiang et al., 2006; Seitz & Watanabe, 2003; Watanabe, Náñez, & Sasaki, 2001). Overall, we argue that an associative process is unlikely to explain the results of the Chapters 3 and 4 and that Experiment 7 should induce an association between a stimulus' spatiotopic location and its radiation.

Commented [DBSDE&S19]: Comment 5 about the difference between Experiments 1-6 and Experiment 7 onward.

For consistency with the previous set of experiments, the adapting stimulus parameters were taken from the Experiments 5 and 6. The adaptation phase should create associations between the spatiotopic location of the stimuli and their radial motion. Pre-test and post-test phases were identical and measured the motion adaptation at the two spatial locations of the motion stimuli before and after the adaptation phase. The method to measure the motion adaptation was identical to the experiments and consisted in psychophysical staircases aimed at finding the physical motion stimulus that nulls the perceived one. An increase in motion adaptation strength between these two phases would indicate that associations between the location of the stimuli and their radial motion had formed, and that these associations lead to an adaptation to the radial motion when the stimuli were presented at their encoded spatiotopic locations.

3.2 Method

3.2.1 *Observers & stimuli*

Five naive observers and the experimenter participated in the experiment. Their ages ranged from 24 to 25 with an average at 24.7 years. There were 2 females and 4 males observers. All had normal or corrected-to-normal vision.

The adapting stimulus – identical to the one used in previous experiment – was composed of 400 dots that formed was either an expanding or contracting radial pattern. The average speed of the dots was 1.47cm/s (see a precise definition in general method section 1.1.2). Individual dots were presented for a random duration and then replaced at another location in the test stimulus (see general method section 1.1.3 for more detail). The initial test stimulus speed was either 1.47cm/s or -1.47cm/s; the psychometric staircase determined the following test speeds.

The Figure 5.1 below illustrates the spatial configuration of the stimuli and how they map onto the spatiotopic and retinotopic reference frames.

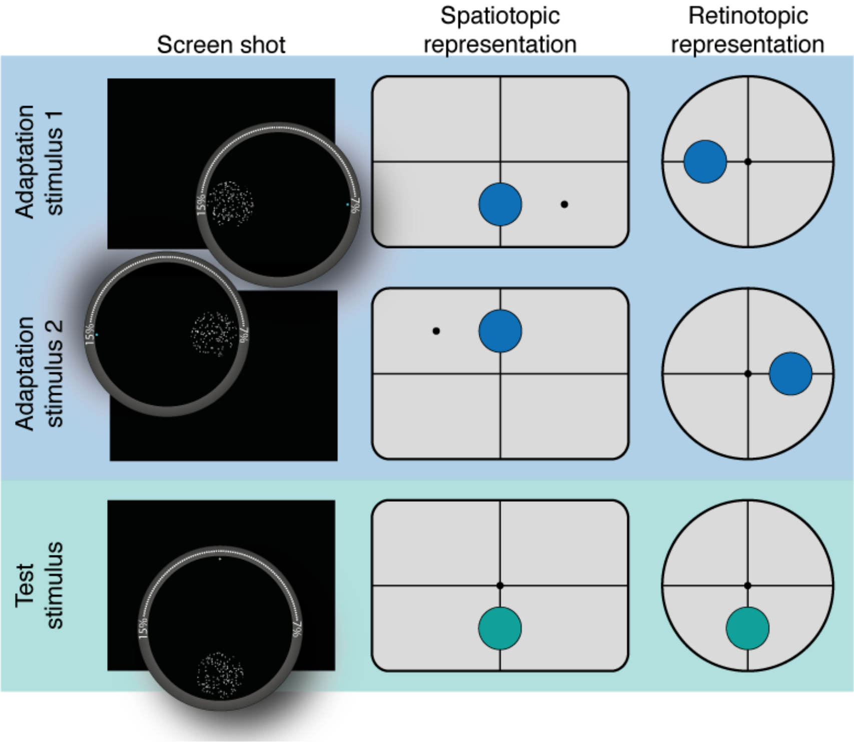

Figure 5.1: Stimulus location's screen shot and illustration of its location in the spatiotopic and retinotopic reference frames. Rows indicate the experiment phase whereas columns describe three ways to understand the stimulus location. The screen shot is at the scale of 1:15 outside the zooming lens and at the scale of 1:6 inside the zooming lens.

The spatial configuration of the stimuli was identical to Experiment 5, see section 7.2.1 for detail. Briefly, the two adapting stimulus were presented at two locations on the spatiotopic representation, 7º above or below the screen's centre; however on the retinotopic representation, the two adapting stimulus were presented at two other locations, 7º to the right or to the left of the centre of the retinotopic representation.

3.2.2 *Procedure*

The experiment was divided into three consecutive phases: a pre-test followed by an adaptation phase and a post-test. The pre-test and post-test phases were identical, except the former took place before the adaptation, whilst the latter took place after adaptation. In the test phase, two independent staircases with opposite starting points probed the intensity of the motion adaptation at the each of the two locations. On average, the test phases lasted 4 to 5 min. The adaptation phase lasted approximately 40min and was composed of one-hundred adaptation trial, which cumulatively adapted each of the two locations for 1000sec. During that phase, observers were given three breaks, one every 10min.

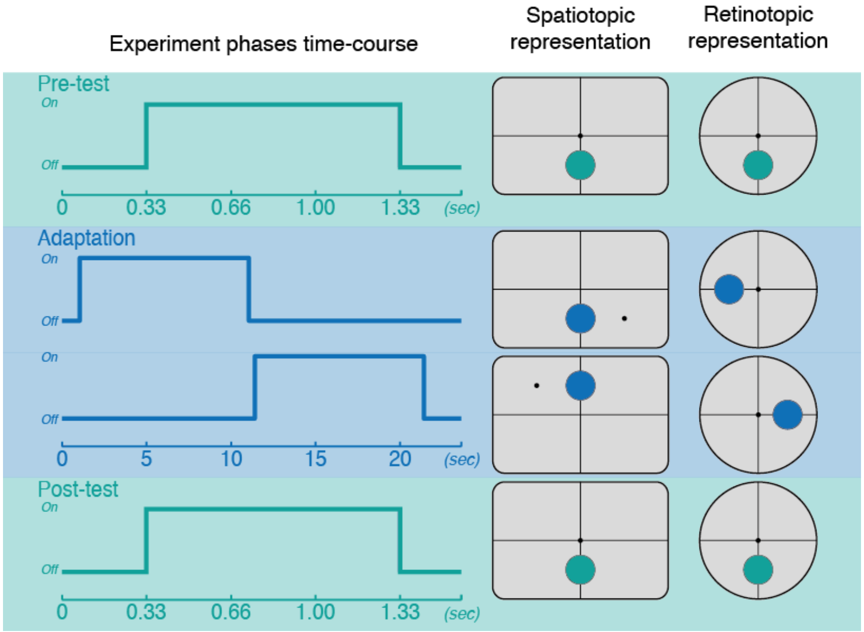

Figure 5.2: A schematic of the main phases of Experiment 7. The illustration describes the time-course of the main experiment phases and their spatial configurations on the spatiotopic and retinotopic representations. The experiment was divided into three phases, a pre-test, an adaptation, and a post-test. During the adaptation, two radial motion stimuli were each presented at spatiotopic location (e.g. an expanding stimulus in the upper part of the screen and a contracting stimulus in the lower part of the screen). During the pre-test and the post-test, the level of motion adaptation of observers was probed at the spatiotopic locations of the two adapting stimuli.

The main components of a single trial are illustrated in Figure 5.2; a finer description of a single trial time-course is given for each condition in the next paragraph. In brief, the pre-test and post-test phases only display the test stimulus, whereas the adaptation phase only displays the two adapting motion stimuli.

The exact time-course for pre-test or post-test phases' single trial was as follow: a fixation point was displayed at the centre of the screen for the 0.35s. Subsequently, the fixation point turned into a fixation cross, and a test stimulus appeared on the screen for 1s as illustrated in the "Test" cyan row in Figure 5.2. The test stimulus on a single trial could be either located in the upper or lower part of the screen, at the two possible spatiotopic locations of the adapting stimulus. When the fixation-cross appeared, the observer was instructed to press a key indicating the direction of radial motion (see section 1.2.3). If no key was pressed within the allocated time (indicated by the fixation cross disappearing), the staircase's step was not incremented and stayed the same (see section 1.2.3).

The time-course for a single trial from the adaptation phase was as follows: a fixation point was displayed at the centre of the screen for the 0.35s and was followed by a 0.35s arrow indicating the next fixation point's location. Once the arrow disappeared, a fixation point was solely drawn on screen for 0.35s and was then drawn in conjunction with the first adapting stimulus for an extra 10s as illustrated in the "Adaptation" first blue row in Figure 5.2. At the end of the "Adaptation 1" period, a 0.35s fixation point was solely displayed at a new location. During the next 10s, the fixation point and the second adapting stimulus were displayed together on the screen as illustrated in the "Adaptation" second blue row in Figure 5.2.

The order of the adapting stimuli was maintained constant throughout an experiment but was counterbalanced across observers.

3.2.3 *Data analysis*

The analysis to obtain a measurement of the motion adaption experienced during the experiment is identical to the previous chapter analysis. In brief, the test stimulus motion velocities presented during the experiment and the responses observers gave for each are linked by a curve to find an index of the motion adaption velocity and the margin of error of this estimate (for a precise description of the process, see section 1.3 of the general method).

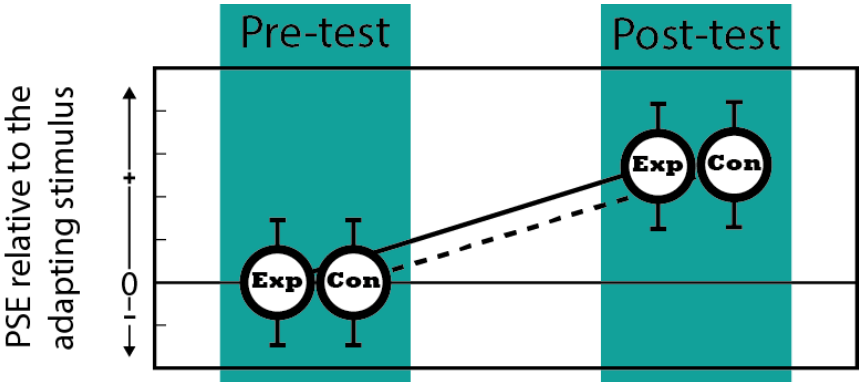

Figure 5.3: Illustration of the experimental hypotheses on the motion adaptation levels before and after perceptual learning motion adaptations. The motion after effect intensity is plotted relative to the adapting stimulus motion vector, so the motion adaptation levels of both expanding and the contracting stimuli are increased by the adaptation phase. Error bars represent confidence intervals. I expect the motion adaptation levels of the pre-test phase to not be significantly different from 0, and the ones of the post-test phase to have significantly increased.

