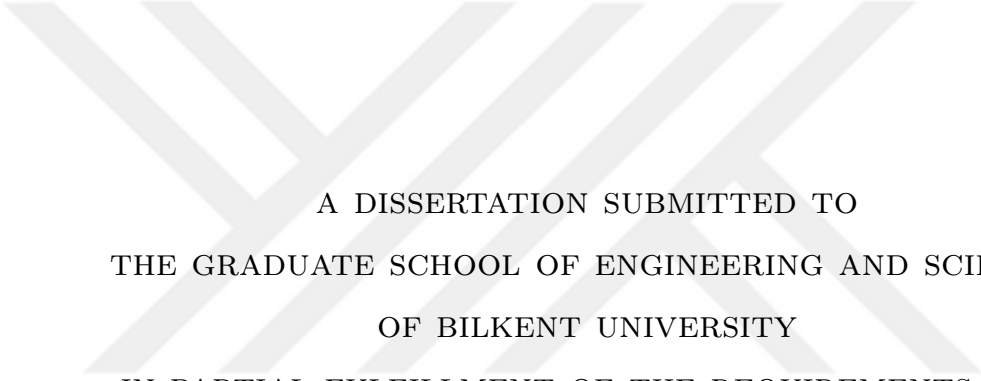


PROBING SENSORY PLASTICITY WITH RAPID FORMS OF MOTION ADAPTATION



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Sibel Akyüz
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MOTION ADAPTATION

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We certify that we have read this dissertation and that in our opinion it is fully adequate, in scope and in quality, as a dissertation for the degree of Doctor of Philosophy.

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ABSTRACT

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Ph.D. in NEUROSCIENCE

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Perception is shaped by both immediate pattern of sensory inputs and previous experience with the external environment. Visual adaptation, a temporary change in perception following exposure to a stimulus, has been widely employed to understand how previous sensory experience on different timescales shapes perception. Visual motion adaptation is a powerful investigative tool to understand sensory plasticity and neural adaptation. However, the neural mechanisms underlying adaptation induced changes by visual motion are still subject to debate. In the present thesis, spatiotemporal dynamics, neural substrates, and functional role of sensory plasticity in the human visual system was examined using rapid forms of motion adaptation paradigm combined with EEG. Specifically, how motion adaption-induced short-term sensory plasticity is reflected at the neural level and parallel with perceptual performance were explored. Participants were adapted to directional drifting gratings for either short (640 ms in Experiment 1; 188 ms in Experiments 2 and 3) or long (6.4 s in Experiment 1; 752 ms in Experiments 2 and 3) durations and used a counter-phase flickering (with constant polarity in experiments 1 and 2; polarity inverting within every step in Experiment 3) grating as a test pattern. Sinusoidal gratings of phi motion were employed in Experiment 1 whereas; square wave gratings were used for phi and reverse-phi adaptations in Experiments 2 and 3 to examine how ON and OFF pathways operate in the visual processing stream. Based on the EEG analyses in Experiment 1, the scalp sites relevant to motion adaptation were identified. Experiment 1 showed that both adapting durations led to significant motion aftereffects and EEG results showed that long adaptation produced stronger aftereffects than the short adaptation condition within 64-112 ms time range over occipital and parieto-occipital sites. Taken together, these findings provide important electrophysiological evidence that motion aftereffects reflect changes in cortical areas mediating low- and mid-level visual motion processing.

They also suggest that adaptation is an active process that involves neural mechanisms operating at different time scales. In Experiments 2 and 3, the short-term adaptation induced changes over these identified scalp sites were further examined based on Experiment 1. Given that the phi and reverse-phi motion mainly engage within (ON or OFF) and across (ON and OFF) pathway mechanisms, the comparisons of adaptation induced changes across these motion types provided further insights into the nature of corresponding mechanisms over visual cortex. The behavioral and EEG findings pointed to efficient convergence of information provided by these pathways and some distinct characteristics of across pathway mechanisms.

Keywords: Neural adaptation, dynamic motion aftereffect, short-term, long-term, event-related potentials, rapid motion aftereffect, phi, reverse-phi, ON-OFF pathways.

ÖZET

DUYUSAL PLASTİSİTENİN HAREKET ADAPTASYONUNUN HIZLI BİÇİMLERİ İLE İNCELENMESİ

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Algı, hem anlık duyuşal girdiler hem de dış çevre ile önceki deneyimlerle şekillenir. Bir uyarıcıya maruz kaldıktan sonra algıda geçici bir değişiklik oluşturan görsel adaptasyon, önceki duyuşal deneyimin farklı zaman ölçeklerinde algıyı nasıl şekillendirdiğini anlamak için yaygın olarak kullanılmıştır. Görsel hareket adaptasyonu, duyuşal esnekliği ve sinirsel uyumu anlamak için güçlü bir araştırma aracıdır. Bununla birlikte, görsel hareketin neden olduğu adaptasyon kaynaklı değişikliklerin altında yatan nöral mekanizmalar hala tartışmaya tabidir. Bu tezde, EEG ile hızlı hareket adaptasyon paradigması biçimleri kullanılarak uzay-zamansal dinamikler, nöral substratlar ve duyuşal plastisitenin insan görsel sistemindeki işlevsel rolü incelenmiştir. Spesifik olarak, hareket adaptasyonunun neden olduğu kısa vadeli duyuşal plastisitenin algısal performansa paralel olarak ve nöral düzeyde nasıl yansıtıldığı araştırılmıştır. Katılımcılar kısa (Deney 1’de 640 ms; Deney 2 ve 3’te 188 ms) veya uzun (Deney 1’de 6,4 sn; Deney 2 ve 3’te 752 ms) sürelerle bir yöne hareket eden greytinglere adapte edilip, test uyarısı olarak zıt fazlı (Deney 1 ve 2’de sabit polarite ile; Deney 3’teki her adımda ters polarite ile) greytingler kullanılmıştır. Görsel işlem akışında AÇIK ve KAPALI yolların nasıl işlediğini incelemek için Deney 1’de phi hareketinin sinüzoidal greytingleri kullanılırken; Deney 2 ve 3’te phi ve ters-phi adaptasyonları için kare dalga greytingleri kullanılmıştır. Deney 1’deki EEG analizlerine dayanarak, hareket adaptasyonu ile ilgili kafatası bölgeleri belirlenmiştir. Deney 1, iki adaptasyon sürelerinin de önemli hareket sonrası algı etkilerine yol açtığını gösterirken aynı zamanda deneyin EEG sonuçları, uzun adaptasyonun kısa adaptasyon koşuluna göre, oksipital ve parieto-okspital bölgelere göre 64-112 ms zaman aralığında daha güçlü etkiler oluşturduğunu göstermiştir. Birlikte ele alındığında, bu bulgular hareket sonrası algının, alt ve orta seviye görsel hareket işlemeye aracılık eden kortikal alanlardaki değişiklikleri yansıttığına dair önemli elektrofizyolojik kanıtlar

sağlamaktadır. Ayrıca, adaptasyonun farklı zaman ölçeklerinde çalışan sinir mekanizmalarını kapsayan aktif bir süreç olduğunu öne sürmektedirler. Deney 2 ve 3'te, Deney 1'e bağlı olarak belirlenmiş kafatası bölgelerinde meydana gelen değişikliklere bağlı olarak kısa süreli adaptasyon kaynaklı değişiklikler daha ileri düzeyde incelenmiştir. Phi ve ters-phi hareketinin esas olarak aynı (AÇIK veya KAPALI) ve karşılıklı (AÇIK ve KAPALI) yolak mekanizmalarını harekete geçirdiği göz önüne alındığında. bu hareket türlerinin adaptasyonundan kaynaklı değişikliklerin karşılaştırılması görsel korteks üzerine karşılık gelen mekanizmaların doğası hakkında daha fazla bilgi sağlamıştır. Davranışsal ve EEG bulguları, bu yolaklar tarafından ortaya çıkan bilginin etkin bir biçimde birleşmesini ve karşılıklı yolak mekanizmalarının bazı farklı özelliklerini ortaya çıkarmıştır.

Anahtar sözcükler: Nöral adaptasyon, dinamik hareket sonrası algı, kısa süreli, uzun süreli, olaya ilişkin potansiyeller, hızlı hareket sonrası algı, phi, ters-phi, ON OFF yolakları.

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Chapter 1

General Background

Vision is essential not only in interpreting and understanding our environment but also crucial for survival. One of the important tools to understand visual perception is the misinterpretation of the physical input. Illusions are great demonstrations of such misinterpretation of visual information. The focus of the current thesis is an illusion called motion aftereffect which has found increasing application as a powerful methodological tool in studies of sensory plasticity and visual processing. In this thesis, the general organization of the visual system, motion adaptation, motion aftereffect, rapid motion aftereffect (rMAE) and, visual motion priming (VMP) will be presented first. The plasticity elicited by MAE and VMP and their neurophysiological basis will also be discussed. Afterwards, the three experiments will be separately introduced in detail. Experimental paradigms were based on rapid MAE and VMP in all of the studies.

1.1 Human Vision

Visual processing starts with a wavelength of light in the visible spectrum reflected by the surrounding objects and striking on the retina. Although perception is initiated with the light hitting the retina, further sensory processes play critical

roles in perception as well. The information provided by the external environment is transmitted to the brain and how the brain interprets it has been a topic of interest to countless number of researchers. Some highlight the stimulus-driven bottom-up nature of perception while others propose that additional top-down processes acquired through prior experiences also play a critical role [11, 12, 13].

Previous research has identified distinct pathways and processing streams specialized for different aspects of visual stimulation. One of the earliest distinction was based on luminance increments (ON pathway) and decrements (OFF pathway). On-center off-surround system, one of the most fundamental systems in the visual system, was initially investigated using the cat visual system [14]. Kuffler's seminal studies showed the existence of two types of retinal ganglion cells, one showing excitation, an "ON" response in response to increased light; the other one an "OFF" response to decreased light. Another major contribution by Kuffler [14] to vision research was to elaborate the mapping of the center-surround relations in the receptive field. He demonstrated that when an ON cell was illuminated in the center it increased its firing rate however, when its peripheral receptive field was illuminated with light, its firing rate decreased. Using the cat visual system, retinal ganglion cells were classified into two groups [15]. X cells, which are more abundant in number and have linear summative characteristics, are more sensitive to the specifications of the stimulus. However, Y cells are less in number, relatively nonlinear in terms of the information they convey to the further steps of the visual system and, more sensitive to identification of change. Retinal ganglion cells transmit the initial signals to the optic nerve to be routed to the LGN (Lateral Geniculate Nucleus) and on to the primary visual areas.

Primate retinal ganglion magnocellular (corresponding to Y cells in cat retina), parvocellular (corresponding to X cells in cat retina) and koniocellular cells project to different areas of the LGN and possess different characteristics in terms of morphology and function. Koniocellular cells are located in the layers between M and P cells. While P cells project to the dorsal areas of the LGN and are numerous in number, they are small in size and smaller in receptive field size compared to the M cells. M cells project to the lateral side of the LGN, are

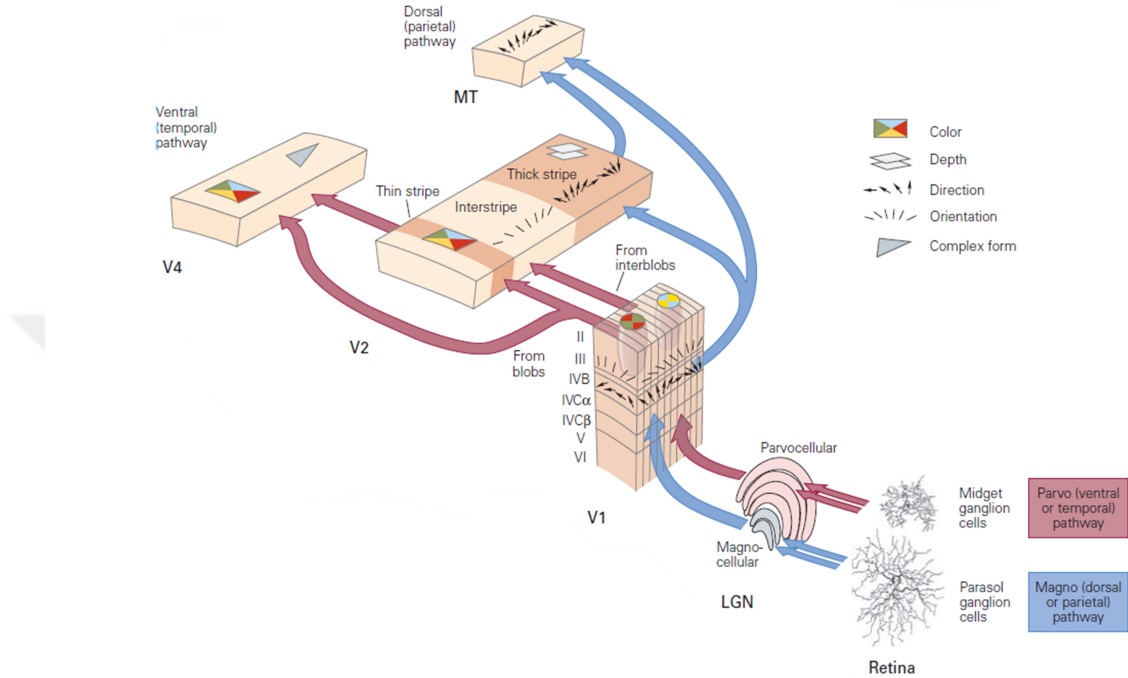


Figure 1.1: Information processing starts in the retina and continues in the dorsal and ventral pathways (Adapted with permission from McGraw Hill LLC, ref. [1]). The dorsal pathway is parvo-dominated whereas ventral pathway is magno-dominated. Parvocellular and Magnocellular cells in the LGN project to distinct parts of V1 (primary visual cortex) followed by a relay to the stripes in V2. Secondary visual cortex (V2) is important for depth, form and direction information, provides input to V4 and MT for further shape and motion processing, respectively.

approximately one-tenth of the P cells in number, bigger in size and receptive field sizes and, relay information relatively faster than the P cells (Fig. 1.1). Also, while P cells have sustained response and they are more sensitive to color stimuli, M cells respond more transiently to stimulation and are more sensitive to black-white low contrast stimuli [16].

LGN has an important role in modulating the afferent sensory signals and projecting them to the initial stages of the visual cortex. The LGN converges and conveys the sensory input to the visual cortex. The primary visual cortex retains the segregation projected from the LGN and, M and P pathways coalesce

in the primary visual cortex [17]. In other words, a segregated organization at the primary visual cortex level is retained. Another fundamental organization of the system is columnar organization in cortex. The presence of orientation columns in the primary visual cortex were shown [18]. They suggested that cells tuned to a specific orientation cluster together and form a columnar organization. Cells with similar feature sensitivity such as orientation are found in a neighbouring columnar structure in the cortex [19]. The cells receiving input from the same eye are grouped together into “ocular dominance columns” in the cortex [20]. Application of Cytochrome oxidase (CO) staining to the visual cortex additionally revealed the blobs and stripes in early visual areas V1 and V2 [21, 22]. These blobs incorporate neurons that are selective to color and relatively less selective to orientation.

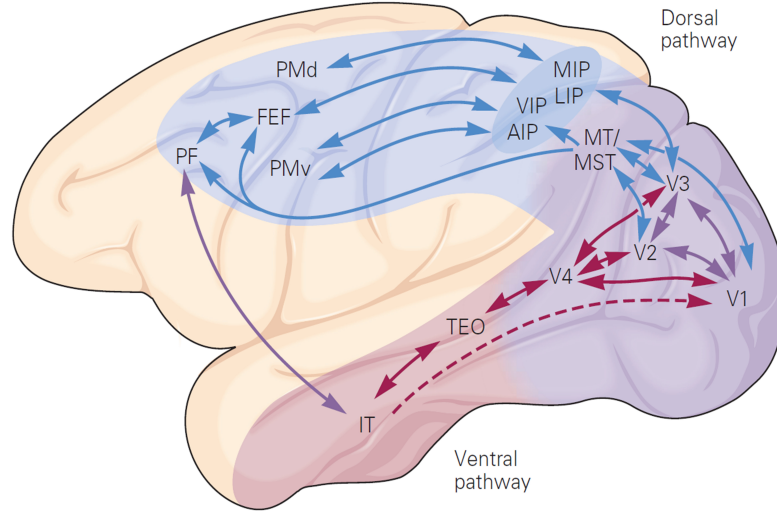


Figure 1.2: Cortical areas of the macaque monkey. Ventral and dorsal pathways are shown. Information progressing streams along the cortical areas are indicated with arrows. The inter- and intra-connections between the regions as they progress to later stages can also be observed (Adapted with permission from McGraw Hill LLC, ref. [1]).

As the signal proceeds into the later stages of the visual processing, the receptive fields of neurons become larger and the retinotopy becomes more conspicuous. Segregated pathways in the earlier areas start to coalesce as the signal progresses to higher areas. For instance, in the area MT, neurons have relatively larger receptive fields than the neurons in the primary visual cortex and the MT neurons integrate the motion information delivered by the primary visual areas. Two mainstream pathways, dorsal and ventral, are defined (Fig. 1.2). The dorsal pathway, which mainly consists of V5 (corresponding to MT and MST in monkey cortex) and plays a critical role for motion perception and action. On the other hand, the ventral pathway dominated by parvocellular input consist of areas, along the temporal cortex (V2, V3, V4, and IT) and it is specialized for object recognition [16].

Visual system also shows evidence for shortcuts to better adapt and respond to visual stimuli that have certain characteristics and may have priority in terms of survival. It is important to stress this interesting line of research that suggests a pathway bypassing early visual areas and directly projects to MT. Fast moving stimuli is mostly associated with this “shortcut”. Researchers used fMRI to measure BOLD signals on the LGN, V1 and MT [23]. They presented the participants with moving dots for 9 seconds at a speed of 6.8° per second in the block design experiment whereas; the speed of dots was increased to 10° in the second experiment (event related design). They found a direct effect of the BOLD response in LGN over MT and this activation was not mediated through V1. Likewise, existence of a probable pathway direct from pre-striatal areas to MT was examined [24]. Using EEG and MEG, they compared the time of arrival of the signal in V1 and V5. They found that signal initiated from a moving stimulus with 22° per second was detected in V5 earlier than it was in V1; when the speed was lesser than 6° per second, the signal arrived at V1 first. ERP latencies in response to a motion stimulus were examined [25]. They found activation in the vicinity of V5 within 30 ms followed by an activation around V1 extrastriate area with a latency onset around 56 ms peaking at 70 ms. Separate asynchronous input to V5 is shown to project asynchronously to perceptual endpoints [26, 27]. In other words, MT does not wait for all the inputs to complete their courses in

order to ignite an output from itself, it rather separately processes inputs arrive in it asynchronously.

1.1.1 Major Motion Models

Visual motion has been an extensively investigated aspect of vision [28, 29, 30]. Several models and motion-systems have been proposed to account for motion detection and discrimination. One of the proposed model is Reichardt detector which is a simple neural circuit of how motion is detected and the direction is computed. For a motion signal to be detected, the input must be received from two spatially segregated receptive fields. Depending on how fast the object is detected at point A and later detected at point B , different cells will fire so that the velocity and the new position of the stimulus can be computed to calculate the direction of the movement. For instance, consider an object moving from point A to point B . Initial signals that arise at the position of A and B are delayed so that they coalesce with A' and B' (latter signals) at the multiplication stage (Fig. 1.3). Leftward motion is perceived if the product of A' and B is greater than the product of A and B' [2].

Reichardt's model was developed for fly motion detection. Later, elaborated Reichardt's model is suggested in order to extend the Reichardt's model to human vision [31]. The model (Fig. 1.4.) is different from the original Reichardt detector in terms of the presence of linear spatial filters (SF) and the temporal integration filter (TA) where temporal averaging is performed.

In an alternative model called Fourier Motion Energy [4], spatial and temporal filters are used to calculate the motion energy (Fig. 1.5). The motion energy model suggests that the input is initially sent to two spatial filters, they pass the signals along to temporal filters, and one of these filters receive the signal with a delay. Following, space – time derivatives of quadrature pairs are calculated to obtain four non-directional inputs (A , B , A' , B'). The information is then passed forward to the next stage to form oriented linear responses. Two left and two

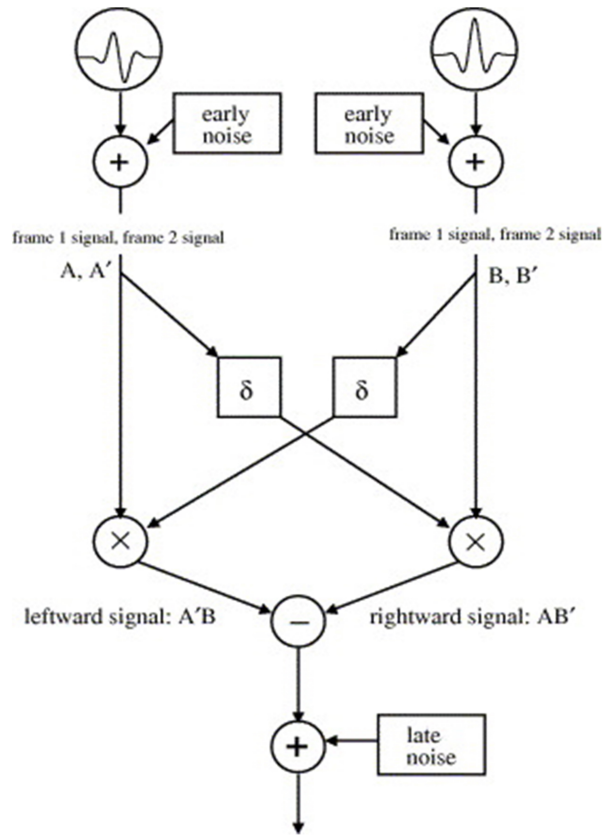


Figure 1.3: Reichardt's detector model. Adapted with permission from Elsevier, ref. [2]. First, a delayed and non-delayed signal from spatial filters are passed to temporal filters. After the multiplication stage, input signals are subtracted from each other to determine the final direction output.

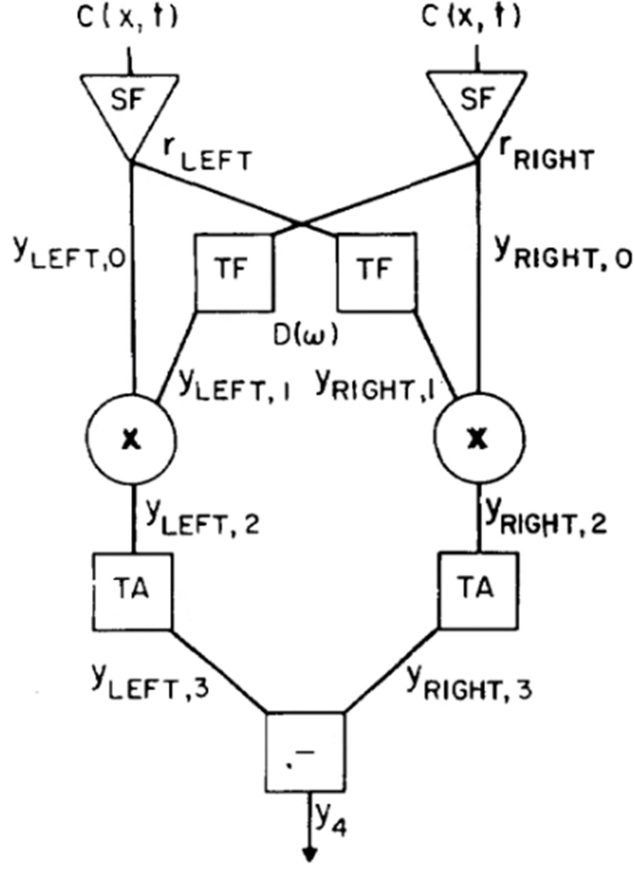


Figure 1.4: Elaborated Reichardt's detector model. Contrast information $c(x, t)$ is sampled from two separate receptive fields by spatial filters named SF. The linear spatial filters (SF) then produces spatial responses expressed as $y_{left,0}$ and $y_{right,0}$. Spatial filters also send a delayed output (r_{left} and r_{right}) to the opposite filter. r_{left} and r_{right} are delayed by the temporal filter, TF, to produce $y_{left,1}$ and $y_{right,1}$. The initial output from SF ($y_{left,0}$ and $y_{right,0}$) and the delayed output ($y_{left,1}$ and $y_{right,1}$) feed into the correlator X to integrate two information and produce $y_{left,2}$ and $y_{right,2}$ at each filter. $y_{left,2}$ and $y_{right,2}$, which are local percepts, are tuned for right or left directional at this point of the stream. $y_{left,3}$ and $y_{right,3}$ produced by the TA (temporal averaging) stage are subtracted to give out global Y_4 , final direction selective output. Adapted with permission from The Optical Society, ref. [3].

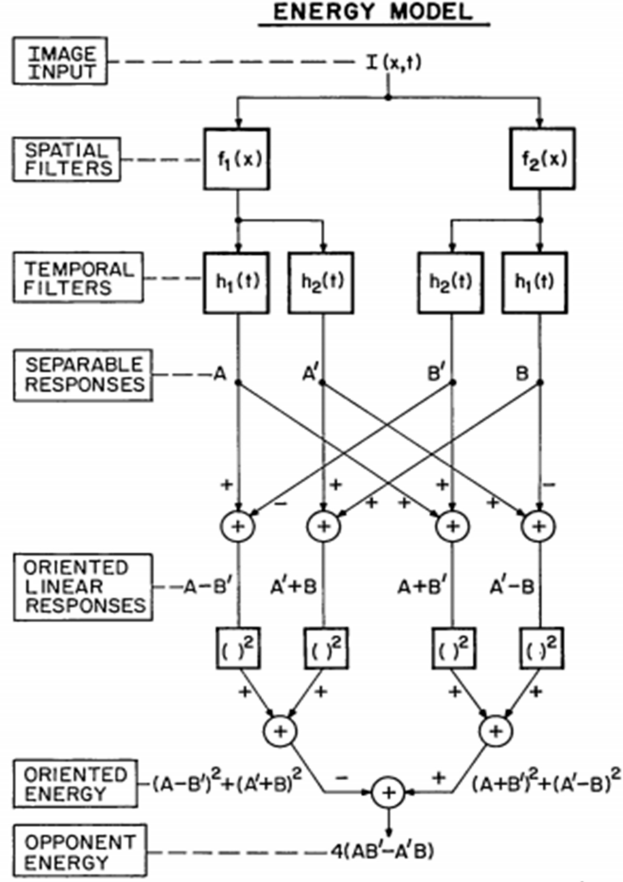


Figure 1.5: Adapted with permission from The Optical Society, ref. [4]. Initial input passes through two spatial filters each to be conveyed to two separate temporal filters one with a delay. Four spatiotemporal separable responses are generated which are later either added or subtracted in the oriented filters. Out of four oriented linear responses, two indicates one direction and the other two indicates the opposite direction. All these responses are squared and same direction energies are summed to form oriented energy responses which are later subtracted from each other to have the final energy output.

right filters are obtained by adding and subtracting the initial non-directional inputs (L_1 , L_2 , R_1 , R_2). Oriented motion energy is obtained by adding sum of squares of the left responses (L_1 and L_2) and, right responses (R_1 and R_2) separately. Finally, the output of these left and right energy is subtracted from each other to have the opponent energy. Direction of motion is inferred from the sign of the difference and if the difference is 0, no net motion is perceived [32].

Original Reichardt model lacks specific features and steps that elaborated detectors and motion energy model have. The initial step in the elaborated Reichardt model, SF step, captures receptive fields that are spatial frequency tuned. Additionally, the TA step converts the local motion signals into global signals which are crucial to form a global motion percept. Initially, Reichardt detector was modelled using point shaped receptive fields. Their filters are linear and time invariant and worked for flies however it is insufficient to interpret human vision. Elaborated Reichardt model expands and applies the original Reichardt model by introducing spatial and temporal filters. On the other hand, elaborated Reichardt detectors are similar to the motion energy model suggested [4]. Sequence of the computations might differ but in the end, their outputs are functionally indistinguishable [3]. Therefore, both elaborated Reichardt and Adelson-Bergen motion models are comparable and valid for human vision.

Single bar and 2 bar responses were examined and it was reported that the results were poorly accurate with a Reichardt detector model [33] however, the predictions from Adelson Bergen model [4] were highly consistent with their results. The motion detection algorithm suggested by Adelson Bergen model [4] was implemented on a vision sensor device [34] and reported highly accurate direction detection performance emphasizing the accuracy of the Adelson Bergen model.

1.2 Visual Adaptation

Visual adaptation refers to temporary changes in the neural activity and the final percept due to continuous presentation of an external stimulus. Adaptation typically causes the adapted neuron population to decrease its sensitivity and cause lingering effects on perception even after removing the adapting stimulus. Why does the visual system have such mechanism? An explanation according to the predictive coding theory states that, regularities in the environment and changes that create irregularities are detected by this mechanism. Prior experience of the environment is used as a top-down apparatus to either suppress or allow sensory input arising from the external environment. This prior information is compared to the incoming feed-forward information with a feedback mechanism, and if there is a mismatch between the two, the information is updated for better prediction of the sensory input in the future leading to an updated, better interpreted template of the sensory input. From an evolutionary perspective, such update of the information operates to aid survival. Simply put, adaptation to repeating stimulus is established, causing the neurons to decrease their sensitivity to it to better detect the abrupt sensory changes in the environment. Besides, long- and short-term forms of neural plasticity related changes occurring on the post synaptic sites eradicate the possibility of excitotoxicity. Updating the system based on the new information is also seen in the visual cortex. Macaque visual areas were examined [35], expecting a remapping occurrence in the extrastriate areas. Receptive fields of neurons were mapped before and after a saccade was made. They found that flashing of a stimulus in the prospective receptive field (the new receptive field after the saccade) of a neuron ignited remapping activity in the 16% of the V3A neurons even before the saccade was initiated and, this rate was lower for the areas V3 and V2.

Sensory inputs starting from early development to the most recent shape how we perceive the environment in our own experience. Plasticity refers to adaptive adjustments in the neural wiring patterns. Long- and short-term plasticity refer to the synaptic changes in synaptic responses for a long or a short period of time. Wiring of neurons continues throughout development and input from

sensory mechanisms affects the way neurons establish patterns. For example, when an early born macaque is deprived of visual input in one eye, unequal ocular dominance wiring is developed as a result of no input in the deprived eye therefore, affecting the development of neural wiring [36] and redefining the perception. This notion is also pertinent to motion perception that is, in response to successive stimulation of motion adaptation, direction selective neurons show changes in synaptic responses.

Plasticity can be reflected in various circumstances over the visual cortex. A deprivation of activity in a group of neurons can be given as an example. In the study, visual stimulus was presented successively [37] to measure the temporal responses of the neurons in the visual cortex. The results indicated that when the stimulus was in the preferred orientation of the neuron, the suppressive response to the latter stimulus was the strongest.

Responses of MT neurons were examined via presenting an adapting and a test stimulus at different locations in the visual field [38]. The aim was to activate different cluster of neurons to assess whether adaptation arises from synaptic depression or rather from intrinsic mechanisms. They found that the adaptation of a group of neuron in a part of the visual field caused attenuation on the firing rates of the neurons that correspond to a separate location on the test stimulus.

Besides the detrimental effects of adaptation on the subsequently presented stimulus, it also can have facilitatory effects under certain conditions. For instance, participants were presented with a Necker cube primed for various durations (0-90 seconds) [39]. The primer stimulus was followed by an ambiguous test pattern that could be interpreted to face one of the two sides. The results suggested a priming effect when exposure to the primer was for shorter periods and, an aftereffect when the primer was presented for longer durations.

