

Context-dependent adaptation in the visual system

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Preface

We live in a world that is highly structured and contains many kinds of different environments, e.g., schools, offices, parks, gyms, forests, beaches, etc. Each of these has its own statistical regularities, including the types and frequency of objects that can be found within, lighting conditions, environment size, location relative to other environments, etc. These regularities, in turn, translate to statistical regularities in the sensory input one is likely to experience when present in that environment. For example, in a “car” environment, one is likely to repeatedly *see* a variety of traffic signs and experience highly regular patterns of optic flow, which may correlate with the type of encountered traffic signs. One may further *hear* common types of sounds, including the “sound textures” generated by surrounding traffic, as well as occasional honking, all of which may be subject to stereotypical transformations (e.g. muffling) of sound passing through the body of the car towards the driver and the passengers. Finally, through the acceleration and deceleration of the car, one may *feel* stereotypical patterns of vestibular sensations.

Taking advantage of these structural regularities is undoubtedly highly useful in our lives, as they, among other benefits, help us better interact with the world through guiding our attention, expectations, and selection of actions that are most likely to be rewarding. However, besides these relatively high-level cognitive effects of knowing the structure of visual environments, it is also possible that the knowledge of these regularities could be used by our sensory systems to optimize their function within these known environments. As of now, the extent to which the dynamics of sensory processing are modulated by knowledge of visual environments remains poorly understood.

In this dissertation, I explore the possibility that repeated experience with visual input containing statistical regularities, which I refer to as “contexts”, can change

how the visual system adjusts its responsiveness to such input. Environmentally-driven rapid changes in neural responsiveness are known as “adaptation” (e.g., Webster, 2011), and Chapter 1 is dedicated to providing the reader with the background knowledge about adaptation necessary to appreciate the experimental work discussed in the remaining chapters. Chapter 1 also reviews past work on adaptation, some of which appears to be consistent with the notion that our visual systems may utilize prior knowledge to influence how we adapt. Chapters 2 and 3 discuss novel experiments that were specifically designed to test the hypothesis that repeated experience with adaptation to visual input containing statistical regularities may speed or otherwise change how we adapt when those statistics are later re-encountered, a phenomenon we term “context-specific adaptation”. Whereas Chapter 2 discusses experiments that use a more traditional adaptation to oriented gratings, Chapter 3 outlines experiments in which participants adapted to a video feed of their surroundings, whose orientation statistics were altered so as to create previously unexperienced adapting conditions. Although both sets of experiments address the same common question, their distinct methodologies allowed us to manipulate a range of variable that may or may not influence whether the visual system engages in learning required for context-specific adaptation to take place.

Although as a whole the experiments provide a mixed pattern of results, they provide some evidence that context-specific adaptation is a genuine phenomenon, and further exploration may be warranted. To this end, Chapter 4 outlines a number of possible directions that future work may pursue, as well as a range of hypotheses about variables that may be crucial for inducing context-specific adaptation, which I was unable to test in the experiments presented in Chapters 2 and 3.

Chapter 1

Context-specific adaptation in visual and motor systems: the common themes

Introduction

Humans and other animals experience frequent changes in their surrounding environments. For example, on a typical day, a person may wake up in a house, go on a jog through a park, and then spend time in a variety of indoor environments, including offices, gym, and restaurants. Because these structural changes can significantly alter both the statistics of the visual input reaching the eyes, and the demands placed upon the motor system, the nervous system needs to continuously adjust its sensory responses and motor commands.

This rapid re-calibration, formally known as neural adaptation, is thought to enhance the efficiency of sensory processing (Fairhall, Lewen, Bialek, & de Ruyter Van Steveninck, 2001; Sharpee et al., 2006; Wainwright, 1999), and the accuracy of motor commands (see reviews by Shadmehr, Smith, & Krakauer, 2010; Wolpert, Diedrichsen, & Flanagan, 2011). For example, neurons in the primary visual cortex adapt to the orientation, motion, and color statistics of the visual input, flexibly changing their sensitivity to optimize encoding of visual information (see reviews by Clifford et al., 2007; Webster, 2011). Similarly, to maintain high accuracy of movements, the motor system dynamically adjusts the strength, or gain, of its efferent commands to cope with muscle fatigue and miscellaneous physical forces exerted on one's body (Wolpert et al., 2011, Shadmehr et al., 2010).

Because adaptation is thought to be a universal property of neural processing, it has received a great deal of attention in research of both sensory and motor systems. However, the vast majority of these studies have treated adaptation as

a process that depends almost exclusively on the recent history of sensory input or motor commands. Although taking this perspective has led to many advances in our understanding of adaptation, it is important to consider how adaptation may function over the long term. More specifically, due to one's extensive experience within the real world, the adult brain has a great deal of predictive knowledge about the spatio-temporal structure of visual and motor statistics encountered throughout the day. For example, as people navigate through the streets on their morning commutes to work, they have accurate expectations about what objects and patterns they are likely encounter at each stage of their journey, as well as the motor demands required to successfully complete the commute.

In the relatively unecological setting of laboratory experiments, adaptation has often been found to be a relatively slow and gradual process, extending over minutes, and even hours (Bao & Engel, 2012; Haak, Fast, Bao, Lee, & Engel, 2014; Kwon, Legge, Fang, Cheong, & He, 2009; Mesik, Bao, & Engel, 2013). However, given the extensive experience we have with functioning in the real world, *it is conceivable that our sensory and motor systems may store information about the statistical structures of different real-world environments, or contexts, and later use this information to adapt more rapidly when these contexts are re-encountered.* For example, the morning commute scenario could be split into several statistically distinct contexts that the commuter encounters. A particular person may initially need to navigate through their home, then pass through a nearby park into the downtown area of their city, and finally access their office in one of the buildings. Each of these contexts may contain statistical regularities, which could, through experience, be stored and later used to adapt more effectively. For example, visual input experienced in the "home" context, may contain energy concentrated predominantly in horizontal and vertical orientations, compared to the "park" context, which will likely have relatively less

energy in vertical and horizontal orientations, and will have vastly different color and luminance statistics. Similarly, motor demands in the “home” context may be different from the other context in its statistics of ground slants, whether a person is wearing shoes, etc. If our visual and motor systems can recognize these distinct contexts and extract their statistical regularities, then adaptation in the real world may function in a more flexible fashion than has been observed in traditional studies.

Is there any evidence that our sensory and motor systems can learn to adapt in a way that selectively utilizes previous knowledge of the statistical regularities in the currently experienced environment? In the rest of this chapter, I will refer to this form of adaptation as *context-specific adaptation*. *The purpose of this chapter is to survey existing literature examining whether motor and visual systems are capable of context-specific adaptation.* These two neural systems were selected not only because neural adaptation is prominent, and well-studied component in both systems, but also because the scientific fields studying the two domains have conducted their research largely in isolation from one another. As such, bringing findings from these two fields together provides a unique opportunity to both look for common themes in these bodies of literature, as well as to draw inspiration from research designs employed in one, but not the other field.

Lessons from animal learning

Although this review focuses on the visual and motor systems, it is important to note that the idea that context in which behavior occurs may play an important role has a long history in the domain of classical and instrumental conditioning (see reviews by Bouton, 1993, 2004). For example, extinction of conditioned behaviors can be made context-specific by conditioning a behavior under one

context and extinguishing the behavior under another context (Bouton & King, 1983). After such a procedure, conditioned responses are renewed when animal is tested in a different context than where the behavior was extinguished. Similar results have also been observed in instrumental conditioning (Bouton, Todd, Vurbic, & Winterbauer, 2011), where an additional finding has been that learning itself does not transfer fully when a behavior is learned in one context, but tested in another.

Besides demonstrating the viability of context-specific learning, the animal conditioning literature has addressed two important issues in studying context-specific learning. First, it emphasizes the difficulty of defining what constitutes a context. Because context can generally be seen as “that which surrounds” a performed task (Smith, 2007), there is an extensive set of possible contextual features that the brain can use for encoding context-specific memories. In addition to obvious contexts, such as the physical location where learning takes place, context can also refer to the time of day, or even internal variables, such as the animal’s mood, hunger level, behavioral goals, or past experiences (Rosas, Todd, & Bouton, 2013).

Second, the animal conditioning literature emphasizes the importance of prediction error in acquiring context-specific memories. That is, associations between the learning context and the learned behavioral responses appear to be formed when an animal experiences outcomes (e.g. not receiving a shock) that do not match their expectations (e.g. receiving a shock). Under these circumstances, the animal may incorporate contextual information into learning in order to better characterize the structure of outcomes. In other words, learning is encoded in a context-specific fashion only when context is useful for predicting outcomes, while uninformative contexts lead to more context-general learning.

Like in animal learning, error signals are also deemed to have critical importance in driving sensory and motor adaptation. For example, the error-correcting functions of motor adaptation depend on one's ability to continuously track the degree to which motor performance matches the intended actions. Large mismatches lead to strong error signals, which in turn lead to large changes in the gain of motor commands. In visual adaptation, computation of error signal is complicated by the fact that an observer may not have access to "intended" visual signal, and thus the error signal may be computed relative to some internal pattern of desired population activity (Benucci, Saleem, & Carandini, 2013).

Contextual adaptation in vision

As stated above, visual adaptation has historically been studied as a very rapid process that continuously adjusts neural sensitivities so as to maintain the visual system's capacity to extract meaningful visual information in an efficient fashion (Clifford et al., 2007; Webster, 2011). As such, relatively little work has touched on the question of how adapting context may influence adaptation dynamics, and whether experience alters these dynamics. However, even though this question has not been the center of attention in adaptation research, results from many related studies can be evaluated from this perspective, and can be informative about whether the visual system does, in fact, use contextual information to alter how it adapts.

McCollough Effect and visual-visual contingent aftereffects

The visual adaptation phenomenon that has, historically, been most discussed as potentially reflecting context-specific processes is the McCollough Effect (ME). In ME generating paradigms, prolonged inspection of a color-orientation combination (see Figure 1) induces a color aftereffect that is only experienced when looking at an achromatic (i.e. grayscale) grating with the *same*, but not

orthogonal, orientation (McCollough, 1965; for review see Howard & Webster, 2011). In other words, the experience of the aftereffect is orientation-*contingent*. It is experienced only for a particular orientation, namely the one that has been used to induce adaptation. For example, if one adapts to a green vertical grating, a physically achromatic vertical grating will appear pinkish, while a horizontal grating will maintain its achromatic appearance.

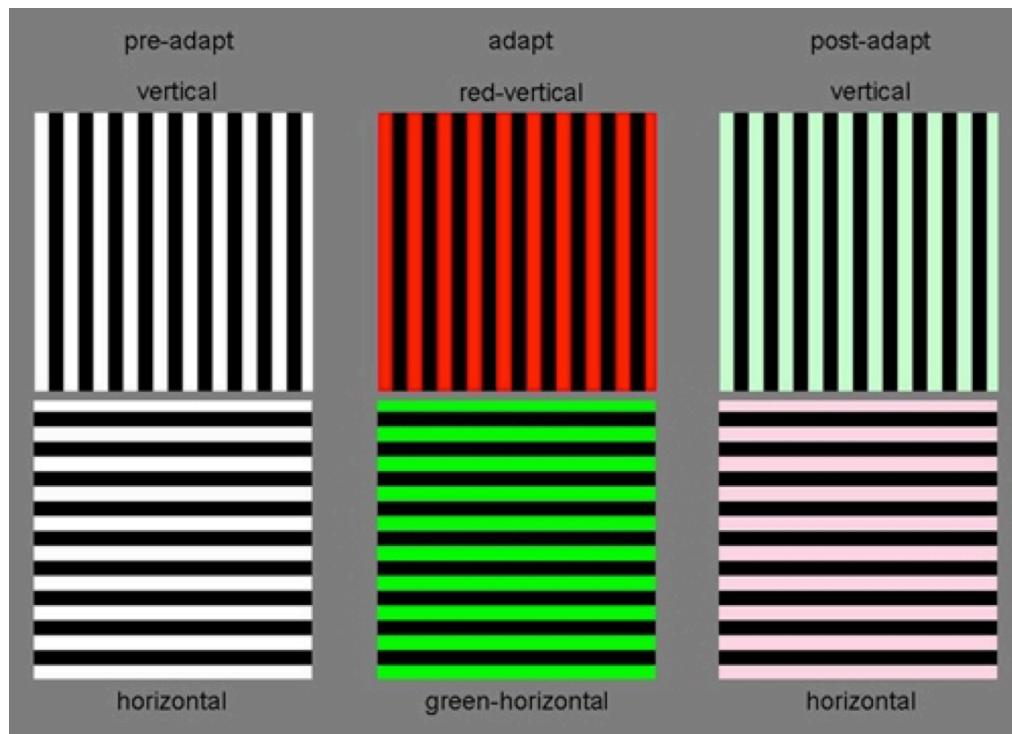


Figure 1. *The McCollough Effect*. Prolonged viewing of colored, oriented gratings (middle column) induces adaptation effects that change the perception of black-and-white gratings from veridical pre-adaptation percept (left column) to illusory tinted percept (right column). This aftereffect is contingent on orientation, such that adaptation to one orientation-color combination causes a color aftereffect just for that orientation. Note: figure reprinted from Howard & Webster (2011) under the CC BY-NC-SA 3.0 license.

Because the aftereffects in the ME are only experienced under very specific circumstances, it can be interpreted as being a context-dependent adaptation aftereffect. More specifically, if one thinks of orientation as a visual context, then the fact that ME is only experienced for the orientation that was used during

adaptation can be interpreted as context-specific adaptation. Indeed, different MEs can be simultaneously induced for multiple color-orientation “contexts,” so that one color aftereffect can be experienced while inspecting a grating of one orientation, while another color is observed when viewing the orientation of a different adaptor.

The question of whether the ME reflects genuine context-specific processes has been extensively debated (Dodwell & Humphrey, 1990; Siegel, Allan, & Eissenberg, 1992; Skowbo, 1984), but even so, the current state of the research does not clearly resolve the true nature of the neural mechanisms involved. The proponents of the contextual account of the ME have used two main arguments in supporting their context-dependent interpretation of the ME. First, as stated above, the ME has a strong intuitive resemblance of being contextual in that the experience of the ME is gated by whether or not the stimuli used to test the aftereffect belong to the adapting context (i.e. the orientation used during adaptation). If the orientation of the test stimulus matches the orientation of the adaptor, the context is interpreted to be identical, and the color aftereffect is experienced. When different orientation is shown, visual system infers a distinct context, and the adaptation is not generalized to this new context.

Second, unlike other forms of visual adaptation, the ME does not fully decay for an extended period of time (Jones & Holding, 1975; Vul, Krizay, & MacLeod, 2008) unless it is actively erased by inspection of the adaptor orientation without the original color pairing. This can be interpreted as the ME being subserved by a memory-like mechanism, which stores the appropriate gains for color-tuned neurons, and which can subsequently be re-used and further updated whenever the orientation context used in ME induction is re-encountered.

In fact, the buildup and decay of the ME can be characterized as a combination of two mechanisms, one of which adapts and decays quickly, and one that is acquired at a slower rate, but appears to have semi-permanent duration (Vul et al., 2008). This long-lasting mechanism could potentially be a signature of the context-specific component of the ME that allows the visual system to store the color-orientation association of the adaptor gratings. On the other hand, aftereffects from classical, non-contextual forms of adaptation involving single visual feature (e.g. orientation or spatial frequency) are not expected to last over a very long duration, because these features are commonly encountered across many visual contexts and thus non-contextual adaptation mechanisms need to continuously re-adapt to the currently prevalent amount of a given feature. The quickly adapting and decaying component of adaptation reported by Vul et al. may, then, potentially reflect a non-contextual aspect of the ME.