I conducted an ANOVA with two within-subjects variables: the testing condition that is the pre-test and the post-test, and the adapting stimulus's radial motion that is the expanding and contracting motion. I expected the motion adaptation induced by the adapting stimuli to be stronger in the post-test than in the pre-test, and I expected this growth to be in positive relative to the adapting stimulus (see Figure 5.3).

The ANOVA's assumptions (i.e. the normality of data distribution, the homogeneity of variance, and the sphericity assumption) were checked by three different tests (see section 1.3.5) and corrections were applied when appropriate.

3.3 Results

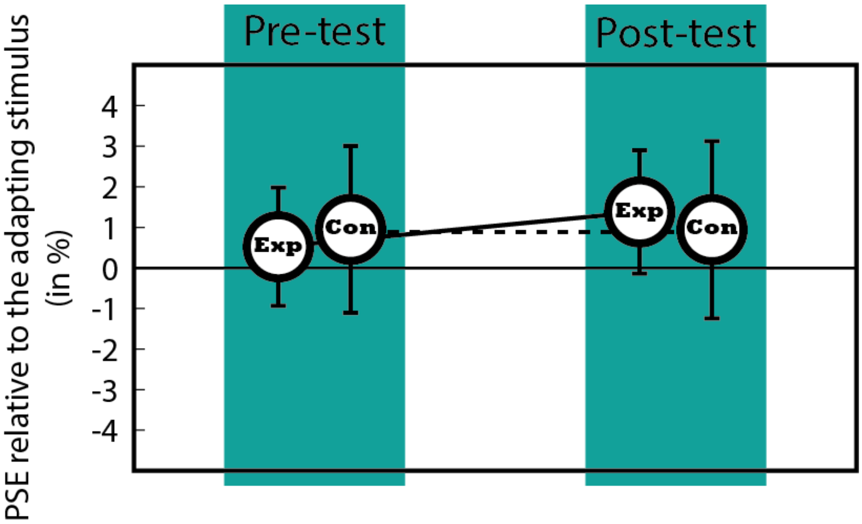

Figure 5.4: Motion adaptation levels intensity before and after 40 min of perceptual learning motion adaptations. The motion after effect intensity is plotted relative to the adapting stimulus motion vector (in %). Error bars represent confidence intervals. None of the motion adaptation levels are significantly different from 0 (95% CI [-0.94 1.98] and 95% CI [-0.98 3.14] and 95% CI [-0.14 2.90] and 95% CI [-1.06 3.32]).

Figure 5.4 shows the magnitude of the motion adaptation levels before and after the 40 min perceptual learning adaptation for the two locations. Inspection of this figure suggests that there was a bias in motion adaptation at the locations of the adapting stimuli (i.e. in the pre-test, observers perceived radial motion to be slightly expanding at the location of the contracting stimulus and slightly contracting at the location of the expanding stimulus), but there certainly is no evidence that this changed as a function of when it was interrogated (pre- or post-test). These observations were confirmed by the results of statistical analysis, which showed that there was no effect of time of testing [$F(1, 6) = 0.204$, $p = 0.661$], no effect of the type of motion radial motion [$F(1, 6) = 1.879$, $p = 0.200$], and no significant interaction between the time of testing and the type of motion radial motion adapted [$F(1, 6) = 0.035$, $p = 0.856$].

3.4 Discussion

Experiment 7 establishes that when observers receive training designed to associate the adapting stimulus’s radial motion to its spatiotopic location, dual adaptation is not apparent. More precisely, the adaptation measured at the two locations was neither altered by the adaptation phase or by the stimulus' radial motion, nor by the interaction of the two. In brief, the visual system did not adapt to the direction of radial motion of the stimuli at their spatiotopic locations.

The absence of dual motion adaptation could be linked to the visual system not being able to associate each direction of radial motion with a specific spatiotopic location. However, Bompas and O'Regan (2006) reported a dual colour adaptation based on a paradigm where adapting stimuli are presented for a much shorter duration than in Experiment 7. The next experiment investigates that decreasing the duration of presentation of the adapting stimuli could lead the visual system to adapt two directions of radial motion based on their spatiotopic locations.

4 EXPERIMENT 8: LEARNING THAT TWO RADIAL MOTION STIMULI ARE PRESENTED AT TWO SPATIOTOPIC LOCATIONS: PART 2

4.1 Introduction

In one experiment reported by Bompas and O'Regan, two colour stimuli were presented after observers made specific eye-movements. The colour stimuli were only presented for a very short duration, 0.4s, and Bompas and O'Regan reported colour adaptation specific to the preceding eye-movements, which suggests that each colour stimulus was successfully associated to a preceding eye-movement.

Experiment 7 failed to find a dual motion adaptation. One difference between the study by Bompas and O'Regan (2006) and Experiment 7 was that the adapting stimuli in Bompas and O'Regan were shorter (0.4s against 10s). In Experiment 8 the duration of the adapting stimuli was decreased from 10sec to 0.4s. It seemed possible that this change might encourage he formation of associations between the radial motion of the adapting stimuli and their spatiotopic location. Apart from this change, the method used in Experiment 8 was identical to the one described in Experiment 7.

4.2 Method

4.2.1 *Observers & stimuli*

Nine naive observers and the experimenter participated in the experiment. Their ages ranged from 24 to 26 with an average at 25.2 years. There were 4 females and 6 males observers. All had normal or corrected-to-normal vision.

The test and adapting stimuli were the same as in section 3.2.1.

The mapping of the stimuli on the retinotopic and spatiotopic representation is identical to the one described in Experiment 7 (see section 3.2.1). In short, the locations adapted on the spatiotopic representation differed from the ones adapted on retinotopic representation.

4.2.2 *Procedure*

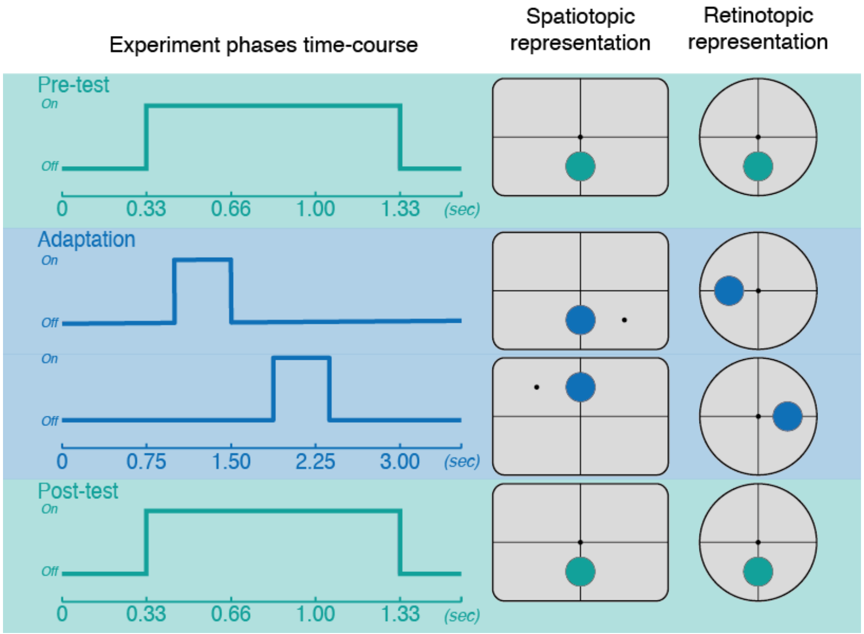

Figure 5.5: A schematic of the main phases of Experiment 8. The illustration describes the time-course of the main experiment phases and their spatial configurations on the spatiotopic and retinotopic representations. The experiment was divided into three phases, a pre-test, an adaptation, and a post-test. During the adaptation, two radial motion stimuli were each presented at spatiotopic location (e.g. an expanding stimulus in the upper part of the screen and a contracting stimulus in the lower part of the screen). During the pre-test and the post-test, the level of motion adaptation of observers was probed at the spatiotopic locations of the two adapting stimuli.

Figure 5.5 illustrates the main stages of a single trial time-course for each experimental phase. The procedure was the same as Experiment 7, see section 3.2.2, with one exception: the adapting stimuli of the adaptation phase were only displayed for 0.5s.

The overall duration of each of the three phases of the experiment was unchanged: 4-5 min for the pre-test and post-test phases and 40min for the adaptation phase. The number of trial in adaptation phase rose from one hundred in Experiment 7 to five hundred in Experiment 8.

4.2.3 *Data analysis (see section 3.2.3)*

The data underwent the same analysis as described in Experiment 7, see section 3.2.3. Briefly, individual data were analysed along the two independent variables (i.e. time of testing and adapting stimulus's radial motion), and a mixed-design repeated measure ANOVA was run to measure the effect of the independent variables at the group level.

4.3 Results

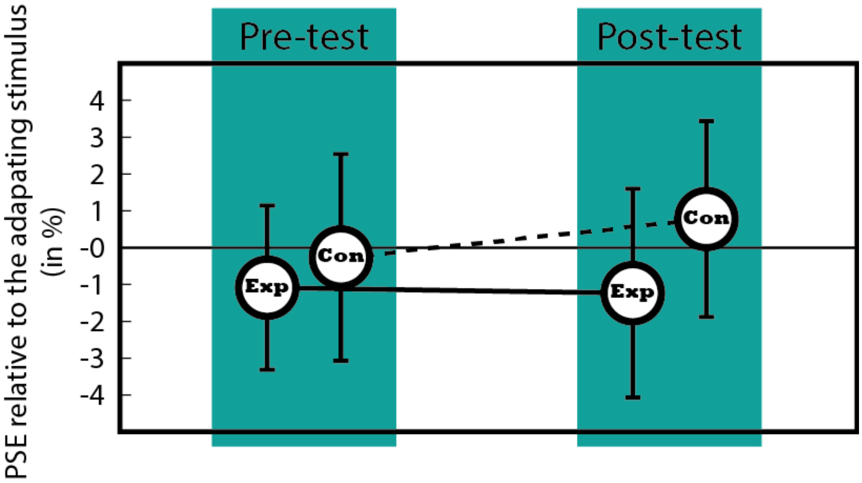

Figure 5.6: Motion adaptation levels before and after 40 min of perceptual learning motion adaptations. The motion after effect intensity is plotted relative to the adapting stimulus motion vector (in %). Error bars represent confidence intervals. None of the group motion adaptation levels significantly differed from 0: (95% CI [-3.32 1.14] and 95% CI [-2.68 2.92] and 95% CI [-4.08 1.60] and 95% CI [-2.34 2.98]).

Figure 5.6 shows the magnitude of the motion adaptation levels before and after the 40 min perceptual learning adaptation for the two locations. Inspection of this figure suggests that there was a bias in terms of motion adaptation (i.e. in the pre-test, observers perceived radial motion to be slightly expanding at the locations of the adapting stimuli) but little evidence that this bias changed as a function of when it was interrogated (pre- or post-test). These observations were confirmed by statistical analysis, which showed that the time of testing and type of motion radial motion adapted had no effect on motion adaptation – respectively [$F(1, 10) = 0.074$, $p = 0.789$] and [$F(1, 10) = 0.211$, $p = 0.651$] – and there was no interaction between these factors [$F(1, 10) = 0.155$, $p = 0.699$].