1.3 Motion Adaptation and Neuronal Response Changes Via Motion Adaptation

Neural plasticity is essential for survival in a dynamic and changing environment. Functional role of sensory plasticity in perception and cognition, the underlying neural mechanisms, and temporal dynamics are still debated. Illusive perceptions play a huge role on altering visual perception and comprehension of ever-changing surroundings. Paradigms based on motion adaptation have been extensively used in this context. After prolonged exposure (i.e., tens-hundreds of seconds) to an object moving in a particular direction and with a certain speed, neurons of the visual system decrease their response to that direction and speed. This phenomenon is known as motion adaptation. Motion adaptation has been used as a tool to adapt neuron groups to study the consequences of synaptic plasticity. The reason visual adaptation is called “the psychologist’s electrode” [40] is because groups of neurons can be adapted without physical interference so their plasticity and firing rates are manipulated. In this thesis, motion adaptation is used as a tool to adapt motion selective neurons (i.e., detectors) in three separate studies. In this way, the percept of an ambiguous test pattern of the test stimulus is modulated.

In an earlier study, it was shown that visual cortex contains motion sensitive neurons [41]. It was proposed that the perceived direction of motion might depend on the ratio of the firing rates of the cells tuned to opposite directions [42]. In line with Sutherland’s ratio rule, adaptation induced changes on rabbit retina has been shown [43]. Motion sensitive cell responses to the prolonged exposure to a random dot pattern were recorded on the rabbit retina and, they found that long-term exposure initially increased the firing rate of the neurons but gradually decreased over time and went down the baseline levels when the stimulus was removed from the display. Alterations in neural responses to rapid presentation of the same stimulus twice is observed and reported in several similar studies.

Directional adaptation followed by a random dot kinematogram was used to probe neuronal responses [5]. As shown in Fig. 1.6., when the adaptation was

in the preferred direction of a neuron, the firing rate gradually decreased as the adaptation was maintained. Firing rates remained around the baseline level when a test stimulus moving in the null direction was presented. The firing rate of neuron was around 75 spikes/sec with a 0% coherence level. Average firing rate was observed when the test stimulus was in the preferred direction. This was also the case for the test stimulus when the test stimulus was static (green lines). Nonetheless, adaptation to the static stimulus did not elicit any changes in the MT neuron's response. Adaptation in the null direction however, did not elicit response for the left direction sensitive neuron. Nevertheless, adaptation to null direction followed by a null direction or 0% coherent test stimulus did not elicit measurable responses. However, a test stimulus in the preferred direction induced responses comparable to the magnitude of the responses when the direction of adaptation and test was congruent.

Adaptation to a stimulus is proven to make a reduction in sensitivity and an opposite direction percept of the subsequent stimulation [44]. Participants were tested with either rightward or leftward moving square wave gratings on various durations [45]. The duty cycle affected the P1 and N1 amplitudes. When the duty cycle was at 5%, N1 component showed the biggest amplitude however; as the duty cycle increased, P1 and N1 reversed their domination in terms of amplitude, and at 80%, P1 simply dominated N1 on all 3 electrode sites. Motion adaptation can also alter the perception of the location of a stimulus. It was shown that when adaptation and the test stimulus had collinear or orthogonal carrier gratings, and the location of a test stimulus appeared to have shifted substantially in its global position [46].

Brief stimulations are shown to exhibit facilitating effects on the neuronal response in some studies. For instance, induced short-term enhancement was reported as well as depression [47]. Enhancement response was shown in V1 [48]. The responses of MT neurons were recorded after adaptation to null and preferred direction of motion [49]. They found that both adaptation types altered responses of MT neurons, but they attributed the adaptation induced changes to earlier areas in the visual tract. Adaptation induced changes were shown in MT

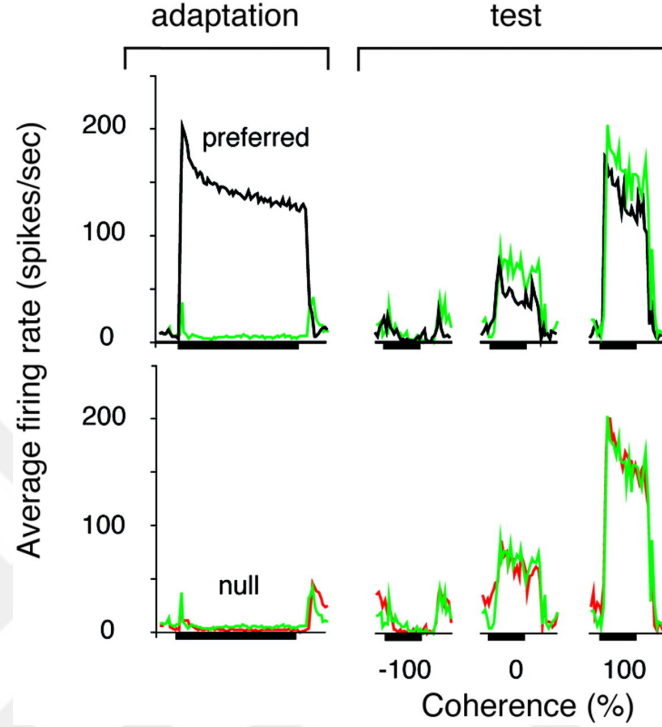


Figure 1.6: A representative MT neuron of a rhesus monkey under different adaptation conditions. Adapters were presented for 3 seconds followed by an ISI (500 ms), and then a random dot kinematogram test stimulus with three different coherency options (null direction: 100%, random movement: 0% coherence, preferred direction movement: 100% coherence) was displayed for 1 second. Neuron's response to preferred or null direction adaptation are shown. The red lines at the bottom correspond to null direction adaptation; the green lines show responses to static pattern used as a control condition (Adapted with permission from The American Physiological Society, ref. [5]).

receptive fields [50].

MAE was examined on cat striate cortex [51]. Square-wave gratings drifting (either in the preferred or null direction) or randomly textured fields were used as adapters for 1 minute. A test stimulus for 1 minute following the adaptation was presented. A control condition in which randomly textured fields were presented was introduced to compare with the adaptation conditions on simple and complex cells. Recordings showed a more rapid onset and decline of simple cells as opposed to complex cells. However, they both showed MAEs of similar strength. The firing rate decreased to a steady state level within 30-60 seconds. Response to

the latter stimuli is shown with a depression in neural response [52]; with a short term depression in the cat visual cortex [53] and; with a more robust but faster dissipating synaptic depression and, a weaker but more persistent response type in layer 2/3 of rat visual cortex [54]. Presentation of a moving stimulus in rapid succession has been reported to cause a reduction in the response to the latterly presented stimulus [55, 53].

Repetitive stimulation suggests a reduction in the neuronal response. It was shown that adapting to a steady high contrast grating for a while reduces the visibility of a grating with low contrast [56]. Responses of rat striate cortex simple cells while responding to drifting stimulus were recorded and shown that the responses to low contrast gratings were reduced after adapting to a high contrast grating for 30 seconds [57]. Postsynaptic potentials on cortical tissue slices were recorded [58]. While they employed repetitive stimulation, they found exponential depression response of the post synaptic tissue. Their findings suggest that the long-term depression caused by adaptation is likely due to declining neurotransmitter release in the presynaptic sites or receptor desensitization.

In brief, most of the studies emphasize a detriment in the motion sensitive neuronal response in response to motion adaptation except those where the adaptation is very brief and a facilitation in neuronal response is observed.

1.4 Motion Aftereffect

1.4.1 Behavioral Basis of MAE

The plasticity effect of motion adaptation renders adaptation a useful tool to investigate the behaviour of neuronal populations. Adapted visual neurons retain their ability to respond to moving objects, and show increased sensitivity to different motion directions and speeds [59]. This well-known phenomenon called motion aftereffect (MAE) shows how adapting to a directional stimulus for a certain amount of time induces a percept of an ambiguous test pattern in the

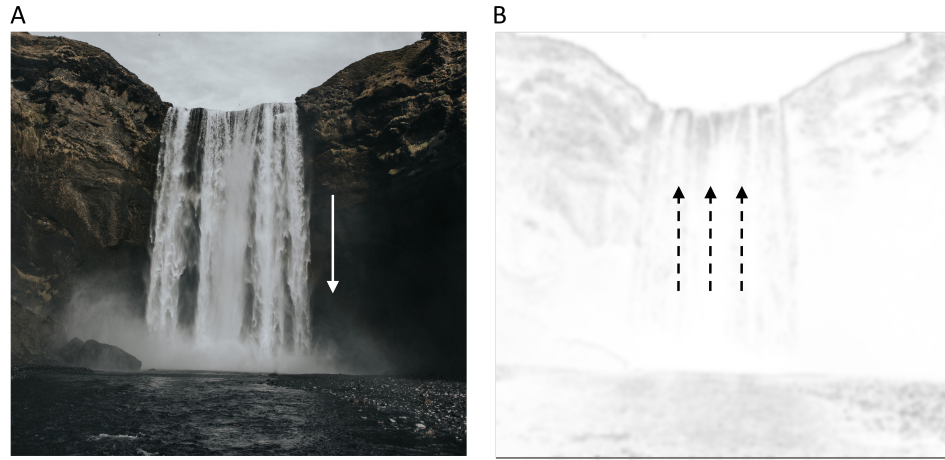


Figure 1.7: Illustration of the waterfall illusion. A. A natural scene depicting a waterfall motion [6]. The white arrow indicates direction of motion. B. Switching the gaze to a stationary surface creates an illusory percept which indicates a perception in the opposite direction to that of depicted by the dashed arrows.

opposite direction. A classic example to explain the motion aftereffect is the waterfall illusion (Fig. 1.7.). This phenomenon has drawn huge interest in motion perception research for decades. After staring at a waterfall with continuous downward movement for a while, followed by a switch of the gaze to a stationary surface, a movement in the opposite direction to that of the original movement occurs.

The classic definition of MAE is known as the perception of an opposite movement direction after adaptation to a directional movement. For instance, the effect of adaptation on the test stimulus was investigated by initially introducing a transparent dot display with half of the dots moving in a vertical direction and the other half moving orthogonally [60]. They presented a cue at the beginning of the trial for hinting the direction of the adaptation stimulus. Then, they asked the participants to identify the cued direction during the presence of the test stimulus for 600 ms. A brief blank interval was followed by the test stimulus for 96 ms. The coherency of the dots in the test was also varied. Participants were asked to identify the direction of the adaptation and the test. They found that when the adapter and test directions matched, the sensitivity was reduced whereas; when they conflicted, the sensitivity was enhanced.

Similar alterations via adaptation were also reported [61]. Prior directional adaptation caused alterations on the perception of the following stimulus presented after a blank interval. These alterations were depressive when both the stimuli were moving in the same direction, when the directions were opposite the response was enhanced, when the second stimulus was orthogonal there was no change in the sensitivity in response to the second stimulus.

Previous research also suggested that physical motion was not even necessary and required for an aftereffect [62]. A new paradigm was introduced in which they presented a still motion depicting picture and tested the participants with dot displays [63]. In their first experiment, they showed a motion depicting picture followed by a dot display containing dots moving either to left or right on each trial. They asked participants to judge whether the dots moved to the left or to the right. In a second experiment, a similar test was applied except that they introduced a 3 second delay between the adaptation and the test stimulus in half of the trials. The purpose of such delay was to test whether implied motion could induce MAE and would further show similar characteristics as the regular MAE. In a third experiment, a reversal of the picture was simultaneously presented against the original picture to create the effect of implied motion to be either inwards, towards the fixation; or outwards to the peripheries. All three experiments of the study resulted in MAE. This study suggests that even pictures that imply motion were sufficient enough to recruit motion selective neurons in MT and shift the perception of the test stimulus that contains dynamic motion to be perceived in opposite direction to that of the test stimuli. In some cases, where participants were asked to imagine directional motion for a period of time, the MAE was also observed [64] [63]. It was shown that a crossmodal induction of motion adaptation can also lead to motion adaptation and aftereffect [65].

1.4.2 Neurophysiological Mapping and Source of MAE

An explanation of MAE is based on motion opponency [66, 59]. It refers to a stage where motion signals are subtracted from each other to form a final net motion

signal. An important component to explain motion opponency is counterphase grating. Two superimposed motion signals both create an energy and when they are combined, they cancel each other out and produce no net motion [67]. Motion sensors in visual area MT confine neural populations whose direction selectivity depends on non-linear interactions between neurons tuned to different motion directions [68, 69]. Motion opponency, consisting of inhibitory connections between neurons tuned to opposite motion direction, is likely to underlie the behavior of these neural responses [70, 67]. In these neural populations, the adaptation of a neuron can reduce the inhibitory input to the other neurons, thereby increasing their response potential. When presenting a stationary or directionally ambiguous test stimulus after the adapting period, the neurons responding to opposite direction are slightly more activated because of the reduced inhibition from cells responding to the adapting direction. Therefore, a motion in the opposite direction is perceived. A similar earlier explanation of Sutherland’s [42] states that adapting direction specific cells for a period of time results in decrements in the firing rates of the adapted neurons. Thus, rapidly presenting a stationary image afterward would produce lesser firing rates in these cells; hence perception of movement in the opposite direction is observed.

Examples of neuronal response changes due to motion adaptation have frequently been shown in the literature. It was shown that 95% of the neuronal population in the extrastriate area V5 (MT) is selective for motion direction [71]. MT (V5) is referred as the motion area and majorly consists of motion sensitive neurons [72]. In a study chemical lesion to MT caused motion detection thresholds of the rhesus monkey to elevate suggesting the effect of the area MT on the perceiving of motion [73].

After showing a depressed neural response of the neurons of rabbit retina in response to adaptation [43], more studies showed the same detrimental effect on cat primary visual cortex [74, 75, 76]. For example, cat motion sensitive cells were adapted for 2 minutes and subsequent responses were measured [77]. They found that, regardless of direction, neuronal responses decreased during and after adaptation on both adapted and non-adapted neurons, however the response was less strong in the null (anti-preferred) direction than those for the preferred

direction with some degree of facilitatory responses. Response decrements have been shown in macaque visual cortex as well [49, 50, 5]. Macaque MT neurons were adapted with sinusoidal drifting gratings and responses were recorded [49]. Using the null direction adaptation, they were able to show that the ability of null gratings to inhibit the responses of simultaneously presented preferred direction stimulation was reduced. Motion sensitive neurons in the area MT of the owl monkey were adapted with either stationary, random or dynamic random dots moving in the preferred or null direction for 20 seconds and 5 seconds later a bar in the preferred or the null direction was shown [78]. When the bar moved in the preferred direction of the neuron, neuronal responses to the bar decreased whereas it was increased for the movement in the null direction.

Variations in the aftereffects over V1 and MT have also been reported. It was suggested that this variability might be a consequence of different stimulus aspects rather than the cortical origin [79]. In this respect, they manipulated the stimulus size and adaptation duration. They showed that response magnitude and neuronal preference changed over V1 and MT depending on the adaptation duration and stimulus size. Preference shifts in both areas occurred. Changes were observed on both small and large stimuli with long adaptation in addition, with large stimuli with short adaptation duration. They concluded that the disparities arise in the results of previous studies are probably a result of stimulus size, not a region-wise difference.

Several studies have provided physiological and psychophysical evidence that motion adaptation can sustain over much shorter timescales (e.g., tens of milliseconds). For example, a stationary test stimulus was presented after deploying a moving adapter for 67 ms [80]. They found perceived and pronounced MAEs specifically around 0-400 ms. To further investigate the temporal extent of the elicited MAEs, they presented adapters varying between 17-58 ms immediately followed by an afterimage presentation until the participants responded. Results showed that near perfect perception of MAE was obtained between 33 and 58 ms. Nevertheless, they were able to demonstrate MAE with an adaptation duration of 25 ms. They also reported significant changes in the activities of MT neurons. The responses of individual MT neurons were higher when the test stimulus was

in the preferred direction than in the null (anti-preferred) direction. These results propose that changes induced by MAE occurs on MT regardless of whether the adapter was consciously perceived.

Besides adaptation induced changes in early visual areas, the neuronal responses of the macaque monkey was examined in higher areas exploring the activation sites for the monkeys' subjective experience to the direction of a moving stimulus [81]. They found that when the monkey perceived visual motion, the area LIP responded strongly whereas, MST responses were relatively weak and the activation vanished in the area MT. The study suggests that the subjective experience of the motion perception and direction discrimination of motion occurred rather in later stages of motion processing. In another words, MT is mostly responsive to motion detection allowing later areas to discriminate the direction of an ambiguous motion. A cortical area (V4) classified as part of the ventral pathway has been reported to indicated motion selective characteristics under certain conditions. It was shown that a portion of neurons in V4 adopted direction selective characteristics after adaptation to motion stimuli [82].

Other techniques such as TMS showed the involvement of various areas in motion perception. Perception of MAE was examined under the influence of TMS disruption on several areas such as MT, dorsolateral prefrontal and posterior parietal cortices [83]. They found no change on the MAE when the magnetic stimulation was applied on dorsolateral prefrontal and posterior parietal cortices however, they found a disturbance on the perception of the MAE when they stimulated MT during the storage interval or the perception of the MAE itself. Another TMS study investigated the involvement of the early areas in motion aftereffect perception [84]. A commonly used experimental paradigm where the leftward or rightward moving sine waves followed by a counter-phase flickering test stimulus was used. Adaptation stimulus was 640 ms followed by an ISI of 120 ms was presented before a test stimulus with 320 ms duration. They also delivered TMS stimulation on different sites such as V1/V2 or MT. The results showed that besides observing minute reduction on MAE when they stimulated V1/V2, a more amplified reduction in the magnitude of MAE was observed when they stimulated the area MT. A transcranial direct current stimulation (tDCS)

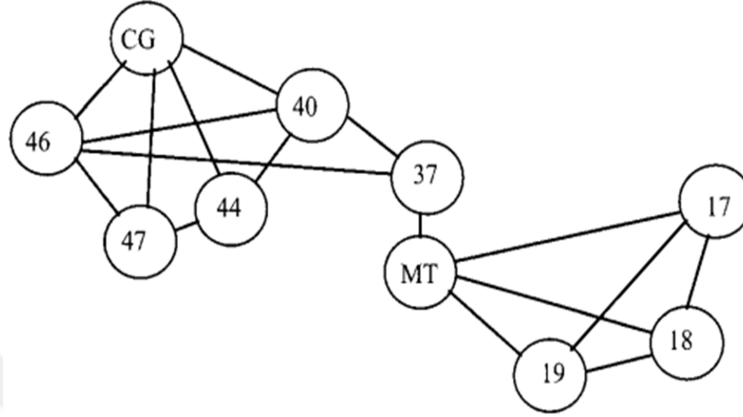


Figure 1.8: Correlational mapping of the areas in relation to MT. Two separate regions (anterior and posterior) were identified for the perception of motion. The two different networks were derived from the inter-correlation coefficients. (Adapted with permission from Elsevier, ref. [7]).

study on MT+/V5 showed the reduction in perceived MAE hence stressing the involvement of MT+ in the perception of MAE [85].

Previous functional magnetic resonance (fMRI) studies also showed the involvement of area MT in adaptation induced changes in motion perception [86] and, MT+ [87, 88, 89]. Neural mapping of MAE was examined using fMRI in detail and identified two main networks; the posterior network consisting of BA; 18, 19, 39 and MT that is responsible for motion analyses and, the anterior network BA; 37, 40, 44, 46, 47 and CG (Cingulate Gyrus) responsible for MAE (Fig. 1.8) [7]. In line with this study, a PET study discussed the involvement of MT+ in MAE and concluded that the involvement of the MAE is constricted exclusively to the motion-sensitive MT area [90].

In general, MT is the major actor in motion perception however, earlier areas such as V1/V2, V4 and further areas such as; hMT+ (MT and MST), LIP, MST are involved as well. Their roles are not as major as the area MT however, their part in direction selective is shown by the studies mentioned above.

1.4.3 MAE Elicited by First- and Second-Order Motions

Differences induced by motion types are shown by studies. In this context, the first-order (luminance-defined) and second-order (contrast- or texture-defined) motions were shown to engage different cortical areas. Using a motion adaptation paradigm combined with fMRI, first-order and second-order motion types were compared [89]. Their results indicated that second-order motion also recruits neurons in low-level visual areas including V1. Additionally, anatomical layouts elicited by first- and second-order motion was quite similar and no segregation of the first- and second-order motion was present in their results. Responses of V1, V2, V3, VP, V4V, V3A, and LO areas to the first- and second-order motion stimuli were examined using fMRI [91] and found no significant differences concluding motion detection mechanisms are not different in the early areas in terms of response to first- and second-order motion. Another line of research suggests the segregation of the processing areas involved [92, 7, 93, 94]. An fMRI study shows the distinctions of the activation locations induced by first and second-order motion [95]. They showed that both motion types can induce strong activation in area MT. Second-order motion was more effective in area V3 than the first-order motion. In lower areas, sensitivity to the first-order motion was greater in V1 and; the second-order motion was represented in a later stage such as V3 and VP probably because of the need to detect second-order features. Macaque V1 and MT neurons were examined to identify their selectivity to the first- and second-order motion stimulus [96]. They found that a small group of V1 and MT neurons exhibited strong selectivity to direction and orientation of second-order motion and almost all cells showed weaker responses to second-order motion than the first-order motion; whereas MT neurons appeared to be sensitive to second-order motion.

It was suggested that MAE magnitude was dependent on spatial frequency when a static test pattern was used [97, 98]. A velocity dependence was suggested when a flickering test pattern was used [99]. All these findings also suggest the presence of two separate stream of information processing for first and second-order motion.

Static and dynamic MAE were shown via first- and second-order motion adaptation. Depending on the properties of the adaptation and test patterns, static or dynamic motion aftereffects were observed [59]. In a study, static and dynamic test were both utilized in which they examined the MAE significance followed by first- or second-order motion adaptation [100]. They found that the MAE was observed when the static test pattern was shown after adapting to a first-order motion, and the counter-phase flickering test was shown after adapting to a second-order motion.

Because of the differences in stimulus characteristics, observed MAE magnitudes were changed resulting in activation differences in motion processing areas.

1.4.4 Tuning and Plasticity of MAE

Motion aftereffect largely depends on various stimulus characteristics. It has been shown to be greatly affected by basic stimulus properties such as spatial frequency, contrast, and luminance [101, 102, 103]. In general, motion aftereffect is associated with long adaptation durations such as tens of seconds. However, short-term adaptations within a few hundreds of milliseconds are also shown to result in motion aftereffects as well [8].

The experimental paradigm by Kanai & Verstraten [8] has been commonly employed to probe rapid forms of motion adaptation (Fig. 1.9). Different combinations of adaptation durations and inter-stimulus intervals (ISI) resulted in distinct perceptions of motion direction [8]. For example, brief adaptation durations (e.g., 80, 160 ms) combined with a brief ISI (e.g., 40, 120 ms; Fig 1.9.B) or an adaptation duration up to 320 ms with an ISI for more than 2 seconds (Fig 1.9. C, D) resulted in a priming effect where the adapter and test stimulus are perceived in the same direction. On the other hand, they showed that increasing the adaptation duration to 320 ms or 640 ms with the same ISI (e.g., 40 ms, 120 ms) resulted in a test stimulus percept in the opposite direction to that of the adapter. Importance of adaptation duration in MAE was previously revealed

[104]. They used linear or rotating motion and adapted the participants for various time intervals between 30 to 180 seconds. They measured the MAE and the decay time. As the adaptation duration increased and when the adaptation stimulus was translational or complex motion, the MAE increased as well.

Besides these temporal properties, similar tuning properties of MAE was reported by prior psychophysical and neurophysiological studies. For instance, direction selective-neurons were adapted to a specific direction in an adaptation paradigm [44]. They found that the motion direction of the test appeared to be shifted by a 30^0 repulsion and disappeared after a 90^0 shift. In other words, adapting to a direction causes the axis of the perceived motion to be shifted to a 30^0 deviation. The aforementioned study [49] showed that after adapting to null and preferred directions, both adaptations altered MT neuron responses, but they attributed the adaptation induced changes to low-level areas in the visual tract. Modulations of MAE can also be obtained via manipulations on the spatial and temporal frequencies. For example, the velocity of the adapting and test stimulus were manipulated and it was demonstrated that slower velocity adapters resulted in MAE when test stimulus was stationary (or close to stationary) and high velocity adapters caused MAE at its highest with a fast velocity test pattern [105]. Another example showed that strength of MAE is dependent on the spatial and temporal frequency of adapting stimulus [101]. Even at low spatial frequencies, MAE was observed when the spatial frequency of the adapting and the test stimulus were similar even at low spatial frequencies such as 0.125 c/deg. They found that the MAE was largest when the counterphase test grating was at 0.125-0.025 Hz. It was shown that different spatial frequencies could result in different magnitudes of MAE [97]. They compared the MAE magnitudes under different spatial frequency values and using a static test stimulus. As in a typical MAE paradigm, they adapted observers to drifting sine-wave gratings. They observed the largest MAE magnitude when the spatial frequency of the adapting and the test stimulus matched, and there was no MAE for stimuli with a spatial frequency less than 0.5 c/deg implying the presence of a minimum threshold for adaptation. It was suggested that measured magnitude of MAE depended on the temporal frequency of the patterns rather than velocity [98]. However, in another

study flickering test patterns failed to cause differences in strength of the MAE perceived [99]. They rather found a difference on the MAE depending on the velocity pointing out that MAE was stronger when the speed of the adapting and the test stimulus were the same.

Other than duration of the adaptation stimulus, spatial and temporal frequency of the stimulus, the context, surrounding the central stimuli has also been shown to alter the brain activation. BOLD signals in the occipital and parietal regions were examined using a moving stimulus [106]. They showed that the signal magnitudes were reduced when the central and surrounding stimulus were moving the same direction however the magnitude was increased when the stimuli were moving in opposite directions.

Adaptation time was manipulated to measure the MAE [107] (see Fig.1.9) . They presented directional movement for 60 seconds, immediately followed by an orthogonal directional movement in varying lengths. Length of the orthogonal motion was manipulated. A stationary stimulus was also presented after the initial two movements to measure the MAE. They found that recovery from the initial adaptation was delayed when it was followed by an orthogonal movement with the same speed.

1.4.5 Static and Dynamic MAE

Static motion aftereffect refers to the illusory percept of a stationary object moving in a direction after prolonged exposure to a directional movement. One of the most common examples to this phenomenon is the waterfall illusion as described previously. Another example to static motion aftereffect could be the illusory percept arising from looking at the road for a while traveling in a moving car; if you maintain looking at the road and when the car stops at the lights, the stationary road is typically perceived as moving forward. Perception of MAE in response to rotational and radial movement adaptation were demonstrated using static test stimulus as well [108]. hMT+ activity were measured using fMRI [87]. They compared the hMT+ response to a static test stimulus in conditions; (1) where

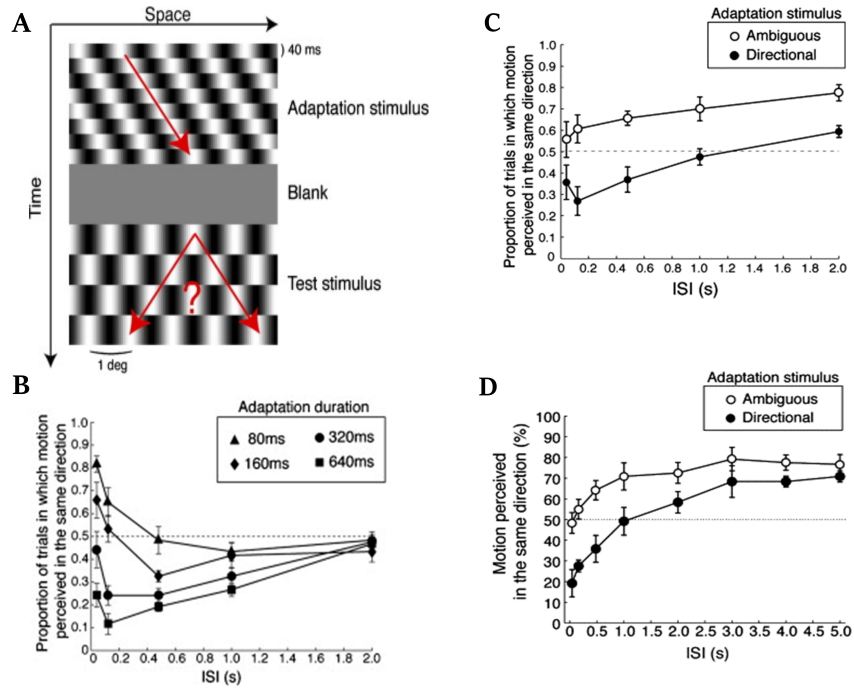


Figure 1.9: Representation of the experimental paradigm used for rapid forms of motion adaptation. Directional and counter-phase flickering gratings were used as the adapter and test stimuli, respectively. Participants were typically asked to compare the directions of the test with the adapter. Other features of the adapter and test stimulus may vary and depend on the specific hypothesis/hypotheses of the experiment. A. The spatiotemporal profile of the adapted and test on a typical trial. B. Results from experiment 1 in the paper where they varied adaptation duration and ISI to observe MAE and VMP responses. C. Results from experiment 2 (320 ms adaptation) in the paper wherein half of the trials adaptation stimulus was a counterphase flickering pattern. D. Results from experiment 3 (320 ms adaptation) in the paper where ISIs more than 2 seconds were added to the x axis (Adapted with permission from Elsevier, ref. [8]).

they introduced a delay (a storage envelope) before presenting the test stimulus or (2) no delay (immediate appearance of the static test pattern). They found that even inserting a dark gap between the adaptation and the test stimulus was ineffective to alter the activation magnitude of the hMT+ or the length of the aftereffect during the perception of the test stimulus.

On the other hand, the dynamic test patterns typically consist of randomly moving dots or counterphase flickering gratings [109] [8]. MAE responses were obtained by introducing a sinusoidal flickering test pattern and it was named ‘flicker MAE’ [110]. The difference from the regular/static MAE was that it was optimal when the adapting grating was at a low spatial frequency, and the aftereffect was increased when adapting and the test stimulus was of high temporal and spatial frequency. The dynamic MAE can also be induced by second-order motion [111]. First- and second-order adaptation and test stimuli were used to test the magnitude of MAE [112]. They showed that adaptation to second-order motion followed by directionally ambiguous test pattern resulted in MAE.

The mechanisms underlying static and dynamic MAE were discussed [113]. They presented static and dynamic test stimuli both in varying orders after adaptation. They found that when the static pattern was presented first, it served to store the static MAE however, when the dynamic stimulus was presented first, preceded by a static pattern, it failed to store the dynamic MAE. In another study, high and low velocity adapters with static and dynamic test patterns were examined [114]. Based on the behavioral findings, they suggested two distinct populations of neurons for static and dynamic test patterns; a group governing with low speed movement adaptation and static test pattern, another group with high velocity adapters with dynamic test patterns. They also showed that dynamic MAE could be perceived with adapters up to three times as rapid as the static MAE adapters.

Static and dynamic test stimuli were used to examine interocular transferability to infer to a probable presence of separate information processing channels for first- and second- order motion processing [115]. They hypothesized that the dynamic MAE should result in better interocular transferability than static

MAE considering it is formed in higher areas. They found that when the test stimulus was static, MAE was observed only when the adapting stimulus was first-order motion and interocular transferability was partial. However, when the test stimulus was flickering, the interocular transfer was nearly perfect for both first and second-order motion adaptation stimuli. Thus, they suggested a higher level information processing stage for dynamic MAE.