The neural mechanisms underlying the McCollough effect remain unknown (Howard & Webster, 2011). One mechanism of implementing the ME (and other contingent aftereffects) as context-specific adaptation has been proposed by Barlow and Foldiak (1989). In their view, neural populations with highly correlated firing (such as correlated activity in color and orientation selective neurons elicited by colored gratings) form mutual inhibitory connections that serve to de-correlate their activities (see Figure 4.4 in Foldiak and Barlow, 1989). Subsequently, when just one of these populations is stimulated (e.g. by viewing a grayscale grating), the non-stimulated population receives inhibitory input that distorts the population response, leading to the percept of a contingent aftereffect (e.g. tinted grating). Hence, contingent aftereffects may be an emergent property of efficient sensory encoding, rather than an “intended” feature. Nevertheless, this implementation can be considered a kind of context-specific adaptation given that the aftereffect is caused by experience-dependent changes in the way distinct populations of neurons interact.

While the context-specific view of the ME is intuitively appealing, there are a number of reasons for caution in concluding that it is indeed implemented in such a way. Most importantly, studies of monkey V1 electrophysiology have identified so-called double-opponent neurons, which jointly encode color-orientation combinations (Johnson, Hawken, & Shapley, 2008). These neurons are tuned such that each neuron only responds to particular combinations of color and orientation, e.g. red vertical gratings, but not to other combinations. Although the nature of neural implementation of the ME remains unclear (Howard & Webster, 2011) it could quite conceivably be caused by adaptation within these neurons. Specifically, perception of chromatic (i.e. colored) contrast may be implemented such that for each orientation the range of colors is encoded by neurons jointly coding that orientation and one of the colors within the range (see Fig. 2). For any color-orientation combination, then, the perceived color would depend on the peak in the population response within these jointly tuned neurons. In an unadapted state (Fig. 2a), a black and white vertical grating should be perceived correctly as black and white and vertical. However, if one adapts to, e.g., a red vertical grating (Fig. 2b), the sensitivity of red-vertically tuned neurons will be reduced, and hence the peak population response to a gray vertical grating will be *shifted away* from red-selective neurons towards ones selective to greenish hues.

The existence of these double-opponent neurons highlights the important possibility that the neural substrates of the ME *could* be pre-wired, as opposed to resulting from associative plasticity between orientation and color-selective populations. In fact, it is worth considering that even simple cells in V1 are selective for specific combinations of orientation, spatial frequency, and location, and thus traditional orientation-selective adaptation of V1 neurons *is* contingent on these jointly encoded features. If the McCollough effect is, in fact,

implemented in this pre-wired fashion, then it does not reflect the kind of *learned* context-specific adaptation that this review is concerned about.

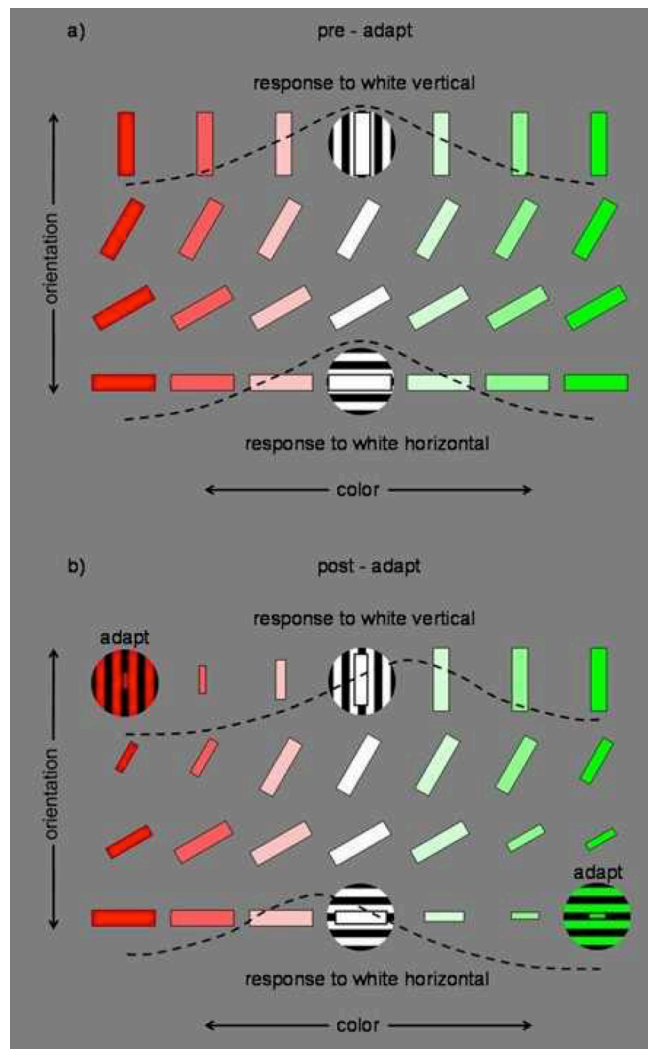


Figure 2: *Double-opponent neuron implementation of the McCollough effect.* Oriented bars in a) and b) represent population of visual neurons tuned to different colors and orientations. The size of the bars represents neural sensitivity. a) In an unadapted state, black and white gratings generate population responses that are centered on black and white. b) When vertically tuned neurons are adapted using a red vertical grating and horizontally tuned neurons using a horizontal green grating, sensitivity of the red vertical neurons and green horizontal neurons decreases (see smaller bar size). Population response to black and white vertical and horizontal gratings in subsequently shifted away from the color of the adaptor orientation. i.e. the vertical grating appears greenish, and the horizontal grating reddish. Note: figure reprinted from Howard & Webster (2011) under the CC BY-NC-SA 3.0 license.

Another reason for skepticism about the ME reflecting context-specific adaptation is that the aftereffect cannot be made contingent on arbitrary visual patterns. While a considerable number of contingent aftereffects akin to the ME have been identified (for review see Durgin, 1996), only relatively basic visual features such as orientation, motion direction, spatial frequency, and color have been successfully used to produce contingent aftereffects. Attempts to elicit a ME contingent on more complex visual patterns such as meaningful objects and scenes have generally failed (e.g. Yamashita, Hardy, De Valois, & Webster, 2005), or induced MEs that could be accounted for based on the low-level features of the inducing and test patterns (Broerse & O'Shea, 1995; McCollough, 2000). These findings lend support to the notion that perhaps contingent aftereffects are restricted to combinations of features that are jointly encoded within pre-existing mechanisms in the visual system.

Overall, while the contextual interpretation of the McCollough effect is intuitively appealing, the current evidence remains inconclusive about its neural implementation (see review by Howard & Webster, 2011). More specifically, while considerable effort has been exerted to determine *where* in the brain the ME may arise (e.g. Barnes et al., 1999; Humphrey, James, Gati, Menon, & Goodale, 1999; Savoy & Gabrieli, 1991; Vul & MacLeod, 2006), relatively little experimental work has been done to elucidate *how* it is implemented. Given that double-opponent neurons with joint color-orientation selectivity are known to exist in the visual cortex (Johnson, Hawken, & Shapley, 2008), the most parsimonious explanation of the ME is that adaptation in these neurons causes the perception of the ME. Alternately, the ME may be implemented through a genuine context-specific mechanism, such as inhibitory interaction between color- and orientation-tuned neurons (Barlow & Foldiak, 1989).

In order to disentangle between these possibilities, an electrophysiological experiment (e.g. in a monkey) of the ME may be needed to determine how correlated the ME perception is with patterns of activity in double-opponent neurons. For example, if inspection of a ME inducing stimuli elicits robust activation in these double-opponent neurons, and if the peaks in population activity within them while inspecting grayscale test stimuli corresponds to the ME percept, then they are likely responsible for the ME perception. Furthermore, if these neural populations subserve the ME, then their electrical stimulation should be capable of modulating the ME percept. Alternately, conducting functional magnetic resonance imaging (fMRI) studies of the ME may also be a fruitful direction given the recent advances in decoding analysis techniques (see review by Haxby, Connolly, & Guntupalli, 2014). Such approaches can successfully distinguish patterns of neural activity elicited by conjunctions of color and form (Seymour, Clifford, Logothetis, & Bartels, 2010), and may therefore be suitable to provide insights into the neural basis of the ME.

Gaze-contingent aftereffects

Despite the insufficient evidence regarding the neural implementation of contingent aftereffects, it can be informative to consider the types of feature combinations that can elicit contingent aftereffects, and the likelihood of their joint encoding. More specifically, if there are pairs of features that can cause contingent adaptation, but are unlikely to be encoded jointly, then the mechanism of adaptation may likely involve some form of associative learning, such as formation of inhibitory connections between the neurons encoding these features.

One sub-class of feature pairs that cause contingent aftereffects, yet appear less likely to be encoded jointly, are ones involved in gaze-contingent visual aftereffects. In this paradigm, the perceived aftereffect depends on the direction

in which one is looking. For example, Mayhew (1973) reported gaze-contingent motion aftereffect (MAE) in which the perceived direction of illusory motion depended on the direction in which a person was looking. When subjects fixated static patterns presented in the gaze direction where they previously observed clockwise motion (e.g. on a display position to subject's left), they perceived a counter-clockwise MAE, while fixating in the direction that previously contained counter-clockwise motion (e.g. display to subject's right) lead to clockwise MAE. Importantly, the retinotopic location (i.e. the position within the visual field) of the adaptors, as well as test stimuli used to quantify the aftereffect strength was the same in each condition, with only difference being the direction in which the subjects were looking. Similar gaze-dependent aftereffects have more recently been also demonstrated with depth (Nieman, Hayashi, Andersen, & Shimojo, 2005), and both the magnitude of MAE and, to a lesser degree, the tilt aftereffect (TAE) were shown to be parametrically modulated by the difference in the gaze direction during adaptation and testing of the aftereffects (Knapen, Rolfs, Wexler, & Cavanagh, 2010; Nishida, Motoyoshi, Andersen, & Shimojo, 2003).

Gaze-contingent aftereffects are a relatively likely candidate for engaging context-specific adaptation mechanisms, as opposed to joint feature encoding. One reason for this is that although neurons sensitive to gaze direction have been identified in visual areas (e.g. Galletti & Battaglini, 1989), the odds that all pairwise combinations of gaze directions and the variety of simple visual features that can be used in gaze-contingent adaptation could be represented with dedicated neurons appears unlikely. In particular, the number of neurons required to encode all pairwise combinations of features grows exponentially as more features are added into mix, a phenomenon more generally known as the combinatorial explosion. This is even more apparent when one considers the fact that all combinations of retinotopic locations, orientations, and spatial frequencies are already represented through joint encoding, and hence adding an array of

gaze directions as another jointly encoded variable would require an enormous number of additional neurons.

The background similarity effect

In recent years, a phenomenon known as the background similarity effect has hinted at the existence of context-specific adaptation mechanisms (N. Qian & Dayan, 2013; Wu, Xu, Dayan, & Qian, 2009). In this phenomenon, an aftereffect is perceived more strongly when the visual statistics of the test patterns background match the ones in the preceding adaptor stimulus. For example, Qian & Dayan (2013) showed that although tilt adaptation from second-order oriented contours generally does not transfer to first-order oriented test lines, when background statistics between the two stimuli are matched, the adaptation does transfer (see Figure 3). In other words, whether the tilt aftereffect (TAE) is perceived is, at least partially, contingent upon visual information that surrounds the adaptor and the test stimuli.

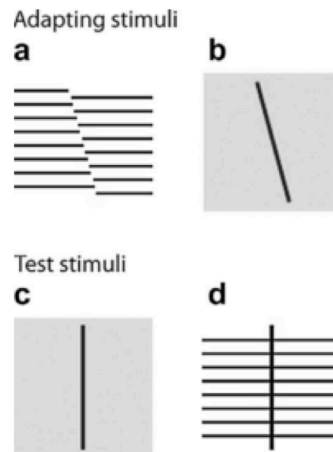


Figure 3. *The background similarity effect.* Illusory perception of tilt, or the tilt aftereffect (TAE), can be induced by adaptation to first-order oriented lines (b) or second-order oriented contours (a). E.g. After adapting to first-order stimulus (b), the first-order test pattern (c) appears tilted slightly clockwise. Adaptation induced by second-order stimuli (a), however, usually does not elicit TAE in first-order test stimuli (c). Qian & Dayan (2013) showed that when the background statistics between the second-order adaptor and first order test stimulus are similar (compare a and d), the aftereffect does transfer, an effect they term “background similarity effect.” Figure reprinted from Qian & Dayan (2013) under the CC BY 3.0 license.

A potentially related effect has been reported by Nakashima & Sugita (2014), who reported a TAE contingent on the geometrical shape that surrounded the adaptor and test stimuli. When one adaptor (e.g. leftward tilted grating) was consistently surrounded by a circle, and another adaptor (e.g. rightward tilted grating) by a square, then the TAE elicited by a vertically oriented test grating depended on the shape of the co-presented surrounding pattern. That is, when the test stimulus was surrounded by a circle, the perceived TAE reflected adaptation to the adaptor with the circular surround and when the test had a square surround, TAE reflected adaptation to adaptor with square surround.

Both the background similarity effect and the surround-contingent aftereffect appear to be strong candidates for engaging context-specific adaptation mechanisms for several reasons. First, these effects capture the intuitive appeal of context specific adaptation, namely that the statistical structure of an entire

environment may be informative about the appropriate states of adaptation for processing that environment. For example in a given context, information such as the characteristic scents, sounds, or colors associated with the context may be useful for inferring the identity of that context and retrieving the relevant context-specific adaptation states for optimal processing of these sensory features. In both phenomena discussed above, the perception of the central stimulus depends on the content of the surrounding patterns. This suggests that the visual system may indeed be able to use statistics in one set of features (e.g. ones in the surround) to infer the adaptation state appropriate for processing another set of features (e.g. ones in the stimulus center).

In a related vein, the fact that the perceived aftereffects depend on the information that spatially surrounds the test stimuli, rather than information that overlaps them, suggests that the effects are unlikely to stem from joint feature encoding (Note: although the test stimulus in Fig. 3d intersects its surround, Qian & Dayan showed that the effect persists when a gap is introduced between the center and the surround). In order to test this, however, it is important to show that the effect does not occur at late stages of visual processing where receptive fields are relatively large and joint encoding of central and surrounding features is theoretically possible. Nakashima & Sugita (2014) tested the spatial transfer of their surround-contingent aftereffect and found that it is retinotopically specific, such that adapting at one location in the visual field and testing at another does not elicit the aftereffect. This suggests that at least in the case of their findings, the effect is subserved by neural populations at relatively early stage of cortical processing, where receptive fields are quite small. In other words, the effect likely depends on formation of some type of associative connections between the central and surrounding features.

Though the above phenomena offer promising hints of context-specific adaptation, more work will be required to explore the nature of their neural implementation. In particular, while they appear to engage context-specific mechanisms, it will be important to show that the neural mechanisms that subserve them are truly contextual in nature. For example, although the McCollough effect can also be elicited with colors that surround, rather than overlap, the adaptor gratings (Siegel et al., 1992), this effect may likely depend on a retinal mechanism that allows color-evoked activity to spread into surrounding retinotopic regions (Pöppel, 1986). As such, it will be important to assess whether some analogous mechanism could somehow account for these phenomena. Furthermore, since there is apparent similarity between background similarity effect and surround-contingent aftereffects in their dependence on visual patterns that surround the test stimuli, future work should also test the extent to which they engage common neural mechanisms.

Cross-sensory aftereffects

Given the multisensory nature of human perception, another possible subclass of contingent aftereffects unlikely to be subserved by joint feature encoding includes aftereffects where responses to sensory features in one sensory system become contingent on features in another sensory system. Recently, a number of such effects have recently been reported (e.g. Hidaka, Teramoto, Kobayashi, & Sugita, 2011; Kuang & Zhang, 2014; Teramoto, Kobayashi, Hidaka, & Sugita, 2013). For example, Hidaka et al. (2011) reported a motion aftereffect that was contingent upon sound. In their experiment, they repeatedly exposed subjects to sounds with high pitch accompanied with visual presentation of rightward apparent motion, and low-pitched sounds accompanied with leftward apparent motion.

Following an exposure period, subjects became more likely to perceive displays with ambiguous (i.e. undirected) motion as containing rightward motion when the high pitch sound was played, and leftward motion when the low pitch was played.