4.4 **Discussion**

Experiment 8 established that the decreased duration of the adapting stimulus had no effect on the association between the radial motion of two adapting stimuli and their spatiotopic location. In this experiment, the adaptation measured at the two locations seems to be unaltered by the decreased duration of the adapting stimulus in the adaptation phase and that whether the adapting stimulus was expanding or contracting. In short, the visual system was unable to adapt to the two radial motion stimuli at their spatiotopic locations.

As with Experiment 7 (see section 3.4), the absence of dual motion adaptation in Experiment 8 could reflect a failure for the visual system to associate the direction of radial motion of the two adapting stimuli to the spatiotopic location of the adapting stimuli. Another important difference between the procedures used in Experiments 7 and 8 and the study conducted by Bompas and O’Regan is that observers were engaged in an attention-demanding task during the adaptation phase. Experiment 9 investigated whether adding an attentional task to the adaptation phase would lead to a dual motion adaptation at two spatiotopic locations.

5 EXPERIMENT 9: LEARNING THAT TWO RADIAL MOTION STIMULI ARE PRESENTED AT TWO SPATIOTOPIC LOCATIONS WHEN ATTENTION IS ENGAGED DURING THE ADAPATION STAGE

5.1 Introduction

Experiment 9 was the same as Experiment 8 with the exception that a shape-discrimination task was added to the adaptation phase. The observers' task was to decide whether the fixation point for the first or the second adapting stimulus had an elliptical shape. I predicted maintained attention during the adaptation phase would help to successfully associate the spatiotopic location of the stimulus with its radial motion, and that the association between the two variables would induce an adaptation for the motion stimulus when a stimulus is presented at the associated spatiotopic location.

5.2 Method

5.2.1 *Observers and Stimuli*

Five naive observers and the experimenter participated in the experiment. Their ages ranged from 24 to 28 with an average at 25.3 years. There were 3 females and 3 males observers. All had normal or corrected-to-normal vision. The test and adapting stimuli parameters were the same as in section 3.2.1. The spatial configuration of the stimuli was identical to Experiment 7, see section 3.2.1. Briefly, the locations adapted on the spatiotopic representation were different from the ones adapted on retinotopic representation.

5.2.2 *Procedure*

The general procedure was identical to Experiment 8, see section 4.2.2, with one exception, the addition of a central attention task. In Bompas & O'Regan's experiment, the trials of the adaptation phase included an attention task where one of the two coloured stimuli has a slight elliptical shape. The task requires that the observers to pay attention to both adapting stimuli in order to solve the task. I fitted their attention task to the experiment, and during the adaptation phase, observers had to indicate whether the fixation point of the first or of the second adapting stimulus had an elliptical shape. To maintain the attention on both stimuli, the elliptical shape was pseudo-randomly assigned on half of the adaptation trials to the fixation point of the first adapting stimulus, and on the other half of the trials to the fixation point of the second adapting stimulus. To maintain attention throughout the adaptation phase, the fixation-point's height-over-width ratio was varied over trials following a staircase procedure, see section 1.1.6, homing at the 75% threshold. The height-over-width ratio of the fixation-point was set in the first trial at 1.05 (i.e. the height was 5% larger than the width) in the first trial.

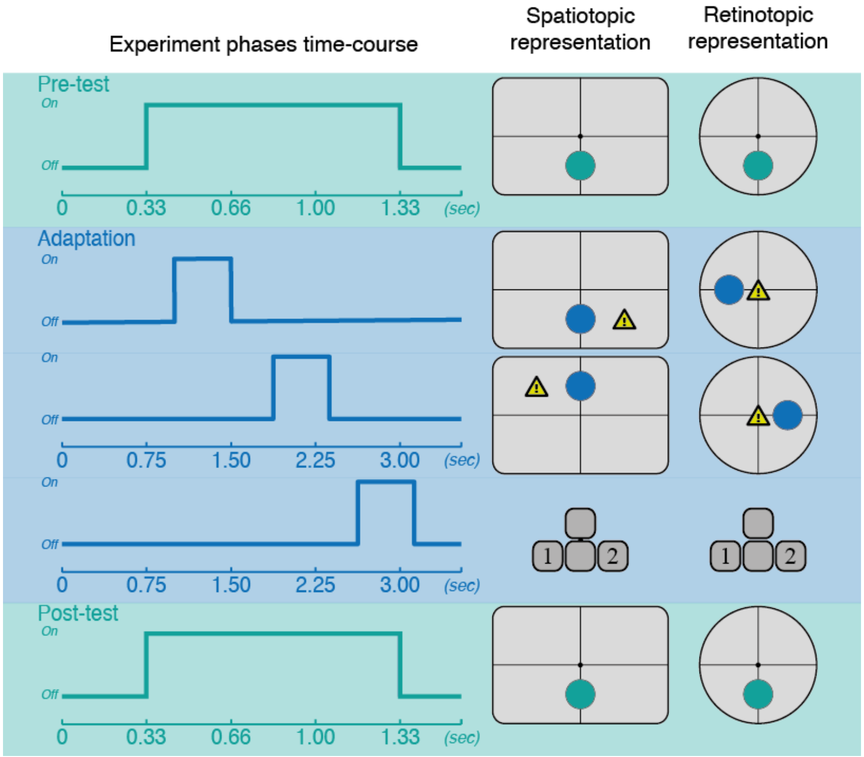

Figure 5.7: A schematic of the main phases of Experiment 9. The illustration describes the time-course of the main experiment phases and their spatial configurations on the spatiotopic and retinotopic representations. The experiment was divided into three phases, a pre-test, an adaptation, and a post-test. During the adaptation, two radial motion stimuli were each presented at spatiotopic location (e.g. an expanding stimulus in the upper part of the screen and a contracting stimulus in the lower part of the screen). The fixation point of the two adapting stimuli also slightly differed in shape from one another. After the second adapting stimulus disappeared, observers were instructed to indicate which of the two fixation points was the oval, and they received feedback once their response given. During the pre-test and the post-test, the level of motion adaptation of observers was probed at the spatiotopic locations of the two adapting stimuli.

Figure 5.7 illustrates the main components of a single trial in Experiment 9; in brief, the pre-test, the adaptation and post-test phases are identical to the ones of experiment 8, see section 4.2.2, with the exception of the adaptation phase which contains an attention task.

In practice, during the adaptation phase, either the fixation point of the first or of the second adapting stimulus had an elliptical shape. The two adapting stimuli are viewed for the same duration – 0.5s – and the same locations as in Experiment 8. The adaptation phase included an additional third stage after the second adapting stimulus, where observers indicated which of the two adapting stimulus’ fixation points was elliptical, and where they received feedback on their response. Observers were given 0.5s to give their response and received feedback for 0.5s once the response was given. If no response was given during the allocated period, observers received negative feedback, and the staircase level probed by the trial was repeated. In total, observers failed to give a response in less than 2% of the trials.

As in Experiment 8, the adapting stimuli parameters - their locations and radial motions – were constant throughout an experiment for an observer, but both the order of the adapting stimuli's location and radial motion were counterbalanced across observers.

5.2.3 *Data analysis*

The data underwent the same analysis as described in Experiment 7, see section 3.2.3. Briefly, data were analysed with two independent variables (i.e. time of testing and adapting stimulus's radial motion), using ANOVA.

5.3 **Results**

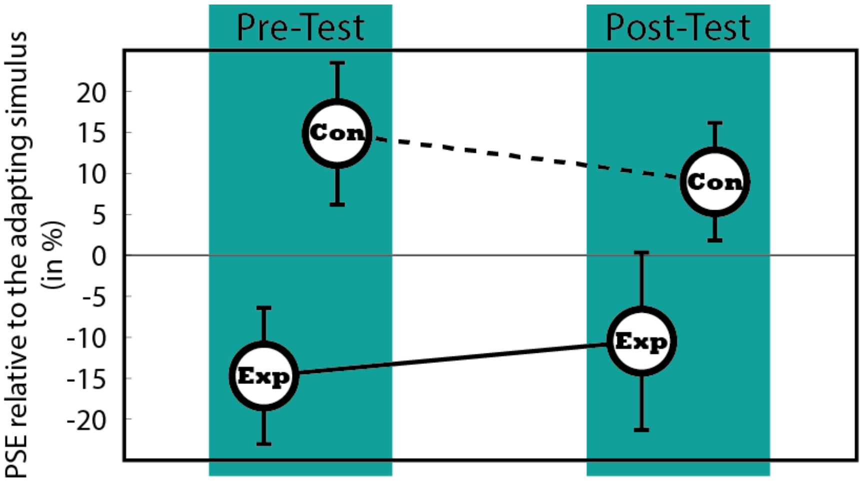

Figure 5.8: Motion adaptation levels before and after 40 min of perceptual learning motion adaptations. The motion after effect intensity is plotted relative to the adapting stimulus motion vector (in %). Error bars represent confidence intervals. Three of the motion adaptation levels are significantly different from 0 (95% CI [-23.0 -6.42] and 95% CI [7.52 24.8] and 95% CI [3.36 17.7]), but the motion adaptation level induced by the expanding stimulus and measured in the post-test condition is not (95% CI [-21.3 0.34]).

Figure 5.8 shows the magnitude of the motion adaptation levels before and after the 40 min perceptual learning adaptation for the two locations in the central attention condition. Inspection of this figure suggests that there was evidence of a bias of motion adaptation (i.e. in the pre-test, observers perceived radial motion to be strongly expanding at the locations of both adapting stimuli), and that this bias weakens after the adaptation phase. Against this last observation, the results of statistical analysis revealed that there was no effect of the time of testing [$F(1, 6) = 0.295$, $p = 0.599$], no effect for the type of motion radial motion [$F(1, 6) = 3.537$, $p = 0.291$], and importantly no interaction between these two factors [$F(1, 6) = 0.505$, $p = 0.493$].

The rather large mean effects measured in both conditions varied considerable across observers, and a careful analysis of the results revealed that outliers drove these large effects. In fact, out of the six observers that took part in this experiment, two were undertaking a psychophysical experiment for the first time, and had MAE scores that strongly deviate from the rest of the group. Without these outliers, the motion adaptation levels in both condition are similar to the ones obtained in the previous experiments, and do not suggest an effect of the independent variables.

5.4 Discussion

Experiment 9 investigated whether or not a task maintaining observers’ attention during the adaptation phase would promote associations between the radial motion of two stimuli and their locations. To this end, I implemented a shape-discrimination task in the adaptation phase where observers had to attend both stimuli (cf. Bompas and O’Regan, 2006). Between the pre-test and the post-test phases, there was no evidence of a change in radial motion adaptation for either of the two adapting stimuli when they were was presented at their associated spatiotopic location. However, in the study by Bompas and O’Regan (2006) attention was directed at the adapting stimulus itself, whereas in the Experiment 9 it is directed at the fixation points 7º away from the adapting stimulus. Experiment 10 examined whether this difference was critical.