1.4.6 Top-Down Instruments Affecting the Perception of MAE

The effect of attention on motion perception has been the topic of discussion for a long time. Some researchers argue that top down factors such as attention has no effect on the motion perception that motion perception is generated in pre-attentive areas [116, 117, 118]. Others suggest that attention could be used to bias motion perception [119, 120, 121]. It was shown that sustained attention extended the perceived duration of movement emphasizing the effect of voluntary attention on the perception of motion [122]. Attentional influences on a third-order motion stimulus was examined [123]. They found that top down attentional control affected perception of motion direction by increasing the perception of certain features of the stimulus. Attentional effects of motion processing were investigated [124]. They presented the participants with ambiguous counter-phase gratings and asked them to attentively search for a radial grating while fixating at the center of the screen. The task produced MAE on a dynamic counter-phase flickering test pattern suggesting that attentional top-down processes may facilitate motion perception processes. A regular motion inducing stimulus was able to induce MAE as well.

In a linguistics task [125], participants were presented with high or low attentional load at the fixation and they were asked to ignore the irrelevant expanding movement distracters presented at the periphery. They examined the fMRI responses of the area V5 (i.e., hMT+). They found that, area V5 exhibited reduced activity when performing the high load task. Their behavioural data

on the motion aftereffect measurements were also in line with the neuroimaging data showing reduced magnitude of motion aftereffects, highlighting the effect of attention on perception of movement. Extrastriatal area activations were investigated using fMRI [126]. They presented high or low load task irrelevant distracters in the center of the screen without effecting the main stimulus. They found that the activation in the visual cortex decreased as the amount of load increased. As it progressed from V1 to higher visual areas such as V4, the amount of decrement was more pronounced. In an attention paradigm, participants were either in attention focused or attention diverted conditions. In the attention focused condition, they were asked to indicate the speed of the stimulus whereas; in the attention diverted condition they were asked to indicate the presence of a vowel [127]. In both conditions, the motion aftereffect percentages were recorded. They found that MAE was significantly greater in the attention diverted condition compared to the attention focused condition, suggesting the modulatory effect of intentional attentive processes on motion perception.

Contrary to the research pointing to a modulatory role of attention, an opposite view suggests a null effect of attention on motion perception within the context of MAE. In a motion paradigm, participants were asked to indicate when the movement of expanding dots stopped [117]. They also presented no-load, low or high attentional load conditions. Aftereffect durations were analysed and there was no difference in terms of the length of aftereffect. Using stimuli in different sizes and types of movement, participants were asked to indicate when the test stimulus appeared to stop [128]. They were also asked to indicate whether a number appeared during the adaptation phase with a key press. In a control condition, they were not engaged in the additional concurrent number task (i.e., no attentional diversion condition). Their results showed that MAE depended on type and the size of the adapting stimulus. That is, when the stimulus size was small, strength of MAE caused by translational adaptation was decreased by the concurrent number detection task. However, rotation or depth adaptation that induced MAE were not affected by the concurrent detection task. The number detection task did not affect the magnitude of MAE when a large adapter was presented.

Inter-sensory interactions also seem to affect motion adaptation. Whether a simultaneously presented visual stimulus would affect the perceived speed of an auditory stimulus was investigated [129]. They found that the direction of the moving stimulus was affected by the visual influence extent to which it often caused the ambiguous auditory stimulus to be perceived as moving in the same direction as the visual stimuli. Another interesting study investigated the effect of visual adaptation on the perception of an auditory stimulus [130]. They presented a moving square in depth followed by a steady sound which appeared to change the direction of loudness in the opposite direction.

Effects of cross modal interactions on the perception of MAE were investigated by using visual and auditory modalities as adaptation and test stimulus [131]. Participants were adapted with a specific a modality and a test stimulus was presented in the other modality. They showed that adapting to auditory motion caused visual MAE on the presented test stimulus, revealing the multisensory nature of MAE.

1.5 Visual Motion Priming (VPM)

In general terms, priming is mostly associated with the increased probability of easily identifying an item as a result of previous experience with it [132]. For instance, in a study participants were asked to identify if the object presented tended to move or stayed still [133]. Behavioral results showed that participants were able to faster identify the object if it was repeated previously. In other words, they were able to make decisions faster about repeated stimuli with respect to the novel stimuli. Characteristics of priming conditions were examined by manipulating the duration, phase degree, and steps of the motion stimulus [134]. They presented a biasing stimulus preceding the probe (adaptation) stimulus. They found that when they used a phase shift of 90° in less than six frames for a duration less than 100 ms, the probe was perceived to move in the biasing direction. A phase shift of 90° with more than six steps or a 270° phase shift appeared to show a detriment on the tendency to perceive the probing stimulus

moving in the direction of the biasing stimulus.

Presence of priming effect was tested through a perceptual task based on the tunnel effect phenomenon. In the tunnel effect, a moving object is occluded by another object [135]. Even though the motion is invisible, participants mainly report motion percept during the occluded period. They wanted to examine whether a priming effect would occur under the conditions in which a part of the motion was invisible to participants. Stimulus was presented for less than 300 ms in different conditions. Behavioral data showed that adaptation to hidden motion biased the perception of the test stimulus to the same direction of the adapting stimulus. In a second experiment, they presented each stimuli to different eye. These two simultaneous views from each eye engaged in binocular rivalry when they were superimposed. On the no-priming condition, participants reported the direction of the movement at chance level. On the priming trials, results showed a robust priming effect and this effect existed robustly regardless of whether the priming motion stimuli was visible (dominance condition) or invisible (suppression condition) to the participant.

Mechanisms underlying VMP were investigated [136]. In the study, they presented a sine-wave grating that induces the priming effect followed by a brief saccade and an ambiguous test stimulus. They manipulated parameters such as; duration, velocity, contrast, and whether the condition was retinotopic or spatiotopic to examine the resulting effects. They first introduced the primer for 167 or 1000 ms durations. An ISI varying from 400 to 3000 ms was introduced where participants either shifted their gaze to a different location or they kept it constant at the initial location. A test stimulus was presented after the ISI for 667 ms. During the test stimulus, a retinotopic (where participants kept their gaze at the shifted location) or a spatiotopic (where participants drifted their gaze to the original location fixation point) condition was presented. They also had a separate condition where there was no saccade during the ISI and the test stimulus for this condition consisted of either full (where the primer and the test stimulus was presented at the same location) or unmatched (where the test grating was presented at a location 180° opposite to the primer) conditions. As they increased the velocity and decreased the contrast, they observed a robust motion

aftereffect. Their main findings were that the priming effects were observed in spatiotopic conditions and retinotopic conditions with an ISI greater than 600 ms whereas aftereffects were only observed in the retinotopic condition. Based on previous studies that relate MAE to low level mechanisms and priming to higher level mechanisms, they suggest that low level mechanisms operate retinotopically as opposed to high level mechanisms operating spatiotopically. The low level motion detectors have been considered to produce an effect opposite to that of the priming. This effect is called negative priming or motion aftereffect by different researchers. Higher order systems that are tuned for detection of second-order motion produces percepts congruent with the adaptor as opposed to the early motion detectors which produce a negative priming percept.

Aside from prolonged exposure to a moving stimuli resulting in MAE or priming, brief exposure is also proven to cause perception of MAE or priming effect. Presence of separate detection mechanisms for first-and second-order motion were examined [137]. They employed a motion experiment setup for each condition where they manipulated the adaptation and ISI durations to examine the magnitude of MAE and VMP. In the first and second experiments they used first-order and second-order motion respectively. They found that longer adaptation durations with 40 ms ISI led to MAE as opposed to shorter adaptation durations causing VMP. For an ISI of 121 ms, both first- and second-order motion adaptations showed MAE.

VMP has been shown in much shorter adaptation scales. In a priming paradigm, participants were presented with a primer for 19 ms and the SOA was manipulated (varied between 0 ms and 200 ms) [138]. In the reaction time condition, participants identified the direction of the unambiguous rotating test stimulus (rotating either clockwise or counter clockwise) and, in this condition priming and the test stimulus was congruent half of the time. In the disambiguation condition, participants indicated the direction of the ambiguously rotating stimulus. In a third condition, participants were asked to judge the direction of the rotating primer. They found that participants performed better in discriminating the direction of the target when the direction of primer and the target was congruent than it was incongruent. This effect was seen even when the primer was

only presented at a duration of 19 ms where its direction cannot be consciously perceived. In the disambiguation condition, the intermediate SOAs resulted in a biased percept. For the third condition, participants mostly reported chance level direction discrimination of the primer however, when the SOA reached 100 ms, they reported the direction of the primer accurately.

In a motion paradigm [139], an unambiguous motion stimulus was presented for durations varying between 50 and 1060.7 ms and the test stimulus duration was 667 ms. Their behavioural data suggested that shorter priming (adaptation) durations resulted in test motion perception in the same direction as the priming stimulus, whereas longer durations induced opposite direction perception.

Priming effect with shorter adaptation is also shown in a paradigm where congruent and incongruent motion is presented. The effect of adaptation duration was investigated by introducing an adaptation paradigm involving a moving stimulus obscured by an occluder [140]. A white ball moved to the opposite side of the screen at a constant speed horizontally (either leftwards or rightwards) until it reached a vertical grey bar at the other end of the screen. Participants fixated on a red dot at the upper center of a black rectangle (the occluder) for 80 (short adaptation) or 600 ms (long adaptation). Before the ball entered the invisible zone (behind the occluder), a texture was presented at the location of the occluder (occluding the occluder). The texture was a random noise (ambiguous movement) moving either in the same or the opposite direction to that of the ball. When the texture was terminated the occluder entered the invisible trajectory (behind the occluder) and participants were asked to indicate the time when the ball reached the grey bar in their imagination. When the texture was congruent long adaptation produced later TTCs (time to contact the target) with respect to incongruent motion. However, the congruent motion combined with short adaptation produced earlier TTCs. Priming effect of short adaptation was shown with respect to the long adaptation condition.

1.5.1 Tuning and Plasticity of VMP

Like motion aftereffect, visual motion priming is affected by various characteristics of the stimulus. These characteristics include features such as contrast, spatial frequency and duration. A pioneering study examined the characteristics of VMP manipulating the spatial frequency, Michelson contrast, duration, and the magnitude of phase shifts [141]. In a motion discrimination task, participants were asked to report the perceived direction of the test stimulus being in the same or the opposite direction to that of the adapting stimulus by a key press. An 80 ms adaptation elicited rapid priming such that the direction of subsequently presented ambiguous stimulus perceived in the direction of adapter's direction. The behavioural findings also showed that VMP was maximum with an adapting stimulus at a phase shift of 90^0 and a test stimulus with an 180^0 phase shift. The priming effect endured when the adapter duration was below 300 ms. VMP was investigated under mesopic conditions [103]. They manipulated parameters such as velocity, luminance, contrast, and the spatial location of adapting and test stimulus. When they presented the adapter and the test at the same location, test stimulus was perceived as moving in the same direction as the adapter stimulus regardless of luminance, velocity or the contrast differences. On the other hand, when the adapter was presented in the periphery and the test was presented at the center, priming was diminished with respect to photopic and scotopic conditions. When the adapter and test stimulus locations were switched (adapter at the center and test at the periphery), the magnitude of priming was reduced in the mesopic condition. On the other hand, the aftereffect was amplified regardless of the velocity or the contrast of the primer in both photopic and scotopic conditions.

Luminance and the velocity of the primer were systematically varied to examine priming under different conditions [142]. They found that as the luminance decreased the positive priming effect nearly disappeared. They also found that low velocities led to a positive priming effect, whereas high velocities elicited negative priming effect (i.e., aftereffect).

1.5.2 Top-Down Instruments Affecting the Perception of VMP

Attention plays a role in the perception of VPM. To examine the role of spatial attention in spatiotopic visual motion perception, a motion priming paradigm [143] was employed. Participants were asked to make a saccade after the adapter to examine the effect on different locations. Then, they were asked to judge the direction of the ambiguous test stimulus. After the saccade, participants were also asked to perform a second task in which they were required to detect the contrast change of a dot. They presented retinotopic and spatiotopic conditions where the adapter was either short (167 ms) or long (1000 ms) and the ISI varied between 400 – 3000 ms. The saccade was executed during the ISI. After a saccade, which was drifted along with the movement of the fixation point, a test stimulus was presented above or below the new location of the fixation dot. In the full or unmatched conditions, the location of the fixation points was not changed hence a saccade was not executed. To control for attention, the participants were instructed to perform a second task where an additional dark grey dot was placed at the location of the upcoming test stimulus (“identical” condition) or the dark grey dot was placed on the opposite side of the fixation dot (“different” condition). The contrast of the grey dot was either increased or decreased. Participants also tracked whether the contrast of the dot changed. They also manipulated the velocity of the primer (adapter). They found that positive priming was exhibited in the spatiotopic condition but not in the full condition. The positive priming was conspicuous in spatiotopic conditions although retinotopic conditions exhibited prevailing negative priming (aftereffect) outcomes. They also observed that spatiotopic conditions required at least 600 ms of ISI to produce positive priming effects. Faster velocities (e.g., 4 hz at 167 ms or 3hz at 1000 ms) produced negative or no priming effects for neither spatiotopic, retinotopic, full or unmatched conditions whereas slower velocities (e.g., 3 hz at 167 ms or 2 hz at 1000 ms) produced positive priming dominantly. When attention was forced away from the location of the test stimulus, positive priming effect at spatiotopic condition vanished. However, when they decreased the ISI and directed the attention at the location of the test stimulus, the positive priming effect increased. Overall,

the effect of attentional manipulation is shown to play a crucial role in producing positive motion priming.

Besides cross model and attentional effects, VMP is also shown to be altered by the number of choices when the participants performed the task. Priming was examined with a test stimulus bearing a maximally ambiguous pattern that could cause the perception to be in more than two directions [144]. Stimuli were presented at different velocities (360, 180, 90, 45, 22.5 d/s). Participants were asked to identify the direction of movement during test. Half of the participants were given two choices (CW or CCW) and the other half were given an additional option to choose from (CW, CCW or “something else”). They found that the number of options given to the participants (2AFC or 3AFC) mattered. In the negative priming condition, similar trends were seen for all velocities regardless of the number of choices given to the participants (i.e. 2AFC or 3AFC). However, the priming effect was decreased for all velocities in the positive priming condition when participants were given a third choice (3AFC), specifically at 90° , 45° and 22.5° . The results suggest that higher order systems are more prone to changes via cognitive influences (whether the participants were given 2 or 3 alternative forced choices) as opposed to lower order systems given the fact that negative priming stayed substantially similar in both 2AFC and 3AFC groups when the positive priming of the 3AFC group were extensively suppressed as velocities decreased.

1.5.3 Neurophysiological Mapping and Basis of the VMP

EEG data was recorded over scalp sites corresponding to low-level visual areas including MT under three experimental conditions: (1) unambiguous motion only, (2) priming condition, or (3) motion reversal condition [145]. In the unambiguous motion only condition, they only presented left or rightward stimuli; in the priming condition, an unambiguous motion preceded an ambiguous motion and, in the motion reversal condition both the priming and the target (test) stimulus

was unambiguous. In the priming condition, they also varied the prime-target interval (ISI) between 200-1000 ms. They found an increased ERP activity around 300 ms in the unambiguous condition over the selected areas mentioned above. They also found that the priming condition revealed an increased ERP around 100 ms and 350 ms after the onset of the test stimulus with respect to the motion reversal condition. In addition, the shortest prime-target interval (200 ms) led to the strongest modulation of behavioural as well as the ERP data. However, the priming effect on both behavioral and the ERP data was abolished beyond 1000 ms ISI.

A comprehensive study functional properties of neuron populations that serve for motion processing were investigated [82]. They used fMRI with a visual priming paradigm on anesthetized monkeys. The repeated exposure to motion reduced the fMRI response and a follow-up sudden change in the stimulus allowed them to investigate whether certain regions of the macaque were involved in the processing of motion. As the adapter, a clockwise or counter clockwise rotating stimulus was presented for 200 seconds followed by exposure to a reversely rotating movement for 100 seconds. They found a significant rebound activity change between the BOLD levels for before and after the motion reversal in the area MT and V4. The interesting finding was that the BOLD directional indices for V4 and MT were not significantly different. V4 response to motion was surprising given the fact that the area V4 contains as many direction sensitive cells as the area V1. They propose that neurons that are classically not attributed to be directionally selective (V4 area neurons) may exhibit directionally selective properties after exposure to motion adaptation. They propose that this activation might be the results of a feedback mechanism arising from MT feeds the area V4. A follow up study investigated the behaviour of V4 neurons in response to motion adaptation [146]. Based on a group of recorded 62 neurons, they found that 86% of the V4 neurons were not directionally selective. They also recorded the activities of the same neurons after adaptation to movement for 1 second. They found that 33% of the non-directional V4 neurons manifested direction selectivity.

Involvement of MT in motion direction and spatial position investigated the

[147]. Participants were presented with two sets of stimuli each of which containing three sinusoidal drifting gratings. The gratings on the left side of the fixation always moved in a bottom-up trajectory, whereas the other three gratings moved horizontally. One of the gratings on the right side of the fixation always moved in the opposite direction to the other two (middle grating never was the odd one). The gratings were presented for 300 ms followed by a blank screen until response. Subjects were asked to indicate the spatial position (experiment 1) or the direction of the movement of the odd grating (experiment 2). Following the response, TMS stimulation over MT/V5 was applied for 500 ms before the next trial started. The analyses were performed on the basis of the previous trial of which the participants were not aware. A main effect of spatial position priming, a main effect of priming of motion direction and an interaction effect was found in which the enhanced spatial priming was observed when repetitive motion direction was presented. TMS stimulation disrupted visual motion priming, however the spatial priming of position was not disrupted. Motion direction was independent of location; however, spatial location was not independent of motion priming from the previous trial. As a result, they suggested that the spatial position is either processed earlier than MT such as in V3 or in higher areas such as posterior parietal cortex. In other words, TMS suppressed motion direction priming but induced no changes on spatial position priming implying that area MT is not responsible for spatial position processing that spatial position is rather processed earlier or later than the MT. Extending their findings, the origins of the spatial position priming were investigated [148]. They stimulated right angular gyrus and both left and right frontal eye fields via repetitive TMS. They found a significant decrease in the perception of motion direction, but spatial position priming was not effected by TMS stimulation. In another study, the detrimental effects of the stimulation were investigated by using a first-order motion and color priming paradigm in which they used TMS to disturb MT and observed [149]. When they applied the stimulation over the area MT, the priming effect was abolished. Motion priming that is seen in the control condition disappeared when the MT was stimulated highlighting the involvement of the area MT in VMP.

Existence of rapid effects in later extrastriate areas such as MT and MST was investigated by adapting the areas with stimulus that is known to respond to expanding and contracting stimulus[150]. The behavioural results indicated only rMAE rather than rVMP. They suggested that complex visual motion exhibits activity in higher areas but motion priming lacks the ability to function in these higher areas. Therefore, they suggested that rVMP mostly operates in earlier areas of motion processing and loses its presence in later stages.

1.6 SPECIFIC AIMS

Motion adaptation is a powerful investigative tool to probe the responses of different neuronal populations and this convenient manipulation allows us to vary different stimulus features such as duration, motion type and spatiotemporal profile of stimulation. This dissertation aims to shed light on the spatiotemporal dynamics of rapid visual motion aftereffect (MAE) and rapid visual motion priming (VMP). Specifically, how short- and long-terms forms of adaptation bias the perception of movement under different conditions and at which sites it takes place are investigated.

The main idea behind this thesis came from two previous behavioural studies [8] [10]. The adaptation duration and adapter type have been shown to alter motion adaptation induced changes, however, an investigation elaborating its neural correlates have not been fully explored. Particularly in here, the differences of the short- and long-term motion adaptations were investigated and how adapter and test types modulate adaptation induced effects were examined.

1.6.1 EEG Study 1

Mounting evidence points to the inhibitory effects of adaptation on the motion sensitive neurons (i.e., detectors). The long- and short-term forms of adaptation have been shown to affect the perception of a latterly presented ambiguous

stimulus direction (MAE). Duration differences has been examined in different contexts using various neurophysiological tools. A sub- and supra-second adaptation difference with EEG has not been investigated yet. In the first experiment, the effects of sub- and supra-second adaptation on an ambiguous test stimulus were examined. *Question 1: Does long term adaptation cause a more definitive and robust difference than the short adaptation over occipital and parieto-occipital sites? Question 2: How do ERPs and topographic distributions vary depending on adaptation duration?*

The first experiment was designed to compare long and short adaptations in terms of both behaviourally and neurophysiologically via event related potentials on various scalp sites. Also, the differences in the spatial domain (i.e., scalp site/electrode location) were sketched out based on the idea whether short- and long-term adaptation to regular motion created region wise differences at the motion sensitive areas. This step was performed to answer hypothesis 1. Furthermore, the source localization analyses were performed to confirm the results at the spatial domain (i.e., anatomical space).

Neuroimaging data allowed to characterize adaptation induced changes in neural activities for both durations. The distinct characteristics of rapid and long adaptation over motion sensitive neurons were elaborated and ERPs were plotted to show component specific differences over occipital and parieto-occipital sites. Furthermore, early component specific characteristics were demonstrated. The voltage distributions over all of the scalp electrodes within the significant time frame were also revealed.

1.6.2 EEG Study 2

Regular phi motion engages the same pathway (ON or OFF pathways) however, a reverse phi motion engages the spatiotemporal correlation across pathways repeatedly (ON and OFF). Two major views of where the two pathways merge indicate that: 1) they merge early in the visual stream [151], 2) they remain segregated until the initial stages of motion processing [152, 153]. In this experiment,

the mechanisms within the same or across pathways were activated with these types of motion stimuli and the activation differences were examined over initial visual processing areas. *Question 1: Do ERPs and topographical plots show distinctive characteristics for aftereffects elicited by each motion type? Question 2: Does engaging same or across pathways make a difference in the neural activities over occipital and parietal scalp sites?*

The second experiment elaborated the differences between short- and long-term adaptations by employing phi or reverse-phi adaptation. The rapid motion adaptation duration was compared to a longer adaptation duration using two types of stimuli and an interaction between the adaptation type and duration was demonstrated [10]. In this experiment, the findings of the original experiment was replicated using fewer adaptation conditions and one ISI to evaluate the interaction between the adaptation duration and motion type. The optimal parameters from the original study [10] were chosen to maximize the MAE. A test stimulus with regular counter-phase flickering motion was used in the experiment. The pre-determined occipital electrodes (occipital ROI) were analysed to see whether differences would occur when comparing duration and type conditions. The effect of motion type would infer to the convergence site of ON and OFF pathways. The duration differences would further provide information about long- and short-term adaptation effects.

The third chapter provides a detailed examination of differences between short and long adaptation durations with regular and reverse-phi motion adaptations. The effects of adaptation type and duration over the extrastriatal sites, particularly motion sensitive MT, and V1 were examined. The differences over the initial visual information processing areas would point out distinct characteristics of across pathway mechanisms compared to adaptation mechanism within each pathway.

The last hypothesis (i.e., research question) focused on determining whether there is a consistency in the traces of conditions via ERPs and the specific differences between components. The early components would emphasize the nature of the ERP in all the conditions. The positivity/negativity of the conditions over

the whole scalp demonstrate voltage distributions across all the conditions.

1.6.3 EEG Study 3

The fourth chapter used the same adaptation stimulus as the previous one, however, the contrast polarity of the test stimulus reversed every 94 ms within each spatial displacement of 180° . A contrast polarity change in the test stimulus was expected to alter the perception of the test stimulus causing the test stimulus to be perceived towards the direction of the adaptation stimulus as suggested [10]. The reverse-phi adaptation adapts across pathway mechanisms compared to the phi motion engaging within pathway adaptation (ON or OFF). Accordingly, the priming effects elicited by reverse-phi motion is expected to be more robust on this test stimulus than the phi motion.

In this study, the spatiotemporal dynamics of and adaptation induced effects test motion were examined over different scalp sites. The aim was to shed light on the spatiotemporal dynamics of motion priming perception under varying conditions. The spatiotemporal characteristics of rapid motion priming were examined at different scalp sites and within identified time-ranges. *Question 1: Do duration-wise differences occur between long and short averaged conditions? Question 2: Does engaging same or across pathways during the test stimulus reverse the sign of the motion and make a difference in activation over occipital and parietal scalp sites, and does reverse-phi adaptation have a more robust effect on the contrast inverting test stimulus? Question 3: Do ERPs show distinct characteristics correlated with different priming conditions?*

The first hypothesis (i.e., research question) is again based on the duration specific differences. First, short and long adaptation conditions were compared behaviourally. Then, electrophysiological analyses within the identified time intervals were performed via averaged potentials. Comparison of motion types helps to further understand whether phi and reverse-phi conditions were able to reverse the sign of the perceived test direction, and whether across pathway adaptation is effective on a contrast inverting test stimulus. To test this possibility, the

pointwise differences on each time point were calculated to find out when the significance occurs between the conditions. The ERP differences were investigated to answer the last question and shed light on the differences on the amplitude and the latency of the conditions. Differences arise from various duration and type conditions were examined in order to elicit condition specific ERP characteristics. The differences in topographical plots for all raw and averaged conditions were also examined to account for a more comprehensive understanding of VMP.



Chapter 2

Short- and Long-term Forms of Neural Adaptation: An ERP investigation of Dynamic Motion Aftereffects

This chapter is based on the publication by Akyuz, S., Kaya, U., Pavan, A., Kafaligonul, H. Short- and Long-term Forms of Neural Adaptation: An ERP Investigation of Dynamic Motion Aftereffects. *Cortex*, vol. 125, pp. 122-134. <https://doi.org/10.1016/j.cortex.2019.12.015>. Reproduced (or reproduced in part) based on the author rights provided by Elsevier Publications.

Adaptation is essential to interact with a dynamic and changing environment, and can be observed on different timescales. Previous research on a motion paradigm called dynamic motion aftereffect (dMAE) showed that neural adaptation can establish even in very short timescales. However, the neural mechanisms underlying such rapid form of neural plasticity is still debated. In the present study, short- and long-term forms of neural plasticity were investigated using dynamic motion aftereffect combined with EEG (Electroencephalogram). Participants were presented with directional drifting gratings for either short (640 ms)

or long (6.4 s) durations. Both adaptation durations led to motion aftereffects on the perceived direction of a dynamic and directionally ambiguous test pattern, but the long adaptation produced stronger dMAE. In line with behavioral results, robust changes were identified in the event-related potentials demonstrated by the dynamic test pattern within 64-112 ms time range. These changes were mainly clustered over occipital and parieto-occipital scalp sites. Within this time range, the aftereffects induced by long adaptation were stronger than those by short adaptation. Nevertheless, the aftereffects by each adaptation duration were in the opposite direction. Overall, these EEG findings suggest that dMAEs reflect changes in cortical areas mediating low- and mid-level visual motion processing. They further provide evidence that short- and long-term forms of motion adaptation lead to distinct changes in neural activity, and hence support the view that adaptation is an active time dependent process which involves different neural mechanisms.

2.1 Introduction

Human perception is shaped by the actual pattern of sensory inputs and previous experience with the external world. Phenomena such as motion adaptation have been extensively employed to understand how previous sensory experience, usually operating over different timescales, contribute to perception [154, 155, 69]. After a prolonged exposure (i.e., tens-hundreds of seconds) to an object moving in a particular direction and with a certain speed, a subsequent motion percept in the opposite direction is produced. This illusion is known as motion aftereffect (MAE), and has been extensively studied by many researchers from different aspects. It has been used as a powerful tool to investigate mechanisms underlying different forms of neural plasticity and their functional roles in perception (see [59] for a review). In order to understand the neural substrates underlying MAE, several adapter types and test patterns engaging distinct stages of motion processing have been frequently used. This resulted in various experimental paradigms based on MAE illusion. An intriguing one is called dynamic motion

aftereffect (dMAE), in which a dynamic test pattern (i.e., a counterphase flickering pattern with no net motion direction) is utilized. Although such dynamic test pattern simultaneously activates early motion detectors sensitive to opposite directions, it is also typically perceived as directional which is determined at higher levels of sensory processing. Some of the previous research highlighted that dMAE has different characteristics than the classical examples of the illusion including only static test patterns. For instance, it is sensitive to second-order motion and can be generated by attention-based position tracking of adapting stimulus [124, 100]. Therefore, these findings suggest that dMAE may affect how later stages of motion processing operate. Conversely, contradicting results have been provided by other studies. For instance, even brief exposure to motion (e.g., tens of milliseconds) was sufficient enough to induce dMAE, biasing the perceived direction of a subsequently presented counterphase flickering test pattern [8]. Rapid forms of dMAE indicated that it can engage low- and mid-levels of motion processing in behavioral setups [137, 150, 156]. Further, V2/V3 and V5/MT (middle temporal) areas were shown to be involved via a transcranial magnetic stimulation (TMS) study using dMAE [84, 157]. Compared to area V5/MT, these TMS findings also pointed out a greater and causal involvement of V2/V3, suggesting that early visual areas play a critical role in rapid forms of dMAE. Although past exploration shows explicit neural substrates for dMAE, the neural mechanisms underlying dMAE induced changes are still subject to debate. In particular, the neural correlates of rapid forms of dMAE and the induced neural plasticity have been poorly investigated, and the resulting framework is fragmentary. In the present study, characterizing the timing and spatial (i.e., scalp) distribution of the dMAE induced changes in event-related potentials (ERPs) were the main focus. Electroencephalogram (EEG) recordings were acquired while participants performed a motion direction discrimination task under several dMAE conditions. Critically, our approach utilized both sub-second (short-term) and supra-second (long-term) adaptation durations. Two explicit objectives were in consideration in having such experimental design. To start with, the exposure time to the adapter has been shown an important parameter for induced aftereffects in general [69]. Past examination additionally showed that an increase in adaptation duration leads to stronger and more robust dMAE

[8, 10]. Following, distinguishing scalp sites and ERP components were planned over which dMAE takes place by utilizing adaptation duration as a critical experimental factor. Second, the adaptation prompted changes in the neural responses can be seen on many timescales even in the same cortical area and neural circuit. For example, the aftereffects on V5/MT neuronal activities have been portrayed in the sub-second time range, seconds and even in minutes [80, 49, 69, 38, 158]. These changes have been proposed to depend on various components of neural plasticity. The duration of both adapter and test stimuli have been frequently manipulated to reveal those mechanisms. Comparing the short-term aftereffects on identified ERP components with those of long-term adaptations, the aim was to determine whether the short- and long-term forms of dMAE rely on different mechanisms even over the same scalp site. If so, particular changes were expected to see in the neural activity for sub and supra-second adaptation durations.

2.2 Methods

In this section, how the sample size was identified, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study were described. No part of the study procedures or analyses was pre-registered in a time-stamped, institutional registry before the research was conducted.

2.2.1 Participants

22 adult human volunteers were recruited. All participants had normal or corrected-to-normal visual acuity and no history of neurological disorders. They were informed about experimental procedures and signed a consent form before their participation. Behavioral performances of 2 participants did not meet the criteria in the training sessions (see Stimuli and procedure) and 1 participant was monitored for excessive EEG artefacts. Accordingly, the data of 19 participants were used in the analyses (10 females, age range 18-33 years). The sample size was

estimated using the G*Power software [159] in order to get a large effect size [160] it was commensurate with previous EEG studies [161]. The inclusion/exclusion criteria were set prior to data analysis. All procedures were in accordance with the Declaration of Helsinki (World Medical Association, 2013) and approved by the local Ethics Committee of Bilkent University and the University of Lincoln.