However, a distinctive feature of these studies is that the reported contingent effects do not manifest themselves as the repulsive aftereffects seen in traditional sensory adaptation literature, but rather as attractive perceptual shifts. That is, repeated presentation of a particular visual feature generally induces sensitivity reduction. If the above experiment with pairings of pitch and motion direction reflected traditional contingent adaptation, then the sound associated with rightward motion should have caused the ambiguous motion to appear to move *leftward*. This is because the context (i.e. sound pitch) during which the rightward motion was presented should be associated with reduced sensitivity of motion sensitive populations tuned to rightward motion (since that direction was repeatedly presented in that context), and hence the population response of motion-selective neurons to ambiguous motion should be shifted towards leftward motion.

These context-specific phenomena therefore appear to engage learning mechanisms that are distinct from traditional contingent adaptation. In fact, these effects are likely related to a broader category of cue combination phenomena in which the brain learns to combine multiple sources of related, yet noisy, sensory evidence to improve the fidelity of the perceptual inference (Haijiang, Saunders, Stone, & Backus, 2006; Knill & Pouget, 2004). While these phenomena can be interpreted as involving context-specific learning, due to their lack of clear relationship with sensory adaptation, they are beyond the scope of this chapter.

Contingent aftereffects: summary

Given the relatively limited amount of evidence for contingent aftereffects elicited by feature combinations that are unlikely to be encoded jointly, the question of whether context-specific visual adaptation can be learned through experience remains open. Importantly, even though psychophysical data discussed above has failed to differentiate between adaptation in populations of neurons that jointly encode multiple features, and more genuine context-specific adaptation (such as via cross-feature mutual inhibition), either implementation could still be possible. As such, more electrophysiology and neuroimaging is needed to elucidate how these contingent aftereffects are implemented.

Aftereffects from adapting to glasses

The vast majority of adaptation literature discussed thus far exposed subjects to highly unnatural visual patterns (e.g. sine-wave gratings) and measured their effects on perception using simple detection and discrimination tasks. Although such paradigms may be excellent for studying many aspects of vision, it is possible that context-specific adaptation may be used predominantly in situations where the visual system has evidence that it is functioning poorly, such as when viewing more natural visual input distorted by a new pair of glasses. For this reason, as well as because they permit long adaptation durations comfortably, studies that examine adaptation to glasses can be highly informative. Because of this potential, I will review them in somewhat more detail than other studies.

In perhaps the most direct and informative investigation related to context-specific visual adaptation to date, Yehezkel et al. (2010) tested whether experience with adapting conditions can change how quickly one adapts. They asked subjects to wear glasses that induced oriented blur (akin to what people with astigmatism may experience), and measured how they adapted in 2 and 4 hours sessions repeated 1-3 times per subject. The average results across sessions revealed that although adapting for just 2 hours led to minimal reduction

in the perceptual distortion caused by the lenses, as well as a strong aftereffect after taking the lenses off, 4 hours were sufficient to significantly reduce both the distortions and the aftereffect. Strikingly, 4 hours of adaptation completely eliminated the aftereffect experienced after taking the glasses off. This suggests that the visual system may have processed the input under the two contexts (glasses on vs. off) differently, and was able to switch between these modes of processing very fast.

Furthermore, the authors tested whether there was any learning across the repeated sessions in a subset of the subjects who completed multiple sessions of the experiment (4 out of 9 subjects). This analysis revealed that on session 1, subjects adapted only partially, but this adaptation carried over to session 2, so that the degree of adaptation started where it left off on the previous session, and continued to improve. In other words, these results suggest that there may be learning processes in visual adaptation that allow consolidation and storage of adaptation states. Although the long-lasting aftereffects seen in the McCollough effect (Jones & Holding, 1975; Vul et al., 2008) hinted at this possibility, learning effects of this sort have previously not been seen with more traditional, non-contingent types of adaptation.

While Yehezkel's results are promising, there are reasons for caution in making strong conclusions about context-specific adaptation. For example, Yehezkel's result showing learning across sessions only used data from 4 subjects who completed multiple sessions of the experiment, and the data from remaining 5 subjects (who, for unstated reasons, only completed a single session) were not included in the estimate of the effects of the first adaptation session. Given the fact that data for 4 hours of adaptation showed significant reduction in perceived distortion across sessions (i.e. an apparent learning effect), inclusion of the data from these 5 subjects would potentially render the learning effect across sessions non-significant. In other words, if these 5 subjects were included in the estimate

of the degree of adaptation in session 1, it is likely that the average amount of adaptation on this session would be much greater, possibly comparable to that on session 2, washing out any apparent changes between sessions.

The authors furthermore omitted showing whether the aftereffect from taking the glasses off changed across days in a similar fashion as the adaptation effect. This is an important piece of evidence that could shed some light on what the learning effect across the sessions actually meant. For example, if the learning across sessions involved learning to distinguish contexts (glasses on vs. off) in order to use separate adaptation mechanisms under each context, then one would perhaps expect that the aftereffect when taking glasses off should be significantly stronger on session 1 compared to session 2. That is, on session 1, subjects may have been less capable of recognizing contextual changes, and may have, therefore, generalized the adaptation from the “glasses on” context to the “glasses off” one, leading to a perceived visual aftereffect. On the other hand, it is also possible that the visual system was able to distinguish the contexts quickly (i.e. within the 1st session), and the learning effect was simply a matter of optimizing the neural gains of the adaptation mechanism for the “glasses on” context. As a speculation, although Yehezkel et al. did not show aftereffects for each session separately, the size of the error bar in the figure showing mean aftereffect across sessions appears quite small, suggesting that perhaps the visual system could employ contextual adaptation quite quickly, and simply needed multiple sessions to calibrate the “glasses on” adaptation mechanism.

Finally, Yehezkel et al. did not test whether subjects could retain the ability to adapt quicker beyond the initial “learning” sessions. As discussed in the introduction section above, the utility of context-specific adaptation lies in the ability to store and reinstate gains that are optimal for processing inputs in various contexts. As such, a key goal in studying context-specific adaptation should be testing whether it can, in fact, be stored and re-used over extended

periods of time. Yehezkel's results showing learning across sessions could, for instance, simply be that the blur adaptation induced by the lenses never decayed between sessions, possibly because the neurons that adapted while wearing the lenses were not engaged sufficiently while not wearing the lenses. Future work should therefore attempt to replicate the experiment with a more standardized paradigm (e.g. all subjects should participate in several sessions), and include additional tests assessing the properties of the adaptation storage, including a longer-term follow-up to assess the duration of the storage.

Another potentially interesting approach to finding evidence of context-specific adaptation is studying visually impaired populations whose members may have developed distinct ways of processing visual input when they are wearing their correction compared to when they are not. One such population is people with astigmatism, which is a visual impairment that induces blur along a particular orientation axis (i.e. astigmats naturally experience the kind of blur similar to what Yehezkel et al. induced using lenses in their subjects). Since most astigmats have long-term experience with both uncorrected oriented blur seen when they are not wearing glasses, as well as with clear input seen when wearing glasses, it is possible that they may be capable of flexibly switching between different context-dependent adaptation states.

Although, somewhat amazingly, no study that I could find has rigorously tested this possibility thus far, several relevant studies comparing habitually corrected astigmats and newly corrected astigmats have been reported. Because the former populations have ample experience with both corrected and uncorrected contexts, while the later population does not, comparing how these populations adapt may reveal hints of context-specific adaptation.

In one study, blur adaptation states of newly corrected astigmats were assessed, over a period of 6 months, as they gained experience with their glasses, and were compared to identical measures in habitually-corrected astigmats (Vinas, Sawides, de Gracia, & Marcos, 2012). Adaptation to astigmatic blur shifts the neutral point of what blur level appears sharp. For example, adapting to a blurry image will make a physically sharp image look sharper than normal. Vinas et al. used adaptive optics, a technique used for precise projection of images onto retina, to measure shifts in this neutral blur point as subjects gained experience with their correction. To do this, authors projected focused images of visual noise onto subjects' retinas, and found how much added (or subtracted) blur along each subject's axis of astigmatism was needed in the images for the visual noise to appear unoriented.

As expected, for previously uncorrected astigmats, a significant amount of oriented blur was needed for the images to appear unoriented; subjects apparently had adapted so that the blur their astigmatism produced appeared unoriented. As the subjects gained experience with their correction over the course of 6 months, this neutral point shifted to the same value found in non-astigmatic control subjects. Strikingly, however, habitually corrected astigmats, who would be expected to have the same neutral point as the control subjects (since their correction provides them with equally sharp input as seen by controls), exhibited a chronic state of blur adaptation despite long-term usage of glasses (see Fig. 4 in the citation). In other words, throughout the 6 months of the experiment, habitually-corrected astigmats required extra blur in the test stimuli, indicating that the physically sharp stimuli projected onto their retinas were perceived to be sharper than normal.

Why would habitually corrected astigmats show such a bias? One possible reason is that because the level of adaptation was tested using adaptive optics

technique, when subjects were not wearing glasses, habitually-corrected subjects may have utilized context-specific adaptation mechanism intended for seeing *without* glasses. More specifically, the visual systems of these subjects may have inferred that because they were not wearing glasses during the measurements, the visual input would be blurry along their axis of astigmatism, and hence they used adaptation state intended to compensate for this anticipated blur. Newly corrected astigmats, on the other hand, may have utilized a non-contextual, general-purpose adaptation mechanism that was still adapted to the glasses worn prior to the testing sessions, and hence their visual systems were adapted for processing sharp input. In other words, habitually corrected subjects may have identified the contextual transition when they took their glasses off for testing and used a context-specific adaptation mechanism, whereas the newly corrected astigmatism did not.

Another potential hint of context-specific adaptation from the astigmatism literature is that both habitually corrected and uncorrected astigmats suffer weaker reduction in acuity when blur is induced along their axis of astigmatism, compared to other orientations (Vinas et al., 2013). Similar to Vinas et al. (2012), subjects in this experiment took their glasses off prior to testing, allowing subjects to detect a contextual switch. As such, it is possible that these results reflect subjects utilizing context-specific adaptation to oriented blur they experience when not wearing glasses. That is, by utilizing neural gains intended to compensate for the blur they typically experience when not wearing glasses, subjects were able to tolerate extra blur along their axis of astigmatism compared to orientations along which they typically do not experience blur. However, the fact that both habitually- and newly-corrected astigmats exhibited a similar effect appears to conflict with findings of Vinas et al. (2012), discussed above, based on which one would expect newly-corrected astigmats to switch between adaptation states optimal for wearing and not wearing glasses at a slower rate. In

other words, based on Vinas et al. (2012), it would be expected that during the experiment, newly corrected astigmats would be still adapted to their glasses, worn prior to the experiment, and hence would not be adapted to compensate for their astigmatic blur.

Because Vinas et al. (2013) did not design their experiment to look specifically for context-specific adaptation, there is an alternative explanation for their results. Specifically, it is possible that astigmats have improved acuity along the axis of astigmatism because of perceptual learning from extensive experience functioning with astigmatic blur, or due to some other form of permanent plasticity. These possibilities would also predict benefits of coping with blur along the axis of astigmatism independent of wearing glasses, and the results of Vinas (2013) therefore cannot be interpreted as strong evidence of context-specific adaptation.

Besides the positive findings hinting at the existence of context-specific adaptation mechanisms, two other studies have failed to find evidence for context-specific adaptation to glasses (Khan, Dawson, Mankowska, Cufflin, & Mallen, 2013; Pesudovs & Brennan, 1993). In one such study, Pesudovs & Brennan (1993) showed that myopes have worse visual acuity (VA) without their glasses immediately following a period of wearing their glasses, compared to a period of not wearing them. In both cases, VA was measured in the same context of not wearing glasses, and hence if context-specific adaptation for “no glasses” context was available to subjects, one would expect that the adaptation states, and hence the VA measures, should be equal in both experimental conditions. The difference in VA between the conditions thus suggest that despite their extensive experience with both blurry and clear visual input, myopes cannot fully and immediately switch between optimal states for seeing with and without glasses. While this result suggests that instantaneous switching between

adaptation states, at least for blur adaptation, may not be possible, it nevertheless leaves a possibility that context-specific adaptation could allow switching between such states to be *faster*. To assess this, it would be important to compare acuities under these conditions between habitually- and newly-corrected myopes. It is possible that while acuity is worse after wearing a correction, the effect could be much more pronounced in someone not experienced with seeing both with and without glasses, or that re-adaptation when switching between the glasses “on” and “off” contexts would be slower.

Another piece of evidence against context-specific adaptation can be found in a study by Khan et al., who compared blur adaptation rates of myopes and normal vision subjects (Khan et al., 2013). Because myopes have extensive experience seeing under blurry conditions, one would perhaps expect that they should be quicker at adapting to blur than normal vision subjects. However, Khan et al. (2013) found that the two groups adapted at the same rate, suggesting that experience with blurry vision does not alter the dynamics of blur adaptation. At the same time, it is possible that even if myopes are faster at adapting to blurry visual input, this advantage would likely be observable for blur levels close to ones caused by their refractive error. In Khan et al. (2013), all subjects were tested with same two levels of myopic defocus, which likely did not match refractive errors that the myopic subjects experienced in daily life.

Overall, although studies of visual impaired subjects have strong potential to shed light onto whether context-specific adaptation does exist, the research done thus far is inconclusive. It will be important to design studies explicitly geared towards assessing context-specific adaptation by testing different ways in which such adaptation could manifest itself. The key directions include conducting more thorough comparisons between experienced and non-experienced wearers of corrective lenses, as well as experiments comparing adaptation dynamics to

visual distortions before and after subjects gain extensive experience with these distortions.

Summary: context-specific adaptation in vision

Because the human visual system possesses a large amount of knowledge about the statistical structure of various visual contexts, an interesting question in the study of visual adaptation is whether the visual system utilizes such knowledge when it adapts to familiar contexts. The literature reviewed here shows that although this possibility has received some limited attention, only relatively weak support for context-specific adaptation has been found thus far. Importantly, most of the reviewed work did not test for context-specific adaptation explicitly, but instead provided informative “hints” about the existence of contextual adaptation mechanisms, which need to be interpreted with caution. As such, the key future direction is to conduct experiments that explicitly test for context-specific adaptation. Because the most suggestive evidence in favor of context-specific adaptation thus far has emerged from an experiment utilizing blur-inducing glasses (Yehezkel et al., 2010), a natural starting point for future work is to employ similar experimental approaches. Paradigms employing free-viewing of the world while wearing glasses may be especially useful in studying context-specific adaptation, as the visual distortion of the world may provide the visual system with strong evidence that visual processing is functioning sub-optimally. Because the poor fidelity of visual information can disrupt one’s ability to perform basic visual tasks such as object recognition and localization, adapting more quickly may be incentivized in these paradigms, maximizing the odds of discovering evidence for context-specific adaptation.

Designing better tests of context-specific adaptation in vision may further be accomplished by drawing inspiration from other fields of research that have devoted more effort and attention to exploring related questions. The next section

will review evidence from research of context-specific adaptation in the *motor* system, and will attempt to uncover useful principles and directions that vision studies should draw inspiration from.

Lessons from contextual plasticity in motor adaptation

Like the visual system, the motor system also adapts, continuously calibrating its efferent commands to cope with changes in muscle properties (e.g. fatigue) and external forces applied to one's body. These adaptation processes have been studied extensively through a variety of paradigms (e.g. Pélişson, Alahyane, Panouillères, & Tilikete, 2010; Shadmehr et al., 2010; Wolpert et al., 2011), which typically measure how limb movements adjust to compensate for externally applied forces. To accomplish such adaptation, the motor system changes the strength of motor commands, known as the motor gain, to minimize error between the performed and intended motions.

In order to produce identical movements in different contexts (i.e. physical states or environments), it is often necessary to use distinct patterns of motor gains. For example, producing equal swimming strokes in an oceanic current and in a calm lake will require much stronger muscle gain in the former situation. Context-specific motor adaptation may therefore be a possible strategy to quickly adapt when a particular situation is reencountered. Unlike the relatively limited scrutiny of context-specific adaptation in vision, the field of motor adaptation has actively studied these effects for the past several decades. As such, this section will survey a narrower, but more focused body of research on context-specific motor adaptation, with the goal of finding principles potentially applicable to vision.