6 EXPERIMENT 10: LEARNING THAT TWO RADIAL MOTION STIMULI ARE PRESENTED AT TWO SPATIOTOPIC LOCATIONS WITH AN ATTENTION TASK CENTERED ON THE MOTION STIMULI

6.1 Introduction

In Experiment 10, I explored whether directing the locus of attention to the features that needs to be associated helps the generate associations between the radial motion of two stimuli and their spatiotopic locations. To this end, I changed the attention task from a shape-discrimination task, that required observers to focus on the fixation points of the adapting stimulus, to a contrast-discrimination task, that required observers to focus directly on the adapting stimuli.

6.2 Method

6.2.1 *Observers and Stimuli*

Nine naive observers and the experimenter participated in the experiment. Their ages ranged from 24 to 26 with an average at 24.8 years. There were 4 females and 6 males observers. All had normal or corrected-to-normal vision. The test and adapting stimuli parameters were the same as in section 3.2.1. The mapping of the stimuli on the retinotopic and spatiotopic representation was identical to Experiment 7 (see section 3.2.1). In brief, the two locations of the adapting stimuli on the spatiotopic reference frame are different from their locations on the retinotopic reference frame.

6.2.2 *Procedure*

The general procedure was identical to Experiment 9, see section 5.2.2, with the exception of the attention task that was a contrast-task centred on the adapting stimuli. During the adaptation phase, the observer had to indicate which of the two adapting stimulus was the dimmest; the contrast of the adapting stimuli was governed by a staircase procedure identical to the one described in Experiment 9.

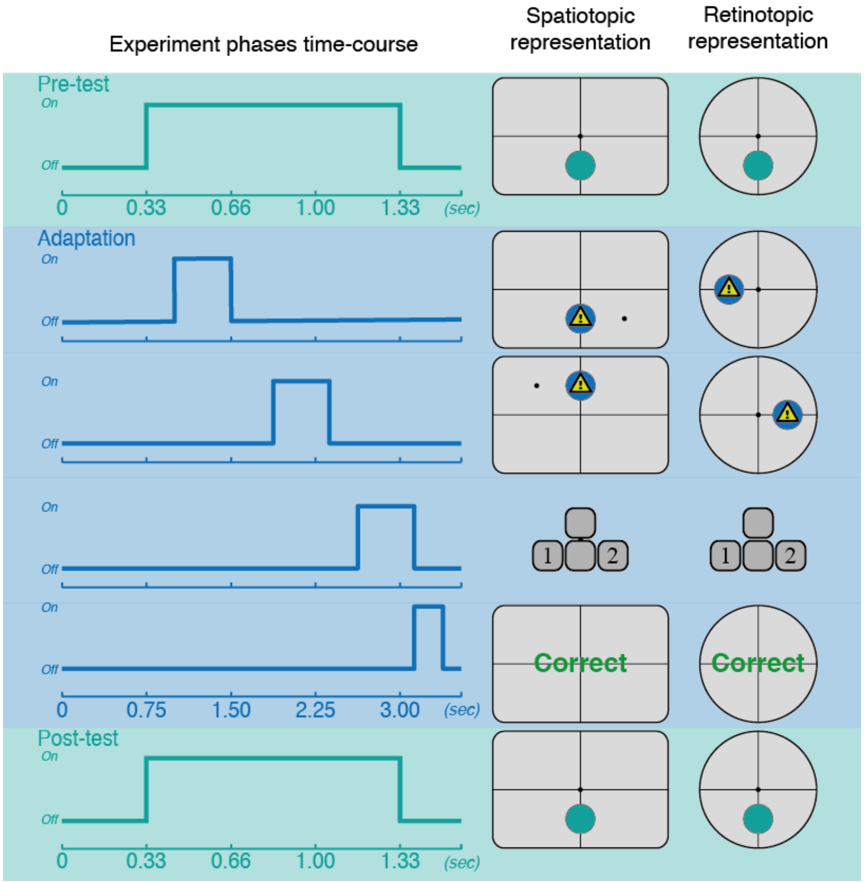

Figure 5.9: A schematic of the main phases of Experiment 10. The illustration describes the time-course of the main experiment phases and their spatial configurations on the spatiotopic and retinotopic representations. The experiment was divided into three phases, a pre-test, an adaptation, and a post-test. During the adaptation, two radial motion stimuli were each presented at spatiotopic location (e.g. an expanding stimulus in the upper part of the screen and a contracting stimulus in the lower part of the screen). The two adapting stimuli also slightly differed in contrast from one another. After the second adapting stimulus disappeared, observers were instructed to indicate which of the two adapting stimuli was the darkest, and they received feedback once their response given. During the pre-test and the post-test, the level of motion adaptation of observers was probed at the spatiotopic locations of the two adapting stimuli.

Figure 5.9 illustrates the principal components of a single trial in Experiment 10; in brief, the pre-test and post-test phases are identical to the Experiment 9, see section 5.2.2, but the attention task in adaptation phase differed slightly to that of Experiment 9, as observers were required to focus their attention directly to the adapting stimulus. This difference aside, a single trial of the adaptation phase is identical to the one described in section 5.2.2 of Experiment 9

The counterbalanced parameters – the order of the adapting stimuli's location and radial motion – of Experiment 10 are identical the ones described in Experiment 9 (section 5.2.2).

6.2.3 *Data analysis*

The analysis conducted in Experiment 10 is identical to the one conducted in Experiment 9, see section 5.2.3. Briefly, individual data were analysed with two independent variables (i.e. time of testing and adapting stimulus's radial motion), using ANOVA.

6.3 Results and Discussion

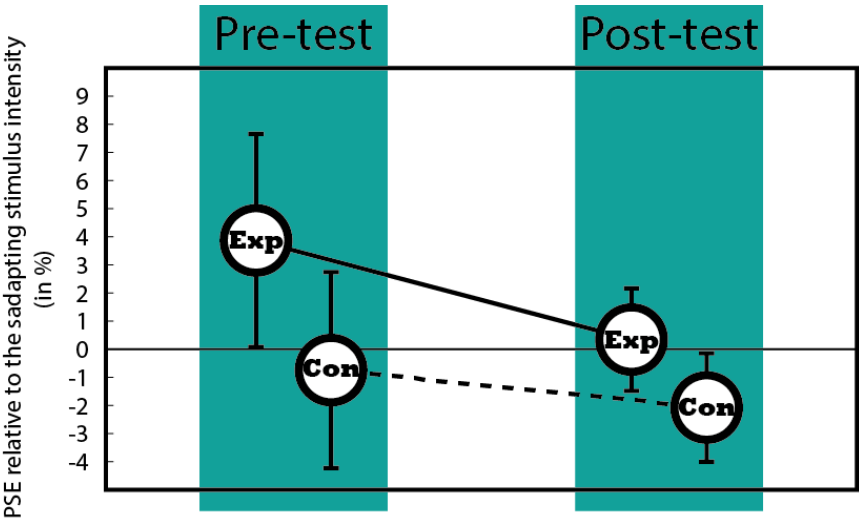

Figure 5.10: Motion adaptation levels before and after 40 min of perceptual learning motion adaptations. The motion after effect intensity is plotted relative to the adapting stimulus motion vector (in %). Error bars represent confidence intervals. The motion adaptation levels at the location of the expanding stimulus in the pre-test phase and at the location of the contracting stimulus in the post-test phase are significantly different from 0 (95% CI [0.08 7.66] and 95% CI [-3.90 -0.04]), but the motion adaptation levels at the location of the contracting stimulus in the pre-test phase and at the location of the expanding stimulus in the post-test phase are not (95% CI [-2.10 4.86] and 95% CI [-1.48 2.16]). .

Figure 5.10 shows the motion adaptation levels before and after the 40 min adaptation phase at the two locations. Inspection of this figure suggests that the motion adaptation decreased after the adaptation phase regardless the radial motion adapted in a given location. ANOVA confirmed that there was a main effect of the time of testing [$F(1, 18) = 5.46$, $p < 0.05$]. A post-hoc test, based on pairwise comparisons table of the time of testing, observed that motion adaptation was decreased in the post-test by an average of 2.96 point of percentage (95% CI [0.3 5.62]). However, the type of motion radial motion adapted onto a location did not influence motion adaptation, and there was no significant interaction between the time of testing and the type of motion radial motion adapted [*Fs* < 1].

Experiment 10 established that changing the locus of attention to the features that needs to be associated does not favour an association between the spatiotopic location of a stimulus and its radial motion. Concretely, switching from a shape-discrimination task targeted at the fixation points of the adapting stimuli to a contrast-discrimination task targeted at the adapting stimuli does not increase the motion adaptation after the adaptation phase.

7 GENERAL DISCUSSION

The aim of Experiments 7-10 was to explore whether observers could associate the spatiotopic location of two stimuli to their radial motion. To this end, I used a paradigm that divided the experiments in three parts: a pre-test phase to show that a motion stimulus was not associated to a spatiotopic location, an adaptation phase to create an association between the spatiotopic location and a motion stimulus, and a post-test phase to measure whether the spatiotopic location was now associated to the motion stimulus. If an association formed during the adaption phase, then observers should show adaptation to the motion stimuli when they are presented at their associated locations. I did not find evidence of a dual motion adaptation mechanism in either of Experiments 7-10, so I concluded that the visual system could not adapt to radial motion stimuli occurring at two spatiotopic locations.

The findings of some studies of perceptual learning are inconsistent with the results reported in this chapter. For example, it has been shown that associations can form between the location on the screen of a stimulus and a rotating stimulus (Haijiang et al., 2006; Jain & Backus, 2010; Jain & Backus, 2013). Moreover, there is already evidence in the literature suggesting that the visual system is capable of a dual adaptation (Bompas & O'Regan, 2006b). In the Bompas and O'Regan experiment, following the presentation of colour stimuli after specific eye-movement, observers' perception of colour stimuli was altered. This result strongly indicates that the visual system is capable of adapting to two colour stimuli depending on the preceding eye-movement made. Consequently, the discrepancy between the results of Experiments 7-10 and the current literature could be related to the nature of the associated features; whilst Bompas and O'Regan (2006) associated a stimulus to an action, I associated a stimulus to a location in space.

The failure to measure any significant spatiotopic MAEs in Experiments 7 to 10 as opposed to Experiments 5 and 6 where one spatiotopic MAE was observed does not allow us to formally claim that these latter experiments were probing a different mechanism. In the introduction, we argued that in Experiments 5 and 6 there was a possibility for subjects to have learned the relationship between the stimuli's locations and radiations. However, since no significant spatiotopic MAEs was ever observed in Experiments 7 to 10, and since these were based on proven perceptual learning paradigm, we are inclined to think that the results of Experiments 5 and 6 were due to a general adaptation of the visual system (i.e. a Phantom MAE), and not to an association between stimuli' spatiotopic locations and radiations.

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The failure to associate a stimulus to a location in space MAE could be explained from an absence of spatiotopic representation, and the fact that we do not perceive information during an eye-movement, known as saccadic suppression, certainly provides evidence in that direction (Matin, 1974). More precisely, the fact that stimuli presented slightly before the start and during an eye-movement are mis-localised seems to contradict the idea that we have an absolute representation of our spatial environment (Morrone, Ross, & Burr, 1997). Overall saccadic suppression combined with the results from experiment 5 to experiment 10 can be taken evidence against the hypothesis that the visual system has access an absolute spatial representation of the world.