2.2.2 Apparatus

Visual stimuli were generated using Matlab 7.12 (The MathWorks, Natick, MA) with PsychToolbox 3.0 [162, 163]. They were displayed on a 20-inch CRT monitor (Mitsubishi Diamond Pro 2070sb, 1280×1024 pixel resolution and 100 Hz refresh rate) at a viewing distance of 57 cm. A digital oscilloscope (Rigol DS 10204B, GmbH, Puchheim, Germany) was used to verify accurate temporal overlapping of triggers and onset times of stimuli in each trial. The oscilloscope was connected to a photodiode to detect visual stimulus onsets and offsets on the screen. Experiment was conducted and behavioral and EEG data were collected in a silent and dimly lit room.

2.2.3 Stimuli and Procedure

A white fixation point (0.3 deg diameter) was located at the center of the screen. The fixation point was surrounded by an annulus of 1 deg diameter at mean luminance value in order to aid fixation. Adapting and test stimuli were vertically oriented Gabor patches presented at the center of the screen (Fig. 2.1). Gabors consisted of sinusoidal luminance modulation enveloped by a static Gaussian. They had a size of approximately 8 deg ($\sigma = 2.22$ deg), and a spatial frequency of 1 c/deg. The Michelson contrast of Gabor patches was fixed at 0.9.

Adapting Gabor patches could be either drifting in one direction (leftward or rightward) or counterphase flickering (i.e., directionally ambiguous), whereas test stimuli were always counterphase flickering patches. A temporal frequency of 6.25 Hz was used. In particular, the directional and counterphase flickering stimuli

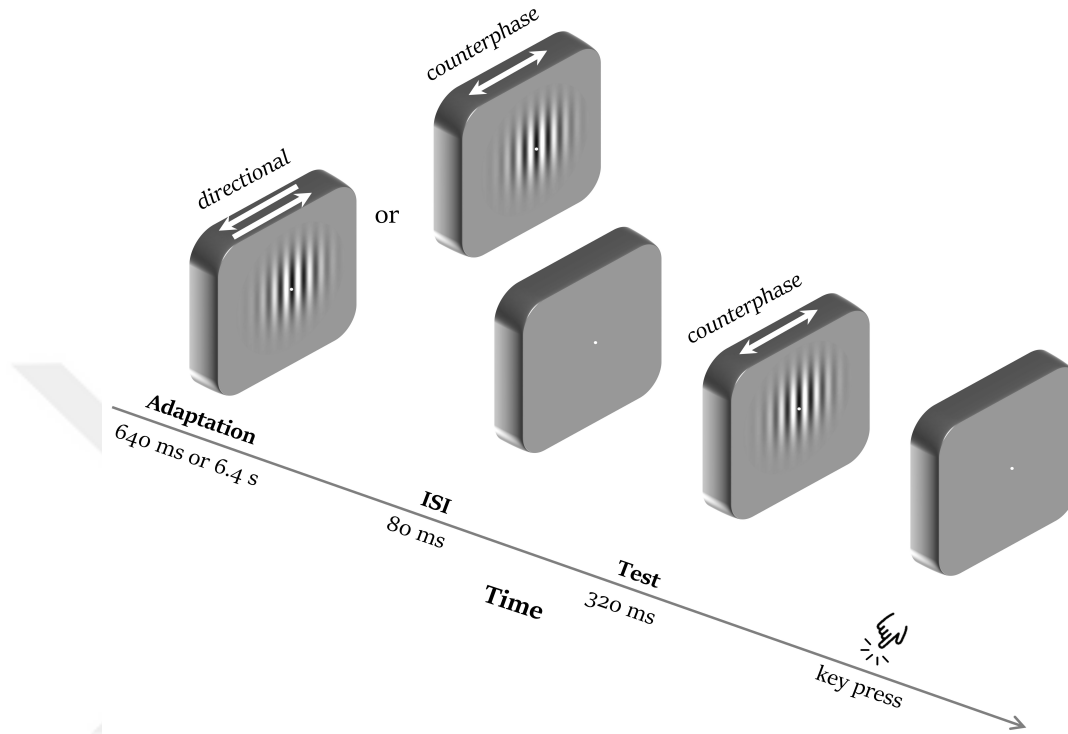


Figure 2.1: Schematic representation of the stimuli and timeline. In each trial, the adapting stimulus was shown first. The adapting pattern was either counterphase flickering or directional (leftward or rightward) and its duration (short: 640 ms or long: 6.4 s) was varied across trials. After an 80 ms adapting-test blank interval, the counterphase flickering test pattern was displayed for 320 ms.

were created by shifting the phase of the sinewave grating composing the Gabor patch. The phase shift was $\pm 90^\circ$ every 40 ms for directional stimuli. On the other hand, the counterphase flickering stimuli were created by shifting the phase 180° every 80 ms based on previous research [8, 137]. This manipulation resulted in directionally ambiguous dynamic patterns (i.e., counterphase flickering) with the same temporal frequency of directional stimuli. On each trial, the starting phase of both adapting and test stimuli was randomized. The parameters of Gabor patches were selected according to the previous dMAE studies [84, 157, 8, 137].

The approach was based on collecting behavioral performance and EEG (electroencephalogram) activity simultaneously. A similar procedure was used to that employed by previous behavioral studies [8, 10, 137]. Each trial consisted of an adapting stimulus and a counterphase flickering test pattern (Fig. 2.1). As already mentioned above, the counterphase flickering patterns were directionally ambiguous with no net motion. The adapting stimulus was presented first and could be either drifting in one direction (directional adapter) or counterphase flickering (counterphase adapter). The counterphase adapter condition was used as a baseline (control) condition. The duration of the adapting stimulus was fixed in each experimental block and pseudo-randomly selected from two values: 640 ms (short adaptation) and 6.4 s (long adaptation). After an adapting-test blank interval of 80 ms (i.e., inter stimulus interval; ISI), the counterphase flickering test Gabor was displayed for 320 ms. The short adaption duration, ISI and test duration values were selected based on previous research to achieve a robust rapid MAE [8, 137]. At the end of each trial, observers were requested to indicate, by a key press, whether the test pattern moved in the same or opposite direction to that of the adapting stimulus. They were also instructed to maintain fixation during each trial. After the keyboard press and a variable inter-trial interval (1-2 sec), during which only the fixation point was present, the next trial started.

Both long and short adaptation conditions were consisted of 100 trials. Within each duration conditions, 50 counterphase-flickering and 50 directional adaptation conditions were presented (25 left, 25 right). Each participant completed one experimental block for each adaptation duration and the order of these blocks was

randomized across participants. Prior to these main EEG blocks, each participant was shown examples of visual stimuli followed by a practice (i.e., training) block for each adaptation duration. In these practice blocks, the same procedure was used but only behavioral data was collected. Participants who reported the test pattern moving in the opposite direction of the adapter in the majority of directional trials were included in the following EEG experiment. This approach allowed us to include participants who performed the task according to our instructions and also experienced the motion adaptation illusion reliably for both duration conditions. During the main EEG sessions, participants performed the perceptual task for all the conditions, and upon debriefing, none of the participants reported any difficulty in performing the task.

2.2.4 EEG Recording and Preprocessing

EEG recording and preprocessing steps were similar to those described previously [161, 164]. In brief, high-density EEG activity was recorded with an MR-compatible system with 64 sintered Ag/AgCl passive electrodes embodied in an elastic cap (Brain Products GmbH, Gilching, Germany). The placement of the cap electrodes was in accordance with a standard 10/20 system. Before the start of each experimental session, the EEG cap was carefully placed on each participant's head. A syringe with a blunt tip and q-tips was used to apply conductive paste (ABRALYT 2000 FMS, Herrsching-Breitbrunn, Germany) and to reduce impedances in each EEG channel. During each experimental session, the electrode impedance values were kept below 10 k to reduce noise to a minimum. The AFz and FCz electrodes were used as ground and reference, respectively. EEG signals were sampled at 5 kHz and band-pass filtered between 0.016 and 250 Hz. EEG data, stimulus markers, and participant responses were stored on a secure hard disk via Vision Recorder Software (Brain Products, GmbH, Gilching, Germany) for further analyses.

Preprocessing of EEG data was carried out offline with BrainVision Analyzer

2.0 (BrainProducts, GmbH, Gilching, Germany). First, EEG signals were down-sampled to 500 Hz and filtered through Butterworth high-pass filter (0.5 Hz cut-off, 24 dB/octave), a 50 Hz notch filter (50 Hz $\pm$ 2.5 Hz, 16th order) and a band-pass filter (1-50 Hz, 12 dB/octave). The data were also re-referenced to a common average and the cardioballistic artifacts were removed using the signal from the ECG channel [165]. Afterwards, the data were segmented into epochs from 200 ms before the onset of the adapter to 1 sec after the offset of the test pattern. To remove common EEG artifacts (e.g., eye blinks, muscle artifacts, any residual heartbeat components), the data was further submitted to independent component analysis (ICA) using the Infomax algorithm. Last, artifact-contaminated trials (i.e., epochs) and bad channels were identified and removed through a combination of automated screening and manually by eye. In the automatic screening, any trial with oscillations over 50 μ V/ms, a voltage change more than 200 μ V or a change less than 0.5 μ V in 100 ms was rejected. Bad channels were reconstructed using spherical spline interpolation [166]. At the end of these standard preprocessing steps, on average 95% of trials were retained per condition.

2.2.5 ERP Analyses

“Cleaned” EEG signals were averaged across trials to compute event-related potentials (ERPs) time-locked to the onset of the test pattern. The final ERPs were baseline corrected using the 200 ms pre-stimulus period before the onset of each adapter. It is possible that adapting stimuli can lead to changes in the evoked activity that are not distinctive to motion direction. These changes can also be dependent on the duration of adapters. To circumvent these potential confounds and to determine direction specific aftereffects on the evoked activity to the test pattern, first the averaged ERPs of the counterphase trials were subtracted from those of directional trials for each adaptation duration. These difference ERPs (directional – counterphase) were used for further statistical analyses. In fact, since counterphase flickering (i.e., directionally ambiguous) stimulation was used

as a baseline (control) condition rather than a static visual flicker, the contribution of any confounding factor even after the test onset is expected to be limited. For instance, it is possible that the physical offset of the adapter may lead to evoked activity after the test onset due to the short ISI used between the adapter and test patterns. However, such offset response is expected to be highly similar in both directional and counterphase adapters. Accordingly, both directional and counterphase adapters should lead to similar motion-offset evoked activities [167, 168] and the subtraction of ERPs for each adaptation duration is expected to eliminate this confound.

The spatiotemporal clusters associated with the changes in the difference ERPs were identified via a cluster-based permutation test integrated into Fieldtrip toolbox [76, 169]. This statistical test is a data-driven nonparametric framework to solve the problem of multiple comparisons (Type I error) and to cluster selected samples (electrode locations and time points) objectively. The difference ERPs of short and long adaptation conditions were compared by paired-sample t-tests at each time point and electrode location. All significant ($p < 0.05$) samples were clustered together based on temporal and spatial contiguity. Then, the cluster-level statistics were calculated by summing t-values within a cluster. A null-distribution of cluster-level statistics was created by randomly permuting the original data (i.e., assigning the original data to one of the two conditions) 10,000 times. The Monte Carlo method was used for these random-permutations. Finally, the observed cluster-level statistics were compared against the generated null-distribution. When the statistics of a spatiotemporal cluster in the real data fell in the highest or the lowest 2.5th percentile of the null distribution, the effect of adaptation duration (*long_{difference}* vs. *short_{difference}*) was considered to be significant. Previous research using a warning stimulus and an imperative (i.e., test) stimulus revealed a component called contingent negative variation (CNV) over fronto-central scalp sites associated with expectancy [170]. Moreover, the amplitude of CNV component starting around 400 ms after the onset of the test stimulus has been found to be correlated with perceptual timing [171, 172]. Therefore, to overcome any unforeseen confounding factor and contamination due to the adapter, the cluster-based permutation tests were performed within the first

400 ms after the onset of the test pattern. Following the cluster-based statistical analyses, time windows and cluster of electrodes (i.e., exemplar sites) were identified over which significant spatiotemporal clusters were mainly located. Using the identified exemplar sites, evoked activities of all conditions were displayed for illustrative purposes. Moreover, ERP amplitudes were averaged within the identified time windows over these locations and performed post-hoc paired and one-sample t-tests on these averaged amplitudes.

2.2.6 Source Localization Analyses

To locate the neural generators of the observed effects at the scalp level, the Standardized Low-Resolution Brain Electromagnetic Tomography (sLORETA) technique [173] was used. sLORETA provides a three-dimensional discrete linear solution that has been shown to estimate the underlying cortical sources of scalp topographies with high and reliable localization accuracy [174, 175]. In its current version, the intra-cerebral volume is partitioned into 6239 voxels with 5 mm spatial resolution. Using a realistic head model from Montreal Neurological Institute (MNI152) template [176, 177] current density at each voxel is calculated. Here, a similar approach was employed to that used in previous research [178]. First, the source estimations for each participant and experimental condition were performed within the identified time window based on ERP analyses. Then, the differences between the voxel-wise normalized estimations of adapter types were computed (directional – counterphase) for each adaptation duration. These voxel-based sLORETA images were compared (*long_{difference}* vs. *short_{difference}*) using the built-in voxel-wise randomization tests with 5000 permutations based on statistical non-parametric mapping [179].

2.3 Results

2.3.1 Behavioral Results

Fig. 2.2 shows the behavioral data. As in previous dMAE studies, the percentage of trials in which the test pattern was perceived to drift in the same direction to that of the adapting pattern is reported for all the adaptation conditions [8, 137, 150]. A percentage value above or below the chance level (50%) corresponds to either motion priming or aftereffect, respectively. The counterphase flickering adapters returned performance values around the chance level for both adaptation durations. On the other hand, the performance values for directional adapters were much lower than the chance level indicating robust motion aftereffects. A two-way repeated measures ANOVA with the adapter type (directional vs. counterphase) and duration (long vs. short) as factors, reported a significant effect of adapter type ($F_{1,18} = 76.298$, $p < 0.001$, $\eta_p^2 = 0.809$). The main effect of adaptation duration was not significant ($F_{1,18} = 0.506$, $p = 0.486$, $\eta_p^2 = 0.027$), but the interaction between the adapter type and duration was significant ($F_{1,18} = 5.732$, $p = 0.028$, $\eta_p^2 = 0.242$).

Post-hoc pairwise comparisons reported that the percentage value of directional adapter was significantly different than that of counterphase flickering at each duration level (short: $t_{18} = -5.564$, $p < 0.001$, Cohen's $d = 1.306$; long: $t_{18} = -8.924$, $p < 0.001$, Cohen's $d = 3.065$). A significant difference between the short and long conditions of directional adaptation was also found to be significant ($t_{18} = -2.709$, $p = 0.014$, Cohen's $d = 0.569$). In terms of percentage values. On the other hand, there was no difference between the counterphase flickering conditions ($t_{18} = 0.629$, $p = 0.537$, Cohen's $d = 0.196$). Overall, this suggests that both adaptation durations led to significant motion aftereffects (i.e., directional – counterphase difference) but the aftereffect induced by the longer duration was significantly stronger.

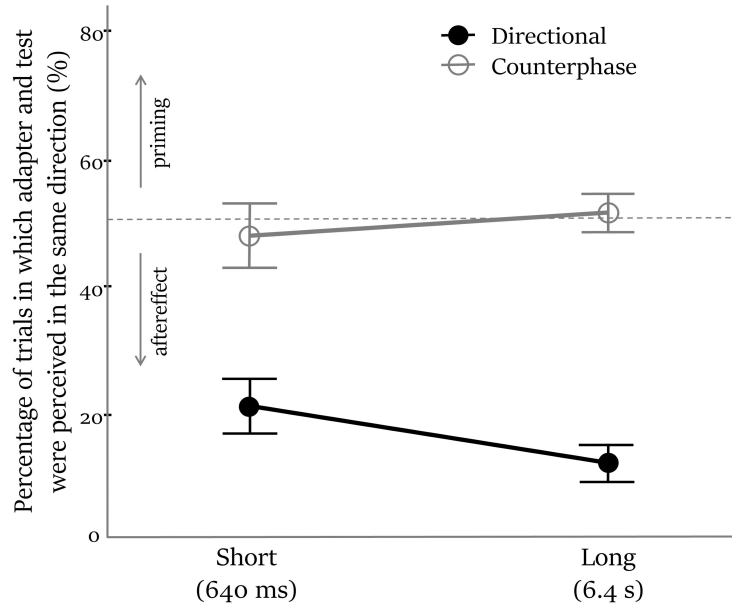


Figure 2.2: Behavioral results ($n=19$). The percentage of trials, in which the adapter and test were perceived to move in the same direction, is displayed as a function of adapter duration. The open and filled circles correspond to the counterphase flickering and directional adapters, respectively. Error bars ± 1 SEM.

2.3.2 Motion Aftereffects on the Evoked Activity

In line with behavioral results, robust changes were found in the evoked activity to the test pattern. A cluster-based permutation test on the difference (directional – counterphase) ERPs revealed a significant effect of duration ($long_{difference}$ vs. $short_{difference}$). The significant spatiotemporal cluster (cluster-level $t_{sum} = 2558.5$, $p = 0.003$) associated with this effect was within 64-112 ms time range and mainly located over occipital and parieto-occipital scalp sites (Fig. 2.3). The cluster also included some of the parietal and centro-parietal electrodes. At these significant scalp sites, averaged difference (directional – counterphase) potentials of long adaptation were higher than short adaptation duration. In agreement with behavioral results, this implies a significant interaction between adapter type and duration over these regions. The cluster-based permutation test also pointed out an earlier (6-32 ms time range) and a later (212-230 ms time range) cluster. However, these spatiotemporal clusters did not return a significant effect

(early: cluster-level $t_{sum} = 730.87$, $p = 0.113$; late: cluster-level $t_{sum} = 146.57$, $p = 0.503$).

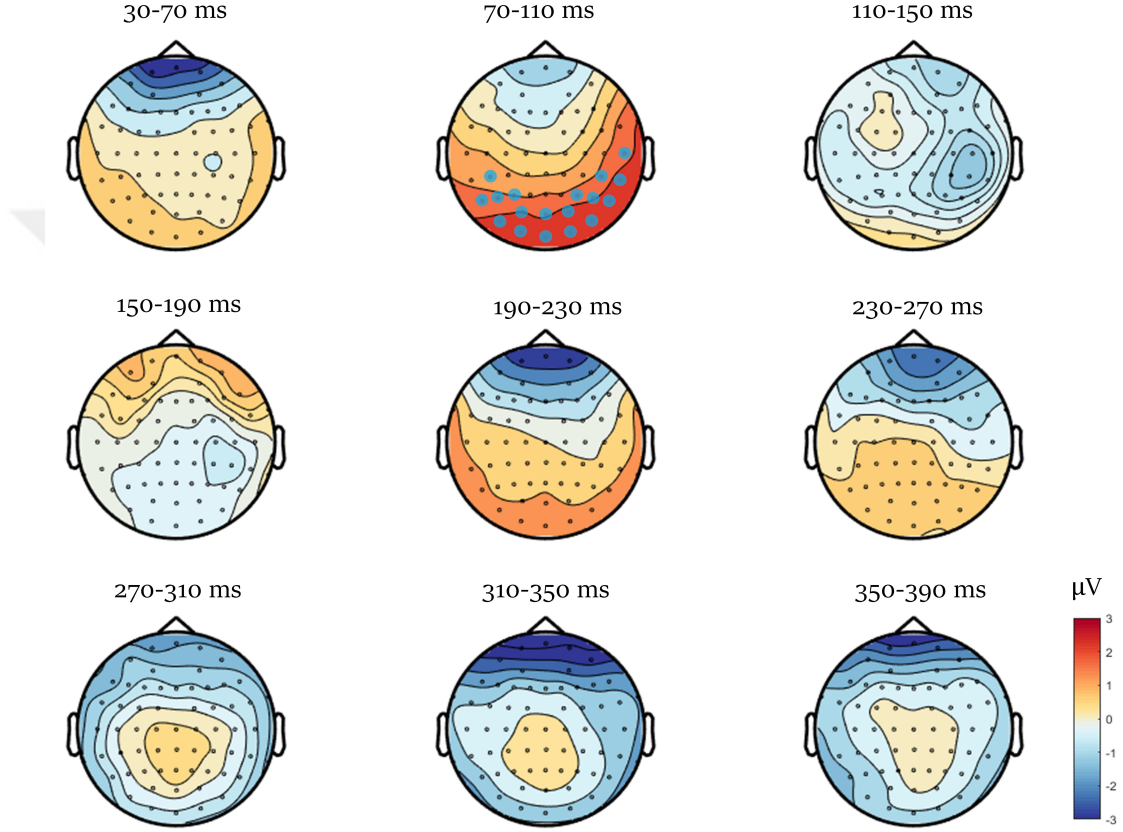


Figure 2.3: Results of the cluster-based permutation test comparing the difference (directional – counterphase) ERPs of the long adaptation duration to those of short condition ($long_{difference}$ vs. $short_{difference}$). Voltage topographical maps of the grand averaged waveforms ($long_{difference} - short_{difference}$) are shown within 40 ms time windows. The electrodes, which were part of the significant spatiotemporal cluster throughout each 40 ms time window, are marked by blue filled circles on the topographical maps. These marked electrodes are $O1$, Oz , $O2$, $PO7$, $PO3$, POz , $PO4$, $PO8$, $P7$, $P5$, $P3$, $P4$, $P6$, $P8$, $CP5$, $CP6$, $TP8$, $T8$.

To understand the functional and neuroanatomical sources underlying this significant effect, source estimations were performed within the 64-112 ms time window (Fig. 2.4). The sLORETA analyses comparing the differences across adaptation durations suggested that this effect was dominant in the left hemisphere and was associated with the activation changes in the cuneus and middle

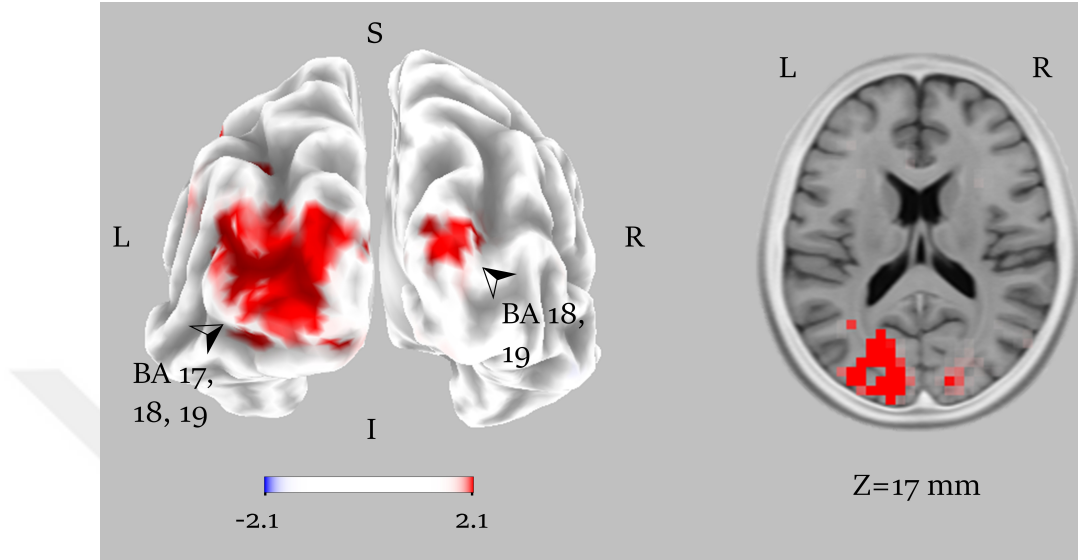


Figure 2.4: Whole-brain t-value maps from sLORETA source estimations within the 64-112 ms time range. Viewing angle of the 3D inflated brain template on the left was arranged according to the significant scalp sites. To better observe the cortical depth, a horizontal slice (T2 MNI-template “Colin 27” of sLORETA) positioned at a coordinate of $Z=17$ mm is also displayed on the right side. The color bar below represents voxel t-values. The sign of the difference between derived waveforms is represented by negative (blue) and positive (red) t-values. Scaling was arranged so that shaded colors indicate (extreme) t-values above 2.1 or below -2.1.

occipital gyrus (Brodmann areas 17, 18 and 19). A relatively small cluster of sources was also found located in the precuneus and superior occipital gyrus.

To display evoked activities to the test pattern and the aftereffects on these activities for illustrative purposes, averaged potentials for the electrodes (i.e., exemplar sites) were computed and marked in Fig. 2.3. As shown by the averaged potentials of these electrodes in Fig. 2.5A, the test pattern showed strong components peaking around 50 ms (C1), 120 ms (P1) and 220 ms (N1). Both C1 and P1 components were mainly present over occipital and parieto-occipital electrodes (Fig. 2.6). Although the P1 component was evident in all the conditions, the C1 component was present and quite robust only in the long adaptation conditions. In terms of difference ERPs, the averaged activities of the long condition were higher within each of these component ranges (Fig. 2.5B). However, as mentioned above, the differential effects of the adapter type (directional – counterphase) for

each adaptation duration only returned a significant spatiotemporal cluster within late C1 and early P1 component range (64-112 ms time range). While the difference ERP of the long condition was located over lateral parieto-occipital and parietal electrodes in this time range, the difference ERP of the short condition was mainly located over the occipital electrodes (Fig. 2.5C).

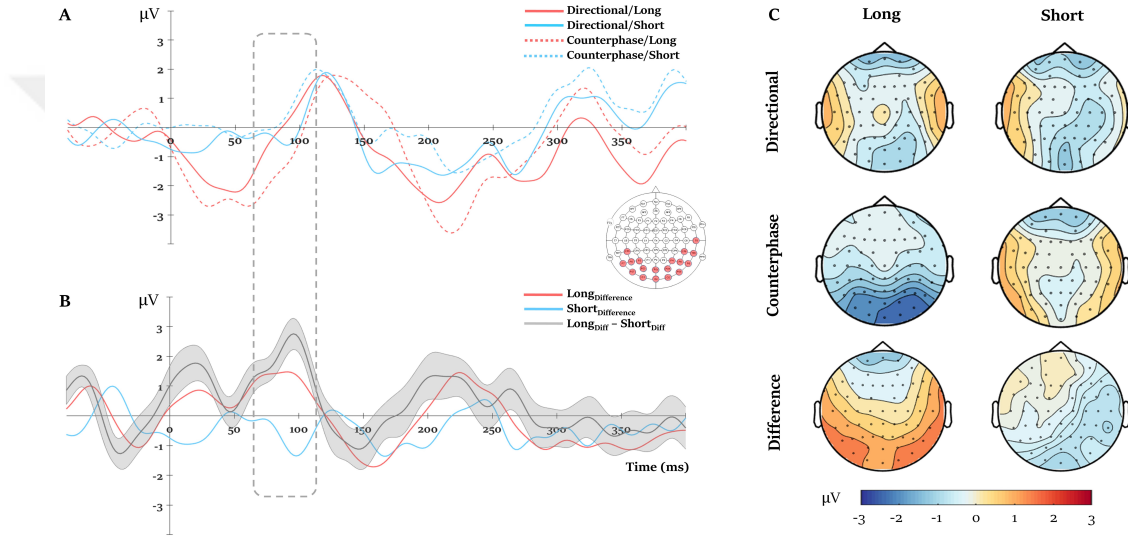


Figure 2.5: A. Averaged activities and derived waveforms from the exemplar scalp site. The exemplar site included all the marked electrodes on a head model ($O1$, Oz , $O2$, $PO7$, $PO3$, POz , $PO4$, $PO8$, $P7$, $P5$, $P3$, $P4$, $P6$, $P8$, $CP5$, $CP6$, $TP8$, $T8$). The averaged ERPs for different adaptation conditions. The ERPs were time-locked to the onset of the test pattern and displayed in the range from -80 ms (i.e., the onset of the blank interval between adapter and test) to 400 ms. The identified time window based on the cluster-based permutation test is highlighted by a dashed rectangle. B. The difference waveforms between conditions. The grey shaded area in the final derived waveform ($long_{difference} - short_{difference}$) represents the standard error (± 1 SEM) across participants. Other conventions are the same as those in the panel above. C. Voltage topographical maps of the grand averaged waveforms within the identified time window (64-112 ms). The voltage topographical map of each adapter type and duration condition is shown in separate rows and columns. The difference topographical maps (directional-counterphase) are shown at the bottom row.

Post-hoc pairwise comparisons on the averaged difference potentials within this range confirmed the significant difference between the two adaptation durations ($long_{difference}$ vs. $short_{difference}$; $t_{18} = 4.78$, $p < 0.001$, Cohen's $d = 1.37$).

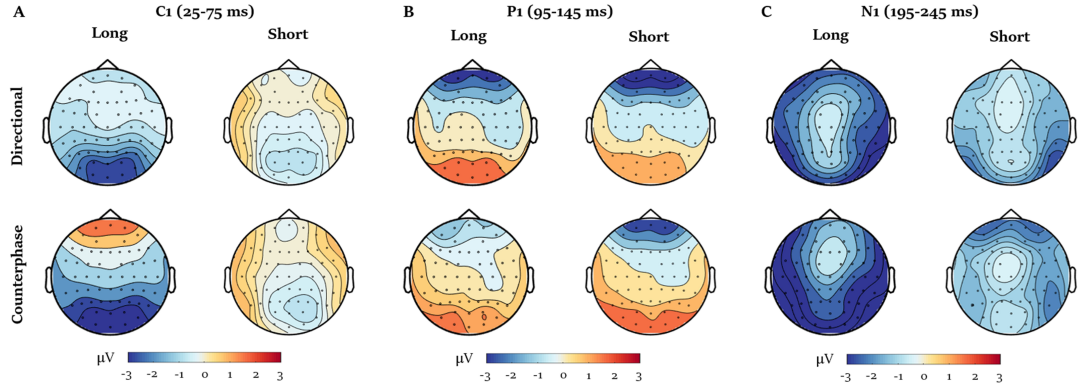


Figure 2.6: Voltage topographical maps of the grand averaged waveforms within 50 ms time range of C1 A, P1 B and N1 C components. The voltage topographical map of each adapter and duration condition is shown in separate rows and columns, respectively.

Hence, this also indicated a significant interaction between the adapter type and duration. To comprehend the underlying mechanisms of this interaction, the average potentials of the directional condition with that of the counterphase at each duration (i.e., directional vs. counterphase) were further compared. The average potential of the directional condition was significantly higher for the long condition ($t_{18} = 4.02$, $p = 0.002$, Cohen's $d = 0.92$) compared to the counterphase. Conversely, the changes in the average potentials were in the opposite direction for the short condition and they were not significant ($t_{18} = -2.03$, $p = 0.058$, Cohen's $d = 0.47$). Using the coordinates by previous research [180, 84, 181] and the electrodes in Fig. 2.5, two sub-clusters (ROIs) were identified mainly located over occipital and parietal electrodes. These occipital and parietal ROIs corresponded to early visual areas (primary visual cortex and neighboring areas) and V5/MT (and also neighboring parietal regions), respectively (Table 2.1). It should also be noted that the occipital ROI included electrodes at the center of the significant spatiotemporal cluster. The averaged activities over these ROIs were highly alike (Fig. 2.7). For both ROIs, there was a significant difference between adaptation durations ($long_{difference}$ vs. $short_{difference}$, Table 2.2) and the average potential of directional condition was significantly higher than that of counterphase (i.e., directional vs. counterphase) for the long adaptation duration. However, the average potentials of short duration were significantly different only for the

Table 2.1: Electrodes designated for the region of interests. In the first column, the marked electrodes in Fig. 2.3 are listed. The selected electrodes for the occipital and parietal ROIs are listed in the second and third columns, respectively.