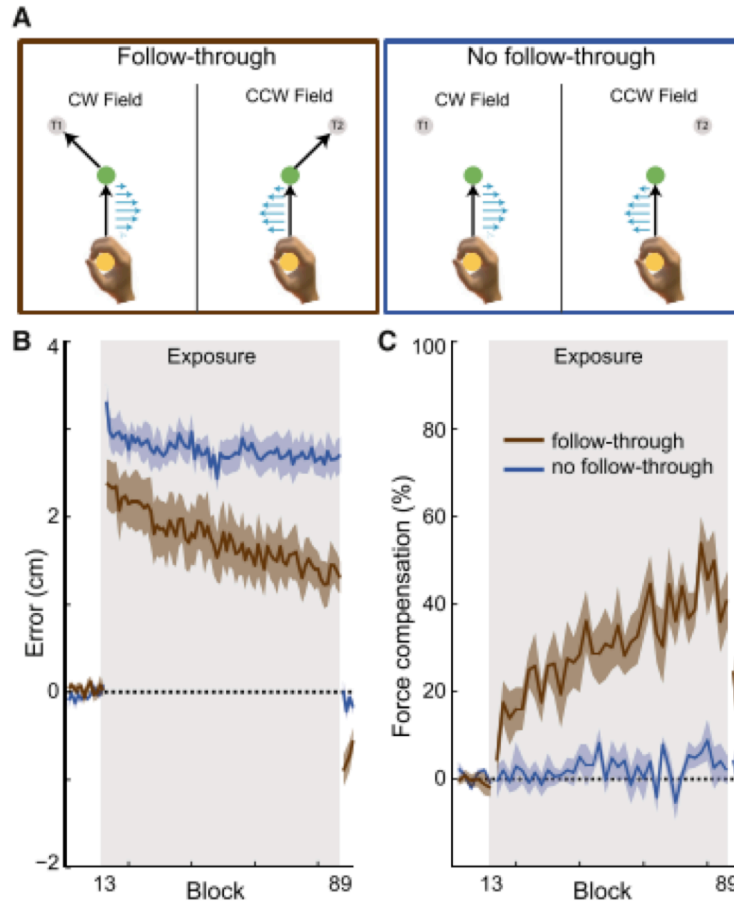


Figure 4. *Force field adaptation paradigm*. Subjects perform reaching movements towards a target (top, green circle), while being subjected to one of two force fields (light blue arrows; brown and dark blue frames show conditions with and without a contextual cue, respectively). As subjects adapt, accuracy of movements gradually improves, which is reflected in declining error distance between reach end point and the target (bottom left) as well as increased compensation for the force field (bottom right). The dark blue trace represents a condition where learning does not occur (no contextual cue), whereas the brown trace (with contextual cue) shows robust learning. Figure reprinted from Howard, Wolpert, & Franklin (2015) under the CC BY 4.0 license.

In one of the most widely used paradigms for studying context-specific motor adaptation, force fields in opposing directions are used on different trials to disrupt subject's attempted limb movements towards a target (see Figure 4). On each trial, the subject grasps a mechanical tool, attempts to reach with it towards the target, and observes the mismatch between the performed and intended motions. This mismatch, termed the error signal, is then used by the motor

system to adjust movements on subsequent trials, allowing the subject to slowly learn to compensate for the force fields and accurately reach the target (Wolpert et al., 2011). The degree of adaptation is usually quantified by measuring the distance between the reach end point and the target, or the force exerted onto the mechanical tool used during the reaching. Furthermore, at the end of the experiment, “error-clamp” trials may be performed, in which the subject reaches towards the target while his or her movement is constrained to reach directly towards the target, leading to a zero error signal. Nevertheless, given the preceding adaptation, subjects continue to exert forces in anticipation of the perturbing forces. These error-clamp trials are intended to quantify the natural decay of adaptation in the absence of error signals, providing an additional measure of the adaptation aftereffect.

Because performing identical movements under oppositely directed force fields requires using opposite patterns of motor gains, a single adaptation mechanism cannot be used to be *simultaneously* adapted to both force fields. For example, to compensate for a force field directed *leftward*, motor gains need to adapt to generate muscle force in the *rightward* direction. If these gains are then used in the context of a *rightward* force field, the resulting movement will be biased significantly rightward away from the target. Consequently, for simultaneous adaptation to both force fields, the motor system needs to adjust and store two separate sets of motor gains, and flexibly switch which mechanism is utilized on a trial-by-trial basis. On each trial, the motor system needs to correctly recognize the current force field context and select the appropriate set of gains to compensate for it.

In this task, failure to process the context correctly will result in *interference* between the contexts, which will greatly limit improvement in the task. If, for example, only one context is inferred, then the error signals on different trials will

produce gain changes in opposite directions. This in turn will cause the net gain change to remain around zero, yielding no visible improvement in performance. Alternatively, if the motor system incorrectly infers the context on some proportion of trials, then the gains will be updated based on performance in a trial from the wrong context, and again performance will not improve (or improve at a slower rate).

Studies with no contextual cues

Using paradigms similar to the one above, two major classes of studies have been conducted that are informative about context-dependent motor adaptation. In the first type, subjects are given no contextual cues about the condition they are in, other than the proprioceptive cues from the force field felt during the completion of each trial. Perhaps unsurprisingly, under these conditions no adaptation occurs to either of two contexts if they are randomly intermixed on a trial-by-trial basis (Karniel & Mussa-Ivaldi, 2002). Lack of explicit contextual cues may prevent the motor system from inferring the correct contexts in this case.

However, when trials from the two contexts are presented in blocks, such that a run of trials in one force field is followed by a run in another, robust adaptation to each of the contexts does occur (Criscimagna-Hemminger & Shadmehr, 2008; D. Lewis, Smith, & McAllister, 1952; Pekny, Criscimagna-Hemminger, & Shadmehr, 2011). In this paradigm, each contextual switch is followed by a pattern of re-adaptation, where initially large motor errors gradually reduce over the course of the block. Whether the ability to compensate for both force fields in these blocked paradigms engages contextually-tuned or some other type of mechanisms has been debated extensively (Karniel & Mussa-Ivaldi, 2002; Lee & Schweighofer, 2009; Pekny et al., 2011; Smith, Ghazizadeh, & Shadmehr, 2006; Wolpert & Kawato, 1998).

Traditionally, results of force field adaptation paradigms have been modeled using fast-adapting and slow-adapting *temporally-tuned* mechanisms (Smith et al., 2006) similar to ones reported in visual adaptation (Bao & Engel, 2012; Mesik et al., 2013; Vul et al., 2008). These models have been influential due to their ability to account for a wide array of motor phenomena. However, under this model of adaptation, each force field context engages the same set of non-contextual mechanisms, so that adaptation in each block *necessarily* interferes with the effects of previous blocks. In other words, under this model it is impossible to be simultaneously adapted to opposite force fields in a way that allows one to successfully compensate for both of them.

This non-contextual model has been challenged with a competing model containing both a non-contextual fast adapting, and contextual slow adapting mechanisms (Lee & Schweighofer, 2009; Pekny et al., 2011; Wolpert & Kawato, 1998), which can also account for the range of phenomena explained by the non-contextual model. In this model, whenever force field context switches, the motor system can infer a change in context through changes in the patterns of error and reward signals, even in the absence of explicit cues, and use this knowledge to switch into using a new contextual mechanism. For example, if context switches from a leftward to a rightward force field, then the first several trials in the new context will result in large magnitude of motor errors, as well as a sudden loss of the reward signals (such as “Great job!” messages) due to unsuccessful performance on these trials. According to the model, these signals are used by the motor system to recognize a change in context, and switch from using the mechanism that led to success in previous context to utilizing and updating a new mechanism intended to produce successful behavior in the new context. A Bayesian version of this model allows for multiple contextual mechanisms to be simultaneously expressed as a combination weighted by motor system’s pattern of uncertainties about the currently active context (Berniker & Kording, 2008).

Pekny et al. (2011) tested this model by reasoning that if one sequentially adapts to opposite force fields A and B, and the motor system does store adaptation states for both contexts, then it should be possible to cue the motor system into expressing both mechanisms. To assess whether this is possible, they adapted subjects in long blocks of trials (384 trials/block) in context B, followed by A, and a brief (20 trial) re-exposure to B. They reasoned, that if by the time of the re-exposure, one has separate mechanisms adapted to each context, then brief re-exposure to context B (whose mechanism should at that time be masked by adaptation to A) should give the motor system a cue to re-express the mechanism for that context. To measure whether this was the case, the BAB block sequence was followed by a block of error-clamped trials, which are used to deprive the motor system of error signals, allowing for the measurement of adaptation uncontaminated by trial-by-trial recalibration. If the mini-block induced re-expression of the adaptation mechanism for B, then the resulting movements in the error-clamped trials should be strongly biased towards the ones observed in the initial adaptation to B. Indeed, when results from this BAB procedure were compared to identical procedure in which the initial B block was replaced by adaptation to null force field (NAB), the movements in error clamped trials were significantly more biased towards B in BAB than in the NAB condition. In other words, although behavior in sequential adaptation to different contexts reflects adaptation to just the most recent context, effects of previous contexts appear to nevertheless be stored, and can be re-expressed when appropriate contextual cues are encountered.

Additionally, Pekny et al. (2011) further showed that gains associated with one context could be reinstated, after being masked by adapting to another context, merely by withholding reinforcement signals, such as the visual feedback associated with successful trials. When adaptation to context B was masked by

prolonged adaptation to null force field, subjects re-expressed adaptation to context B in error-clamp trials if the visual feedback for trial success was withheld in a small number of error-clamp trials. In contrast, the same procedure in which all error-clamp trials provided “success” visual feedback did not elicit re-expression of adaptation to context “B.” In other words, by virtue of providing subjects with visual feedback associated with unsuccessful trials, previously learned contextual mechanisms can be recovered, presumably due to the motor system’s inference that the old context’s mechanism may lead to more successful performance. This suggests that context-specific adaptation not only depends on error signals used to update adaptation mechanisms, but it can also be influenced by more abstract reward signals (e.g. rewarding pictures) similar to those used in classical conditioning literature.

Effects of contextual cues on limb movement adaptation

The second major class of motor adaptation studies are ones in which different contexts are accompanied by explicit cues. These studies have shown that whether or not the motor system can acquire context-dependent motor “memories” crucially depends on the type of contextual cues used to distinguish between the contexts (Hirashima & Nozaki, 2012; Howard, Wolpert, & Franklin, 2013, 2015; Imamizu et al., 2007; Wada et al., 2003). Randomly intermixing trials from two contexts *can* elicit robust adaptation to both contexts quickly (within a single experimental session) and reliably when the contextual cues allow the motor system to infer that in different contexts, the subject’s body is in distinct physical states.

For example, Howard, Wolpert, & Franklin (2013) showed that it is possible to adapt to two oppositely directed force fields when the different force field directions are associated with different *apparent* locations of the task. More specifically, when the visual depiction of the starting position, target, and the

cursor representing the arm position were offset to one side of the screen for one context and the opposite side of the screen for the other context (while maintaining the same physical arm position), subjects were able to distinguish between contexts on a trial-by-trial basis and rapidly learned to compensate for both contexts. Similar effects were also observed when the limb is physically placed in different locations in the workspace (Howard et al., 2013; Hwang, Smith, & Shadmehr, 2006), or when contexts are linked to movements that subject performs *following* each trial (Howard et al., 2015; e.g. moving arm leftward after each trial in one force field context, and rightward in the other context).

On the other hand, the use of more arbitrary contextual cues, such as the color of a fixation point, or peripherally presented motion has yielded more conflicting results. Shorter, single session experiments have shown virtually no context-specific adaptation with these cues (Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Howard et al., 2013), whereas experiments with many blocks or multiple sessions have elicited context-dependent adaptation (Addou, Krouchev, & Kalaska, 2011; Imamizu et al., 2007; Krouchev & Kalaska, 2003; Wada et al., 2003) that is relatively weak. The slower rate of learning with these cues suggests that trials from each context significantly interfere with adaptation in the other context's adaptation mechanism, possibly due to motor system's failure to *consistently* attribute the observed motor errors to the appropriate context.

Although the reasons for the discrepancy between the efficacies of different cues are unclear, a possible explanation is that the two classes of contextual cues engaged distinct mechanisms of context-specific adaptation. On the one hand, cues that provide the motor system with evidence that in each context the body is in a different state may engage mechanisms that map body states to actions appropriate for those body states. As such, this type of context-dependent

adaptation may be better thought of as state-dependent adaptation, which likely has tremendous importance in everyday life.

Although the physiological substrates of state-dependent adaptation remain unclear, it could potentially be implemented through prewired circuitry dedicated for association of body states to appropriate gains. Such circuitry could possibly be located in the cerebellum, which has a crucial role in production of accurate movements, and which has been shown to be involved in motor learning (Raymond, Lisberger, & Mauk, 1996). Lesioning of the monkey cerebellum has been shown to disrupt the ability to learn associations between different contexts and arm movements (Lewis & Tamargo, 2001), and electrical stimulation of cerebellum in humans can modulate acquisition and retention of motor adaptation to force fields (Herzfeld et al., 2014).

Contextual cues that are more arbitrary and elicit slower, less efficient contextual adaptation may, on the other hand, engage some kind of associative mechanism capable of mapping patterns of motor gain to arbitrary contextual cues. This may reflect a more classical type of learning mechanism similar to ones seen in the classical conditioning literature. More work is, however, needed to determine whether the slow contextual adaptation with arbitrary cues is, in fact, subserved by an associative learning mechanism, or whether it simply reflects a slowly devised cognitive strategies for compensating for the force fields (Addou et al., 2015; Howard et al., 2013).

Contextual cues in saccadic adaptation

In addition to adaptation of limb movements, context-specific adaptation has also been investigated with adaptation of saccadic eye movements. Adaptation in eye muscles is induced by shifting the saccadic target during the saccade either

closer to, or farther away from the initial point of fixation. The former perturbation causes the saccade to over-shoot the target and hence induces gain reductions on subsequent saccades, whereas the latter manipulation induces gain increases (Pélisson et al., 2010). Contextual effects in saccade adaptation have been investigated by measuring whether one can simultaneously acquire two sets of saccadic gain patterns appropriate for opposite saccadic perturbations, and switch between them in a context-specific manner.

Analogous to arm movement adaptation, the ability to induce context-specific adaptation depends on the type of contextual cue used. Cues that influence the body state, such as the pre-saccade eye position or head tilt (Alahyane & Pélisson, 2004; Havermann, Zimmermann, & Lappe, 2011; Shelhamer & Clendaniel, 2002) are effective for contextual adaptation. One could argue that this kind of context-specificity is likely pre-wired given that each context corresponds to different initial muscle states, which means that different muscle groups may be utilized under distinct contexts. This is not the kind of context-specificity this chapter is concerned with. However, the motor system has the flexibility to use eye position such that if it is not informative about the experienced perturbation, then adaptation acquired at one eye position transfers to other eye positions (e.g. Albano, 1996; Frens & van Opstal, 1994; Semmlow, Gauthier, & Vercher, 1989). In other words, the motor system *can*, but does not necessarily have to, utilize eye position for usage of separate contextual mechanisms.

Visual cues that are informative for saccade planning, such as pre-saccade target motion direction and velocity, are likewise effective for inducing context-specific adaptation (Azadi & Harwood, 2014). For example, when a saccade shortening perturbation is linked with high pre-saccade target velocity, and saccade lengthening perturbation with low target velocity, robust context-specific

adaptation is observed. Because Azadi & Harwood had subjects fixate prior to making the saccades, the muscle states were identical between contexts, and hence the ability to adapt to both perturbations cannot be explained as simple recalibration of distinct groups of eye muscles.

Instead, these results suggest that the motor system learns and uses the associations between target features (e.g. velocity or motion direction) that are informative about perturbations, and the appropriate compensatory saccadic gains. Importantly, these target features may be special, because they are necessary for saccade planning. That is, pre-saccade target velocity or direction informs the visual system about where the target will be in the next time point, and hence they are crucial target properties for motor planning. As such, in order for a contextual cue to be capable of supporting context-specific adaptation, it may be important for the cue to have pre-existing relevance in motor planning. Indeed, more arbitrary visual features such as target color and shape, which do not have obvious *a priori* utility in motor planning, have generally failed to induce context-specific adaptation (Azadi & Harwood, 2014; Bahcall & Kowler, 2000; Deubel, 1995; but see Herman, Harwood, & Wallman, 2009 for a positive result).