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The remaining difference between the paradigm used in Experiment 10 and the Bompas and O'Regan's experiment lies in the nature of the event that are associated together; whereas I aimed – and failed – to generate associations between the spatiotopic location of a stimulus to its radial motion, they aimed – and succeeded – in generating associations between an eye-movement to the colour of a stimulus. If observers can generate a dual adaptation following an association between a colour stimulus and a preceding eye-movement, they should also be able to generate a dual adaptation following an association between a motion stimulus and a preceding eye-movement. Evidence in the literature suggests that motion stimulus should not be a particular case for a adaptation mechanism (Durgin et al., 2005), and that following the constant conjunction of a self-movement and a motion stimulus, the visual system should adapt for this new relationship (Wallach & Kravitz, 1965; Wallach & Frey, 1969). The next chapter will investigate based on Experiment 10, but assessed whether a preceding eye-movement can be associated to a radial motion stimulus and generate a dual radial motion adaptation.

Chapter 6

DUAL SENSORIMOTOR ADAPTATION IN MOTION PERCEPTION

1 EXPERIMENT 11

1.1 Abstract

It has been suggested that our visual system shows eye-movement dependent colour adaptation (Bompas & O’Regan, 2006b). However whether the visual system can adapt to the direction of radial motion of two stimuli if they are preceded by specific eye-movements remains an open question. To answer this question, I investigated whether or not the visual system can associate two specific eye-movements with different radial motions. The results indicated that the two associations between the eye-movement preceding the stimulus and its direction of radial motion were formed, and that the visual system had adapted to the two direction of radial motion.

1.2 Introduction

The example given in the general introduction describes a situation where a high-speed optic flow can induce an adaptation of the visual system (Denton, 1966). But, can the visual system adapt to more than one radial optic flow? For example, could the visual system learn that after an eye-movement to the right, toward the opposite side of the motorway, the optic flow will be expanding, and that after a smaller eye-movement to the right, toward your side of the motorway, the optic flow will be contracting? This type of dual adaptation resembles the one probed by split-field goggles procedure, where eye-movements were associated with specific colours (Kohler, 1962).

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In Kohler (1962), observers were given split-field goggles with opposite colours: the left halve of the frame contained a yellow filter and the right halve a blue filter. Observers wore the split-field goggles for several weeks, and when they removed them, an eye-movement to the left induced a blue percept, and an eye-movement to the right induced a yellow percept: the adaptation process depended on the direction of the eye-movement. This double colour adaptation indicates that observers had simultaneously adapted to two different perceptual distortions in the same situation. However, this result failed to be replicated with better-controlled experiments (Harrington, 1965; McCollough, 1965).

Recently, two experiments demonstrated with colour-split goggles and with a more precise computer-controlled adaptation that sensorimotor adaptation was possible (Bompas & O'Regan, 2006b). In the computer-controlled version, the experiment was divided into three phases: a pre-test measuring the colour adaptation of two stimuli at different locations, an adaptation phase creating a contingency between two eye-movements and two colour stimuli (i.e. each colour stimulus was presented after a specific eye-movement), and a post-test phase identical to the pre-test phase. In the pre-test and in the post-test phases, observers made the same series of eye-movement as in the adaptation phase before being probed on their level of colour adaptation.

The results showed that after the adaptation phase, colour adaptation levels were changed according the colour stimuli presented during the adaptation phase (i.e. observers perceived colour in the shade of green at the location of the red adapting stimulus, and they perceived colour in the shade of red at the location of the green adapting stimulus). One interpretation of these results that is consistent with the classical literature (Kohler, 1962) is that each colour stimulus became associated with its preceding eye-movement; therefore forming two associations that each induce a specific colour adaptation, a dual colour adaptation. Instead Bompas and O'Regan argued only one relative association is formed: the difference in colour between the two stimuli (e.g. red to green) became associated with the eye-movement required to go from one-colour stimuli to the other.

Bompas and O'Regan argue against the dual sensorimotor adaptation based on the findings of an additional experiment probing each hypothesis (i.e. absolute sensorimotor encoding and relative sensorimotor encoding). In this experiment, observers were presented both colour stimuli, but only made a single eye-movement (i.e. the one from the first to the second colour stimulus). Dual colour adaptation still occurred. However, this experiment does not rule out absolute sensorimotor encoding due to the conjunction of two factors. First, the relative eye-movement between the two stimuli corresponds to the absolute eye-movement to the second stimuli. Second, the task did not measure the adaptation occurring after each eye-movement individually, but relatively (i.e. observer indicated if the second patch was redder or greener than the first patch). Therefore, the experiment does not differentiate between the result induced by a single absolute sensorimotor adaptation (i.e. the association between the second coloured stimulus and the eye-movement to the second stimuli) and a relative sensorimotor adaptation (i.e. the association between the two coloured stimuli and the eye-movement between the two stimuli).

At a theoretical level, encoding the relative difference between two stimuli and two self-movements seems to be advantageous because instead of forming two associations, we only from one. Yet, this argument does not hold when there are more than two stimuli each associated to more than two eye-movements. In this case the visual system needs to encode more pairs of associations (i.e. relative encoding) than single association (i.e. absolute encoding). Bompas and O’Regan argue that relative encoding permits to achieve colour constancy (i.e. our perception that objects have relatively stable colours irrespective of dramatic variations in ambient light (Maloney & Wandell, 1986)); however, given that we perceive more than two colours, this process of relative encoding is likely to be involved in situation where more than two pairs of colour stimuli and eye-movements. In such case, absolute encoding would prove more efficient in terms of the number of association to store than relative encoding. Therefore, the findings of Bompas and O’Regan are more likely to reflect a dual absolute sensorimotor adaptation than a single relative one.

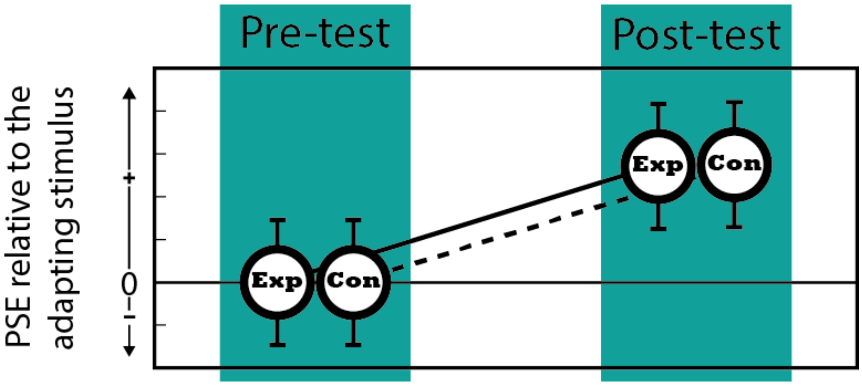

Figure 6.1: Illustration of the experimental hypotheses on the motion adaptation levels before and after perceptual learning motion adaptations. The motion after effect intensity is plotted relative to the adapting stimulus motion vector, so the motion adaptation levels of both expanding and the contracting stimuli are increased by the adaptation phase. Error bars represent confidence intervals. I expect the motion adaptation levels of the pre-test phase to not be significantly different from 0, and the ones of the post-test phase to have significantly increased.

If two different colours can be associated to two different eye-movements, I suggested that in light of the previous research on dual adaptation, it should be possible to associate the different radial motion stimuli to two different eye-movements. To this end, I adapted the design the Experiment 10, which presented two radial motion stimuli at two constant spatiotopic locations, to include specific eye-movement before each radial motion stimulus. During the tests phases (i.e. pre-test and post-test), the task was changed to measure the level of radial motion adaptation, and during the adaptation phase, the two opposing radial motion stimuli were always each preceded by a specific eye-movement. I hypothesised that each eye-movement command would be associated with a direction of radial motion; therefore as in Experiment 10, the level of radial motion adaptation would be increased between the pre-test phase and the post-test phase in the direction of the adapting stimuli's radial motion (see Figure 6.1).

1.3 Method

1.3.1 *Observers & stimuli*

Five naive observers and the experimenter participated in the experiment. Their ages ranged from 24 to 25 with an average at 24.7 years. There were 2 females and 4 males observers. All had normal or corrected-to-normal vision.

The adapting stimuli were identical to those used in my previous experiments and were composed of 400 dots that were expanding or contracting at an average speed of 1.47cm/s. The test stimuli were similar to the adapting stimuli but its speed depended on a psychometric staircase that had starting values of 1.47cm/s or -1.47cm/s. Individual dots of the test stimulus were presented for a random duration and then replaced at another location in the test stimulus (see general method sections 1.1.2 and 1.1.3 for more detail).

An illustration of the stimuli spatial configuration and their mapping onto the retinotopic and spatiotopic location is given by Figure 6.2.

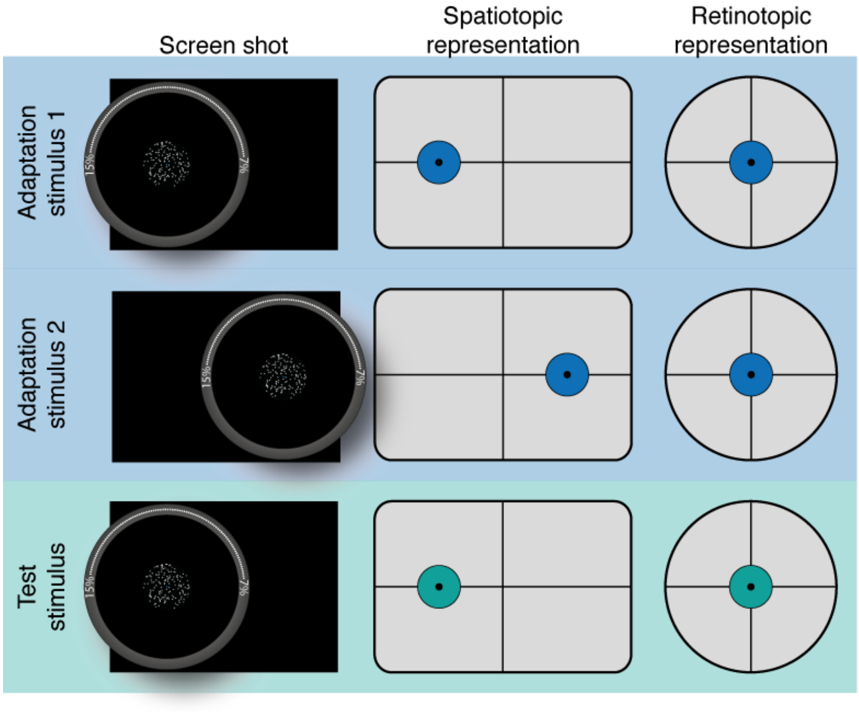

Figure 6.2: Stimulus location's screenshot and illustration of its location in the spatiotopic and retinotopic reference frames. Rows indicate the experiment phase whereas columns describe three ways to understand the stimulus location. The screen shot is at the scale of 1:15 outside the zooming lens and at the scale of 1:6 inside the zooming lens.