Electrodes	Significant Electrodes	Occipital ROI	Parietal ROI
	O1, Oz, O2, PO7, PO3, POz, PO4, PO8, P7, P5, P3, P4, P6, P8, CP5, CP6, TP8, T8	POz, O1, Oz, O2	Cp5, Cp6, P5, P6, P3, P4

occipital ROI ($t_{18} = -2.27$, $p = 0.036$, Cohen's $d = 0.52$). There was no such difference for the other parietal ROI ($t_{18} = -1.63$, $p = 0.120$, Cohen's $d = 0.37$). Overall, these additional analyses suggest that the short-term motion aftereffects were dominant over occipital scalp sites corresponding to low-level visual areas.

It is intriguing to observe that the waveforms in Fig. 2.5A also underline a duration aftereffect not specific to motion adaptation (i.e., adapter type). Additionally, a cluster-based permutation test was run to investigate the main effect of adaptation duration. The ERPs of two adapter types were combined (i.e., averaged) then, these two combined waveforms were compared across adaptation durations using a cluster-based permutation test ($long_{combined}$ vs. $short_{combined}$). The results revealed a significant effect of duration (cluster-level $t_{sum} = -3730.3$, $p = 0.003$) only within the C1 component range (10-75 ms). The C1 amplitudes of short adaptation durations were greater than those of long conditions. The significant spatiotemporal cluster was mainly present over occipital and parieto-occipital sites (Fig. 2.8 and 2.9) and included most of the exemplar electrodes shown in Fig. 2.5.

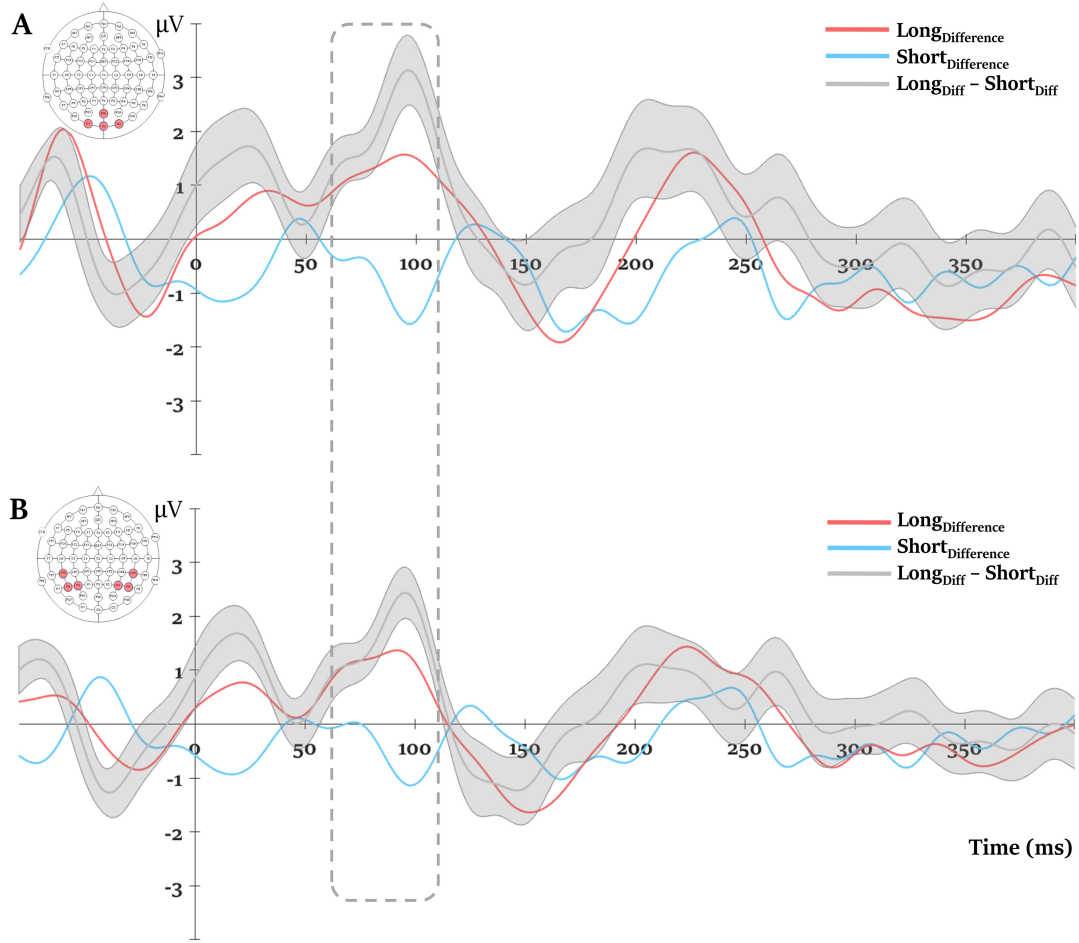


Figure 2.7: Averaged difference potentials across the occipital. (A) and parietal (B) ROIs. The electrode locations are shown on the left insets. The activities were time-locked to the onset of the test pattern and displayed in the range from -80 ms (i.e., the onset of the blank interval between adapter and test) to 400 ms. The identified time window based on the cluster-based permutation test is highlighted by a dashed rectangle. The grey shaded area in the final derived waveform ($long_{difference} - short_{difference}$) represents the standard error (± 1 SEM) across participants. Other conventions are the same as those in Fig. 2.5B.

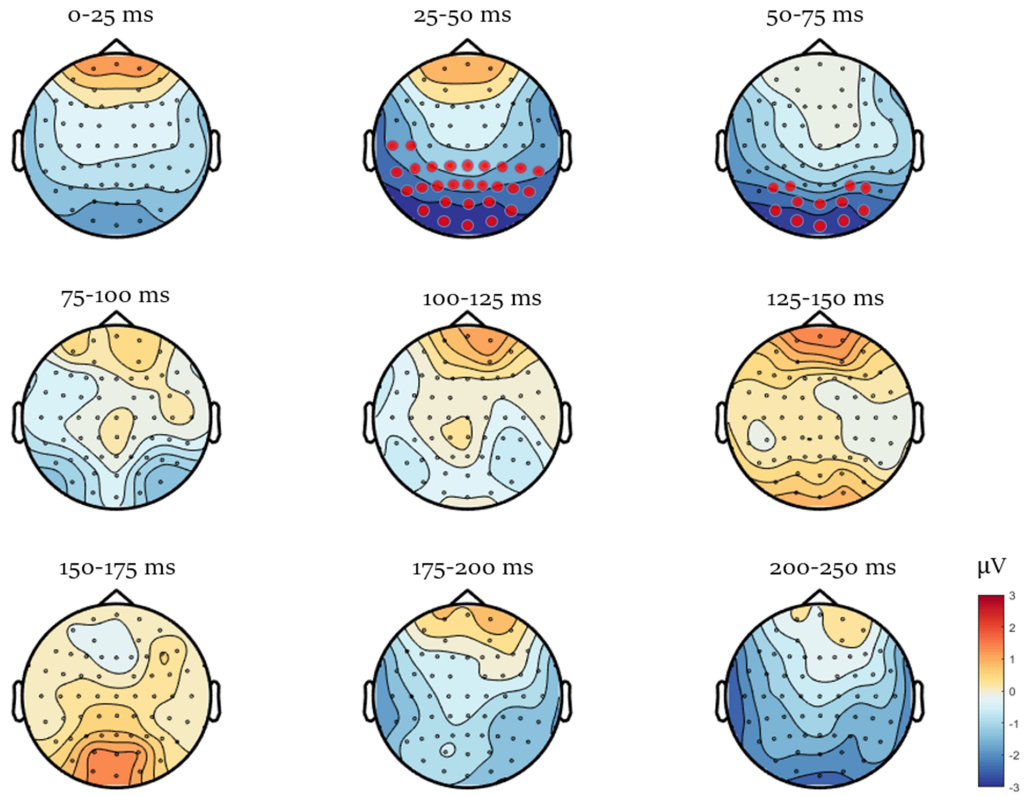


Figure 2.8: Results of the cluster-based permutation test comparing combined (i.e., averaged) ERPs of the short adaptation duration to those of long condition ($long_{combined}$ vs. $short_{combined}$). Voltage topographical maps of the grand averaged waveforms ($long_{combined} - short_{combined}$) are shown within 25 ms time windows. The electrodes, which were part of the significant spatiotemporal cluster throughout each 25 ms time window, are marked by red filled circles on the topographical maps. These marked electrodes are $T7$, $C5$, $TP7$, $CP5$, $CP3$, $CP1$, CPz , $CP2$, $CP4$, $CP6$, $TP8$, $P7$, $P5$, $P3$, $P1$, Pz , $P2$, $P4$, $P6$, $P8$, $PO7$, $PO3$, POz , $PO4$, $PO8$, $O1$, Oz , $O2$ for 25-50 ms time window and $P5$, $P3$, $P4$, $P6$, $PO3$, POz , $PO4$, $O1$, Oz , $O2$ for 50-75 ms time window.

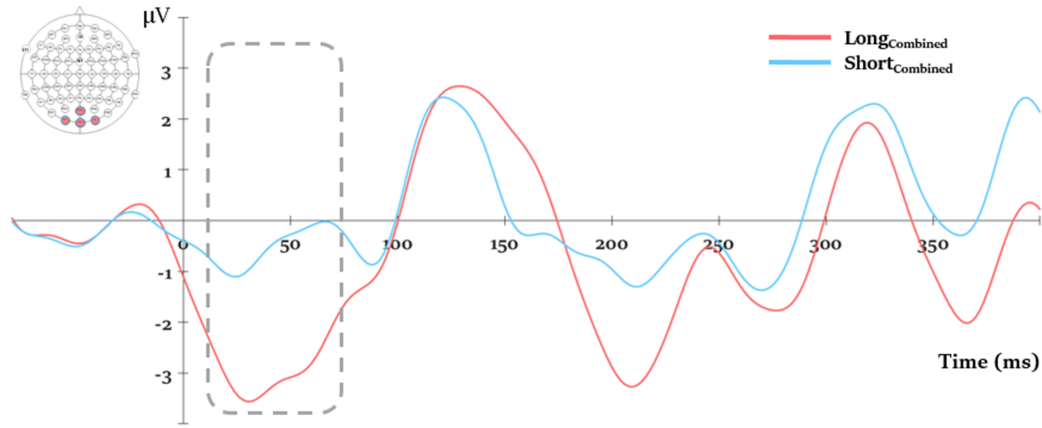


Figure 2.9: Averaged combined waveforms across all the electrodes (*POz*, *O1*, *Oz*, *O2*) located at the center of the significant spatiotemporal cluster in Fig. S3. The combined waveforms were time-locked to the onset of the test pattern and displayed in the range from -80 ms (i.e., the onset of the blank interval between adapter and test) to 400 ms. The identified time range based on the cluster-based permutation test is highlighted by a dashed rectangle.

Table 2.2: The results of the post-hoc t-tests and descriptive statistics for the occipital and parietal ROIs. The values of each ROI are grouped in separate rows. For each ROI, the comparison of difference potentials across adaptation durations (*long_{difference}* vs. *short_{difference}*) is shown first. Then, the statistical results comparing directional and counterphase conditions (i.e., directional vs. counterphase) condition at each adaptation duration are shown in the following rows. Significant *p* values ($p < 0.05$) are highlighted in bold.

	t_{18}	p	Cohen's d	Mean (μV)	SEM (μV)
Occipital ROI					
Long _{diff} vs. Short _{diff}	4.357	<0.001	1.316	2.201	0.505
Long _{diff}	3.481	0.003	0.798	1.324	0.380
Short _{diff}	-2.268	0.036	0.520	-0.877	0.387
Parietal ROI					
Long _{diff} vs. Short _{diff}	4.463	<0.001	1.260	1.635	0.366
Long _{diff}	4.102	0.001	0.941	1.106	0.270
Short _{diff}	-1.634	0.120	0.375	-0.528	0.323

2.4 Discussion

In the present study, short- and long-term forms of dynamic motion aftereffect (dMAE) were investigated using both psychophysical and EEG techniques. Behavioral results indicated that both adaptation durations led to aftereffects, but the aftereffects by the long-term were significantly stronger. Accordingly, considering the adaptation duration (i.e., long vs. short) as a critical experimental factor, scalp sites and ERP components were identified. The adaptation duration significantly influenced aftereffects on the ERPs within the 64-112 ms time range (between the late C1 and early P1) and mainly over occipital and parieto-occipital electrodes. These findings point at the fact that dMAE takes place over visual areas that play an important role in low- and mid-level of motion processing. Thus, they provide important electrophysiological support for previous behavioral and brain stimulation (TMS) results [84, 157, 137]. This study is the first systematic EEG investigation on the rapid form of (dynamic) MAE and also provides novel insights into the nature of this adaptation. In particular, specific comparisons between short and long adaptation durations highlighted important information about this type of motion adaptation. The additional ERP analyses showed that short adaptation gives rise to significant aftereffects mainly over occipital scalp sites. On the other hand, the significant aftereffects of the long adaptation duration were evident over both occipital and parietal electrodes. This suggests that the recruitment of early visual areas for the dMAE also depends upon the timescale used. Previously, it was found that rapid MAE is strongly reduced when either areas V2/V3 or V5/MT are disrupted with repetitive TMS [84]. However, the stimulation over V2/V3 weakened rapid motion aftereffect much more than V5/MT stimulation did. Our results are in line with these findings by highlighting the important and causal involvement of low-level visual areas in rapid MAE. In addition, the results here pinpoint the distinct nature of aftereffects induced by each adaptation duration. Compared to the baseline condition (i.e., counterphase flickering), the directional adapters led to aftereffects on the evoked activity in the opposite direction for each duration. In other words, the rapid MAE on the evoked activity were in the opposite direction, emphasizing the distinct characteristics and nature of rapid MAE. Building upon

these findings, one can hypothesize that rapid MAE may lead to distinct sensory plasticity and engage different neural mechanisms even in the same cortical area. This hypothesis is also supported by previous models of rapid and long MAEs. Using a modified and extended version of Adelson-Bergen motion energy sensors, studies systematically investigated the effect of adaptation duration on MAEs [182, 183]. To account for adaptation effects over different timescales, these sensors included multi-stage leaky integrators. Their simulation results revealed that the amount of time needed by the motion sensor to lose most of its gain and approach the asymptotic baseline activation is a key factor to identify distinct characteristics of rapid and long MAEs. They further reported that the first-order leaky integrator was sufficient to implement adaptation effects of long durations which can span many seconds. However, a second-order leaky integrator, which causes the sensor to require a finite amount of time to react to a sudden change in stimulation, was critical for the rapid form of MAE [183]. These findings clearly demonstrate that the neural mechanisms operating over different timescales can be supported and recruited in the same neural substrate. According to previous research [183, 184], the temporal dynamics of adaptation may reflect a balance between adapting rapidly to avoid short-term saturation and adapting slowly (over longer timescales) to avoid instability in the absence of changes in image statistics. This is because changes in natural scenes occur over multiple timescales, therefore short- and long-term adaptations in the visual system might be expected to occur over a correspondingly diverse range of timescales. Previous EEG recordings on motion adaptation were mainly based on monitoring changes in motion-onset visual evoked potentials (i.e., motion-onset VEPs). In motion-onset VEP paradigms, the motion specific potentials are identified by comparing the cortical activities to a motion display with those to the preceding stationary period of the same stimulus [185]. In the adaptation experiments of motion onset VEP paradigm, an adapter moving in a specific direction was typically displayed for a few seconds and then the test stimulus was shown. However, to identify aftereffects on the motion onset VEPs, the test stimulus included both a stationary and a coherently moving period. These studies consistently reported aftereffects on a negative component peaking around 150-200 ms time range [45, 186]. This motion specific component, which is also known

as N2 component, has been associated with the activity of human area V5/MT+ [187, 188]. The aftereffects on this component were also found to be direction specific to some extent [189, 190]. Relatively more comparable experimental designs to the present EEG study have been used in recent neurophysiological recordings in area MT [191, 192]. During each trial of these recordings, a 3 sec adaptation period was used and after a blank interval (300 ms) a test pattern was displayed for 300 ms. Similar to the experiment here, directional or dynamic adapters with no net perception of directional motion (i.e., random-dot kinematograms with either 100% or 0% coherence level) were used. However, the test pattern employed was always directional. The long conditions of the current study are similar in terms of adaptation duration and types. They reported adaptation induced modulations over the evoked local field potentials (LFPs) in 50-70 ms and 90-110 ms time ranges. Furthermore, these modulations were specific to motion direction and the later modulations were stronger. Compared to the previous motion-onset VEP experiments, these findings highlight earlier aftereffects on the evoked activity and they are highly similar to the time range observed here. EEG recordings in this experiment for the long adaptation durations confirm these modulations in the LFP activities to some extent. It is important to note that rapid MAE can only be generated with dynamic ambiguous test patterns (e.g., counterphase flickering) but not with stationary test patterns [156]. Therefore, future neurophysiological recordings systematically investigating the effect of different test patterns (static, dynamic/directionally ambiguous and directional) on these early modulations will be informative to further extend our understanding of the mechanisms and principles underlying rapid MAE. Interestingly, results here also indicated duration aftereffects (not specific to the adapter type) on the C1 component. In both directional and counterphase adapters of the long condition, the average potentials were lower within the C1 range. On the other hand, the C1 component was almost absent for the short adaptation conditions and the average potentials were close to the baseline level. In a recent study, the evoked activity to a visual apparent motion was systematically examined under different time interval adaptation conditions [164]. Their design included both auditory and visual sub-second time interval conditions. Moreover, they defined two main adaptation conditions (short vs. long) which were

shorter and longer than the time interval demarcated by the apparent motion frames. Similar to the findings here, they found significant aftereffects on the C1 component within 50-80 ms time range. For visual time interval adaptations, the average potential of long condition was lower than that of the short. On the other hand, the aftereffects by auditory time intervals were in the opposite direction such that the short adaptations resulted in lower average potentials. In addition to time interval aftereffects within the C1 component range, these findings further indicated that these aftereffects were distinct for each modality. It is well established that C1 component receives major contributions from the earliest retinotopic regions of the visual processing and this component is associated with the early processing over primary visual cortex (V1) of Brodmann area 17 [193, 194]. In line with these basic features, the C1 component has been found to be sensitive to low-level visual manipulations [195, 196]. By showing duration and time interval aftereffects on this component, the current and previous EEG findings within the context of visual motion suggest that C1 component may be also linked to timing and temporal processing. Indeed, this fits well with previous behavioral results showing that duration aftereffects on perceived timing are narrowly tuned to the location of the visual adapters and hence spatially specific [197, 198, 199]. Using a series of additional manipulations in the visual domain, it was also demonstrated that low-level mechanisms play an important role in encoding the duration of visual events in a retinotopic frame of reference (see ref. [200]). Moreover, there is recent TMS evidence suggesting that temporal information at V1 and V5/MT is encoded in retinotopic spatial frames [201]. On the other hand, it is still possible that other factors may have contaminated the main effect of duration adaptation on the C1 component. For instance, previous research also pointed out that the C1 component may be modulated by attention under some circumstances [202, 203]. Future experiments designed to control other factors (e.g., attention) and to specifically understand the role of C1 component modulations in visual timing and time perception will be informative. To conclude, the current findings indicate that dynamic motion aftereffects take place over ERP components at occipital and parieto-occipital scalp sites. Thus, they provide electrophysiological evidence that dynamic motion aftereffects tap both low- and mid-level motion sensors. In terms of scalp sites and the direction

of modulations, our data further showed some distinct characteristics of aftereffects by short- and long-term directional adapters. Accordingly, these findings, in conjunction with a variety of related converging evidence, support the general view that sensory plasticity is an active time-dependent process which involves different mechanisms.



Chapter 3

Probing ON and OFF Pathway Interactions Via Rapid Motion Aftereffect

ON and OFF pathways are specialized pathways that processing luminance increments and decrements, respectively. Both phi and reverse-phi motion has been shown to recruit motion selective neurons and reduce their firing rates. Phi adaptation activates the same polarities (ON or OFF) repeatedly therefore, engage each pathway whereas; reverse-phi motion activates both ON and OFF pathways simultaneously. Both motion types are shown to elicit MAE. In this study, either phi or reverse-phi motion adaptation was used to induce activation in each pathway (ON or OFF) or; ON and OFF pathways together to observe the consequential effects over occipital and parieto-occipital sites. Since a reverse-phi percept is observed when ON and OFF pathways are activated together, this motion type is expected to merge in the processing stream to produce a final motion percept. Some researchers suggest that the two pathways merge in early visual processing sites [151]; while others suggest that they merge later in the stream right before the global motion signals are produced [152]. A systematic EEG investigation elaborating differences on voltage activation around the occipital and parietal ROIs would exhibit response characteristics of early visual

motion processing sites and provide a comprehensive explanation on the location where ON and OFF pathways coalesce. In this study, two types of adaptation (phi or reverse-phi) and two duration times (188 or 752 ms) were used. A 121 ms ISI followed the adaptation stimulus. Afterward, a counterphase-flickering test stimulus was presented. MAEs on behavioural responses and evoked activities were analysed. An effect of duration on behavioural reports was found, despite a non-significant motion type effect, a difference between the long conditions were observed. The long and short conditions were combined to analyse neural activities and these analyses pointed to differences in C1 component over occipital ROI. Type-wise differences on the long conditions were examined as well. A difference over occipital and parietal sites emerged around P1 component range. A supplementary analysis for phi and reverse-phi combined conditions also supported $long_{phi}$ vs $long_{reverse-phi}$ comparison results by revealing a difference between the conditions around early P1 component range. Further ANOVA analyses on the electrophysiological data within the C1 and P1 range on the combined conditions showed a main effect of type as well as a main effect of duration indicating a segregated processing of the ON and OFF channels. The duration-wise differences observed in Chapter 2 were also found here. These results indicate efficient convergence of information provided by ON and OFF pathways and also distinct characteristics of these across pathway mechanisms.

3.1 Introduction

3.1.1 Phi and Reverse-phi Motion

Phi motion is perceived when two spatially segregated bars are successively presented and perceived as moving in a certain direction. Conditions of whether two successively presented bars will be perceived as a moving object or not depend on different characteristics of the objects such as luminance, spatial range and temporal interval. It was proposed that the objects in two consecutive frames should be similar to an extent in order to be perceived as coherently moving and

it was called as the “correspondence problem” [204]. Ullman further suggested that characteristics such as contrast or luminance should be corresponding to an extent in both frames for the sequence to be perceived as a clear movement. Also, it was shown that similar spatial frequencies were required in both motion frames to have a coherent percept [205]. On the other hand, a reverse-phi illusion is obtained by reversing contrast in each motion frame. By engaging ON and OFF pathways consecutively, an illusory perception of motion direction can be induced. When the same photograph is presented consecutively with a small spatial displacement, perception of motion towards the direction of the latterly presented stimulus (forward phi/ regular phi) is obtained [206]. However, when a graphic negative of a picture is presented after the original one, the perceived movement is towards the direction of the initially presented picture, which is opposite to the physical displacement (reverse-phi). In other words, the reverse-phi motion is perceived when the contrast polarity of the initial frame is reversed and presented with a spatial shift right after the original frame. This polarity change is executed in each spatial displacement, and the change causes perception of movement to be in the opposite direction to the physical displacement. However, in the regular motion, no polarity change is introduced therefore, a phi motion (regular motion) is perceived. Fig. 3.1 illustrates the difference of phi and reverse-phi in the space-time domain. The contrast reversals are thought to alter the balance of motion energy towards the opposite direction. Motion energy models of reverse-phi movement will be discussed in the following sections.

Not only the stimulation structures in Fig. 3.1 result in motion perception but also random dot kinematogram (RDK) is proven to result in motion perception as well. It is suggested that for an RDK to be perceived as moving or not highly depends on the spatial difference of the subsequently presented frames. This upper displacement limit is found to be 15 min arc [207] and is much less as opposed to a regular apparent motion. The upper spatial displacement limit for reverse-phi motion was examined and they found that foveal reverse-phi upper limit was comparable to that of regular RDK [208].

Many researchers showed interest in the characteristics of phi and reverse-phi

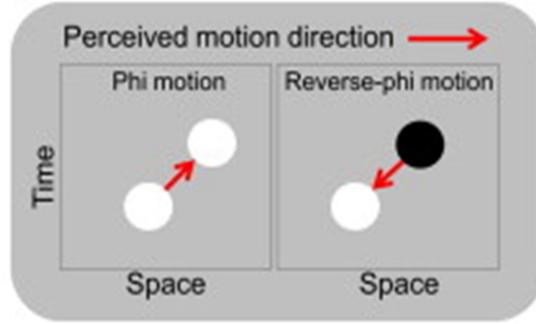


Figure 3.1: Representation of phi and reverse-phi motion in the spatial and temporal domains. In the phi motion, a physical displacement is introduced without a change in the contrast polarity of the dot whereas; in reverse-phi motion, contrast polarity is changed along with a shift in space. The red arrows show the physical shift for each motion type. Both phi motion and reverse-phi motion are typically perceived as a movement to the right even though the direction of the physical displacement is in the opposite directions (Adapted with permission from Elsevier, ref. [9])

motion and they examined both movement types in different aspects. Another line of research examined the location where perception of movement was initiated for both motion types. Detection stage theories will be discussed in the next section to broadly provide information about the prominent views.

3.2 Detection stage theories

3.2.1 Early Stage

Sensitivity of phi and reverse-phi motion was measured [151] to test whether ON and OFF cells are processed separately or through a combination of signals from both channels that operate in an interactive manner. Step size and temporal interval were manipulated to compare the resulting sensitivity curves. They found similar sensitivity tuning curves for both phi and reverse-phi movement and concluded that motion detectors are equally adept at combining signals arising from same or different polarities that the signals progress in an interactive manner. They suggested that both phi and reverse-phi motion is generated by

using low-level contrast correlations. In another study, researchers investigated how blocking an ON channel can modulate the way ON center and OFF center affects the neurons in the primary visual cortex [209]. Blockage of the ON cell at the retina affected the responses of the ON center cells at the LGN level however, it remained ineffective at the OFF center responses. Nonetheless, the blockage affected light-edge responses at the primary visual cortex suggesting that ON and OFF cells begin interacting at the striate level. Similarly, Schiller (1992) suggested that ON and OFF cells start off as segregated units and they converge at the primary visual cortex.

3.2.2 Late Stage

Another view on the processing of ON and OFF pathways suggests that prior to the area that produces global motion processing, ON and OFF pathways converge [152]. In their study, they investigated parallel pathway interactions of ON and OFF pathways at the high level motion stage. They used coherent random dots and asked the participants to indicate the global direction of the stimulus (up or down). First, they tested whether dark and light stimuli were processed by different pathways but they found no independent mechanisms. They measured thresholds of the light and dark stimuli to test whether the signals coalesce before the global motion signal is formed. They found that the threshold (in terms number of dots) leading to a motion percept was the same for light only stimuli and the 50% light and 50% dark stimuli, suggesting that ON and OFF channels are not processed separately. They also tested the thresholds with polarity change and without polarity change conditions and found that polarity reversal was ineffective on the global motion mechanism. At the end, they examined whether regular and reverse-phi motion conditions had the same thresholds. They showed that only the partial polarity change condition showed a different threshold than the opposing vector conditions. They also compared the no contrast polarity change with the polarity change condition, in terms of effectiveness in driving the global motion system. Overall, these results suggest that ON and OFF pathways remain bifurcated until the initial motion detection stages but then they

converge prior to the global motion signal extraction. Threshold delays of successively presented stimuli for dark and light stimuli were investigated and they found that threshold diameters for motion to be perceived for bright lines were twice as large as the dark pairs [153]. This suggests that ON and OFF pathways exhibit separate characteristics due to the spatial segregation throughout early stages of motion processing.

3.3 Motion Models

In order to examine mechanisms underlying phi and reverse-phi, computational models have been designed and developed by researchers. Early modelling studies suggested a common mechanism can account for phi and reverse-phi motion [210, 4, 211]. Different types of models have been introduced to understand the mechanism of the reverse-phi motion adaptation. Three major models will be discussed in the subsections.

3.3.1 Evidence based model

Early views called “evidence based models” emphasize the activation shifts in low-level motion detectors [212]. For instance, in the Mo-Koch model, when a constant-contrast stimulus is presented, the output of a motion detector is enhanced as much as when a contrast-inverting stimulus moving in the opposite direction is presented. This was called evidence based model simply because the polarity inverting stimulus induces direction selective neurons that are tuned to opposite way. In other words, polarity inverting stimulus aids oppositely tuned neurons in MT.

3.3.2 Counterevidence Model

Detection mechanisms of reverse-phi motion and motion aftereffect were studied to examine whether they share similar detection mechanisms [213]. In the model, authors argued that different contrasts arising from reverse-phi motion stimulation reduced the activity in the low-level motion detectors thus leading to a motion percept in the opposite direction. In other words, the neurons tuned to a phi movement in a certain direction is suppressed by a reverse-phi movement in the same direction. In their study, they used both phi and reverse-phi motion and suggested a similar reduced activity for reverse-phi motion and motion aftereffect. Hence, they suggested that an inhibition at the motion detection stage must be already present so that motion perception in the opposite direction was perceived.

3.3.3 Complex Motion Model

Similar to regular adaptation, reverse-phi motion adaptation is shown to produce MAE [213]. In fact, researchers have shown a reduction in the direction selective MT cell responses as well as on its behavioral responses after adapting the monkey to a reverse-phi illusion [68]. In their study, they showed that monkeys were able to perceive reverse-phi motion like humans. Monkeys were able to perceive rightward motion with regular phi movement and leftward movement with reverse-phi movement. They showed that a neuron, directionally selective to phi motion in a specific physical direction showed similar activation to a reverse-phi movement in the opposite direction. They concluded that MT was the origin of the perception of reverse-phi movement and the perception is not merely a linear subtraction of Fourier components but rather a more competitive and selective activation pattern which fits the behaviour of the direction selective neurons. They proposed a more complex model involving competition of all the Fourier components each of which might have influences in different extents when combined with another component. They propose that components other than preferred and opposite

preferred directions also contribute to perception of motion, and these components have multitudes that do not contribute linearly. Even though the weights of the components were known one by one, a linear sum did not explain the net MT neuronal behaviour. This distribution of competition between all Fourier components make up for a better explanation of the neuronal behaviour at MT level. Another study found that adaptation for 2 seconds was sufficient enough to diminish perceived speed while it improved speed discrimination in both humans and monkeys [69]. Both of these studies suggest that adaptation is not a mere result of fatigue but a much more complicated process that might facilitate the encoding of a stimulus aspect while it may impede others.

3.3.4 Comparison of the Motion Models

In the Bours-Kroes-Lankheet model [213], the output of a detector, which is tuned to a constant-contrast stimulus moving in a particular direction, is suppressed by a contrast-reversing and moving stimulus in the same direction. Accordingly, the contrast reversing motion stimulus provides evidence for the opposite direction in the Mo-Koch model [212], whereas Bours-Kroes-Lankheet model provides a perspective highlighting a suppression mechanism in which motion perception in one direction with constant-contrast stimulus (i.e., phi movement) is suppressed by a contrast-inverting stimulus (i.e., reverse-phi movement) in the same direction, providing evidence against it. In other words, a reverse-phi motion in right direction could create a leftward motion percept by means of; excitation of left movement tuned neurons (Mo-Koch evidence model) or; inhibitions of the neurons tuned for right direction (Bours-Kroes-Lankheet counterevidence model).