Context specificity in visuo-motor adaptation

Besides saccade and force field adaptation, adaptation to sensory-motor manipulations, such as when visual input is shifted or inverted using prism goggles, provides further evidence for context-specific motor adaptation. In visuo-motor adaptation, a subtype of the larger class of sensory-motor adaptation, the motor system adapts to compensate for distortions in the mapping between motor and visual coordinates. For example, prisms that invert the visual world render information coming from above to appear in the lower visual field, and the motor system needs to learn that to interact with objects in lower visual field, one needs to reach upwards. Like in limb movement and saccadic adaptation studies,

adaptation to multiple contexts has been studied in visuo-motor adaptation (e.g. Cunningham & Welch, 1994; Fogt & Henry, 1999; Ghahramani & Wolpert, 1997; Kravitz & Yaffe, 1972; Martin, Keating, Goodkin, Bastian, & Thach, 1996; Tuan & Jones, 1997; Welch, Bridgeman, Anand, & Browman, 1993).

In one such study, Tuan and Jones (1996) used a combination of contact lenses and spectacle lenses to induce prismatic shifts in the visual input, and measured how subjects adapted to this distortion. Using a behavioral task that tracked the errors in pointing towards a target, the authors found that pointing accuracy improved over the course of the experiment. This improved accuracy remained high when the glasses were removed, and the adaptation state appeared to be stored and re-used when the glasses were put on again after several minutes. In other words, the subjects appeared to maintain two separate adaptation states that were used selectively, depending on whether or not the subject was wearing the glasses. Fogt and Henry (1999) replicated these findings and further showed that such adaptation can be stored for at least 4 days, and hence can accommodate people who use multiple different prescriptions.

These studies along with a number of others demonstrate that context-specific adaptation to multiple distinct distortions of visuo-motor mapping is possible (Cunningham & Welch, 1994; Ghahramani & Wolpert, 1997; Kravitz & Yaffe, 1972; Martin, Keating, Goodkin, Bastian, & Thach, 1996; Welch, Bridgeman, Anand, & Browman, 1993). Although this rich body of literature is certainly valuable to our understanding of context-specific adaptation, its closer review is beyond the scope of this chapter.

Lessons for visual studies

Given that context-dependent adaptation has received much more attention in the motor adaptation field than in vision research, there are a number of lessons

from motor literature that can be applied to vision. Most importantly, in future work it will be important to design studies that explicitly test whether context-dependent visual adaptation mechanisms do exist. The paradigms used in motor literature can quite easily be “adapted” to vision studies. For example, adaptation to one type of distortion in visual statistics (e.g. reduction in oriented contrast) can be used as one visual context, and opposite distortion (i.e. contrast enhancement for same orientation) can be used as the second context. Periodical switching of these distortions while measuring the degree of adaptation through both behavioral and neural measures can then be used to assess whether, over time, the visual system learns to maintain and switch between multiple contextually-tuned adaptation mechanisms.

Secondly, a key take-home from motor literature is that the type of contextual cues used to give the motor system predictive information about the current context is crucially important. Specifically, as shown in saccadic and limb adaptation, some cues are much better for acquisition of context-dependent adaptation, while with others, the different contexts may significantly interfere with each other’s mechanisms (Azadi & Harwood, 2014; Howard et al., 2013). As such, selection of appropriate contextual cues may also be critical for whether the visual system can utilize context-specific adaptation mechanisms. In the motor system, contextual cues that indicate to the motor system that the body is in different states in each context appear to be the most effective cues for contextual adaptation. Analogously the visual system may also respond strongly to cues that inform it of its “visual state.” However, what these states may be in vision is somewhat unclear.

One intuitive possibility is that these “visual states” could correspond to being situated in distinct physical locations, which is often associated with distinct visual statistics. Adapting to one visual distortion in one location and an opposite

distortion in another location may thus allow for adaptation and expression of distinct contextual mechanisms. On the other hand, the results showing gaze-contingent visual aftereffects (Mayhew, 1973; Nieman et al., 2005; Nishida et al., 2003) suggest that visual states may possibly correspond to spatial locations encoded in an ego-centric coordinate system. That is, rather than context-specific adaptation as a function of physical locations, these mechanisms may be encoded relative to one's own body. Finally, the mere presence of some consistent visual feature in the visual field, such as the frame of the glasses, may be sufficient to signal to the visual system that it should be functioning under a different set of contextual mechanisms. Yehezkel's (2010) experiment showing that experience wearing blur-inducing glasses can lead to increases in adaptation rate are consistent with this view, and suggest that context-specific adaptation may be implemented through neither world- nor ego-centric coordinate systems. One of the goals of future research should be to elucidate the nature of context-specific adaptation mechanisms by testing which of these possibilities, if any, is most effective for inducing contextual adaptation.

The third lesson, albeit somewhat speculative, is that behaviorally relevant error signals may be important for inducing context-specific adaptation. In motor adaptation, subjects consciously perceive the mismatch between their intended and actual movements and use this information to re-calibrate their movements. Additionally, reward signals indicating trial success have been shown to have influence on expression of contextual mechanisms that previously led to trial successes (Pekny et al., 2011). The nature of error signals in vision is currently poorly understood, and especially in traditional adaptation studies utilizing simple patterns such as sine-wave gratings and plaids, it is non-obvious how the visual system determines the mismatch between the "optimal" and "actual" visual response. In these situations, the error signal may be quite abstract, such as the difference between the population activity at a given moment and some "optimal"

pattern of activity, perhaps one that is equalized across the population (Benucci, Saleem, & Carandini, 2013). However, studies that induce adaptation in natural viewing conditions, such as through blur-inducing glasses, allow subjects to perceive that the world is distorted, and may therefore incentivize learning how to adapt to such distortions in a context-specific fashion. Indeed, the success of Yehezkel et al. (2010) in finding evidence suggestive of context-specific adaptation may potentially be due to their use of such naturalistic visual input. Therefore, in future studies, it may be crucial to provide subjects with behaviorally relevant error signals in order to elicit context-specific visual adaptation.

In addition to the use of various blurring lenses, behaviorally relevant error signals may also be generated through the use of altered reality systems similar to one utilized by Bao & Engel (2012). This approach has an advantage in that it allows for more customized way to alter visual statistics, and hence can be used to study adaptation to wide array of visual distortions. Using altered reality, context-specific adaptation may be incentivized, for example, through the reduction of visual information available to the subjects through attenuation or scrambling of visual features such as orientations, colors, or spatial frequencies. The relatively large difficulty in perceiving the world under such conditions may drive the visual system to learn and store context-specific adaptations for each type of distortion to which the subject is exposed.

Finally, it should be acknowledged, that despite the similarities between visual and motor adaptation, it is entirely feasible that context-specific adaptation mechanisms may not exist in vision, or may only exist in some limited form. One reason for this is that due to the highly dynamic nature vision, the visual input may not be sufficiently predictable to make context-specific adaptation mechanisms desirable. This may be especially true for low-level visual features such as orientations, spatial frequencies, and colors. In other words, although

there may be underlying statistical regularities for these features in different environments, the moment-to-moment variability of the visual input may be too high for the storage of gain patterns for different contexts to be desirable. Due to input variability, context-specific visual adaptation would, at best, be a kind of a “best guess,” or a heuristic, for the visual system to set the neural gains at a reasonable starting point, from which it would nevertheless need to deviate on a moment-to-moment basis.

Higher-level visual features, such as objects and faces, may, on the other hand be predictable enough to warrant context-specific adaptation mechanisms. For example, it is possible to adapt separately to male and female faces, or faces of different ethnicities (Jaquet, Rhodes, & Hayward, 2007; Little, DeBruine, & Jones, 2005), and obtain gender- or ethnicity-contingent face aftereffects. These aftereffects can be seen as being context-specific in that they are only experienced when a face of a given gender or ethnicity is observed. However, these high level contingent-aftereffects are thought to be implemented through neurons with complex joint-encoding profiles that are sensitive to high-level characteristics like gender and ethnicity. As such, while context-specific adaptation with high-level visual objects may be possible, it is likely that these aftereffects do not reflect the type of context-specific adaptation explored in this dissertation. Nevertheless, given that processing of high-level visual features is still not understood thoroughly, further exploration of these high-level context-specific aftereffects may likewise be a worthy future direction.

In conclusion, this chapter has addressed the possibility that visual and motor systems may be able to learn and retain neural adaptations for optimal functioning in distinct environments, or contexts. This kind of learning may potentially be very useful in everyday life, as it allows the visual and motor systems to rapidly adapt whenever a given context is re-encountered. The

possibility that such adaptation mechanisms exist is particularly interesting, because it would suggest that even low-level neural phenomena such as adaptation may be subject to memory-like effects, which are, at least in vision, thought to operate at later stages of neural processing. Here, I have reviewed a body of evidence that hints that such mechanisms may exist, suggesting that further exploration of this possibility is warranted. Furthermore, I reviewed evidence from motor adaptation literature, which suggests that the motor system does use context-specific adaptation mechanisms. I argue that due to the similarities between visual and motor adaptation, the field of vision research should draw inspiration from the paradigms and findings reported in motor adaptation literature, and design experiments that utilize what has been learned from that field.

Chapter 2

Repeated experience with adapting to biased orientation ensembles does not alter contrast adaptation dynamics

Introduction

The visual system continuously adjusts its sensitivity so as to optimize its performance (see Chapter 1, and reviews by Clifford et al., 2007; Webster, 2011; note that overlap between this and previous chapter are to aid publication of this chapter as a paper). This process, known as neural adaptation, is a fundamental property of sensory processing, and thus its thorough characterization is important for our system-level understanding of the brain.

The majority of work on visual adaptation has used a contrast adaptation paradigm (e.g., Blakemore & Campbell, 1969), where high contrast sinusoidal gratings are used to induce robust, orientation-selective reduction in neural gain (See Chapter 1 for more detail). Adaptation is quantified behaviorally by measuring, e.g., elevation of detection thresholds, or repulsive shifts in the perception of orientations around the adapted orientation.

Although past work has addressed a wide range of important questions, it has generally assumed that neural adaptation is a process with relatively hard-wired properties. That is, aside from the observation of some modulatory effects of attention (Lankheet & Verstraten, 1995; Ling & Carrasco, 2006; Rhodes et al., 2011), adaptation is seen largely as a “bottom-up” or stimulus-driven process unaffected by experience (but see Yehezkel et al., 2010; Dong, Gao, Lv, and Bao, 2016).

However, different environments in the real world are filled with statistical regularities (Torralba & Oliva, 2003) that could, in theory, be detected and

recognized by the visual system to adapt faster. For example, forests tend to have relatively large amounts of contrast energy along vertical orientations, and are generally green in color, while cities contain both vertical and horizontal energy and are comparatively more grayish and bluish in hue. With sufficient experience, the visual system could learn these statistical regularities and use them to adapt more quickly when the familiar environment is encountered. This may be advantageous, because the moment-to-moment visual input is variable and thus purely bottom-up adaptation may be relatively slow in reaching a state that is optimal for the average statistical structure of the environment. As such, having prior knowledge of the environmental structure may provide a good starting point from which the optimal gain for the *current* circumstance may be achieved at a faster rate.

In this chapter, we report the results of two experiments that address the question of whether the dynamics of contrast adaptation can change with experience. Specifically, we test whether repeated experience with orientation statistics induces some form of learning that speeds adaptation dynamics when the same adaptors are re-encountered.

In contrast to the standard usage of a single oriented grating as an adaptor, we used statistically defined adaptors to emulate the fact that different visual environments (e.g. forests, cities, or mountains) all have different visual statistical structures. Although the moment-to-moment visual input in these environments may be variable, on average the overall input statistics contain stable biases. We term these statistically defined analogues of visual environments “*contexts*,” and our hypothesized effects of experience-dependent changes in adaptation dynamics “*context-specific adaptation*.”

Participants viewed rapid sequences of sinusoidal luminance gratings whose orientations were, in different conditions, sampled from distributions biased towards either clockwise or counterclockwise orientations (Figure 2.1.1). Adaptation to biased ensembles like these reduces neural gain in the population of neurons tuned to the dominant orientation (Benucci, Saleem, and Carandini, 2013). This gain reduction can, in turn, be quantified behaviorally by measuring, e.g., shifts in orientation perception near the dominant orientation, a phenomenon known as the tilt aftereffect (TAE). For example, in one of our conditions participants viewed grating ensembles with 15 deg clockwise orientation bias, which induces a small repulsive shift in perception of orientations around 0 deg, causing test gratings to appear slightly more counter-clockwise (e.g., 0 deg may appear to be -2 deg).

The most common interpretation of this effect is that following adaptation to a clockwise bias, a 0 deg vertical grating elicits an activation pattern across the orientation-selective population that is slightly weaker in clockwise-tuned neurons, and hence the peak of this activity pattern occurs at slightly counter-clockwise-tuned neurons. This pattern of activation is, then, “read-out” or interpreted by later stages of visual processing as a counter-clockwise tilt, leading to the perception of the TAE. In contrast, adapting to an ensemble of gratings with no orientation bias leads to an unbiased symmetric activation pattern when a vertical grating is presented. This results in a veridical perception of a 0 deg stimulus, because the entire orientation-selective neural population is adapted evenly, leading to no shifts in the peak of the activation pattern.

To aid the visual system in identifying and distinguishing contexts from one another (e.g. +15 deg vs -15 deg context), we simultaneously presented adaptors and “*contextual cues*,” which were peripherally presented images defined by either low-level orientation features (Exp. 2.1) or meaningful natural scenes (Exp.

2.2). These cues were uniquely temporally linked with each context such that the visual system could, in theory, learn to infer the statistical structure of the context based on the cue alone.

We measured adaptation to these visual contexts in an hour-long session on each of four consecutive days, and assessed whether the buildup and decay of TAE changed across sessions. If the visual system can learn the structure of adapting contexts through repeated experience with them, and is capable of using this knowledge to more rapidly adjust its gain, then we should observe across-session increases in adaptation speed and/or strength.

Experiment 2.1

In this experiment we tested whether relatively short but repeated exposure to sequences of gratings with biased orientation statistics, can lead to changes in contrast adaptation dynamics.

Methods

Eight observers participated in Experiment 2.1. All gave informed consent in a protocol that was approved by the University of Minnesota IRB. Two participants were excluded from analyses due to their data not showing TAE in any condition or session.

Observers participated in four sessions on consecutive days, each of which consisted of 20 task blocks split into 4 runs. During each 2 min task block (Fig 2.1.1), subjects fixated while attending a pair of rapid sequences of adaptor gratings (33 ms / grating, 85% contrast, 3 cycles per deg, 3.25 deg diameter, random phase), presented on opposite sides of the fixation (left-right or above-

below, counterbalanced across participants). The sequence on one side of the fixation always served as a *neutral* sequence, and its orientations were sampled from a uniform distribution over 12 evenly spaced orientations between 15-180 deg. The other sequence was the *adaptor* sequence, and its orientations were sampled either from the neutral distribution, or from one of two biased distributions where either +15 or -15 deg had a probability of 66.6%, while the remaining probability mass was split evenly among the other 11 orientations (Fig 2.1.2). In total, there were three adapting distributions (contexts) in different blocks of this experiment: Neutral, -15 deg, and +15 deg.