Concisely, the spatial configuration of Experiment 11 resembles the one from Experiment 4, where two locations are adapted on the spatiotopic reference frame but only one in the retinotopic reference frame.

The first adapting stimulus and its fixation-point were co-located 7º left of the screen centre and the second adapting stimulus and its corresponding fixation-point were co-located 7º right of the screen centre. The test stimulus and its fixation-point were located 7º away from the screen centre, either at first adapting stimulus location or at the second adapting stimulus location. The co-location of the adapting stimuli and their fixation points indicates that all adaptation takes place at the centre of the retina, so all the adapting stimuli are encoded at the same location on the retinotopic representation. On the spatiotopic representation, however, the adapting stimuli are presented at two different locations, 7º left and right of the screen centre.

1.3.2 *Procedure*

The general procedure was identical to the one used in Experiment 10 (see Section 6.2.2) where the experiment is divided into three phases: a pre-test phase probing any pre-existing motion adaptation at either of the two post-saccadic locations, an adaptation phase with an attention task aimed at associating an eye-movement to a consequent radial motion stimulus with the aid of a contrast-discrimination task, and a post-test phase identical to the pre-test phase and probing the motion adaptation induced by the adaptation phase. For the contrast-discrimination task, observers had to indicate which of the two adapting stimulus was the dimmest; the contrast of the adapting stimuli was governed by a staircase procedure identical to the one described in Experiment 10.

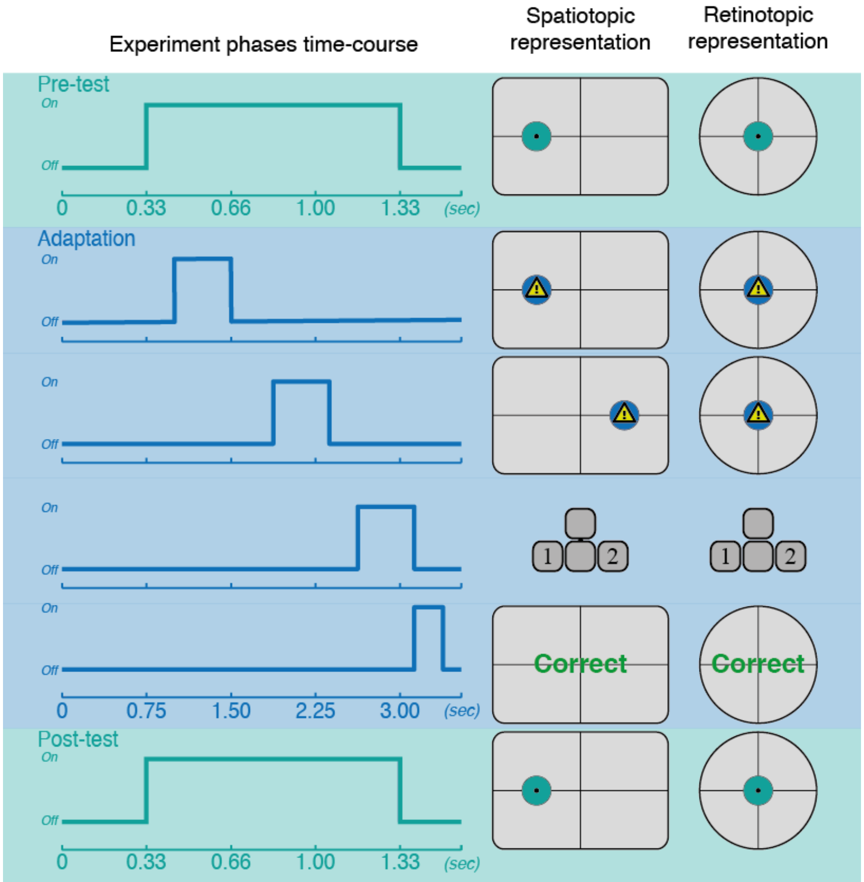

Figure 6.3: A schematic of the main phases of Experiment 11. The illustration describes the time-course of the main experiment phases and their spatial configurations on the spatiotopic and retinotopic representations. The experiment was divided into three phases, a pre-test, an adaptation, and a post-test. During the adaptation, two radial motion stimuli were each presented after specific eye-movement (e.g. a left eye-movement followed by an expanding stimulus and a right eye-movement followed by a contracting stimulus). The two adapting stimuli also slightly differed in contrast from one another. After the second adapting stimulus disappeared, observers were instructed to indicate which of the two adapting stimuli was the darkest, and they received feedback once their response given. During the pre-test and the post-test, observer had to make the same specific eye-movements as in the adaptation phase but instead of presenting the adapting stimuli, their level of motion adaptation was probed.

The main sections of a single trial in Experiment 11 are described by Figure 6.3. Briefly, the temporal time courses of the three experimental phases are similar to the ones of Experiment 10 with one exception, the number of location tested per trial in the pre-test and post-test phase.

During a single trial of the adaption phase, observers viewed each adapting stimuli 0.5s after making an eye-movement, once the adapting stimuli disappeared, they had to indicate which of the two adapting stimuli was the darkest. Once their response given, they received feedback on it.

During a trial of the test phase, observers viewed a motion stimulus at the locations of one of the adapting stimuli, and they had to indicate whether the motion stimulus was expanding or contracting. If no key was pressed within the allocated time, the staircase's step was not incremented and stayed the same (see section 1.2.3).

During the test phases, the two locations were probed in the same order as in the adaptation phase, and the central fixation dots at the beginning of a trial was only displayed every two test trials. To this end, the adapting stimuli were presented in the same order as in the adaptation phase, the eye-movement required before each adapting stimulus were also identical to the ones observers had to make in the adaptation phase.

As in Experiment 10, the locations and radial motions of adapting stimuli were constant throughout an experiment for an observer, but their order was counterbalanced across observers.

1.3.3 *Data analysis*

I used the analysis described in the general method section to estimate of the strength of motion adaptation (see Section 1.3). In short, the velocities of the test stimuli presented during the experiment and the responses observers gave for each are linked by a curve to find an index of the motion adaption velocity. This curve was then bootstrapped to obtain a margin of error of this estimate (for a precise description of the process see section 1.3.4 of the general method).

I used the same inferential analysis as in Experiment 10 to assess whether the adaptation phase induced stronger motion adaptation in the direction of the associated radial motion than the motion adaptation measured in the pre-test. To this end, I ran an ANOVA with two variables: the test condition (i.e., that pre-test or post-test), and the adapting stimulus's radial motion (i.e., expanding or contracting motion). I expected the motion adaptation induced by the adapting stimuli to grow stronger between the pre-test and the post-test. As before, ANOVA's assumptions (i.e. the normality of data distribution, the homogeneity of variance, and the sphericity assumption) were assessed (see section 1.3.5) and corrections were applied when appropriate.

1.4 Results

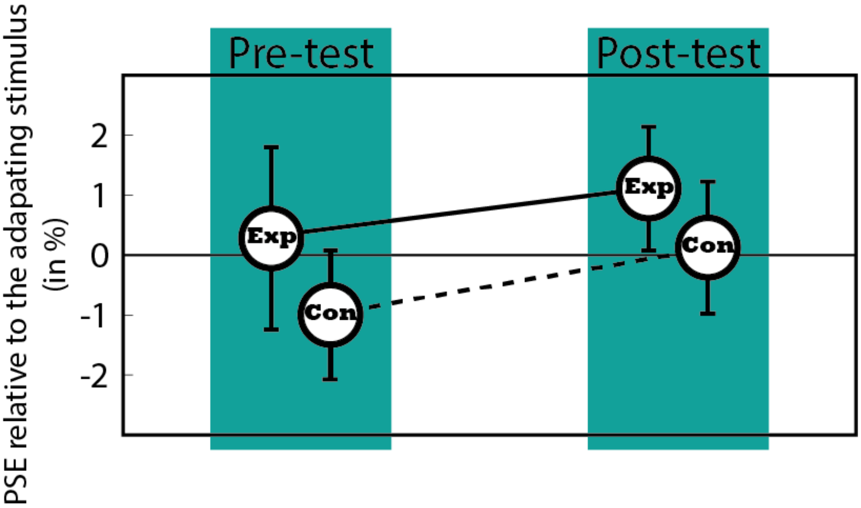

Figure 6.4: Motion adaptation levels before and after 40 min of perceptual learning motion adaptations. The motion after effect intensity is plotted relative to the adapting stimulus motion vector (in %). Error bars represent confidence intervals. The only motion adaptation level significantly different from 0 was experienced during the post-test phase at the location of the expanding stimulus (95% CI [0.34 2.06]), none of the other conditions presented motion adaptation levels significantly different from 0: (95% CI [-1.38 1.66] and 95% CI [-2.04 0.06] and 95% CI [-1.26 0.94]).

Figure 5.10 illustrates the magnitude of the motion adaptation levels before and after the perceptual learning adaptation phase. Inspection of the figure reveals that the motion adaptation levels grew stronger relative to their adapting stimuli after the adaptation phase. More specifically, during the pre-test the motion adaptation measured at the location of the expanding stimulus is slightly contracting, and that the motion adaptation measured at the location of the contracting stimulus is reversed compared to the contracting stimulus, and therefore slightly contracting as well. The first observation is confirmed by the results of the statistical analysis that shows a main effect of the time of testing [$F(1,10) = 6.35$, $p < 0.05$]. There was no significant effect of type of motion radial motion adapted, or of the interaction between the time of testing and type of motion radial motion [$Fs < 1$]. The second observation, regarding a bias to perceive radial motion stimuli as slightly contracting, was not confirmed by post-hoc test either at the location of the expanding stimulus (95% CI [-1.38 1.66]) or at the location of the contracting stimulus (95% CI [-2.04 0.06]).

1.5 Discussion

The current experiment investigated whether or not a feature of the adapting stimulus – its radial motion – can be associated with the preceding eye-movement. To this end, a specific adapting stimulus was always presented after the same eye-movement (e.g. the contracting stimulus always required a 7º left eye-movement). The motion adaptation levels measured after the adaptation phase were stronger relative to their adapting stimulus' direction of radial motion than the one measured before the adaptation phase. In line with the hypothesis, this result indicates that eye-movements were successfully associated with the incoming radial motion stimuli, and this association allowed the visual system to anticipate the incoming radial motion stimulus upon an eye-movement.

The finding that a self-movement can become associated with a constant motion feature of the visual scene is consistent with previous empirical observations. In 1973, a similar paradigm measured a motion adaptation for circular motion stimuli and eye-movements after only 10min of adaptation: after an eye-movement, an illusory motion percept was seen in the opposite direction to that of the circular motion stimulus (Mayhew, 1973). Mayhew (1973) had already argued that an adaptation process had taken place between the eye-movements required before each rotating stimulus and the rotating stimuli. More recently this adaptation mechanism was observed with coloured stimuli; the repeated presentation of a coloured motion stimulus after a specific eye-movement induced an adaptation of the visual system, and if a grey stimulus was presented after the associated eye-movement, observers saw a colour percept opposite to that of the associated colour stimulus (Bompas & O'Regan, 2006b; Kohler, 1962; Richters & Eskew, 2009).