To compare counterevidence (Bours-Kroes-Lankheet) and, evidence only (Mo Koch) models, tuning curves of constant and inverting contrast stimulus were examined in areas V1 and MT [214]. They compared the experimental data to the predicted outputs of these models. They found that in V1, population tuning curves were consistent with the counterevidence model whereas in MT, tuning curves resembled evidence only predictions better than the evidence only

model. They corrected this inconsistency with a nonlinear summation of the V1 neuron responses and suggested that the consequence of the constant- or inverting-contrast stimulus presentation manifested itself as early as V1.

With all the models discussed in the chapter, Duijnhouwer Krekelberg [214] suggested that Bours-Kroes-Lankheet model provide a better explanation to reverse-phi motion perception with emphasis on the differences occurring early stages of motion processing.

3.4 Aims of the Study

As discussed in Chapters 1 and 2, the rapid forms of MAE are generated by presenting observers with brief durations of adapting stimuli and with a particular brief ISI followed by a test stimulus. It was shown that a response arose in MT direction selective cells even after a 67 ms adaptation period [80]. Characteristics of rMAE were observed by using stationary or dynamic (counterphase flickering pattern) test patterns [156]. By varying certain characteristics such as adaptation duration, temporal frequencies, test duration, ISI, and phase shift, they investigated the underlying mechanisms of rMAE. They found that rapid forms of motion aftereffect are largely dependent on the spatiotemporal characteristics of the stimulus presented. While evidence suggests that reverse-phi motion also induces activity in V1 and MT [213, 215, 68], the spatiotemporal characteristics of motion perception induced by opposite contrast polarities is still largely unknown [214]. Research suggested that in order to understand the nature of reverse-phi directional selectivity, the activation of both pathways (e.g. ON and OFF) is required, in fact activating both ON or OFF pathways only could give insights to the nature of the regular motion [212].

Two main approaches as to how these within (either ON or OFF) and across (ON and OFF) pathways function, it was suggested that they are initially segregated and they converge 1. prior to the extraction of the global motion signal [152], 2. they converge at lower motion detection stages [213, 212]. In the present

study, using the same paradigms as in the ref. [156], the aim was to identify the neural correlates of rapid forms of MAE with several alterations to the stimulus. The voltage changes were investigated mostly on the electrodes that correspond to the areas responsible for visual motion processing. As discussed earlier in Chapter 2, parietal (*CP5, CP6, P5, P6, P3, P4*) and occipital (*O1, O2, Oz, POz*) regions of interests were the basis of ERP analysis in this experiment as well. Electrode activations provided us with further information in regard to the differences and similarities of neural basis of classical and rapid forms of MAE. Differences between long and short durations were found with several ISIs [10]. They also showed that differences occurred between phi and reverse-phi conditions in particular ISIs. They showed that the differences in behavioural reports occurred after inducing simultaneous induction of ON and OFF pathways. In this study, electrophysiological basis of this modulation was examined to better understand ERP differences over occipital and parietal ROIs. The outcome of this study will also be informative about processes in visual pathways specifically at the striate level by implementing regular motion and reverse-phi motion adaptation paradigms. Employing both motion types would activate within or across pathways to provide a deeper understanding over different timescales.

3.5 Methods

Experimental setup and testing room described in Chapter 2 was also used for this study.

3.5.1 Recruitment of Participants

Through the Bilkent University mailing lists, university students were informed about the study and participants were scheduled upon their voluntary requests. 30 volunteers (19 females, age range 18-25 years) who were given course credits were tested. All other conventions regarding participant recruitment was the same as in Chapter 2. 6 participants (2 females) were eliminated due to their

behavioural performances in the experiment (see Procedure). Participant elimination was performed according to the elimination criterion and remaining 24 subjects were included in the behavioral and EEG analyses.

3.5.2 Apparatus

The apparatus and settings were the same as those in Chapter 2 except the screen was set to 85 Hz refresh rate. A minimum luminance of 0.36 cd/m^2 , a maximum of 98.95 cd/m^2 and a background luminance of 16 cd/m^2 were used.

3.5.3 Stimuli

The experimental paradigm and stimulation were similar to those of [10]. A red fixation circle with 12 arc-diameter was displayed at the center of the screen in all trials (Fig. 3.2). Adapting stimulus was vertical square drifting gratings (1 cpd) either moving rightwards or leftwards. The gratings (i.e., both adapter and test) were presented in a 160 diameter circular aperture placed at the center of the screen. The phase shift for the adaptation stimulus was ± 90 degrees either rightward or leftward (Fig. 3.3.A). To obtain a regular phi movement, the contrast polarities remained the same in each motion frame (94 ms each) however, reverse-phi motion required a contrast polarity reversal at each spatial displacement (Fig. 3.3.B). For both phi and reverse-phi adapters, the test stimulus was also square-wave gratings were either darker (5 cd/m^2), or lighter (27 cd/m^2) than the background (16 cd/m^2) except with a $\pm 180^\circ$ phase shift. The regular and reverse-phi motion adaptations with 188, and 752 ms and an ISI of 121 ms were presented. Subsequently, a directionally ambiguous flickering test stimulus for 752 ms was presented. A jitter for inter-trial intervals were introduced (random between 1-2 seconds) to prevent habituation of the brain activity.

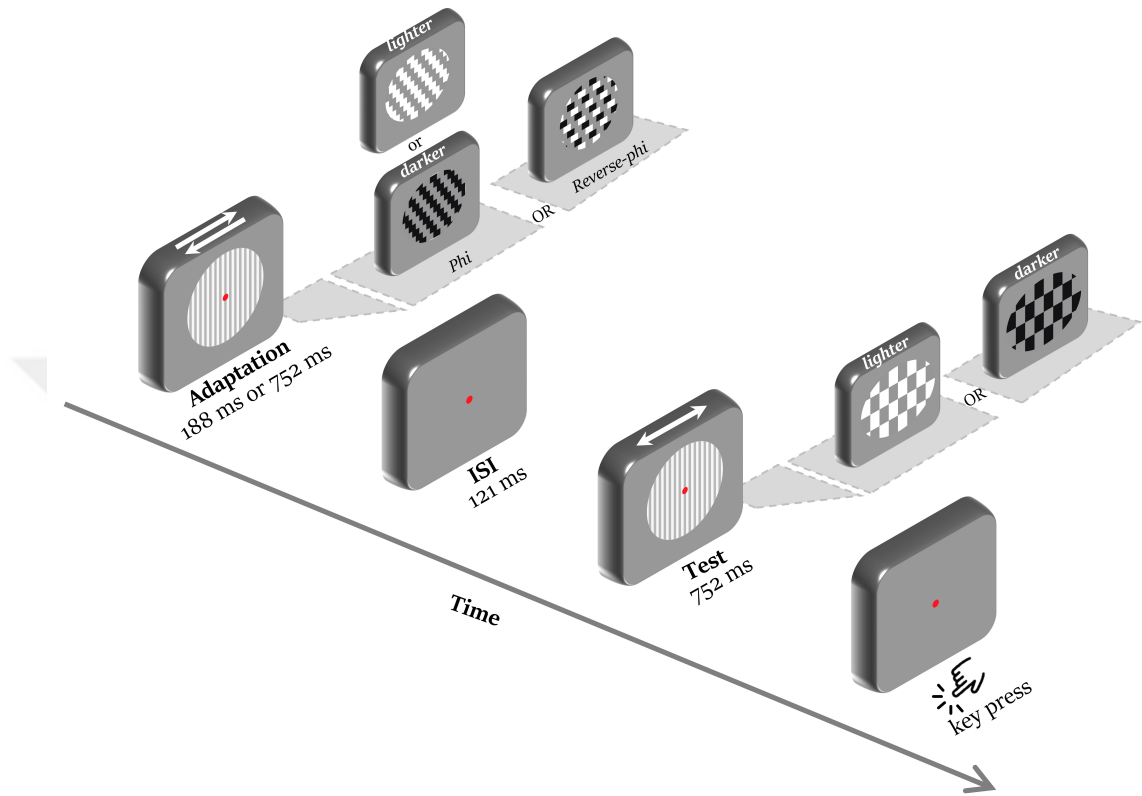


Figure 3.2: Schematic representation of the experimental design. An adaptation stimulus was followed by a blank interval and a test stimulus. Same convention was applied for each trial. Two adaptation type options were possible (i.e. phi and reverse-phi). Phi condition was presented with square wave gratings either darker or lighter than the background. The contrast polarity of the test stimulus and phi adaptation stimulus was matched. The contrast of a test stimulus following a reverse-phi adaptation was pseudo-randomly selected. The contrast polarities were reversed on every motion frame and the initial contrast polarity was randomly selected for the reverse-phi adaptation. Long (752 ms) and short (188 ms) duration options were possible for adapting stimulus. The test stimulus was always displayed for 752 ms.

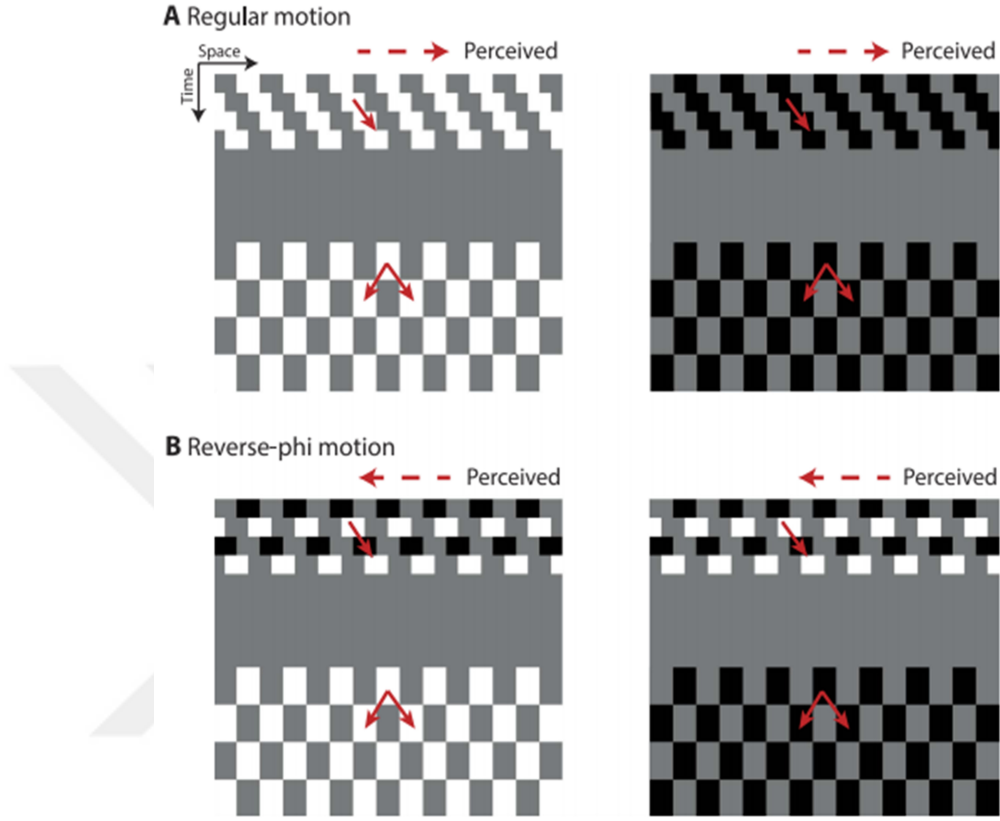


Figure 3.3: Space-time plots of stimulation for each condition. A. For adaptation stimulus, each flip was presented for 94 ms shifted for 90° to the left or to the right on the horizontal axis. There was no polarity change for phi adaptation. B. Polarity alternated between dark and light for reverse-phi adaptation. Test stimulus was presented for 188 ms for every flip and shifted by 180° and the gratings were either lighter or darker than the background. Horizontal axes correspond to space and vertical axes correspond to time domains. Adapted with permission from SpringerNature, ref. [10].

3.5.4 Procedure

The experimental procedure by ref. [10] was applied. However, in the current EEG study only one ISI (121 ms) and two adaptation durations (i.e. long; 752 ms and short; 188 ms) were used (Fig. 3.2.). The test stimulus (i.e., counterphase-flickering test pattern) duration was the same (752 ms). At the end of each trial, the participants were asked to indicate with a key-press whether they saw the test stimulus moving in the same or opposite direction to that of the adaptation stimulus. Four conditions were possible based on two adapters (phi adaptation, reverse-phi adaptation) and 2 adaptation durations (i.e. long vs short adaptation).

Participants first went through a training session where they were tested whether they were able to perceive and report both adaptation types in the expected directions. The expected direction for regular phi adaptation referred to a perception in the direction of the physical displacement and, for reverse-phi adaptation it referred to the perception opposite to the physical displacement. The same adaptation stimulus from the experimental conditions was used in the training session with both adaptation durations (i.e. long and short). Phi and reverse-phi training sessions were run separately. Training trials were presented 60 times per session (2x60 trials for the training session). Participants who indicated responses in the expected direction more than 70% of the time were proceeded to participate the experimental sessions. If the participants indicated that both adaptation and the test stimulus were moving in the same direction for more than 50 percent of the trials per condition, they were excluded from the analyses. Rationale for the criterion indicated was the lack of aftereffect responses in the performance, resulting in exclusion from the participant pool.

In the experimental blocks, participants were asked to fixated on a red circle and indicate whether adaptation and test stimulus were moving in the same direction. During the ISI, only the red fixation circle was present on the screen. Same stimulus iterations were restricted to three subsequent times at most. The adaptation durations were run in a random order. In the reverse-phi condition,

starting polarity of the test stimulus in each trial was pseudo-randomly selected. Phi and reverse-phi blocks were run separately in a random order with 100 trials each. Each block had 50 long and 50 short adaptation trials. Breaks were given between all blocks to prevent the participants from getting exhausted.

3.5.5 EEG Data Acquisition, EEG Preprocessing and Analyses

All EEG data acquisition protocol was the same as the first study. An average of 88% of the trials remained after preprocessing of the EEG data. ERP analyses in this study was conducted by averaging electrodes that are predetermined from the study in chapter 2. An occipital and a parietal ROI were determined in the previous study based on the designated electrodes. Trials were averaged and point by point (i.e., time points) comparison across conditions were performed with FDR corrected t-tests to reduce type 1 error [216, 217]. When there was continuous activation difference for 20 ms between conditions, that interval was considered significantly different [218].

Since the experimental questions and the setup address questions regarding visual motion perception, temporal limits are set to 400 ms. The electrodes corresponding to the early visual sites have been identified as *O1*, *O2*, *Oz* and, *POz* in the first experiment, therefore the same electrodes were averaged to perform all the analyses in this experiment. A main temporal interval between 64-112 ms was also identified in the first experiment hence; the same interval was tested for all analyses accordingly. ERPs were plotted to examine component specific characteristics of the differences.

3.6 Behavioral Results

As seen in Fig. 3.4, both phi and reverse-phi conditions were perceived in the expected direction (towards the direction of the physical displacement for phi

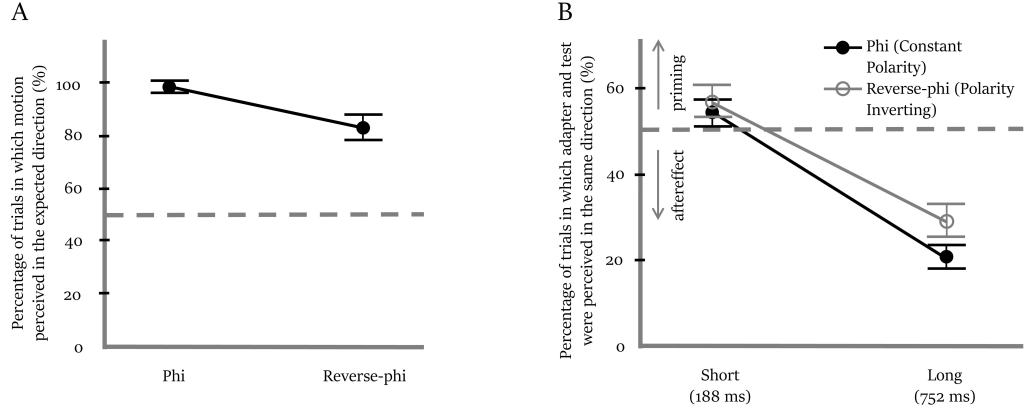


Figure 3.4: The left side of the figure shows percentage of trials in which motion is seen in the expected direction as a function of motion type. The right side of the figure shows the behavioral results of the experiment (N=24). For each adaptation duration, the percentage of trials in which participants judged both the adapter and the test stimulus moving in the same direction is plotted as a function of stimulus duration. Error bars represent $\pm 1\text{SEM}$

motion and opposite to the reverse-phi motion). Phi condition was perceived correctly for 98% of the time with 3.7 standard deviation whereas; reverse-phi condition was perceived correctly 83% of the time with a standard deviation of 3.9.

A two-way ANOVA with the adaptation (motion) type and duration conditions was performed. A significant main effect for adaptation duration ($F_{1,23} = 69.04$, $\text{MSE} = 23562.66$, $p < 0.0001$, $\eta_p^2 = 0.75$) was found. However, the main effect of adaptation type ($F_{1,23} = 3.205$, $\text{MSE} = 580.167$, $p = 0.087$, $\eta_p^2 = 0.122$) was not significant. The two-way interaction between these factors was not significant either ($F_{1,23} = 1.133$, $\text{MSE} = 160.167$, $p = 0.298$, $\eta_p^2 = 0.047$). Further t-tests on each adaptation type showed a difference between phi long ($M = 20.833\%$) versus reverse-phi long ($M = 28.33\%$) was significant ($t_{23} = -2.739$, $\text{SEM} = -7.5$, $p = 0.012$, Cohen's $d = 0.483$).

3.7 EEG Results

In accordance with the significant duration effect indicated by behavioral results, we grouped conditions and performed statistical test on the EEG signals. A main effect of duration and, a difference between $long_{phi}$ and $long_{reverse-phi}$ conditions were identified as a result of the behavioral analyses therefore, point by point FDR corrected t-tests were performed based on the difference of behavioral results.

3.7.1 $Long_{combined}$ vs $short_{combined}$ Comparison

$Long_{combined}$ condition was obtained by averaging over $long_{phi}$ and $long_{reverse-phi}$ conditions while $short_{combined}$ condition is obtained by averaging over $short_{phi}$ and $short_{reverse-phi}$ conditions. A t-test on the difference between $long_{combined}$ vs $short_{combined}$ conditions were performed within the first 400 ms of the test stimulus. ERPs were plotted to examine component specific characteristics of the differences.

Even though a persistent significant difference was not present between 64-112 ms interval, two other main significant intervals were identified (i.e. 0-88 ms, 128-160 ms) between $long_{combined}$ and $short_{combined}$ ($p < 0.05$, FDR corrected) conditions. The responses in Fig. 3.5.B showed that an initial peak around C1 was present for the $short_{combined}$ condition where the $long_{combined}$ condition cruised around the baseline level with no salient peaks. A P1 peak for both $long_{combined}$ and $short_{combined}$ conditions were evident as marked on Fig 3.5.B. Another peak with a relatively smaller amplitude was seen between 64-112 ms.

Topographical plots showed that short adaptation induced a more positive voltage distribution as opposed to the long adaptation in both significant 0-88 ms interval and, the pre-determined 64-112 ms interval. An activity reversal is observed within the second significant interval (128-160 ms) in terms of short and long adaptation durations. Within this interval, the long adaptation duration induced a more increased response compared to the short adaptation. Although

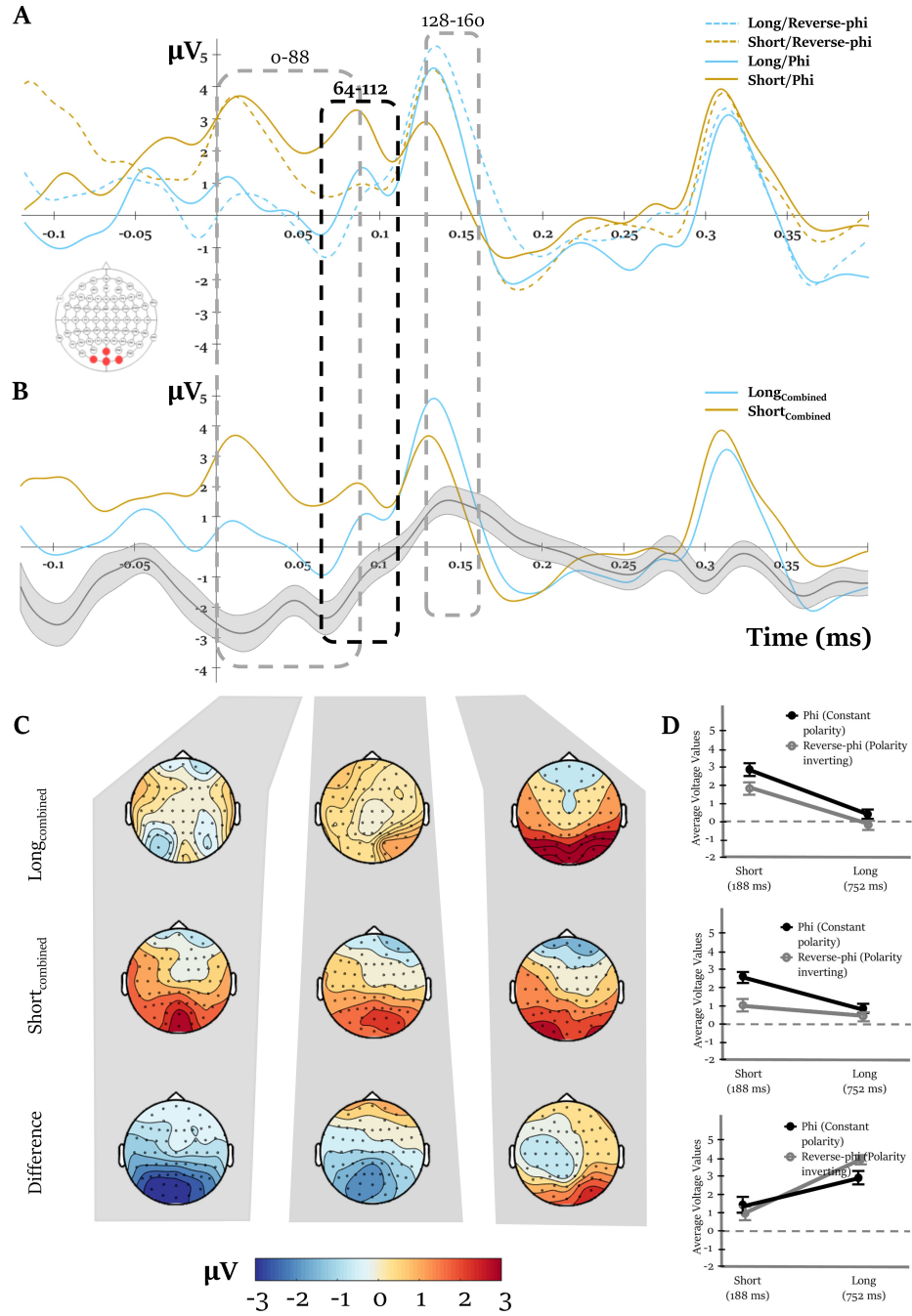


Figure 3.5: Average ERP amplitudes (N=24). A. All 4 conditions are plotted. B. ERPs for *long_{combined}* vs *short_{combined}* conditions are shown. The grey line indicates the difference values between the conditions and grey shaded region indicates the standard error across observers. C. Topographical plots of *long_{combined}* vs *short_{combined}* conditions and difference distributions are plotted for three significant intervals. D. Average voltages for all 4 conditions are shown with corresponding error bars for all three intervals (top: 0-88 ms, middle: 64-112 ms, bottom: 128-160 ms)

Table 3.1: The results of the repeated measures ANOVA for the occipital ROI. The values of each time window are grouped in separate rows. For each time window, the comparison of combined potentials across duration (long vs short) is shown first. Then, the statistical results comparing type (constant polarity vs polarity inverting) and the two-way interactions are shown in the following rows. Significant p values ($p < .05$) are highlighted in bold.

	F	p	η^2	MSE (μV)
0-88 ms				
Duration	19.972	<0.001	0.465	5.642
Type	3.963	0.059	0.147	3.545
Interaction	0.82	0.375	0.034	2.718
64-112 ms				
Duration	5.024	0.035	0.179	5.259
Type	5.279	0.032	0.187	3.808
Interaction	2.001	0.171	0.08	8.808
128-160 ms				
Duration	9.891	0.005	0.301	4.68
Type	10.773	0.003	0.319	4.12
Interaction	0.135	0.717	0.006	0.459

not significant, another notable pattern of activity within these intervals is the overall increment in the activity when the phi adaptation is utilized vs. reverse-phi adaptation.

Topographical maps (Fig. 3.5.C) demonstrate the voltage distribution across all electrode locations. Evidently, *short_{combined}* condition is more positive at the occipital sites than the *long_{combined}* condition within the first 112 ms envelope, which is attributed to visual processes. Difference distributions portray more negativity within the earliest time period followed by a gradual increment in the occipital ROI.

Fig. 3.5.D. indicates mean values for the four conditions (i.e., short directional, short counterphase, long directional, long counterphase). Intervals identified by

FDR corrected t tests show duration differences. In order to examine whether any type differences occur within the intervals, repeated measures ANOVA was performed (Table 3.1.). Duration differences can be seen in all three time windows however, type differences were observed within the predetermined 64-112 ms interval along with 128–160 ms time interval.

3.7.2 *Long_{phi}* vs *Long_{reverse-phi}* Comparison

Based on the behavioral data, ERP differences on *long_{phi}* vs *long_{reverse-phi}* were also examined. The t-tests were performed within the first 400 ms. Four occipital electrodes (i.e. *O1*, *O2*, *Oz*, *POz*) were analyzed. For illustrative purposes, ERPs were plotted (see Fig. 3.6C)

One main window between 152-184 ms is identified as a result of the pairwise t-tests ($p < 0.05$, FDR corrected). ERP plot in fig. 3.6.A. elicited a positive peak around 130 ms. The lack of a C1 peak on the difference between *long_{phi}* and *long_{reverse-phi}* condition is notable. Also, *long_{phi}* vs *long_{reverse-phi}* conditions were compared within the pre-determined time window (64-112 ms), and no significant difference was found between the conditions in this interval. However, repeated measures ANOVA analyses suggest a main effect of adaptation type for 64-112 ms (Table 3.1.). Therefore, a difference in the *short_{phi}* vs *short_{reverse-phi}* ought to be present. Overall these results infer to a difference between *short_{phi}* vs *short_{reverse-phi}*. Behavioral difference seen in *long_{phi}* condition was overall more negatively distributed than the *long_{reverse-phi}* condition within 152-184 ms. Topographical plots showed that the difference between the conditions were apparent over the occipital sites around 152-164 ms. On the other hand, 64-112 ms time interval elicited a more intermixed distribution. While overall voltage values for *long_{phi}* condition showed decreased response as opposed to *long_{reverse-phi}* condition within 64-112 ms interval, it was the other way around within 152-184 ms interval.

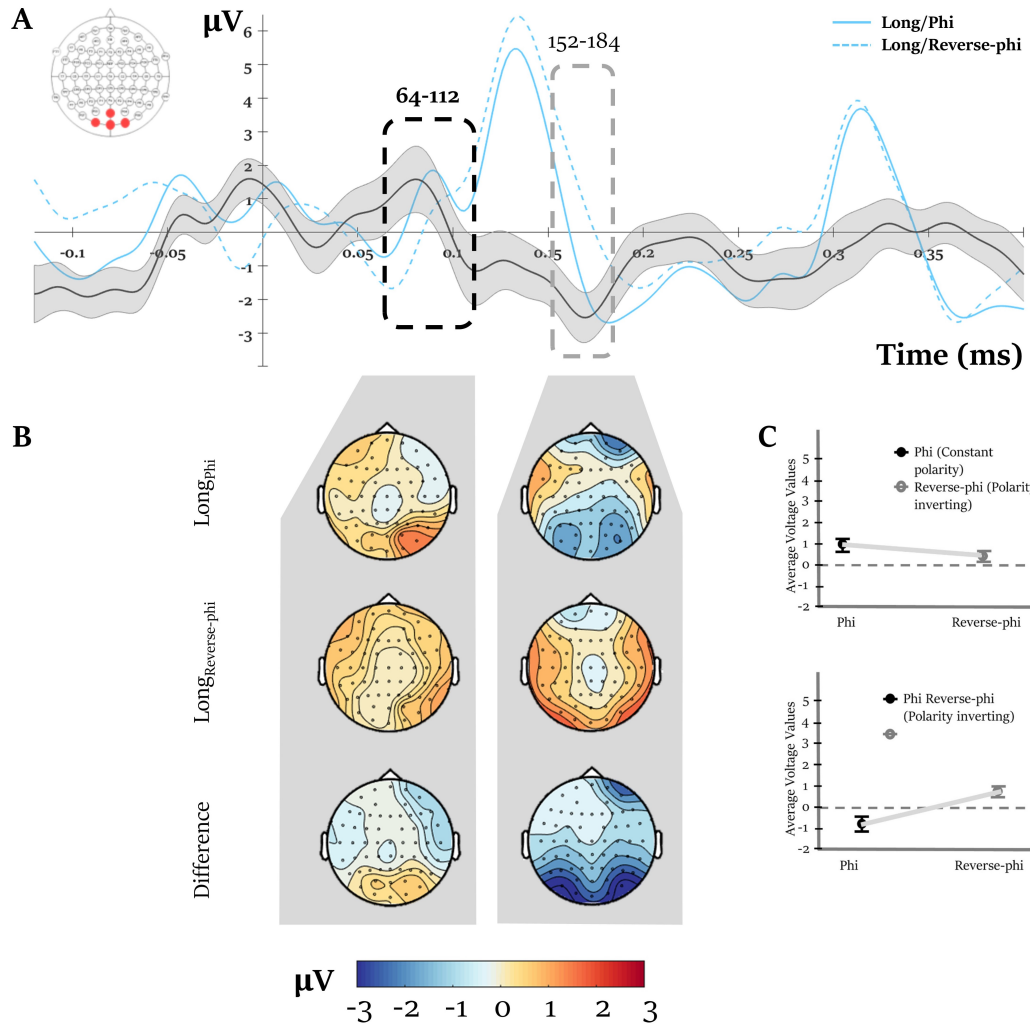


Figure 3.6: ERP results for $long_{phi}$ vs $long_{reverse-phi}$ comparison. A. ERPs for $long_{phi}$ vs $long_{reverse-phi}$ conditions are shown. Grey line indicates the difference values between these conditions and grey shaded region indicates the standard error. B. Topographical plots of $long_{phi}$ vs $long_{reverse-phi}$ conditions and difference distributions are plotted for three intervals. C. Average voltages for all 4 conditions were shown with corresponding error bars for all three intervals.

3.7.3 $\phi_{combined}$ vs $Reverse - \phi_{combined}$ Comparison

A comparison between $\phi_{combined}$ vs $reverse - \phi_{combined}$ was conducted regardless of the behavioral results (i.e., as a planned contrast). Since there was a behavioral difference between $long_{\phi}$ vs $long_{reverse-\phi}$ conditions and significant main effect of type within 64-112 ms and 128-160 ms in Table 3.1., a more scrutinized ERP analyses between the $\phi_{combined}$ and $reverse - \phi_{combined}$ conditions would be more reassuring. Nonetheless, an FDR corrected t-test on the average ERPs across all selected occipital ROI electrodes (Fig. 3.7) pointed out differences between $\phi_{combined}$ and $reverse - \phi_{combined}$ conditions within the 68-98 ms and 130-166 ms time window.