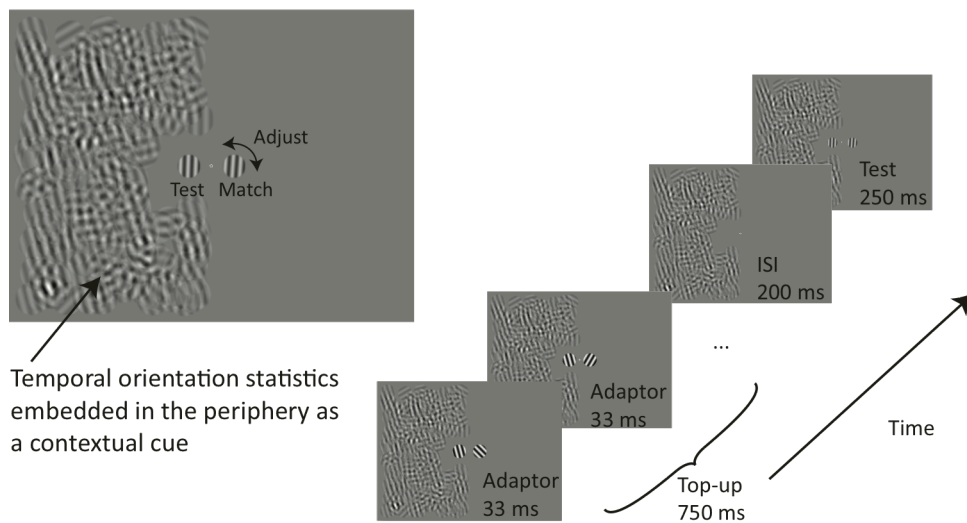


Figure 2.1.1 Trial structure

In each block, two sequences of 85% contrast gratings were presented simultaneously to the left and right of the fixation at a rate of 33 ms / grating. Each 750 ms “top-up” period was followed by a blank ISI period of 200 ms, and a 250 ms presentation of a pair of 35% contrast gratings. One of these gratings, on the same side as the adaptor sequence, was a “test,” and had an orientation of either -2, 0, or +2 deg (chosen randomly on each trial), while the other was a “match” grating, whose orientation the subject adjusted using a mouse to perceptually match the test. The matching could take place over several top-up periods. Once a satisfactory match was achieved, subject clicked the mouse, and the next trial automatically began.

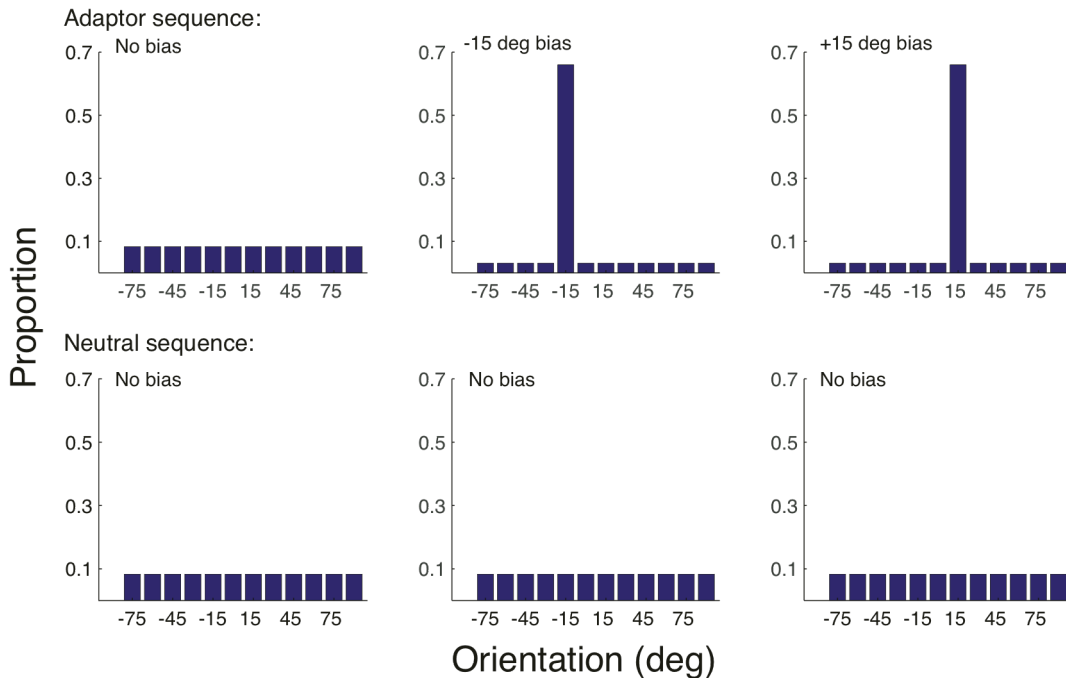


Figure 2.1.2 Statistical structure of adaptor and neutral sequences.

Orientations in the “Adaptor sequence” (top row) were sampled either from a uniform distribution (left), distribution biased towards -15 deg (middle), or distribution with a +15 deg bias (right). The “Neutral sequence” (bottom row) was always sampled from a uniform distribution

The adaptor and neutral grating sequences were interleaved with an orientation matching task to quantify effects of adaptation. After a 750 ms period of “top-up” grating sequences, there was a 200 ms blank period, followed by a 250 ms period in which a near-vertical test stimulus appeared in the location of the adaptor sequence, and a match stimulus, initially randomly selected to be between ± 45 deg appeared in the location of the neutral sequence. Both of the test and match stimuli had same parameters as the adaptor sequence, except their size was 2.5 deg and contrast was 35%. The purpose of the smaller size was both to make the task stimuli easy to distinguish from the adaptors, and to make our measures of adaptation robust to small changes in gaze direction, i.e., microsaccades. We used lower contrast to minimize the amount of adaptation decay caused by the test and match stimuli. Subjects moved the mouse leftward

and rightward to adjust the orientation of the match stimulus to replicate the perceived orientation of the test stimulus. This process continued over as many top-up periods as needed to produce a satisfactory match, at which point participants clicked the mouse to submit the response and begin the next trial.

Because trial completion was self-paced, the number of submitted responses varied from block to block. To minimize the time required to complete each trial, subjects heard real-time auditory feedback for each 1 deg orientation step taken during the matching, allowing them to continue with adjustments during the top-up periods despite the test/match stimuli not being on the screen.

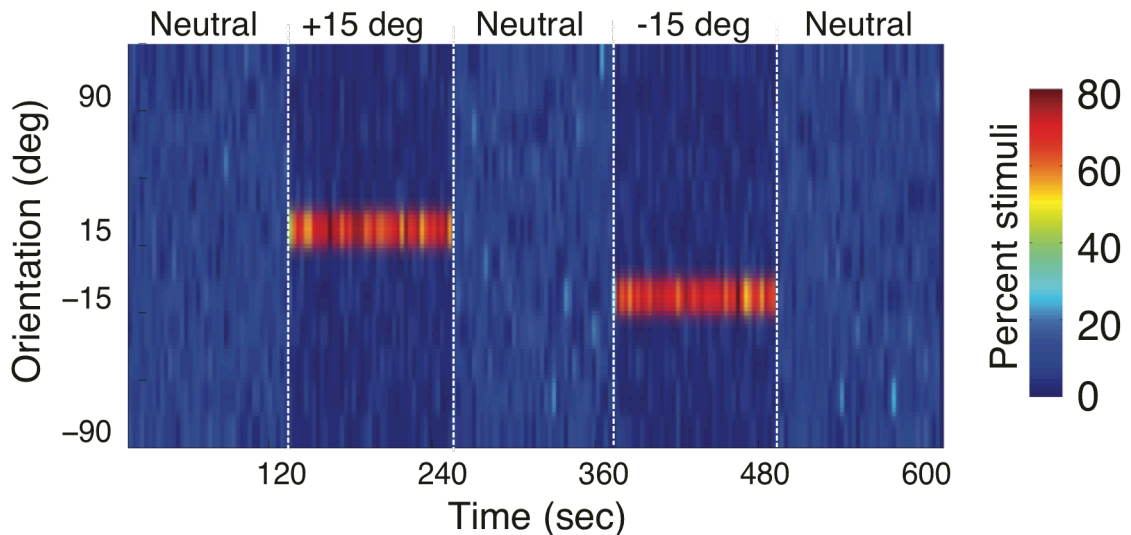


Figure 2.1.3 Run structure

During each task run, there were five 2-minute blocks. Color in the plot depicts the proportion of each orientation (y-axis) as a function of time (x-axis) for sample adaptor sequences. The run always began with a neutral condition and then the adaptor sequence alternated between biased and neutral conditions. The neutral sequence (not pictured) was always sampled from a uniform distribution, i.e. same as the neutral blocks in the diagram. The order of biased conditions was counter-balanced across subjects, and alternated both across runs and days.

In order to encourage subjects to use their perception of the test stimulus, rather than memorizing a generic match response (e.g. “vertical”), the test orientation was randomly selected on each trial to be -2, 0, or +2 deg (relative to vertical).

Prior to the beginning of the main sessions, each subject performed four to five brief practice sessions to train them on the task and verify that they were able to perform it quickly, consistently, and that their responses indeed tracked the different test orientations.

To differentiate the adapting contexts, and hence facilitate the hypothesized contextual learning, the side of the screen with the adaptor sequence contained a *contextual cue* (Fig 2.1.1) consisting of a spatial array of 250 gratings (15% contrast, 3.5 deg) whose orientation statistics matched the probability distribution (Fig 2.1.2) used to sample the adaptor sequence. The center of each grating was randomly positioned, but to ensure homogeneous spatial distribution, the portion of the screen containing the array was divided up into 5 sectors, each of which received a number of gratings proportional to the area of the sector. There was a 2.5 deg gap between the adaptor sequence location and the contextual cue to minimize the magnitude of center-surround interactions between the adaptors and the cue. Additionally, in order to reduce low-level retinal adaptation induced by the contextual cue, the cue changed every 5 sec and was replaced by one of nine arrays with the same orientation statistics. The same cue exemplar could appear multiple times / block, but never twice in a row.

Each of the 4 runs in a session consisted of 5 blocks (Fig 2.1.3). The adapting contexts began with neutral one, and then alternated between -15 or +15 deg and neutral, with each biased context appearing once per run. This sequence allowed us to obtain a clean, relatively adaptation-free baseline measure in the beginning of a run, and then measure both the buildup and decay of TAE through the pairings of biased sequences followed by neutral sequences. The initial biased context (i.e. whether the bias was +15 or -15 deg) was counterbalanced across subjects, and alternated both across runs and sessions (e.g. On session

1, the initial bias in run 1 may have been +15 deg, but for run 2 it was -15 deg, as was the case in run 1 on session 2).

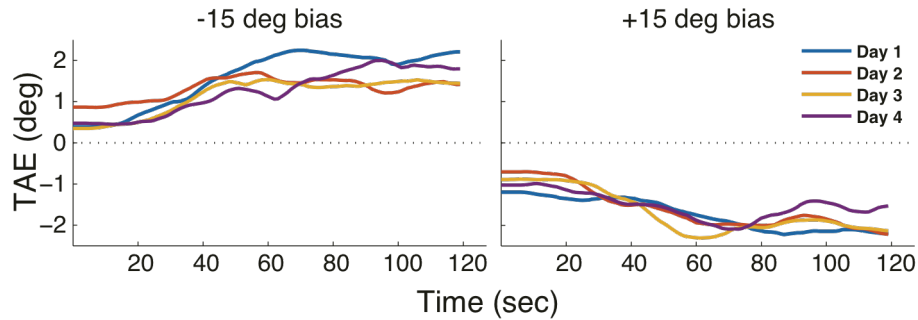
Following each run, subjects were given a one minute break. Five seconds prior to the beginning of the next run, a brief beep was played to notify the subject to get ready for the upcoming block. The total duration of each experimental session was 44 minutes.

For each participant, we computed within-block TAE buildup and decay dynamics for each context by interpolating match responses for each of the 3 test orientations, and then averaged across these curves together. This was motivated by the observation that the TAE magnitude was comparable for the 3 test orientations, making the average of these curves a more accurate estimate of the overall dynamics. The TAE curves were then averaged across participants for each day to compare the dynamics across days, and to perform group-level statistical analysis.

Results

Adaptation to the biased contexts induced a robust tilt aftereffect whose direction was repulsively shifted away from the most common orientation of the adaptor sequence (Fig. 2.1.4A), i.e. clockwise TAE from counter-clockwise bias, and vice versa (15 deg context: $P < 0.005$, 1 – 2.4 deg 95% CI; -15 deg: $P < 0.001$, -1.3– -2.4 deg 95% CI). The TAE then decayed back towards baseline in the ensuing neutral blocks (Fig. 2.1.4B).

A. TAE Buildup



B. TAE Decay

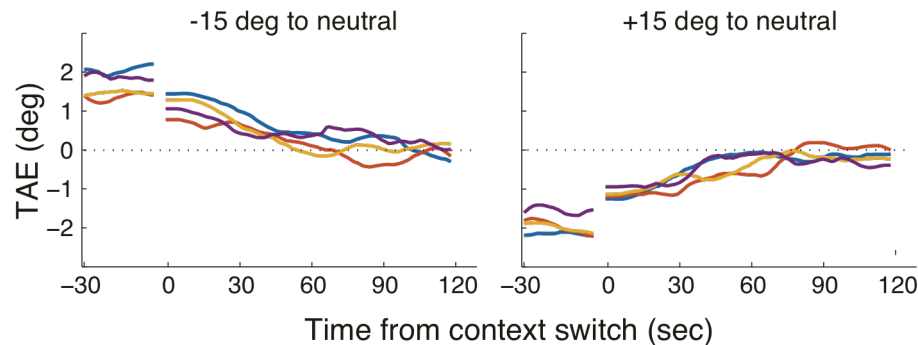


Figure 2.1.4 Dynamics of orientation matching in Exp 2.1

(A) Adaptation to each orientation bias produced robust, repulsive shifts in the perception of the test stimuli. On all 4 days, this effect built up over the course of the block to about 1.5-2 deg TAE. (B) During the subsequent neutral blocks, the TAE decayed back towards the baseline level of 0 deg TAE.

However, we observed no indication of experience-dependent changes in the dynamics of adaptation. First, we tested whether the overall *strength* of the TAE induced by the two adapting contexts changed across days (Fig. 2.1.5). For each day we computed each participant's asymptotic level of TAE in both conditions by taking the mean TAE in the final 30 sec of the growth curves, and then computed the slope of a linear fit across days for both conditions. These slopes did not differ significantly from zero ($P > 0.5$ and $P > 0.2$ for -15 and +15 deg contexts, respectively), indicating that with 4 days of experience, our adaptors became no more (or less) potent at inducing TAE than they were at the beginning of the experiment. A simpler analysis where we compared the peak TAE on first and last days of the experiment showed similar results.

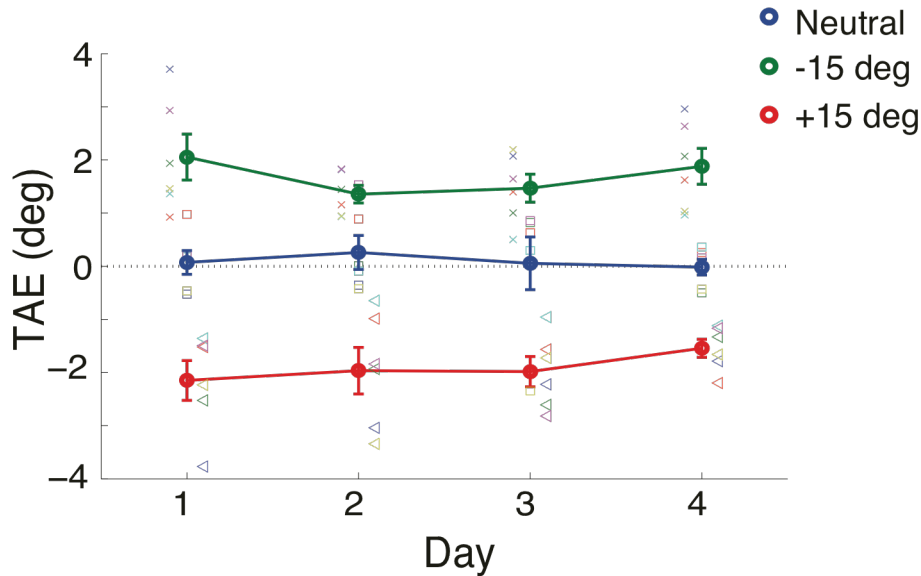


Figure 2.1.5 TAE asymptotes across days

The figure plots asymptotes (average of last 30 sec of the block) as a function of days for all conditions. The large circles are group averages ± 1 SE, while the smaller symbols are results for individual subjects (small x-axis offsets were applied for better visibility). The data reveals no systematic shifts in this TAE asymptote metric.