The current results suggests a dual radial motion adaptation induced by two associations as opposed to a single relative association (cf. Bompas and O'Regan, 2006) and is in line with current experiment (Dam, Hawellek, & Ernst, 2013). In the adaptation phase of Experiment 11, observers had to make a first 7º eye-movement from centre of the screen to the first adapting stimulus. According to Bompas and

O'Regan, it is the second eye-movement from the first adapting stimulus to the second that becomes associated to the change in visual property of the adapting stimuli (e.g. from expanding to contracting), so this first eye-movement should not be associated to the first adapting stimulus, and should not have induced a motion adaptation. Yet, I measured a radial motion adaptation induced by the first eye-movement, which suggests that the first eye-movement had become associated to the first adapting stimulus. In short, I conclude that in the light of the results and in line with the literature (Dam et al., 2013) not one but two associations had formed during the adaptation phase: one for each pair of adapting stimulus and eye-movement.

Chapter 7

GENERAL DISCUSSION

Anyone having driven on a motorway for a long time knows the feeling of exiting it: an impression that speed at which you are cruising is slower than the one indicated by your speedometer. This impression is the result of an adaptation of the visual system: a change in sensory characteristics as a result of the high-speed optic flow (Denton, 1966). Yet whilst driving on a motorway, there is more than the single optic flow generated by the speed at which we are travelling. On the same side of the road, cars are overtaking you; therefore generating a contracting optic flow, whilst on the opposite side of the road, cars are going in the opposite direction; therefore generating an expanding optic flow. Is it possible that we adapt to these two radial optic flows? The results presented in this thesis suggest this dual adaptation only occurs in very specific situations.

Commented [DBSDE&S23]: Comment 10.10 (minor formating details)

I raised the question of whether the visual system was capable of simultaneously adapting to two different radial optic flows in three different conditions. In Chapter 3 and 4, I asked whether the visual system was capable of adapting to two radial optic flows through MAEs. More specifically in Chapter 3, I conducted a series of experiments that investigated whether a fast low-level adaptive system was capable of generating a MAEs at the spatial locations of the adapting motion stimuli (i.e. their spatiotopic locations). In Chapter 4, I increased the frequency of presentation of the radial motion stimuli to test if it would impact the dual spatiotopic adaptation of the visual system.

In the second part of the thesis, in Chapter 5, I probed whether the visual system – via a perceptual learning mechanism – was capable of simultaneously adapting to two radial optic flows based on their locations in space. More precisely, I examined whether the visual system could predict two radial optic flows consistently occurring at two different spatiotopic locations.

In the final part of this thesis, in Chapter 6, I tested whether the visual system was capable of simultaneously adapting to two optic flows based on two preceding self-movements. Below, a brief summary of the results of each chapter is given as well as a summary of the discussion for the main results.

1 EXPERIMENTAL RESULTS

In Experiments 1 to 5 of Chapter 3, I explored spatiotopic MAEs induced by radial optic flows. More precisely, I explored radial motion MAEs, an illusory motion percept that follows the presentation of a radial motion stimulus, and I probed whether two radial MAE induced by opposite radial motion stimuli could be observed at two different spatiotopic locations. To answer this question, I first conducted a series of four experiments to ensure the validity of the main experiment on dual spatiotopic MAEs.

Out of the four results, two were particularly important for the main experiment. First in Experiment 2, a single MAE could be measured at the spatiotopic location of the radial motion stimulus. This result allows to further extend the findings of Turi and Burr (2012) that reported a spatiotopic effect after the presentation of another complex motion stimulus.

The second result of importance for the main experiment is from Experiment 3: two MAEs can be measured at the retinal location of the radial motion stimuli. This result, in line with previous evidence (Cameron et al., 1992; Wade & Salvano-pardieu, 1998), suggests that the paradigm used can measure two MAEs, so the paradigm should be able to measure two MAEs at two spatiotopic locations.

The experiment on the dual spatiotopic MAEs, Experiment 5, revealed that only the most recent radial motion stimulus can induced a measurable spatiotopic MAE. The results of the experiments of Chapter 3 can not differentiate between the two following conclusions: either the paradigm did not allow for the production of two spatiotopic MAEs, or the visual system is not capable of generating two MAEs at two spatiotopic locations.

In Experiment 6 of Chapter 4 investigated the possibility that the absence of dual spatiotopic MAE was due to infrequent adapting stimuli. To this end, I increased the frequency of radial motion stimuli with the idea that more frequent radial motion stimuli would generate two spatiotopic MAEs. There was no effect of increasing the frequency of the radial motion stimulus; I still measured a spatiotopic MAE at the location of the latest radial motion stimulus presented.

The finding that one but not two radial motion stimuli can be encoded on the spatiotopic reference frame seems to reflect an actual limitation of the visual system rather than an erroneous result. In Experiments 2, 5, and 6 of Chapters 3 and 4, not only did I replicate the finding that a complex motion stimulus can be encoded onto a spatiotopic reference frame (Melcher, 2005; Turi & Burr, 2012), but I replicated this finding under three different conditions. The possibility for observers to perceive a MAE at the same spatial location as the preceding complex motion stimulus seems to reflect an actual capacity of our visual system. Moreover, the failure to measure two spatiotopic MAEs when two retinotopic MAEs can be measured suggests that the test method was sensitive enough to probe two MAEs, when they were encoded onto a fully defined reference frame.

One way to account for the results is to assume that the brain does not have a spatiotopic map, but rather a spatiotopic pointer, a visual memory that would keep track of the spatiotopic location of the latest relevant information. For instance the analysis of the expanding motion stimulus generated when walking contains information that allow us to produce a relevant response (e.g. avoiding collisions, intercepting objects; see Gibson, 1955), and by being able to localise this motion stimulus after an self-movement without having to re-analyse the visual scene, the visual system could save precious time; therefore allowing it to react faster to these crucial motion information (i.e. the information that either something is coming toward us or that something is escaping us).

Since in Experiments 5 and 6, the spatiotopic MAEs induced by the first adapting stimulus were constantly reversed (i.e. the motion aftereffect measured was in the same direction as the adapting stimulus), an alternative explanation to the spatiotopic pointer could exist. Because the two adapting stimuli contained opposite direction of radial motion, this MAE reversal, although never significantly different from 0, could be attributed to the second adapting stimulus. More precisely, because radial motion stimuli are processed by MSTd neurons (Burr, Morrone, & Vaina, 1998), whose receptive field can cover the locations of both adapting stimuli (i.e. MSTd receptive field can measure up 40º (Duffy & Wurtz, 1991), and because the motion adaptation was not tested at its default retinotopic location, the second adapting stimulus could have erased and replaced the motion adaptation induced by the first adapting stimulus by its own; therefore inducing a phantom MAE (i.e. in the direction of the second adapting stimulus) at the location of the first adapting stimulus.

Commented [DBSDE&S24]: Comment 1 about the role of the Phantom MAE and comment 10.10 (minor formating detail)

In Experiments 7 and 8 of Chapter 5, I approached the second question of the thesis on whether the visual system can learn that two radial motion stimuli occur at two spatiotopic locations. A recent study suggested that the visual system could be trained to associate a property of the visual system to a specific location within the visual scene (Haijiang et al., 2006). Could the visual system be trained to associate two radial motion stimuli with two spatiotopic locations? Models of human learning suggests that if such an association were to occur, a shift in coding strategies for radial motion perception – a visual adaptation – would be observed at the trained locations (Barlow, 1990; Friston & Kiebel, 2009). The absence of adaptation in Experiments 7 and 8 of Chapter 5 could be due to the paradigm used, which did not allow the visual system to associate radial motion stimuli with their spatiotopic locations.

In Experiments 9 and 10 of Chapter 5, I explored the possibility that the absence of adaptation for radial motion was due to the paradigm used. In previous studies, an attention task was used during the training part of the experiment (Bompas & O’Regan, 2006b; Haijiang et al., 2006). Moreover, behavioural experiments have also emphasised the role of attention in associative learning (Kattner, 2014). Consequently, I hypothesised that the addition of an attention task, would help the association of the radial motion stimulus to its spatiotopic location; therefore inducing a radial motion adaptation at each spatiotopic location of the stimuli. Two experiments investigated whether adding an attention task contributed to forming associations between the radial motion stimuli and their spatiotopic locations, but neither found a radial motion adaptation effect. In conclusion, the results of experiment 7 to 10 of Chapter 5 suggest that the visual system is not capable of associating radial motion stimuli to specific spatiotopic locations.

In Experiments 11 of Chapter 6 evaluated the third concern of the thesis: whether the visual system can learn that two radial motion stimuli occur after specific eye-movements. Previous studies suggests that radial motion stimuli are associated to walking movement (Durgin et al., 2005; Wallach & Flaherty, 1975). Recently, a study indicated that observers could be trained to associate colours with eye-movements (Bompas & O'Regan, 2006b). In Experiment 11, during the training period, each radial motion stimulus was always presented after a specific preceding eye-movement. This training period was aimed at inducing a shift in coding strategies identical to the one hypothesised in the experiment 7 to 10 of Chapter 5: radial motion adaptation. During the experiment, I measured radial motion perception before and after the training period. After the training period, the level of radial motion adaptation had increased based on the contingency introduced during the training period (e.g. in the training period, an expanding radial motion stimulus was constantly presented after a left eye-movement, and once this training stopped, the visual system was adapted to expanding stimulus after a left eye-movement). This result constitutes a further indication that the visual system is capable of learning eye-movement contingent consequences within visual scene, as reflected in dual adaptation to two radial motion stimuli.

2 POSSIBLE LIMITATIONS OF THE EXPERIMENTS

Regarding to the three main questions developed in this thesis, the experimental results point toward three main conclusions:

1. The visual system is not capable of adapting to more than one radial stimulus based on their positions in the real world.
2. The visual system is not capable of learning to adapt to two radial stimuli based on their positions in the real world.
3. The visual system is capable of learning to adapt to two radial stimuli based on a preceding action.

Commented [DBSDE&S25]: Comment 10.6 about a 1,2,3 conclusion

Each of these conclusions can be assorted to limitations. Here is a brief outline of the four main ones. First, according to Experiment 2, a radial motion stimulus can induce a single spatiotopic MAE, and that even if a delay is present between the presentation of the stimulus and the MAE (see section 4.4). However, this experiment only probes the MAE at its spatiotopic location, and not at an unmatched location (i.e. a location that corresponds to neither a location on the retinotopic or the spatiotopic reference frame), so the MAE recorded could correspond to a general adaptation of the visual system and not one specific to the spatiotopic location. Second, the visual system does not seem to be capable of learning to associate radial motion stimuli with their respective spatiotopic locations; however previous experiments have consistently reported at least a single adaptation of the visual system to spatiotopic (Haijiang et al., 2006; A. Jain & Backus, 2010; Anshul Jain & Backus, 2013). Third, the visual system can learn to associate different eye-movements with different radial motion stimuli. However, the strength of the motion adaptation reported in Experiment 11 – + 1% of motion adaptation after the training (see section 1.5) – could undermine this explanation. Fourth, none of experiments presented in this thesis contained eye-tracking data, which could at first glance indicate that participants did not maintain fixation as was required.