The differences between $\phi_{combined}$ and $reverse - \phi_{combined}$ conditions were also seen within 72-100 and 132-158 ms over parietal ROI electrodes (Fig. 3.8.).

These results are consistent with the repeated measures ANOVA tests (Table 3.1.). ANOVA results also suggest a type difference around similar intervals for the occipital ROI electrodes. A second significant time window on Figs. 3.7. and 3.8. are alike with the difference seen between $long_{\phi}$ vs $long_{reverse-\phi}$ comparison plotted on Fig 3.6.

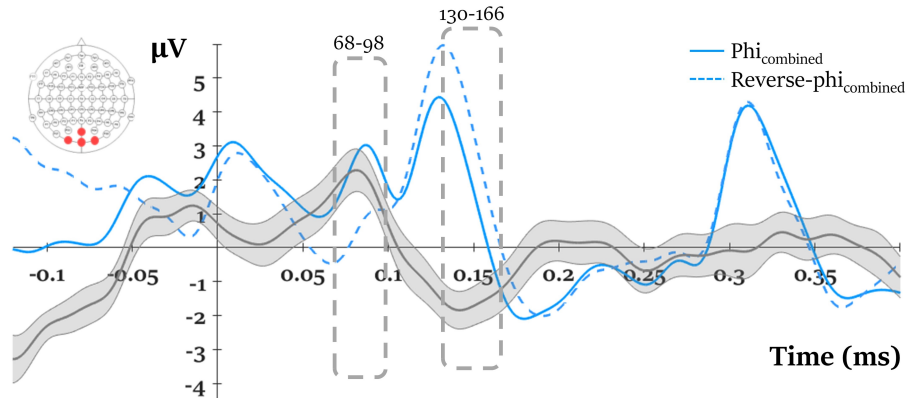


Figure 3.7: ERP results for $\phi_{combined}$ vs $reverse - \phi_{combined}$ comparison over V1 electrodes ($O1, O2, Oz, POz$). The grey curve indicates the difference values between the conditions and grey shaded region indicates the standard error.

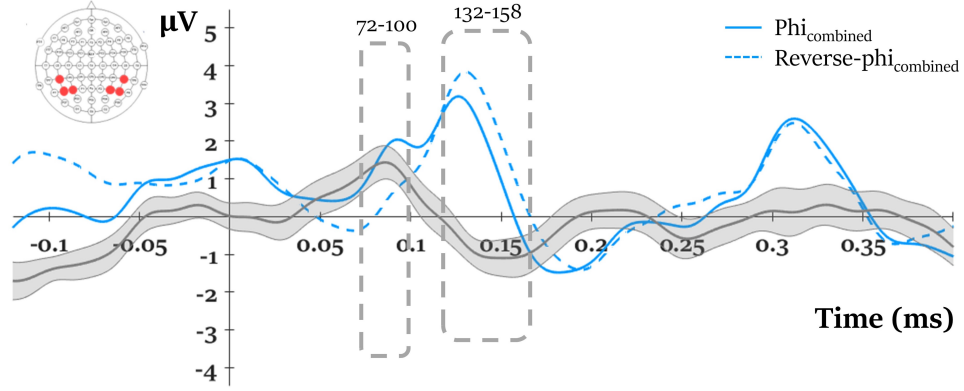


Figure 3.8: ERP results for $\phi_{combined}$ vs $reverse - \phi_{combined}$ comparison over MT electrodes ($CP5, CP6, P5, P6, P3, P4$). The grey curve indicates the difference values between the conditions and grey shaded region indicates the standard error.

Given the type differences based on ANOVA results on table 3.1., it can be concluded that type differences emerge from short adaptation that appear around 64-112 whereas differences emerge from long adaptation appear around 130-166 ms.

3.8 Discussion

This experiment investigated the short-term adaptation effects of phi and reverse-phi motion on the perception of a directionally ambiguous moving pattern. The purpose of the study was to examine how ON and OFF pathways operate at the initial stages of visual processing. Some of the previous studies suggested that the two pathways remain segregated until the initial motion detecting sites [152, 153] while others suggested that they merged as early as V1 [213, 151, 209, 19, 219]. In this study, the aim was to investigate the EEG correlates of within and across pathway interactions within the context of rapid motion aftereffect. Same (phi; either dark or bright stimulus) and different (reverse-phi; both dark and bright stimulus) polarities were presented to induce within and across pathway activation, respectively. In the end, both behavioral and EEG results were analyzed to

reveal the differences between these conditions.

This study is the first systematic study that investigates the EEG correlates of rapid forms of both phi and reverse-phi motion adaptations. A robust main effect of adaptation duration was the main remark of the experiment. Both *long_{phi}* and *long_{reverse-phi}* adapters in this study proved to result in aftereffects on a directionally ambiguous test stimulus. However, when both adaptation types were presented for a short temporal interval (188 ms), the motion aftereffect was at chance level. As shown in Fig. 3.4, a slight difference was notable between the *long_{phi}* and *long_{reverse-phi}* conditions. A pairwise t-test returned significant results implying that both types of adaptation produced motion aftereffects on a counterphase flickering test stimulus. However, *long_{phi}* adaptation condition produced a more robust motion aftereffect compared to *short_{phi}* adaptation. This study was designed based on ref. [10]. In their study, they found a duration main effect but not a main effect of type. They also found an interaction effect between adaptation duration and type. In the present study, a robust main effect of duration was observed and no main effect of type was found likewise. Difference between the two studies was the absence of an interaction effect. Despite the absence of an interaction effect in the present study, a difference between phi and reverse-phi conditions emerged at long duration. After *long_{phi}* adaptation (640 ms) with a 120 ms ISI, a strong MAE was seen and *short_{phi}* adaptation (160 ms) resulted in chance level responses [8] as it did in this experiment. In terms of duration differences, this study is consistent with the first experiment in this thesis (see post-hoc comparisons).

EEG results provided support for the behavioral data such that *long_{combined}* vs *short_{combined}* comparison provided significant differences in two main intervals. Raw ERPs elicited a difference around C1 and a peak around 130 ms (P1) was also observed. A more increased activation through the first significant (0-88 ms) and the pre-determined (64-112 ms) interval is seen in the ERP responses however, a later time range (128-160 ms) seems to elicit a switch in the activity over primary visual areas. In this study, a difference between *long_{combined}* and *short_{combined}* conditions was observed over the primary visual areas within the C1 range. This difference was in line with the behavioral results. In other words,

long and short adaptation differences were evident within C1 and whether short or long duration was used can be predicted by looking at the averaged evoked potential patterns on the test stimulus. This result is consistent with the results presented in Chapter 2 where a difference between long and short duration was demonstrated around 64-112 ms. Both behavioral and EEG data suggest that temporal component of the adaptation is critical with respect to perception of the test stimulus that activates same or different polarity pathways. These results could portray the underlying pattern regarding the difference between long and short conditions. In the additional analyses of Chapter 2, a difference between *long_{combined}* vs *short_{combined}* comparison was seen between 10-75 ms interval. Duration-wise differences from this chapter is also consistent with the *long_{combined}* vs *short_{combined}* comparison found in the previous chapter; both providing evidence for a C1 component difference for combined duration-wise comparisons. Topographical plots also show similar activation patterns for C1 component when *long_{combined}* vs *short_{combined}* differences are plotted. Both studies show a negative voltage distribution for *long_{combined}* and *short_{combined}* comparisons.

Based on the behavioral results, *long_{phi}* vs *long_{reverse-phi}* comparisons were performed on the electrophysiological data as well. A difference around 152-184 ms was present on the EEG data over occipital scalp sites. A peak around P1 component was present in both conditions. Nonetheless, voltage values of *long_{reverse-phi}* condition were overall diminished as opposed to *long_{phi}* condition within the 64-112 ms interval (Fig. 3.6A), whereas the pattern was reversed within 152-184 ms. Also, topographical distributions look rather intermixed within 64-112 ms (Fig. 3.6.B.) and this is perhaps due to the inconsistent ERP activity pattern. Inducing same polarity pathway for adaptation and test in the long condition resulted in a more robust perception of aftereffect behaviorally, and topographical distributions also point at a more negative distribution on *long_{phi}* than *long_{reverse-phi}*. Inducing same polarity pathways in long adaptation condition proved more effective in this study in terms of MAE perception.

In order to examine type differences within the specified intervals, ANOVA analyses were performed. ANOVA results within 64-112 ms and 128-160 ms indicates a main effect of type. This difference is not present in the behavioral

results in the form of a main effect however, electrophysiological evidence is quite robust. Following additional ERP analyses (Fig. 3.7.) on $\phi_{combined}$ (constant polarity) and $reverse - \phi_{combined}$ (polarity inverting) conditions, a difference around C1 component along with a difference around the P1 range emerged at early visual sites. These results provide support for the main effect of type observed on the ANOVA analyses (Table 3.1.). A behavioral main effect of type is absent in the study however a difference between ϕ and $reverse-\phi$ was seen in longer durations. Nonetheless, short duration adaptation brought the behavioral effect up to chance level. But, this overall doesn't necessarily mean that the ERP differences would not occur in early sites. The reason there is no type effect in the behavioral results might be because the pathways remain segregated up to the initial motion detection sites (hence the electrophysiological differences around the occipital and parietal ROIs), and they efficiently converge prior to the extraction of global motion signal [10, 152] therefore, the absence of a main effect of type in the behavioral results is observed. Apparently, the detection occurs in the early sites, segregation of ON and OFF pathways may be retained over the early occipital sites, therefore, the type difference is still seen on the ERPs but perhaps this difference persists until the global motion signal is extracted. Therefore, when the adaptation duration is very short, further discriminatory processes are affected, resulting in chance level behavioral performance.

$\phi_{combined}$ vs $reverse - \phi_{combined}$ difference seen on the EEG data could be due to same or across pathway activation induced by ϕ or $reverse-\phi$ adaptation. An initial N1 followed by a P1 peak around 250 ms was shown [220]. In their study, they adapted observers to ON and tested with OFF test stimulus and vice versa. They investigated aftereffects on the evoked potentials to the test stimulus. The cross polarity adaptation conditions (ON-OFF or OFF-ON), which are suggested to engage cortical interactions between ON and OFF pathways, revealed distinct changes in the evoked activities (up to 300 ms over occipital sites) compared to the same polarity conditions (ON-ON or OFF-OFF). The differences seen within the two main windows on Figs. 3.7 and 3.8 could be arising from similar ON-OFF channel dynamics. In combination with the observations in differences in ref. [220], the differences in this study between $\phi_{combined}$ and

reverse – *phi*_{combined} conditions over the occipital and parietal ROI electrodes emphasize that across pathway mechanisms have distinct characteristics and can be reflected by the cortical activity over scalp sites corresponding to the low-level visual areas.

According to the ERP plots, the duration differences (Fig. 3.5.A: *long*_{combined} vs *short*_{combined}) emerge before the type differences (Figs. 3.6, 3.7, 3.8: *phi*_{combined} vs *reverse* – *phi*_{combined}). The timeline from this study suggests that over the occipital ROI, the duration dependent differences emerge on the ERPs first, followed by type related differences, both to be terminated around 184 ms.

Chapter 4

Probing ON and OFF Pathway Interactions Via Rapid Visual Motion Priming

In this chapter, a replication of the Experiment 2 from ref. [10] was employed to examine the EEG correlates of rapid Visual Motion Priming (VMP). An ISI of 35 and, long (752 ms) or short (188 ms) duration conditions were adopted [8, 10] studies.

To engage within (i.e. ON or OFF) or across (ON and OFF) pathways, phi and reverse-phi adapters were utilized. Reverse-phi adaptation was expected to show a more robust effect in this experiment since a contrast inverting test stimulus was used. The results showed that, short (188 ms) adaptation caused VMP as in [10]; however, long (752 ms) adaptation caused MAE here, contrary to their chance level results. Adaptation type did not lead to significant alterations in this experiment as well. In addition, robust ERP differences were observed within the C1 component between long and short combined waveforms suggesting a strong duration effect. Further ANOVA analyses indicated that type differences were observed within C1. These findings also point out to efficient convergence and integration of the ON and OFF pathways right before the extraction of the motion

signal as in Chapter 3.

When the results of short conditions from Chapters 3 and 4 were compared, a reversal of motion direction with short adaptation was observed. Behavioral comparison between *short_{combined}* conditions did not suggest a significant main effect of adaptation type or an interaction effect. A shift from chance level performance to VMP responses could be due to; 1) the test stimulus, 2) ISI 3) an interaction between these experimental factors. While the information acquired from short comparison results is limited, the ISI is perhaps a more plausible candidate as the reason for these VMP differences. Moreover, the long adaptation led to MAE in both Chapters 3 and 4 even though a different type of test stimulus was used. If the test type had been the major contributor to the differences in the short comparison, the long adaptation duration would have led to different responses in Chapter 3 than in 4. Additionally, the duration differences in the C1 range was evident over occipital ROIs. The short adaptation results from Chapters 3 and 4 showed no difference until late P1. This study is complementary to Chapter 3 suggesting a duration-wise behavioral and ERP differences. Both chapters also are in agreement in behavioral and ERP results in terms of type differences.

4.1 Introduction

4.1.1 Rapid Visual Motion Priming

In addition to the inhibitory effects of adaptation, the facilitatory effects have also been observed under certain conditions [48]. A facilitatory effect of the adapting stimuli on the test stimuli lasting for hundreds of milliseconds was described [141]. They termed it VMP. It was shown that a perceptual bias of the perception of the test stimulus towards the same direction of the adaptation pattern (visual motion priming, VMP) [137]. A response increment in response to prior stimulation has also been shown [47]. It was shown that a VMP perception can be elicited with either small ISIs (e.g., 35 ms) or very large ISIs (e.g., 2 seconds) [8]. In another

similar study, it was shown that shorter ISIs such as 35 and 121 ms were more effective in producing VMP [10].

VMP has tuning characteristics. For instance, motion priming is present for both first- and second-order motion adaptations [221]. In the study, they suggest that both levels of motion processing retain retinotopic organization passed MT but earlier than the area MST. Also, it was shown that VMP was able to sustain for hundreds of milliseconds, and the VMP magnitude reached a maximum when the shift was 90 degrees [141]. Short adaptation durations (80 ms, 160 ms, 320 ms, 640 ms) were used and the ISI was manipulated between 40 ms and 2 s [8]. Brief adaptation durations (80, 160 ms) combined with a short ISI (40, 120 ms) resulted in a priming effect. Similar priming was observed for a relatively longer adaptation duration (e.g., 320 ms) with an ISI higher than 2 s.

Based on the findings of ref. [8] and ref. [10], an ISI of 35 ms was employed in this experiment to induce an optimal rapid priming effect. ISI was then followed by a contrast polarity by changing test stimulus to reverse the effect. Normally, a setup with constant contrast test stimulus suggests that both phi and reverse-phi adaptations would induce an aftereffect with long (752 ms) adaptation and, the aftereffect would typically be around chance level performance with short (188 ms) adaptation [10]. They also showed that both phi and reverse-phi adapters elicit aftereffects on a constant contrast test stimulus (without a polarity change) when the adaptation duration is around 752 ms. As the adaptation duration was decreased, aftereffects were lost. On the other hand, both adapters led to priming on a contrast inverting test stimulus (with polarity reversal) and, this effect was only present at short adaptation durations. Here, the consequences of a polarity reversal in the test stimulus were examined along with the comparison of short adaptation results between Chapters 3 and 4. In addition to behavioral comparisons, the spatiotemporal differences in the EEG activity were investigated between long and short duration conditions as well as phi and reverse-phi type conditions. Type differences will also be addressed in order to address whether the information provided by two pathways merge and across pathway mechanisms has distinct characteristics. If the two major pathways remain segregated until right before producing the motion signal, then a difference in behavioral and

neurophysiological data would occur. In addition, reverse-phi adaptation should dominate the VMP effect since a contrast inverting test stimulus is used here. Two major questions, duration and type differences, will be investigated in this chapter. Additionally, a comparison between Chapter 3 and 4 will be explored.

4.2 Methods

All procedures and protocols of this experiment were the same as those in Chapter 3 except for changes in the test stimulation. Behavioral and EEG data were collected in the same testing room and the environmental conditions were identical to those of the experiment in Chapter 3.

4.2.1 Recruitment of Participants

The participants from the Chapter 3 took part in this experiment as well. They were instructed accordingly before the start of the experiment. Participants were eliminated according to their behavioral performance as described in Chapter 3. After this behavioral screening, 6 participants were eliminated due to insufficient priming responses providing a different set of subjects to remain in the subject pool. After the objective elimination steps, 24 participants (14 females, aged between 18-32) remained for the analyses.

4.2.2 Apparatus

The apparatus was the same as those used in the previous experiments (Chapters 2 and 3).

4.2.3 Stimuli

The adaptation and test stimuli were the same as those in the previous experiment described in Chapter 3. However, the contrast polarity reversed within each spatial displacement and motion frame (i.e., 94 ms) in the test stimulus. The period of reversal (i.e., a 180-degree phase shift) was 188 ms (Fig 4.1.). An ISI of 35 ms was used in this experiment.

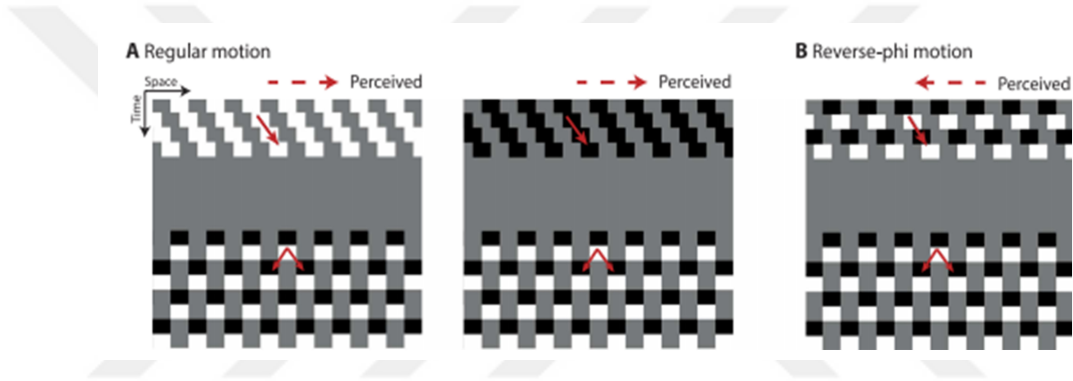


Figure 4.1: The spatiotemporal profile of adapters and test stimuli. Horizontal axes correspond to space, and vertical axes correspond to time domain. In the adaptation stimulus, each flip was presented for 94 ms, shifted for 90° to the left or the right on the horizontal axis. In each flip, which lasted for 188 ms, the test stimulus reversed its polarity every 94 ms and, shifted by 180° , and, the gratings were either lighter or darker than the background. A. There was no polarity change for phi adaptation. B. Polarity alternated between dark and light for reverse-phi adaptation. Adapted with permission from SpringerNature, ref. [10].

4.2.4 Procedure

The procedure was the same as those described in Chapter 3 (Fig 4.2), except a 35 ms ISI was used to have an optimum rapid priming effect [10].

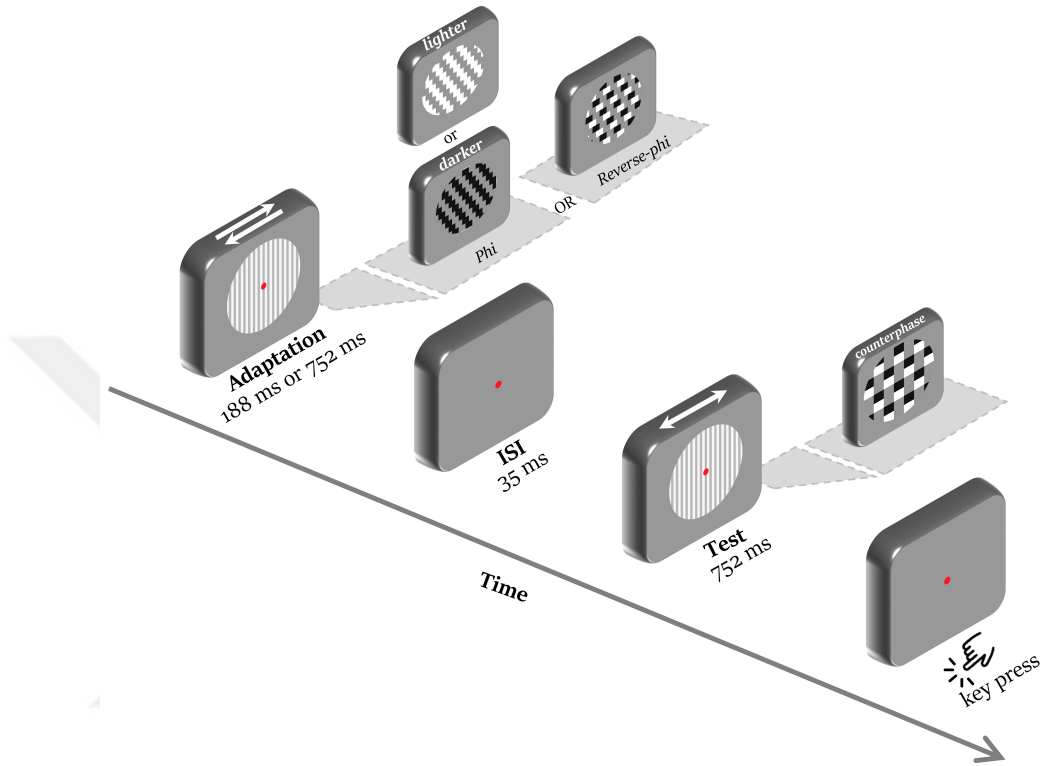


Figure 4.2: Schematic representation of the experimental design. On each trial, an adaptation stimulus was followed by a blank interval and a test stimulus. Two motion types were used as adapters (i.e. phi or reverse-phi). Square-wave gratings were used. Phi gratings were either darker or lighter than the background. For the reverse-phi adaptation, the contrast polarity was reversed on each motion frame, and the initial contrast polarity was randomly selected. Long (752 ms) and short (188 ms) adaptation duration conditions were used. The test stimulus was always displayed for 752 ms.

4.2.5 EEG Data Acquisition, Preprocessing and Analyses

The conventions were the same those as in Chapters 2 and 3. Average trial number remained after preprocessing of the EEG data was 85%. The ERP analyses were performed to examine voltage changes as a function of time over designated electrodes (from Chapter 2). Significant windows were identified based on FDR corrected t-tests. The voltage values were averaged occipital ROI for long and

short conditions to obtain $long_{combined}$ and $short_{combined}$ matrices. Same analyses performed in Chapter 3 were performed in this chapter as well. Looking at the FDR corrected t statistics, significant time frames were identified. Analyses were separately performed to compare the short conditions on the participants who were not eliminated from either experiments in Chapters 3 or 4. The results were presented in separate subsections below.

4.3 Behavioral Results

Fig. 4.3. shows the percentages of expected directions for phi and reverse-phi conditions. The values for phi and reverse-phi were indicate a motion percept in the same and opposite the direction of physical displacement, respectively. The proportion in which participants perceived phi motion moving in the same direction as the physical displacement was 98.67% with a standard deviation of 0.77, a minimum of 85% and a maximum of 100%. The reverse-phi motion resulted in a mean percentage of 83.88% reported in the opposite direction, a standard deviation of 6.68, a minimum of 75% and a maximum of 96.66% (Fig. 4.3A).

A two-way repeated-measures ANOVA with the adaptation type and duration condition as factors were performed (Fig. 4.3.B). There was a significant main effect of adaptation duration ($F_{1,23} = 138.156, p < 0.0001, \eta_p^2 = 0.857$). However, a non-significant main effect of adaptation type ($F_{1,23} = 0.018, p = 0.89, \eta_p^2 = 0.001$) and two-way interaction ($F_{1,23} = 0.447, p = 0.51, \eta_p^2 = 0.019$) were reported.

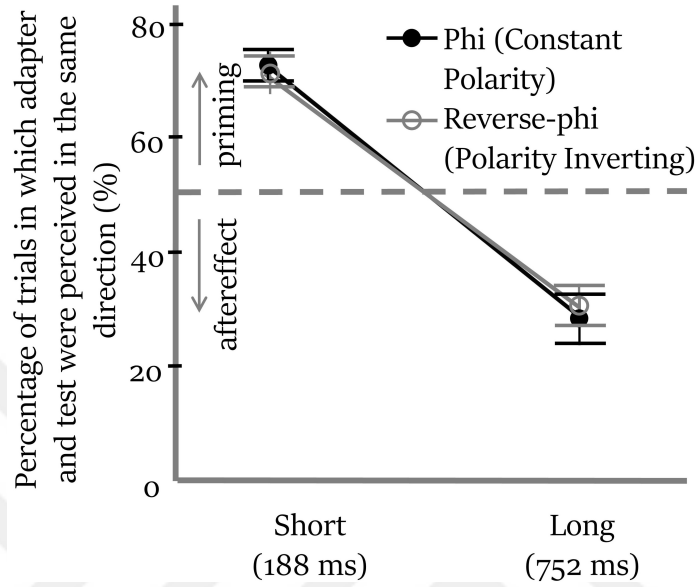


Figure 4.3: The plot the behavioral results of adaptation experiment are shown (N=24). For each adaptation duration, the percentage of trials in which participants judged both the adapter and the test stimulus moving in the same direction is plotted as a function of stimulus duration. Error bars represent (± 1 SEM).

4.4 EEG Results

The ERP analyses were performed and plotted in accordance with the significant effects reported in the behavioral results (Fig. 4.4).

4.4.1 $Long_{combined}$ vs $Short_{combined}$ Comparison (N=24)

FDR corrected running t-tests were performed across $long_{combined}$ and $short_{combined}$ conditions. A difference between 0-110 ms and 334-352 ms was evident between the conditions ($p < 0.05$, FDR corrected). All 4 conditions were plotted in Fig. 4.4.A. Combined values were plotted in Fig 4.4.B. All ERPs seem to peak around 110-120 ms range (P1). A continuous difference for 20 ms between the conditions was observed including the pre-determined time window (64-112 ms from Chapter 2), confirming the robust duration-wise differences within that interval. Additionally, both combined conditions showed a trough around 65 ms.

The differences were mainly within the C1 component range.

Topographical plots showed that long adaptation caused less negativity than short adaptation during the presentation of test stimulus within the first significant time frame (0-110 ms). Similar activity profiles were observed for 64-112 ms and 334-352 ms time intervals. In agreement with Chapter 3 results, a strong positivity of *short_{combined}* condition within C1 was mainly present over occipital and parieto-occipital sites. Topographical plots also indicated similar distributions within C1 for *long_{combined}* vs *short_{combined}* conditions in comparison with the Chapter 3 results. Also, as in Chapter 3, the mean voltage values within the significant and the predetermined time windows (Fig 4.4.D) were similar for all 4 conditions within the C1 range.

According to the mean (average) potentials within all time windows, the reverse-phi adaptation caused a more negative activation than the phi adaptation. This difference was seen between long and short conditions within both significant time frames (i.e. 0-110 ms, 334-352 ms) displayed on Fig. 4.4.D. Phi adaptation seems to induce a more positivity within all the time windows except the long condition within 334-352 ms.

To further examine any type effects, repeated measures ANOVA results for *long_{phi}*, *short_{phi}*, *long_{reverse-phi}*, and *short_{reverse-phi}* comparison within three time windows (including the predetermined time window) are shown on Table 4.1. ANOVA statistics can be found on the respective rows. First and second rows show main effects and the third row within each group shows the interaction effect results. Aside from duration differences observed in the initial FDR corrected t tests, type wise differences are also found within C1 as well. This difference was also observed within the non-significant predetermined time window. Existing of similar differences along 0-110 and 64-112 ms is expected due to overlapping time points in each time intervals. Aside from early emerging differences, a duration difference in the 334-352 ms interval is also seen.

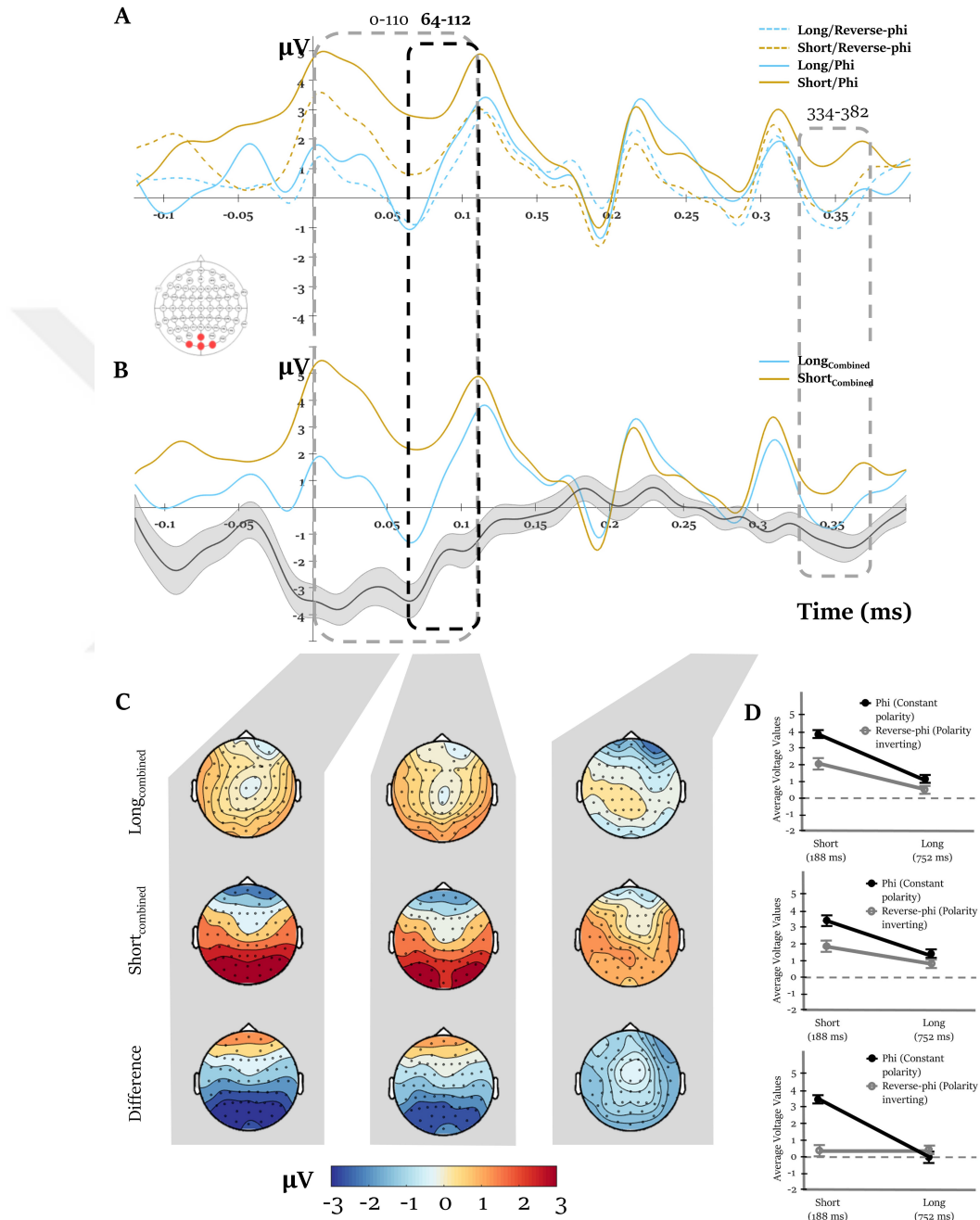


Figure 4.4: Average ERP amplitudes (N=24). A. The ERPs of all conditions are displayed. B. ERPs for *longcombined* vs *shortcombined* conditions are shown. Gray line indicates the difference values between these combined waveforms and grey shaded region indicates the standard error across observers. C. Topographical plots of *longcombined* vs *shortcombined* conditions and the distributions of difference waveform are plotted for three identified time intervals. D. Average voltages in each time interval are displayed in separate plots. Error bars correspond to (± 1 SEM).