Second, we tested whether the speed of TAE buildup changed across days. To this end, we computed the time required to reach 80% of the peak TAE for each day and condition, determined as the median of time points that came within 0.25 deg of this TAE value. We then computed slopes for the linear fit to these durations across days. These slopes, again, did not significantly differ from zero ($P > 0.35$ and $P > 0.6$ for the two contexts) indicating that experience did not affect the rate at which participants adapted.

Third, because the neutral context is also an adaptor in its own right (albeit one that equalized gain across orientation-selective populations), one could expect repeated experience with it to lead to faster decay of TAE accrued in the preceding biased conditions. In fact, the neutral context was experienced three times as frequently as each biased context, making it arguably the most likely condition to show behavioral changes. We tested for changes in the rate of TAE

decay following switches from biased to neutral contexts by computing the slopes over the time required for TAE to decay to 20% of its peak magnitude and compared these slopes against zero. Again, we observed no changes ($P > 0.8$ and $P > 0.35$, for -15 and $+15$ deg, respectively), consistent with experience not altering adaptation dynamics. We also tested whether there was any change in the rapid decay occurring in the first 10 sec following a contextual switch to neutral condition (Fig. 2.1.6). The slope of this quantity across days, likewise, did not differ from zero ($P > 0.9$ and $P > 0.6$).

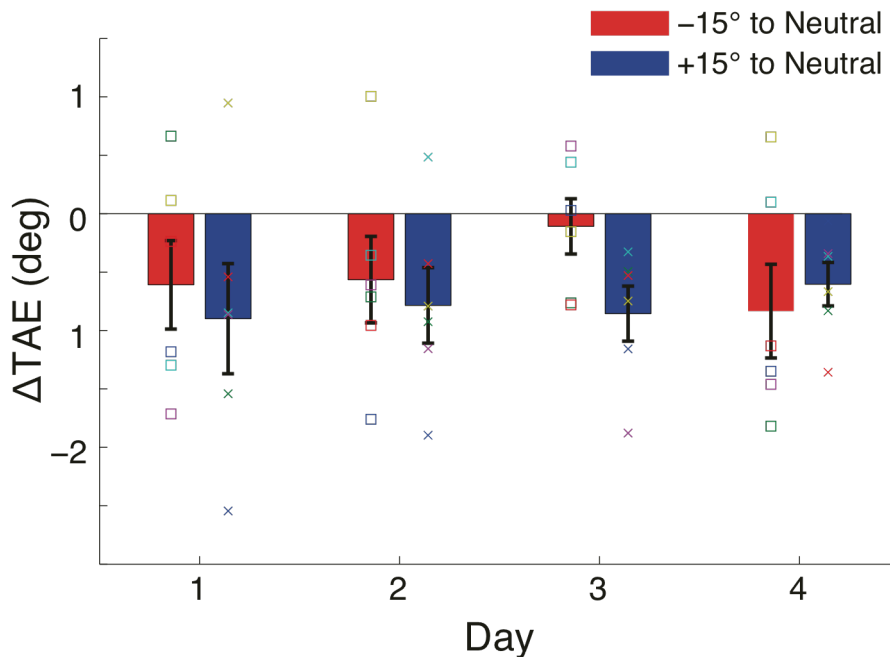


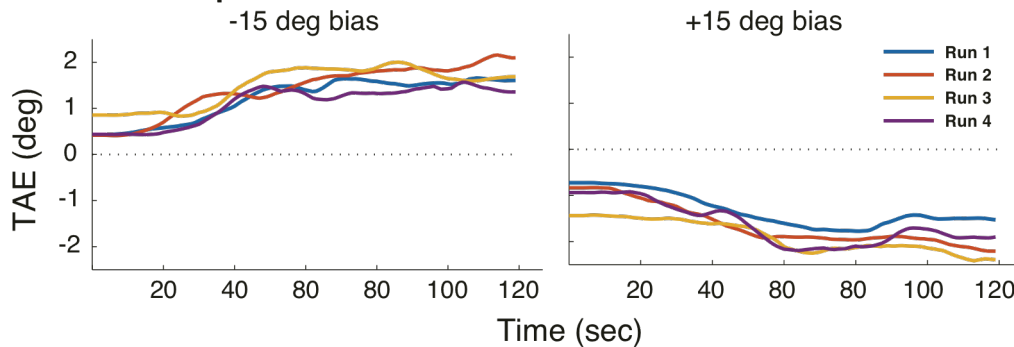
Figure 2.16 Rapid decay across days

The graph shows rapid TAE decay occurring during the transitions from the biased conditions to neutral condition, as a function of testing day. This rapid decay was quantified as the difference between the mean TAE in the initial 10 sec of the unbiased condition and the mean TAE in the final 30 sec of the preceding biased condition. This metric reveals no systematic changes across days. Given the pattern across the 4 days, the lack of fast decay in the -15 deg to neutral condition transition on day 3 is likely an outlier.

In an additional series of analyses, we tested for much shorter-term changes in adaptation dynamics, occurring on the timescale of a single session (i.e. across

runs). For these analyses, we averaged data across days for each of the 4 runs (Fig 2.1.7), and computed the same statistical tests as described above for across-days changes. Similar to the across-days analyses, we found no significant changes in any of the metrics of adaptation dynamics. These analyses suggest that adaptation dynamics tend to be unaffected by experience on both shorter (tens of minutes) and longer (days) timescales.

A. TAE Buildup



B. TAE Decay

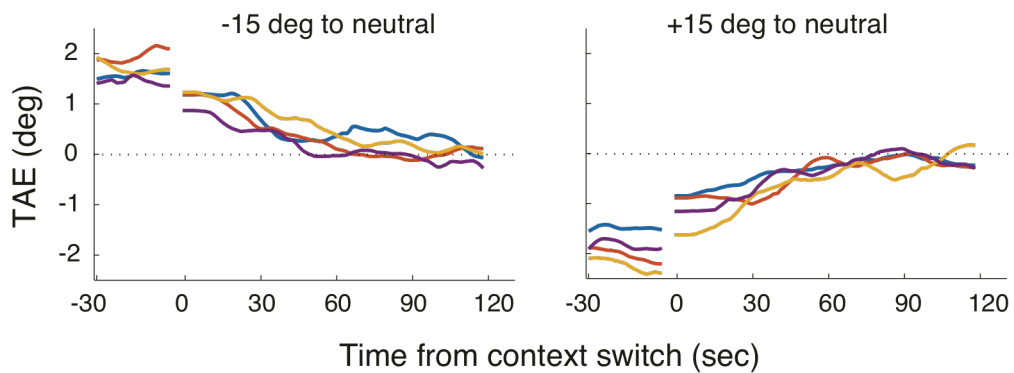


Figure 2.1.7 Timecourse of TAE over runs

The adaptation growth (A) and decay (B) curves are plotted separately for each of the four runs, averaged across the 4 sessions (see plot color legend). In all runs, adaptation produced robust TAE. The growth and decay patterns, however, did not change in a systematic way over the course of the session, in line with our analyses of change over days.

Discussion

In experiment 2.1, we tested whether repeated experience adapting to different contexts led to changes in the buildup and/or decay of the tilt aftereffect. We found no changes in these dynamics, consistent with the hypothesis that adaptation is *not* modulated by prior knowledge.

Nevertheless, it is possible that we failed to find an effect of experience for methodological reasons, rather than the null hypothesis being true. One possibility is that there was interference between our three adapting contexts (Qian, Jaeger, & Aslin, 2012). Specifically, in order to learn the statistical structure of our adapting contexts, the visual system needs to be able to differentiate between the three conditions: That is, the visual system needed to accumulate moment-to-moment orientation statistics separately from each context, so that over time it could learn and use this knowledge to appropriately compensate for the biases via gain changes in its orientation-selective neural populations.

However, such learning will not be possible if the visual system either fails to recognize that there are three contexts in our experiment, or fails to reliably detect contextual transitions. In such a case the learning process may continue accumulating evidence across multiple contextual transitions, for example arriving at the conclusion that there is a single context with a bimodal distribution with peaks at both +15 and -15 deg (or some other incorrect distribution). Alternatively, failure to detect some changes in the input statistics could have led the visual system to infer that the adapting context is unpredictable or unstable, and hence its structure is not worth learning. Whatever the case, it is possible that our failure to observe contextual learning may have been caused by poor

detectability of contextual transitions leading to the failure of the visual system to build appropriate internal models for the three contexts.

Note that we included *two* biased contexts, rather than just one, to make sure that any change in adaptation dynamics would be due to some type of learning, rather than the engagement of previously observed temporally tuned adaptation mechanisms (Bao, Fast, Mesik, & Engel, 2013; Bao & Engel, 2012; Mesik et al., 2013). The reasoning for this is that with one adapting context, an adaptation mechanism with long time constant could become adapted and stay adapted between sessions, while a fast mechanism with short time constant could be used to rapidly adjust to transient changes in the input statistics. In this case, adaptation on subsequent sessions could appear to be faster due to lingering effects of the already adapted slow mechanism. Inclusion of two orientation biases producing opposite, but equally strong TAE thus provides a stronger test of whether the learned adaptor statistics can actually be used to alter adaptation dynamics, since slow temporally-tuned mechanisms would, in this case, cancel each other's effects out. As such, any changes in dynamics across days are unlikely to be explained via such temporally-tuned mechanisms.

We attempted to help subjects distinguish contexts by including a contextual cue in the surround of the adaptor sequence. However, because these cues were essentially a spatial analogue of the temporal statistics of the adaptor sequence, the cues may have been too "low level" for visual system to pick up on. It is possible that a different, semantically meaningful, cue may allow for learning to occur. Indeed, in motor learning literature where context-specific adaptation has been repeatedly demonstrated, such learning critically depends on the cues used to differentiate between trials for different adapting contexts (Howard et al., 2013).

Another reason we may have failed to find contextual adaptation is that both our adapting contexts had very strong bias, since each orientation sample had a 66% probability of being the dominant orientation. As such, the bottom-up drive from these adaptors may have been so strong that there was little need for top-down, experience-driven image to speed the already rapid adaptation dynamics. We chose this adaptor strength in order to increase our signal-to-noise ratio (SNR) for detecting the TAE, but paradoxically, we may have reduced our SNR for finding experience-driven effects.

Finally, although our paradigm tried to loosely mimic the real world in that the adapting contexts were stochastic, yet contained statistical regularities, it differed from real-world experience in a potentially very important way. Specifically, in real world, contexts are generally encountered one by one and the visual input thus reflects the structure of a single environment. However, in our experiment whenever participants were in a biased context, they viewed *two* adaptor sequences that differed in their statistical structure, one on each side of the screen. Because the neutral sequence was always sampled from a uniform distribution, input on half of the screen corresponded to one context, while the other half reflected a different context. It is possible that for contextual learning to take place, the visual system may need a clear signal that the statistical structure of the current context applies to the entirety of the visual world.

Experiment 2.2

In the second experiment, we addressed some of the possible reasons, discussed above, for our failure to find changes in adaptation dynamics.

It is possible that learning of context in the previous experiment was difficult because the adapting contexts were only present on half the screen, and most

enduring contexts in real life may be more global. To add this real world feature to Exp 2.2, the statistics of each context were applied to a larger portion of the screen by using a single, centrally presented sequence of gratings (vs two sequences in Exp 2.1). As before, the orientations in the central sequence were drawn from one of three distributions (-22 deg bias, Neutral, and +22 deg bias), each corresponding to a different adapting context.

In order to further facilitate contextual learning of the orientation distributions, each condition was associated with a semantically meaningful image category (cities, beaches, and mountains), images from which were presented in the background of the adaptor sequences as a contextual cue. This made it more likely that participants would notice contextual transitions, as the changes in the background image category are more salient than the comparatively subtle changes in orientation statistics of the background textures in Exp 2.1.

This experiment also used orientation distributions with greater orientation variability than in Exp 1, with the goal of slowing down the buildup of TAE. As a result, we hypothesized that learning the orientation distributions associated with each context would be more useful for the visual system, since there is greater potential for significant time saving in reaching the optimal adaptation state.

Methods

Experiment 2.2 was run on 6 participants (3 females), all of whom gave informed consent in a protocol that was approved by the University of Minnesota IRB.

To make contexts more similar to the real world (see above), we used just one, centrally presented adaptor sequence that covered the retinotopic location of both the test and match stimuli (Fig 2.2.1). The adapting gratings were 11 deg in

size, had a spatial frequency of 0.75 cpd, and were presented in 1.6 sec top-up periods at a rate of 9.44 Hz. As in the previous experiment, the orientation statistics of these sequences were neutral (i.e. sampled from a flat orientation distribution) in odd blocks and biased in even blocks. To minimize transfer of adaptation to the match stimulus, the spatial frequency of the match was 3 cpd, i.e. 2 octaves higher than that of adaptor and test stimuli (Shapley & Lennie, 1985).

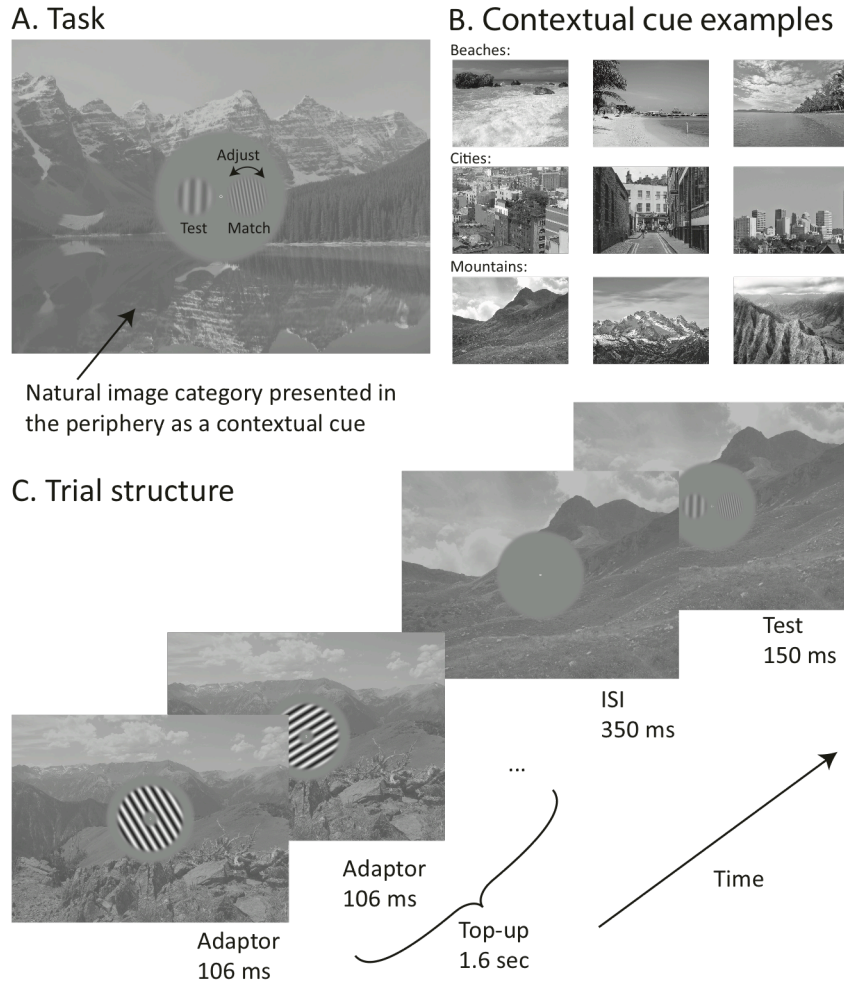


Figure 2.2.1 Trial structure in Exp 2.2

(A) Participants performed the same matching task as in Exp 2.1, except the “match” grating had a higher spatial frequency than the “test” (3 vs 0.75 cpd). The surrounding area contained a natural image, which served as contextual cue about the adaptor statistics. Central stimuli were separated from the background image by a 15 deg central aperture to minimize center-surround interactions between the contextual cues and the grating stimuli. (B) Contextual cues were sample image of beaches, cities, or mountains (overall 5 per category). (C) Trials were interleaved with 1.6 sec top-up periods, during which a large 0.75 cpd adaptor was presented at 9.44 Hz. Following each top-up, there was a 350 ms ISI, followed by a concurrent presentation of the test and match gratings. As in Exp 2.1, each trial could last through multiple top-up periods, and was terminated by subject submitting their match response via a mouse click.