2.1 The Phantom MAE

Since none of the experiments of Chapter 3 and 4 probed the MAE at an unmatched location, then the single spatiotopic MAE could actually correspond to a non-specific adaptation of the visual system. Given the controversy existing in this field of research, many studies have actually probed the MAE at three types of locations (Knapen, 2009; Turi & Burr, 2012): they probed the MAE at its retinotopic location, at its spatiotopic location, and at an unmatched location. Knapen (2009) reported that if they did measure a spatiotopic MAE, that MAE was equal to the one reported at the unmatched location, so the adaptation induced by the motion stimulus is more likely to correspond to a general adaptation of the visual field rather than a specific spatiotopic adaptation.

The reversed MAE induced by the first adapting stimulus in Experiments 5 and 6 could also point toward a general adaptation of the visual field. More precisely, because radial motion stimuli are processed by MSTd neurons (Burr et al., 1998), and because MSTd neurons have receptive field as large as 30º - 40º (Duffy & Wurtz, 1991), the two adapting stimuli – only separated by 14º – could be processed by neurons with the overlapping receptive fields. In this case, the motion adaptation induced by the first adapting stimulus could be erased and replaced by the adaptation induced by the second adapting stimulus. The two adapting stimuli having opposite direction of radial motion, the MAE induced by the second adapting stimulus at the location of the first adapting stimulus would be reversed, and a negative MAE would be measured. However, Experiment 5 and 6 both probed the effect of a dual adaption on spatiotopic MAEs and both reported that only one location presented a significant spatiotopic MAE. If the spatiotopic adaptation actually corresponded to a general adaptation of the visual field, then the presentation of the second radial motion stimulus would have adapted the entire visual field; therefore the MAE generated by the second radial motion stimulus would have been observed at either location probed. Given that both Experiment 5 and 6 only reported a single spatiotopic adaptation, the idea that the entire visual field was adapted seems implausible.

Commented [DBSDE&S26]: Comment 1 about the Phantom MAE

2.2 The (too) short adaptation period

A second possible limitation targets the conclusion of Experiments 7-10 of Chapters 5 and 6 where the visual system seemed incapable of learning to associate two radial motion stimuli with their respective spatiotopic locations. One caveat of Experiments 7-10 could be the duration of their training period: 40min. Previous studies reporting a learned association between a visual property and a location in the visual field used training session ranging from 1 hour to 3 hours spread over 3 days (respectively Jain and Backus (2010), and Haijiang and colleagues (2006)). Consequently, it is possible that a longer training period could have resulted in an association between the radial motion stimuli and their spatiotopic location, and so in an adaptation of radial motion perception. However, the training duration was identical to the one used in Experiment 11 and it did induce a radial motion adaptation. So the fact that an adaptation of radial motion perception did occur in Chapter 6 suggests that the visual system can much more easily anticipates the consequence of its own self-movement on the visual scene than it can learn the consequence of radial motion that consistently occur at precise locations in the visual scene.

2.3 The (too) small effect of Experiment 11

The third limitation of this thesis concerns the strength of the effect reported by Experiment 11. A dual recalibration of radial motion perception did occur after a 40min-training period where each eye-movement was followed by a specific radial motion stimulus. However, when looking at the results, the effect is rather small:

radial motion perception was modified by only 1% as a result of the training period. Moreover, if both eye-movements had impacted the following perception of radial motion stimulus in the correct direction, the effect reported after right eye-movement toward the contracting stimulus is due to a negative pre-test radial motion perception (i.e. during the pre-test, observers perceived the radial motion stimulus that followed the both eye-movements to be slightly expanding; therefore in the reversed direction compared for the contracting stimulus). Yet, since the negative level of radial motion perception in the pre-test for the contracting stimulus is similar to the one for the expanding stimulus: observers perceive a slight expanding stimulus after either eye-movements, and this bias could be related to the larger number of MSTd cells tuned to expansion motion compared to contracting motion (Meng et al., 2006). Taken these two observations into account, it seems if the effect reported in Experiment 11 is relatively small but valid.

The opposite results of Experiment 4 and Experiment 11 despite their very similar experimental design also reinforces the conclusions that the effect reported in Experiment 11 is relatively small but valid. During both experiments, two adapting stimuli were presented at two spatiotopic locations but at one retinotopic location, and during both experiments, the adapting stimuli were presented for roughly 45 min. Yet, subjects experienced two MAEs at two locations only in Experiment 11. This difference can be explained by the testing phase of each experiment: Experiment 4 was designed to measure spatiotopic MAEs so subjects had to fixate a point and the test stimulus was presented at the spatiotopic location of the adapting stimulus; Experiment was designed to measure sensorimotor adaptations so subjects had to make the same eye-movement pattern as in the adaptation phase. Since only Experiment 11 reported two radial MAEs, it seems reasonable to conclude that it was the eye-movement pattern of the adaptation phase in combination with the two adapting stimuli that allow the visual system to adapt.

Overall, these two different justifications seems to point toward the same conclusion, I argue that the results reported in Experiment 11, two radial MAEs measured at two difference locations, are in favour of the sensorimotor adaptation of the visual system.

Commented [DBSDE&S27]: Comment 10.4 about the similarities and difference between experiment 4 and 11.

2.4 Eye-tracking data

A fourth limitations lies in the absence of eye-tracking data, which could explain the absence of effects observed in experiments where there was no attention task. An immediate effect of this limitation would be the variability of effects reported across subjects: different observers would have had different eye-movement pattern during the experiment and all should have reported different level of motion adaptation. However, Experiment 9 aside, the results observed in all experiments are similar across subjects, which tends to suggest that there were all probing a similar mechanism. Moreover, the method used to probe the MAE, a psychometric staircase, would not have been able to converge toward a consistent point at the individual level: from one trial to the other a subject would have made different type of eye-movement and induced a motion adaptation a different location and so there would not have been a consistent motion adaptation threshold for the staircase to converge to. A brief glance at the individual staircase profile suggests otherwise, as all are converging toward a consistent threshold. As for Experiment 9, the average 75% threshold reached by all subjects during the attentional task suggest that subjects were indeed fixating at the right locations, and that the variability in the results is due to the variable manipulated during the experiment. Overall, the idea that participants did not fixate at the instructed location seems to be implausible.

Commented [DBSDE&S28]: Comment 6 about eye-tracking data

3 FUTURE DIRECTIONS

The main results and conclusions I report in this thesis suggest further investigation in two different topics. First, the relatively short duration of the training period (i.e. 40min) in Chapters 5 to 6 seems to be a problem for both type experiments as it is either insufficient to induce an adaptation of radial motion perception (i.e. Chapter 5) or the effect of the induced adaptation of radial motion perception is small (i.e. Chapter 6). It is possible that increasing the duration of the training period could result in a stronger adaptation of radial motion perception, in both type of experiments (i.e. whether the association with the radial motion stimulus takes place with a preceding self-movement or at a precise spatiotopic location). Consequently, I suggest adopting the training duration used in Haijiang and colleagues (2006), 1 hour of training for 3 consecutive days. By increasing the exposure of the visual system to the correlation between the radial motion stimulus and a preceding self-movement or a precise spatiotopic location, the chance of the two events to be associated increases.

Second, the existence of the spatiotopic pointer suggested in light of the results from Chapter 3 and 4 could also be explored. In brief in Experiment 5 and 6, I consistently measured a single spatiotopic MAE induced by the latest motion stimulus presented, but I never measured two spatiotopic MAEs. To account for these results, I suggested that the visual system only keeps tracks of the most recent stimulus (i.e. transform its retinotopic coordinates into spatiotopic ones). This process would permit the visual system to immediately have access to the location where a motion stimulus was presented regardless of our own self-movement. In that sense, it would act as a compass that when you move still indicates “the north”.

Keeping track of radial motion stimuli can be extremely important. For instance, expanding motion stimuli either indicate that something is running away from us or that we are running toward something, and being able to keep track of this change as we move by transforming its retinal location into a spatial one could be very useful. Moreover, the advantage is not only to transform the location of where the motion stimulus occur in spatiotopic coordinates, but also to have an immediate access to this information via the MAE without having to re-process the entire visual scene. The spatiotopic MAE could save precious milliseconds in localising this movement; therefore allowing the visual system to react faster to the event.

To bring further evidence to the existence of a spatiotopic pointer for motion stimulus, I suggest two possible routes. First, since the objective of the spatiotopic pointer is to indicate the latest location of a motion stimulus, then by presenting two changes simultaneously on the screen, it should be possible to detect two spatiotopic

MAEs. If the proposed experiment resembles the ones used in the dual spatiotopic experiments, in Experiments 5 and 6 the two motion stimuli were consequently presented, so presenting them simultaneously would force the visual system to keep track of both changes. Second, as mentioned in Chapter 3 and 4, the spatiotopic location (i.e. the location of an object in the real-world coordinate) is not separated from the craniotopic location (i.e. the location of an object in reference to the head) in Experiments 5 and 6, it would be interesting to separate the two reference frames to see if the spatiotopic pointer is truly spatiotopic.

4 OVERALL CONCLUSION

The question of whether the visual system is capable of adapting to two simultaneous changes in the environment (i.e., two radial flows) is important, and the results presented in this thesis suggest that such dual adaptation only occurs under relatively circumscribed conditions. This thesis explored three aspects of dual simultaneous motion adaptations: when it occurs immediately after the presentation of motion stimuli at their locations in space (i.e. Chapters 3 and 4), when it occurs following the sustained presentation of the two motion stimuli at two locations in space (i.e. Chapter 5), and when it occurs following the combination of self-movements and two motion stimuli (i.e. Chapter 6). Only in the last condition did a dual adaptation occur. These results bring three different answers to the main problem of dual simultaneous adaptation. The results of Chapter 3 and 4 suggest that dual adaptation linked to different locations in space does not occur: the presentation of radial motion stimuli does not induce a fast low-level adaptations on a reference frame of the external world (i.e. the spatiotopic reference frame). The results of Chapter 5 indicate that dual adaptation did not occur when the visual system receives 40min to learn to associate a motion stimulus with its location in space. The results of Chapter 6 show that the visual system is capable of learning to associate self-movements with different visual properties of the environment. The idea that the visual system is better prepared to learn that a visual stimulus (e.g. radial motion) is associated with a self-movement (e.g. an eye movement) has several precedents (e.g., Durgin et al., 2005; Von E, 1950; Wallach & Kravitz, 1965). I conclude, based on the results of the different experiments and the current literature, that dual simultaneous adaptation is only possible if the change is induced by a self-movement. This conclusion emphasises the role of self-movements in allowing the visual system to adapt to new properties of the visual environments. In brief, we only adapt to new properties of the visual environment if these properties affect the way we interact with our environment. With regard to the example presented at the start of this thesis, our visual system only adapts to optic flows on opposite sides of the motorway either retinotopically or through a process of learning involving eye-movements.

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Commented [DBSDE&S29]: Comment 10.10 about minor foprmating detail