Table 4.1: The results of the repeated measures ANOVA for the occipital ROI. The values of each time window are grouped in separate rows. For each time window, the comparison of combined potentials across durations (long vs short) is shown first. Then, the statistical results comparing type (constant polarity vs polarity inverting), and interaction results are shown in the following rows. Significant p values ($p < .05$) are highlighted in bold.

	F	p	η^2	MSE (μV)
0-110 ms				
Duration	28.899	<0.001	0.557	3.803
Type	9.307	0.006	0.288	3.148
Interaction	4.192	0.154	0.154	2.207
64-112 ms				
Duration	12.592	0.002	0.354	4.238
Type	10.925	0.003	0.322	2.615
Interaction	3.752	0.065	0.14	1.833
334-352 ms				
Duration	8.894	0.007	0.279	2.959
Type	3.242	0.085	0.124	3.446
Interaction	2.507	0.127	0.098	2.081

4.5 Discussion

Mounting evidence indicate that ON and OFF pathways remain mainly segregated until the primary visual cortex [19, 219]. Studies argued that this segregation persists until the early motion-detecting sites resulting in a segregated motion detector mechanism [152, 153]. Understanding the integration of the two separate streams of information is vital to grasp the underlying mechanism of motion perception. In this study, sub-second adaptation effects of phi and reverse-phi movement was examined on a test stimulus that changed its contrast polarity every 94 ms and hence engaging an interaction and spatiotemporal correlation between these pathways. This experiment is the first systematic EEG study to investigate the differences in the neural responses that rapid phi or reverse-phi motion adaptation makes on a test stimulus that changes its polarity. Since a change in polarity engages both ON and OFF pathways, polarity switch of the test stimulus was expected to reverse the direction of motion aftereffect resulting in a perception that is towards the direction of the adaptation stimulus (VMP). Our behavioural results showed only a significant main effect of adaptation duration for both motion types. Exposing the participants to longer adaptations resulted in aftereffects regardless of whether phi or reverse-phi motion was used, and priming effects by the short adaptation duration was also present for both adaptation types. Such strong priming effect is also in agreement with ref. [10]. These results suggest that adaptation duration is a more compelling factor than the motion type to elicit VMP. Long adaptation resulted in chance level responses; however, a strong aftereffect was seen in this experiment [10]. It was also found that a 640 ms phi adaptation followed by a brief ISI (40 ms, 120 ms) resulted in MAE [8]. They also showed that 160 ms adaptation (short) followed by a 121 ms ISI resulted in chance level performance (in line with the results from Chapter 3) whereas; when the ISI was reduced to 40 ms, a priming effect was seen (in line with the results from this chapter). Even though the test stimulus was a polarity inverting stimulus in this experiment, similar results to ref. [8], where a constant contrast test stimulus was used, were found. Despite the lack of type main effect in the behavioral data, a main effect of type is seen in the electrophysiological data. This means that the type of adaptation induced different activations over

the occipital ROI during the perception of the test stimulus. Inducing ON and OFF pathways vs ON or OFF pathways made a difference over the occipital sites, suggesting segregation of the pathways to some extent. In other words, adapting same or across pathways left different signatures over the occipital scalp sites.

VMP found in this chapter was stronger than it was in ref. [8] where they introduced a very similar adaptation duration and ISI (160 ms short adaptation followed by a brief 40 ms ISI). Overall, the behavioural results raise the question of whether engaging ON and OFF channels alone is sufficient enough to observe a priming effect or whether it is instead a more complicated configuration that involves multiple components that produce such modulations. In ref. [10], a main effect of duration was present however a main effect of type was not seen in the behavioral data. Results in this experiment support their findings. However, they also reported an interaction effect on the behavioral data which was not a part of the results of this experiment. In other words, the behavioral data suggests that engaging similar or different contrast polarities did not have an impact on the perception of direction that duration of the adaptation stimulus contributed much more. However, additional analyses on the electrophysiological data implies a different more elaborate underlying story about how ON and OFF pathways behave over the occipital areas (Table 4.1).

The ERPs pointed out differences around the first 110 ms (Fig 4.4.A and B). This suggests that the differences due to adaptation duration were mainly present around extrastriate areas. *Long_{combined}* vs *short_{combined}* comparison results were comparable to the experiment in Chapter 3 such that an ERP difference over occipital ROI within C1 range was observed between the conditions. Additionally, this difference endured until the early stages of P1 complementary to the results found in Chapters 2 and 3. Topographical plots (Fig. 4.4.C) show similar distribution characteristics for long and short (*long_{combined}* vs *short_{combined}*) differences within the 334-352 ms time interval as the other specified intervals; however, the latest time frame is further on the time axis. Instead, it may be attributed to discrimination mechanisms as suggested by [222].

The reverse-phi adaptation was expected to show a more prominent priming

effect on the test stimulus since both stimuli are contrast reversing stimuli. However behavioral results did not show any difference for either adaptation durations. On the other hand, ERP comparison of constant contrast polarity (within pathway) vs polarity inverting (across pathway) test provided a more comprehensive perspective about behavioral differences. Specifically, additional ANOVA analyses indicated a main effect of type within the first two specified intervals, which majorly overlap (Table 4.1.). A main effect of type on the electrophysiological data suggests that inducing same or different polarities during adaptation and test lead to differences over occipital sites. In other words, within and across pathways may operate separately and these distinct processing may be reflected by the activation difference across adapting with polarity inverting stimulus and constant polarity stimulus. However, the fact that long and short adaptation duration caused different percepts behaviourally suggests that this segregation of the two pathways does not seem to go further than the motion sensitive areas. It suggests that they merge around V5 therefore variations on the behavioral data emerge. ON and OFF signals stay segregated before the motion signal is formed. Electrophysiological data from Chapters 3 and 4 are consistent in terms of occipital scalp site activations of phi vs reverse-phi comparison. Behavioral difference caused in this study originates from the test stimulus characteristics which was set to invert its polarity every 94 ms. As a result, a VMP in the short condition is observed instead of the MAE seen in Chapter 3.

Moreover, the results here are complementary to those in Chapter 3 in terms of the significant effect of motion type in the ANOVA tables (3.1., 4.1.). Therefore, the results of this experiment also support the view that ON and OFF pathways remain segregated until the initial stages of visual processing, and they also efficiently merge at early-stages of cortical processing and hence cannot be identified by the evoked activities over visual cortex.

4.6 Differential Effects of Short-term Adaptation on Test Stimulus Types

The behavioral difference in the short conditions from Chapters 3 and 4 provide us to perform further analyses on behavioural and ERP waveforms. Therefore, additional comparisons were performed using the data of 18 common participants. Independent variables will be referred as such; 1) adapter type, 2) experiment number. Experiment number was used as an independent variable (IV) because there were two concurrent changes made in experiment 3; ISI used and test stimulus used. Therefore, an IV name of “experiment number” would be suiting for this comparison.

4.6.1 Behavioral Results

Short adaptation resulted in chance level responses in Chapter 3 whereas it resulted in priming responses in Chapter 4 (Fig. 4.5.). To examine whether this difference was significant an ANOVA (with adapter and test type as factors) was run on the results of 18 common participants who were included in both experiments. A non-significant main effect of adapter type (whether it was phi or reverse-phi adaptation) ($F_{1,17} = 0.312$, $p < 0.584$, $\eta_p^2 = 0.018$), and two-way interaction effect was observed ($F_{1,17} = 2.714$, $p < 0.118$, $\eta_p^2 = 0.138$). However, whether it was experiment 2 or 3 was significant ($F_{1,17} = 42.437$, $p < 0.0001$, $\eta_p^2 = 0.714$).

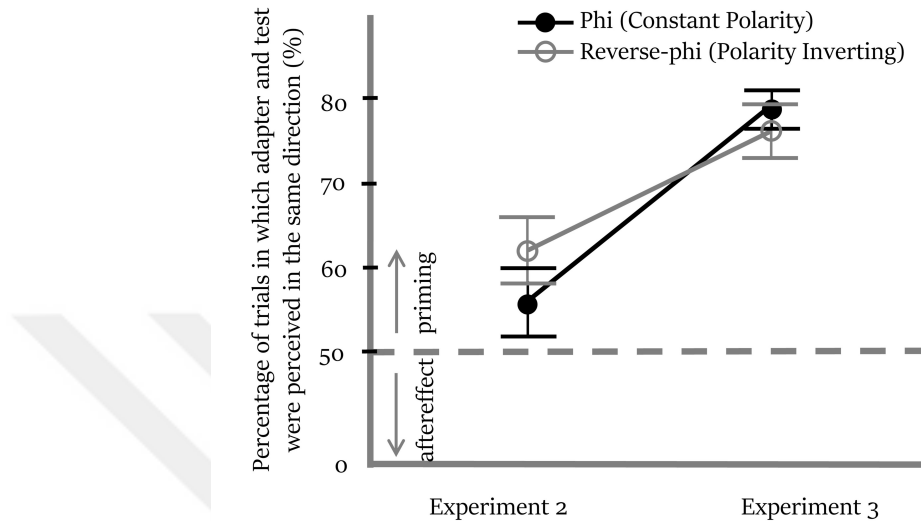


Figure 4.5: The behavioral results of short adaptation durations (N=18). For each adaptation type, the percentage of trials in which participants judged both the adapter and the test stimulus moving in the same direction is plotted as a function of experiment number (i.e experiment 2 or 3). Error bars represent (± 1 SEM).

4.6.2 EEG Results

Short conditions were higher in amplitude in the C1 range in both Chapters 3 and 4. This indicates a consistent pattern that short adaptation elicits effects on the ERPs. *Short_{combined}* conditions were obtained by averaging phi and reverse-phi conditions in both studies in Chapters 3 and 4 for 18 common participants. FDR corrected t-tests were performed, and significant time windows for at least 20 ms were; 164-184 ms, 200-244 ms and, 362-386 ms (Fig. 4.6.).

T-test results for *short_{combined}* conditions from chapter 3 and 4 are compared. Comparisons performed within four time windows (including the pre-determined time window) are shown on Table 4.2. First, a paired sample t-test was conducted across constant polarity and polarity changing conditions and the respective t statistics can be found on related rows. Second and third rows show t results when the conditions were compared to the baseline zero.

All conditions showed a peak to an extent around 100 ms. The amplitude of this peak was not the same for all conditions (Fig. 4.6.A). The averaged potentials are plotted in Fig. 4.6.B did not provide a significant difference until 154 ms. Topographical plots showed that within the predetermined time frame (64-112 ms) short conditions from both experiments elicited positive activations around occipital and parieto-occipital ROIs (Fig. 4.6.C). Consistent with the behavioral plots, the positivity observed over occipital ROIs within the predetermined time window was higher in the *short_{combined}* condition of experiment 3. Although the last two time frames are later on the time axis, they also showed similar distributions compared to earlier time windows. Fig 4.6.D. shows average voltages for 4 time intervals. The average values of phi conditions were only higher than those of the reverse-phi condition within the predetermined time frame. The rest of the ranges showed a smaller amplitude in phi conditions.

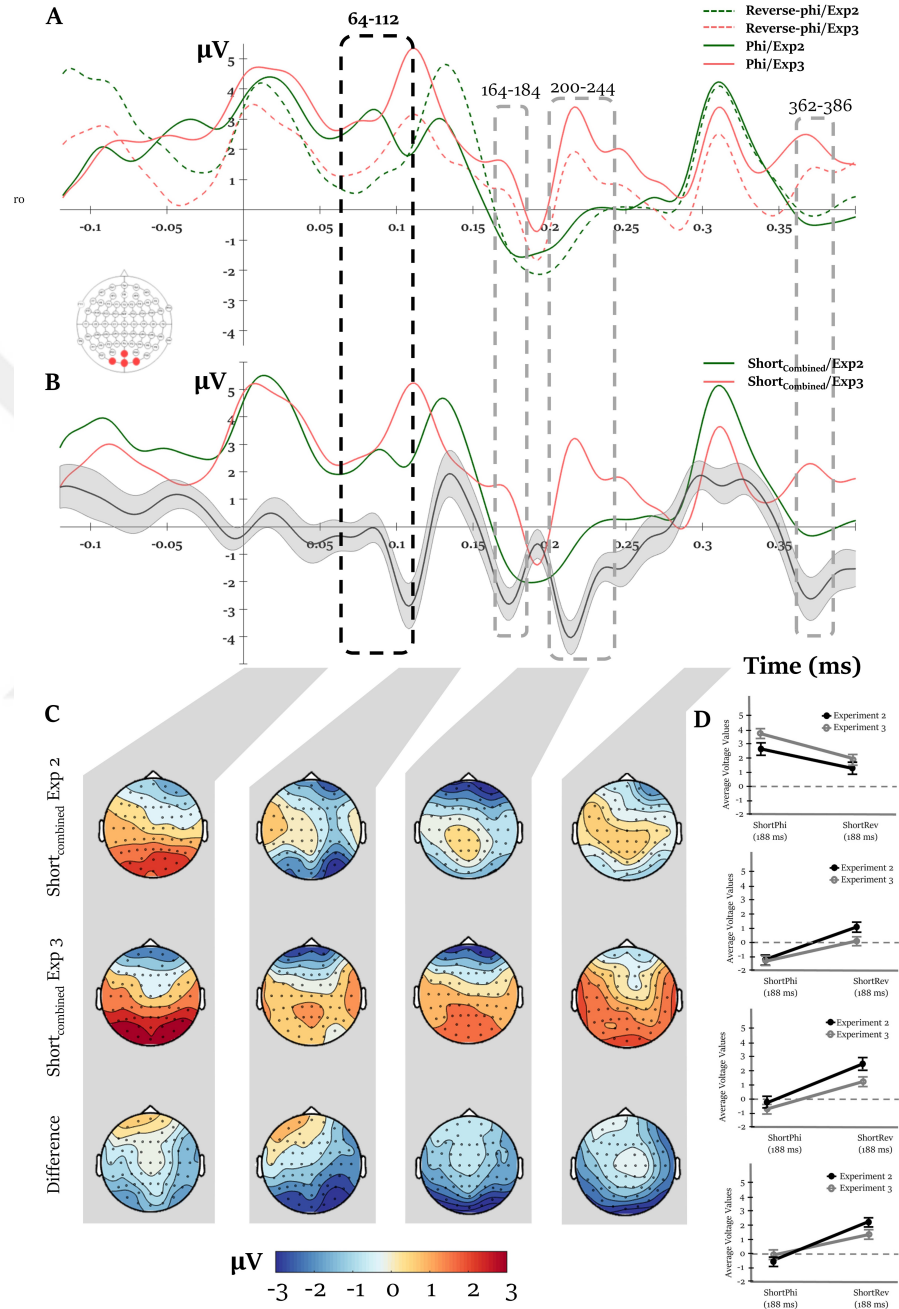


Figure 4.6: Average ERP amplitudes (N=18). A. All 4 conditions are plotted. B. ERPs for *short_{combined}* conditions from experiments 2 and 3 are shown. Gray line indicates the difference values between the conditions and grey shaded region indicates the standard error. C. Topographical plots of *short_{combined}* conditions from experiments 2 and 3 and, difference distributions are plotted for three significant intervals. D. Average voltages for all 4 conditions are shown with corresponding error bars for all three ranges.

Table 4.2: The results of the post-hoc t-tests and descriptive statistics for the occipital ROI. The values of each time window are grouped in separate rows. For each time window, the comparison of combined potentials across short conditions (*constant polarity* vs *polarity inverting*) is shown first. Then, the statistical results comparing *constant polarity* and *polarity inverting* conditions at each experiment are shown in the following rows. Significant p values ($p < .05$) are highlighted in bold

	F	p	η^2	MSE (μV)
64-112 ms				
Exp 2 or 3	4.055	0.06	0.193	4.445
Type	9.020	0.008	0.347	4.622
Interaction	0.304	0.589	0.018	0.615
164-184 ms				
Exp 2 or 3	14.287	0.001	0.457	3.913
Type	1.543	0.231	0.083	3.370
Interaction	3.752	0.422	0.038	3.669
200-244 ms				
Exp 2 or 3	31.124	<0.001	0.647	1.919
Type	4.973	0.04	0.226	1.613
Interaction	1.525	0.234	0.082	2.001
362-386 ms				
Exp 2 or 3	9.034	0.008	0.347	7.684
Type	0.244	0.627	0.014	3.084
Interaction	3.567	0.076	0.173	1.729

4.6.3 Discussion

It is important to note that short adaptation resulted in different behavioral outcomes in Chapters 3 and 4. In the short adaptation conditions, engaging ON or OFF pathways led to no aftereffect (chance level performance in Chapter 3) whereas engaging both pathways during test along with an ISI reduction led to a percept in the direction of the adapter (VMP performance in Chapter 4). According to the results here, a brief ISI along with short adaptation was also required to produce a strong VMP. A 121 ms ISI following a short-term adapter seems to create a percept in the direction of the adapter in Chapter 4 whereas no changes arise from short adaptation followed by a 121 ms ISI in Chapter 3 (chance level performance). This difference in two experiments is due to either the ISIs or the test stimuli used. One thing for sure is that no priming effect was observed in Chapter 3 but a strong priming effect was observed in Chapter 4 for the short adaptation condition. Therefore, engaging both ON and OFF channels during test is a requirement but perhaps not adequate by itself for observing a priming effect.

As mentioned above, the difference might be due to the ISI or the test stimulus used in each study. However, considering the fact that long adaptation resulted in motion aftereffect even with an ISI of 35 ms in this chapter, one should perhaps avoid assuming that the difference arises from the polarity change on the test stimulus or the ISI used. It is more likely that the adaptation duration caused the MAE in both experiments. Additionally, a significant difference seen between $long_{phi}$ and $long_{reverse-phi}$ in Chapter 3 was not seen in Chapter 4. Long adaptation caused perception of aftereffect in both experiments regardless of the ISIs or the test stimulus used. It makes sense to talk about a robust adaptation duration effect in comparing long adaptation outcomes between Chapters 3 and 4.

Another similarity between Experiments 2 (Chapter 3) and 3 (Chapter 4) was the oscillatory patterns short adaptation exhibited. Averaged short conditions from experiments 2 and 3 did not provide a significant difference until 154 ms

and this implies that short conditions exhibited similar oscillations in both experiments. In other words, short adaptation exhibits a quite consistent activity pattern that can be visibly seen by looking at its amplitude within the first 150 ms. Interestingly, the similarity in Chapter 3 where MAE was observed, *short_{combined}* condition fluctuated very similarly to the *short_{combined}* condition in Chapter 4 where a VMP perceptual effect was seen. Even though the test stimulus changed its contrast polarity and induced VMP, similar oscillatory patterns were observed until 154 ms. Looking at the difference ERP, a trough is seen around 110 ms however the FDR corrected t-tests did not return a significance for this interval. Topographical plots also show that no difference emerged at the predetermined time window (64-112 ms) because short conditions from experiments 2 and 3 were quite similar in terms of elicited activations. Further windows showed tangible differences that could perhaps be attributed to discriminatory processes.

Chapter 5

General Discussion

Our visual processes are constantly exposed to motion stimulus in our daily lives and how repetitive motion affects visual perception has been a great interest to researchers for decades. Adaptation characteristics of the stimulus (e.g., size, orientation, luminance, contrast, duration and position) have been investigated by different researchers. A substantial number of researchers have focused on the effects of duration on motion perception. In this thesis, repetitive motion is used as a tool to adapt direction selective neurons without physical interference as referred by [223]. The overall aim was to take advantage of this investigative tool to adapt motion selective cells in various conditions and probe the differences in perception while an ambiguous test stimulus was present. Specifically, the long- and short-term adaptation differences were investigated. The motion after-effects induced by different adaptation durations have been investigated by other researchers using different methodologies such as psychophysical, fMRI, intracranial EEG, TMS and MEG. A comprehensive investigation on long vs. short (i.e., rapid) adaptation was explored in this thesis via measured scalp surface electrical activity. First study investigated the difference between adaptation durations by comparing the sub- and supra-second intervals. In the second and third studies, the aftereffects or priming elicited by rapid sub-second adaptations were further examined.

Using a well-known motion adaptation paradigm, an exploratory analysis was performed in the first experiment. The main purpose was to explore where and when specifically the difference between long and short conditions emerges and form a spatio-temporal core for the induced changes. Meaningful clusters were identified based on their space and time characteristics to pinpoint the scalp sites. A secondary purpose was to utilize those designated sites to further investigate how these sites operate in conditions where constant contrast and polarity inverting stimuli are presented (Experiments 2 and 3). In these experiments, the systematic comparisons also allowed to compare within (ON or OFF) and across pathway mechanisms within the context of visual motion. Similar conventions were used for all three experiments. On each trial, an adapter was followed by an ambiguous test pattern with an ISI. The effects of adaptation duration on an ambiguous test stimulus was one of the major questions investigated through the experiments of this thesis. All three experiments highlight a major duration effect on the directionally ambiguous stimulus. Moreover, in the last two experiments, the adapter and test types were also manipulated to probe the convergence of information provided by the ON and OFF pathways in the visual system. The results of Chapter 1 are highly consistent with the existing literature, however, the main purpose of Experiment 1 exploratory cluster-based permutation tests were run for this purpose.

5.1 Duration as a Critical Factor

In all three experiments, the differences between the long and short adaptation durations were evident in both behavioral and neural responses. The long adaptation durations in all experiments led to motion aftereffects whereas the short duration in Experiment 3 led to priming. Of note, the term “long” does not correspond to exactly the same duration in Experiment 1 (Chapter 2) compared to Experiments 2 and 3 (Chapters 3 and 4). In Experiment 2, the long duration was a supra-second envelope (6.4 sec) whereas short duration was almost as close to the long conditions in Experiments 2 and 3. However, in all three experiments, adaptation durations above 640 ms led to an aftereffect. Even though the ISIs

were different in each experiment, the long adaptation condition resulted in aftereffect. Previous research indicated an increase in duration of adaptation results in stronger aftereffect [8, 10]. In combination of short ISI values, the decrease in adaptation durations can even lead to motion priming [140]. In this respect, the behavioral results of Experiments 2 and 3 are line with the previous literature. Considering the fact that a short duration in Experiment 1 roughly corresponded to long durations of Experiments 2 and 3, a MAE in the short duration of Experiment 1 is also reasonable. A duration effect on the EEG data emerged in all three experiments. Experiments 1 and 2 showed an effect of duration on the amplitudes of C1 and P1 components regardless of the test stimulus type. The scalp topographies also indicated similarities within C1. With short adaptation, while chance level behavioral performance (Fig. 3.4B) in Experiment 2 induced more positive activity to some extent (see Fig. 4.6C, first row of 64-112 ms interval), a more pronounced change was observed in Experiment 3 (see Fig. 4.6C, second row of 64-112 ms interval) where participants perceived priming. Additionally, where long adaptation was used and behavioral data suggested a MAE, topographical plots showed distributions around baseline zero for Experiments 2 (Fig. 3.5B) and 3 (Fig.4.4B), however, when the short adaptation was used, the chance level behavioral performance caused a fainter positivity (see Fig. 3.5C.) than the distributions corresponding the priming conditions (Experiment 3, Fig 4.4.C). It is also worthwhile to note that short duration of Experiment 1 and long durations of Experiments 2 and 3 led to similar oscillatory patterns that is around the baseline level within the C1 and P1 range over occipital sites, possibly due to the similar lengths in duration (i.e., 640 ms for the short condition in Experiment 1, and 752 ms for long conditions from Experiments 2 and 3).

Aside from C1 and P1 components, an additional late positive peak on the raw ERPs was observed in Experiments 2 and 3. A nicely visible positive peak around 310 ms is present over the occipital electrodes for both long and short conditions. Visual P300 is regarded as an emerging component present as discrimination processing [222]. Therefore, this common P3 peak can be interpreted as the process of discrimination of the stimulus.

All three experiments highlight a major consistent finding electrophysiologically: raw long condition is more negative than the short condition around the first 120 ms in over primary visual areas including motion detection sites. This is in line with the basic descriptions of motion adaptation in the literature [41, 43, 42]. They showed that motion selective cells initially increased their firing rate to a motion stimulus but then constant exposure to motion decreased their firing rates. In all three studies of this thesis, exposure to a motion stimulus for longer durations resulted in lower average voltage values than shorter durations over occipital and parietal sites around within the first 100 ms. Moreover, the behavioral results of Experiments 2 and 3 are highly consistent with ref. [8]. They found that with an ISI of 120 ms, long adaptation resulted in MAE while, short adaptation resulted in chance level responses; with an ISI of 40 ms, long adaptation returned strong MAE responses while it returned VMP responses.

5.2 Where ON and OFF Pathways Meet

In Experiments 2 and 3, a similar design to that of ref. [10] was employed to assess the characteristics of information processing within and across ON-OFF pathways. In both experiments, phi and reverse-phi motions were used as adapters. However, Experiment 2 included an ambiguous counterphase flickering test pattern engaging either ON or OFF pathway while Experiment 3 included an ambiguous test pattern engaging both the interactions between ON and OFF pathways by having polarity reversal in each frame. In both Experiments 2, the reverse-phi motion elicited effects comparable to regular phi motion, suggesting that it is processed as the regular motion and can alter the perception of a subsequently presented ambiguous stimulus. This highlights efficient convergence (i.e., interaction) of information provided by ON and OFF pathways.

A robust effect of duration is also notable in these experiments such that, long adaptation duration dominated the motion (adapter) type on the behavioral output. Electrophysiological data provided more insight into the progression of the information through within (ON or OFF) and across (ON and OFF) pathways.

Even though there were not any type differences on the behavioral data, the main effect of adapter type was present in both experiments within C1 (Experiments 2 and 3) and P1 (Experiment 3). This information provides insights about how within and across pathways work. A difference in the activation within C1 and P1 range suggests that within and across pathways remain segregated before forming a net motion signal. This information is consistent with the view that suggesting some distinct characteristics of each motion type [152, 153, 10]. It is also important to note that both experiments show distinct activation patterns for the duration and type on the electrophysiological data.

In the behavioral results, phi and reverse-phi adaptation showed similar sensitivities [151] resulting in similar strength on the behavioral output. However electrophysiological data suggested that type-wise differences emerged around occipital and parietal ROIs for both of the experiments. Behavioral data also suggested a similar pattern as in ref. [10]. However, Experiments 2 and 3 suggested that across pathway motion processing may have distinct characteristics. These results are also consistent with the previous findings of ref. [224] where the strength of reverse-phi motion adaptation was shown to be weaker with respect to phi adaptation.

It is important to note that short adaptation resulted in different outcomes in Experiment 2 than in 3. After short adaptation, engaging either ON or OFF pathway during the test phase resulted in no bias however, engaging both pathways and the interactions between them through test stimulation caused perception to be biased in the direction of the adaptation stimulus. In other words, in order to perceive the priming effect, one needs to have been adapted from a short adapting stimulus so that the contrast reversing test stimulus can switch the perception of the motion aftereffect to motion priming. A biasing effect from short adaptation seems to be present in the third experiment whereas no biases arise from short adaptation in Experiment 2. This small difference between the two experiments can be attributed to the ISI or the test stimulus used. One thing for sure is that no priming effect was observed in Experiment 2 but a strong priming effect was observed in Experiment 3 with short adaptation so, engaging both ON and OFF channels within the test stimulus may be a requirement but not enough by itself

for producing a priming effect.

5.3 Future Directions

This thesis highlights the crucial role of adaptation duration on the subsequent directionally ambiguous test pattern, and that distinct characteristics of across pathway mechanisms. In order to arrive at a more definitive conclusion about the extent to which the ISI or the adaptation type contributes in reversing the sign of the motion direction, a control experiment with two ISIs (35 ms and 121 ms), three adaptation durations (80 ms, 376 ms, 752 ms based on ref. [8] and two adaptation types (phi and reverse-phi) can be employed using the same paradigm. Main reason for selecting the two ISI durations and 3 adaptation durations is based on the results from the ref. [10]. Robust MAE was seen at 121 ms whereas the strongest priming effect was seen at 35 ms. The three adaptation durations would also provide information about a transition in the spatiotemporal profile. Also in Experiment 2, short adaptation duration returned chance level performances therefore prolonging the duration to an extent that will lead to MAE in phi and reverse-phi conditions would be proper.

Aside from the changes in the ISI used, different results arose when they provided a third option to participants [144]. It would be interesting to see how the responses would change when the participants were presented with an option that indicates the perception of no net motion, where any trial dismissed would be presented again until they complete a specific number of trials per condition. Variations - or no variations- on the electrophysiological data would provide a better and precise interpretation of the components that emerge around the occipital sites. Through this way, the disadvantage of forced-choice which enforces participants to indicate a motion direction even on the trials they do not perceive a motion direction would be avoided. It is doubtful that the main message of the results would change however, it would be intriguing to see the extent of the changes in the oscillations around C1 and P1 components over the occipital areas.

As mentioned in above, robust duration specific differences on the behavioral and EEG data were observed along with type differences on the EEG data alone. Previous studies showed that perception of VMP and MAE is highly dependent on the duration and/or ISI used [8, 10]. On the other hand, reverse-phi adaptation is shown to result in lower sensitivity as opposed to phi adaptation [224, 10]. In Experiments 2 and 3, the proportion of correct responses was lower for reverse-phi motion than phi motion as well. This information also indicates that reverse-phi is less powerful to induce a motion percept with respect to phi motion. This could be due to the total duration each ON or OFF pathway is adapted, considering the effect of duration and type on motion perception. For instance, while a within pathway adaptation would last for 752 ms and would adapt the same polarity pathway for all along, a stimulus that adapts ON and OFF pathway would end up adapting each pathway half the time (376 ms). Perhaps the weaker sensitivity arising from inducing reverse-phi adaptation is due to this reason. In light of this information, it seems reasonable to fine-tune the duration of the reverse-phi adapting stimulus to match the effect of phi adaptation. Then, a comparison of the EEG data as well as the behavioral data could be discussed. Another way of matching the observed effect could be established by increasing the duration of each flip on the reverse-phi stimulus. Reverse-phi motion is perceived to be faster than the phi stimulus therefore, increasing the duration of each step could prove effective in matching the effect of phi motion [224].

Introducing a baseline condition in Experiments 2 and 3 as in Experiment 1 would provide more sturdy and powerful conclusions since the processes lag from the adaptation period might affect visual information processing during the test stimulation. However, it would be surprising to see a major change in the main implications of the results.

Although this thesis replicated duration and type effects shown in refs. [8] and [10] and examined the neurophysiological basis of these conditions, a further step could be to reverse the process and interpret the conditions from the EEG data. By classifying the oscillations, it would be possible to refer to the condition that the participant is experiencing from looking at the EEG data. Therefore, the distinct signatures of the short, long, phi, or reverse-phi motion could be

recognized from the amplitude of event-related oscillations.



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