To make our adaptors *weaker* and more *variable* (see discussion above), we sampled orientations in the two biased conditions from von Mises distributions (i.e. roughly Gaussian on a circular domain), as opposed to a combination of

uniform and impulse distributions used in Exp 2.1 (Fig 2.1.2). The new distributions were centered at ± 22 deg and had a concentration parameter of 7.64 (a standard deviation of approximately 7.5 deg). This change made the variability of the presented orientations considerably higher than in Exp 2.1, and consequently reduced the detectability of the bias. To accommodate for this intended weakening of adaptation, we increased the block duration from 120 to 150 sec.

Since the orientation matching task does not require paying attention to the adaptor sequence, we attempted to direct participants' attention to the adaptor via a secondary task. In addition to performing the matching task, participants also were asked to detect spatial frequency shifts from 0.75 to 0.3 cpd in the adapting grating, lasting 212 msec (i.e., duration of two samples in the adaptor sequence). Shifts occurred every 4-8 adaptor top-up periods. Observers indicated detection via a button press.

Because the contextual cues, consisting of oriented patterns of gratings, used in Exp 2.1 did not appear to attract participants' attention, and because real-world contexts are generally more semantically meaningful (e.g. different locations have different statistics), we decided to use more high-level contextual cues (Fig. 2.2.1A-B). To this end, we presented the grating sequences embedded in background natural images (in a gray 15 deg circular aperture). We used three different natural image categories, each of which had 5 different image samples and was associated with one of the three contexts (including the neutral context). The image categories included pictures of cities, mountains, and beaches, and the association between image categories and conditions was counterbalanced across participants.

Note that while in real world environments the contextual category (e.g. forest) and biased statistics (e.g. more vertical energy) are tightly linked, our cue-bias pairings were arbitrary. Although this is a potential weakness of our contextual cues, we chose to do so because finding real context categories with ± 22 deg orientation biases is unlikely to be possible, and more importantly because the usage of such categories could be disadvantageous due to contextual learning effects being already complete from participants' prior experience with those contexts.

We attempted to increase participants' awareness of these semantically meaningful contextual cues in two ways: First, prior to the beginning of each block, sample natural images from the current category were presented for 5 sec at a rate of 2 images per second. These images were shown in isolation, i.e., in the absence of adaptor gratings, and participants were instructed to freely look at them. Second, every 4-8 test-match presentations, the test-match stimuli were omitted, and instead the full background image (i.e. without the central gray aperture that normally underlay the gratings) of the current context cue sample was shown for the same duration. Participants were instructed to freely look at the natural image during these brief periods so that over time, they would become more aware of the contextual cues. Although the efficacy of these two manipulations is unclear, we implemented them to *maximize* the odds that the contextual cues would be associated with the statistics of our adaptor sequences.

Based on participant feedback that the experiment was tiring, we introduced a longer break in the middle of each experimental session. The duration of this break was determined by the participant, but was forced to be at least 1 minute long. The other two inter-run periods (i.e. after runs 1 and 3) contained a 1 minute break, as in Exp 2.1

Observers participated in several practice sessions to become proficient in the orientation matching and spatial frequency change detection tasks. All participants completed three practice sessions with 10 neutral blocks each. Halfway through each practice session, participants received feedback about their speed, average accuracy, and response variability. This way, they had an opportunity to adjust their strategy and see the outcome at the end of the practice session. To be eligible to participate in the main experiment, participants needed to meet performance criteria by the last session: 1) Complete 10+ trials per block, 2) Have across-block mean error range of 1 deg or less, and 3) Have within-block response variability (mean absolute deviation) of 1 deg or less.

All other paradigm details were identical to Exp 2.1.

Results

As in Exp 2.1, adaptation produced reliable tilt-aftereffects. Whereas neutral adaptors maintained the orientation matches around the veridical test stimulus orientation (with a small, statistically significant counter-clockwise bias, $P < 0.05$, $-0.002 - -0.70$ deg 95% CI; see Fig 2.2.3), the two biased conditions (Fig 2.2.2A) induced a robust, repulsive TAE that grew over the course of the block, reaching an average size of 0.9 deg (-22 deg context: $P < 0.005$, $0.42 - 1.28$ deg 95% CI; +22 deg context: $P < 0.001$, $-0.6 - -1.28$ deg 95% CI). This effect then decayed back towards baseline in the following neutral block (Fig 2.2.2B).

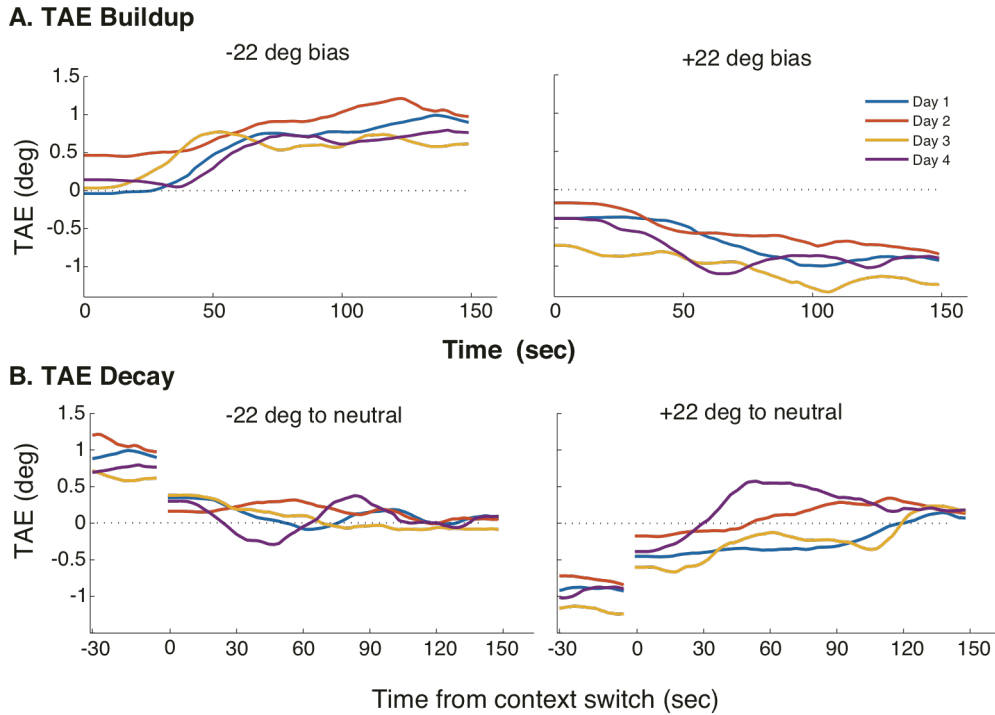


Figure 2.2.2 Dynamics of orientation matching in Exp 2.2

(A) During the biased blocks, perception of test stimuli was subjected to the TAE, which grew stronger over the course of the block. (B) In the subsequent neutral blocks, responses TAE gradually decayed back to baseline.

However, consistent with our previous results, we failed to observe changes in adaptation dynamics over the 4 sessions of the experiment. First, we tested for across-day changes of peak TAE induced by each condition (Fig 2.2.3). Slopes of the linear fit to the peak TAE as a function of day did not differ significantly from zero ($P > 0.27$ and $P > 0.66$ for -22 deg and +22 deg contexts, respectively), suggesting that the overall strength of adaptation stayed constant across days. We found parallel results in an alternative analysis comparing only the difference of peak TAE between days 1 and 4.

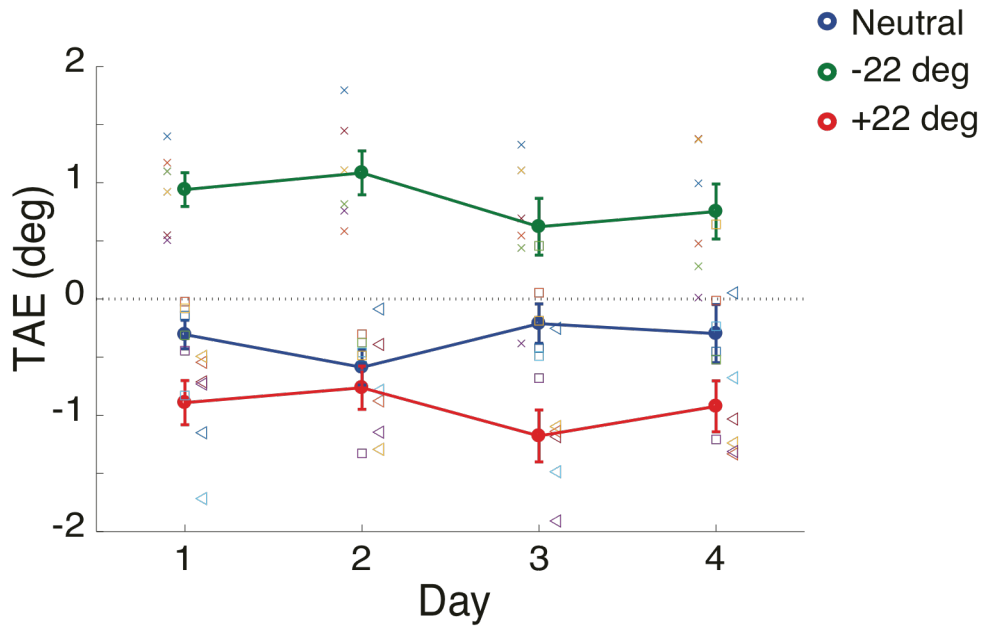


Figure 2.2.3 TAE asymptotes across days

TAE values for each session reflect the average the final 30 sec of each condition. Error bars indicate ± 1 SE. Data from individual participants is plotted in smaller font (x: -22 deg, □: Neutral, ▷: +22 deg), with small x-axis offsets for de-cluttering purposes.

Second, we tested for changes in the speed of TAE buildup. For each context and day, we computed the time to reach 80% of the peak TAE strength and fitted the values for all four days with a linear function. The slope of this fit did not differ significantly from zero for either context ($P > 0.4$ and $P > 0.5$), indicating that the shape of TAE growth did not change over the course of the experiment.

Finally, we tested for changes in the TAE decay following contextual switches from biased to neutral contexts. We compared the time required for TAE to decay to 20% of its peak strength across days, but found the slope of the fit to these values indistinguishable from zero ($P > 0.9$ and $P > 0.1$ for the two contexts). We also tested for rapid decay of TAE following switches from biased to neutral conditions (Fig 2.2.4). This was computed as the difference between the mean of the first 10 sec of the decay function in the neutral condition and the mean of the last 30 sec in the preceding biased context. Linear fits to these decay values as a

function of test day did not differ from zero ($P > 0.46$ and $P > 0.79$ for -22° deg and $+22^\circ$ deg). These results all support the hypothesis that experience does not affect adaptation dynamics

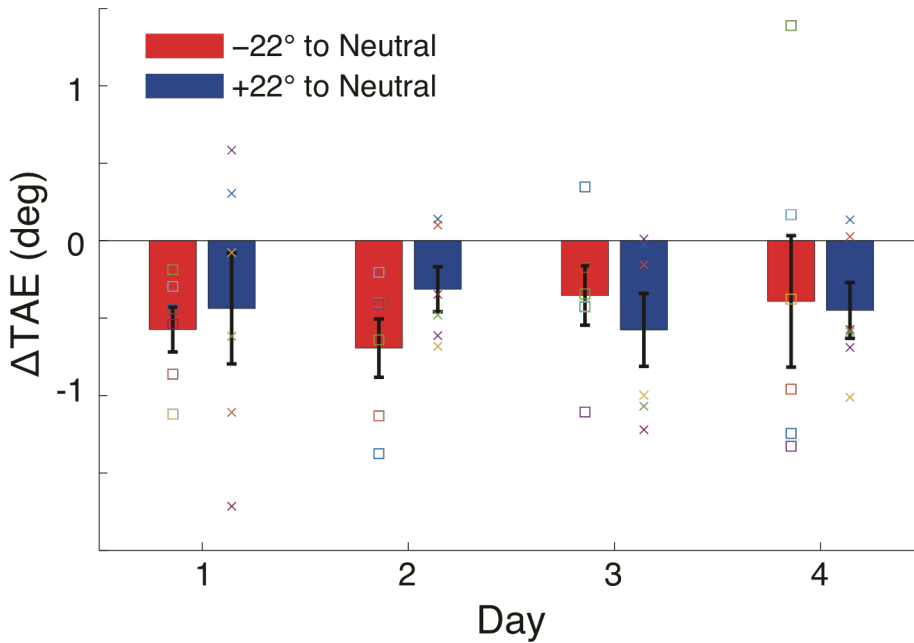


Figure 2.2.4. Rapid decay of TAE across days.
(Same as Fig 2.1.6 above)

Informal post-experiment debriefing revealed that participants did notice the different natural image categories in the experiment, but did not explicitly associate them with different adaptor sequence biases. As such, it is unclear if explicit awareness of adaptor biases would produce different pattern of results, for example via conscious expectation of tilted percepts of the test gratings.

In addition to comparing adaptation dynamics across testing sessions, we also tested for changes in adaptation occurring on a much shorter, within-session timescale. For these analyses, we averaged each of the four runs in a session

across days, and repeated the identical statistical tests as above to test for changes over the course of individual session. We found no within-session changes in adaptation dynamics. Together, these results suggest that repeated experience with adapting to visual contexts does not alter adaptation dynamics at shorter (~50 min) nor longer (days) timescales.

General discussion

If knowledge of the statistical structure of the adapting environment influences adaptation dynamics, then one should observe changes in these dynamics as experience is gained with said statistical structure. In the two experiments described here, we tested this hypothesis by repeatedly adapting participants to three sets of low-level statistical regularities, i.e. contexts, and comparing the buildup and decay of TAE across sessions. We found no evidence of either between-, or within-session changes in adaptation dynamics, consistent with the null hypothesis, i.e., that adaptation processes operate largely in a bottom-up fashion, with the moment-to-moment input dictating the buildup and decay of adaptation.

However, there are several important limitations to our results. First, learning of contexts may happen on a different timescale than the one tested in our experiment. In the real world, the visual system is often re-exposed to the same environments over the course of days, months, and even years, and extracting their statistics could potentially happen on any one of these longer timescales. In our experiment, we tested subjects on a relatively short timescale, where each of four experimental sessions contained ~50 minutes of visual stimulation split between the 3 orientation distributions. It is conceivable that these timescales are insufficient to induce learning. Indeed, it appears that habitual, long-term wearing of colored spectacles leads to faster chromatic adaptation when putting the

spectacles on or taking them off (Engel, Wilkins, Mand, Helwig, & Allen, 2016). Speculatively, one reason why long timescales may be needed for experience-dependent changes in adaptation to take place is that the visual system needs to acquire evidence that the adapting environment has long-term relevance, justifying the devotion of neural resources to storing its parameters.

On the other hand, Dong et al. found changes in the strength of both motion and contrast adaptation to be occurring at timescales comparable to ones in our experiments (Dong, Gao, Lv, & Bao, 2016). In their study, participants adapted to either coherent random dot motion or a high contrast grating in multiple short sessions, which, in their case was sufficient to reveal weakening adaptation effects across days. Although their paradigm contained a higher number of sessions (6 or more, depending on the experiment), the weakening aftereffect strength was already apparent during the early sessions of the experiment. While our results are, on their face, inconsistent, it is possible that the timescale required to induce contextual learning is proportional to the complexity of the adapting environment. For learning to take place in our experiment, a longer timescale could be necessary since we utilized multiple contexts, each with a statistical structure much more complex than in the study of Dong et al.

Another reason for our null results could be that learning comes at a cost of neural resources, and the visual system may only employ it when it is deemed necessary. In the case of a psychophysical experiment like ours, there is little explicit incentive for the visual system to devote resources to learn the statistics of the adaptors. After all, adapting slowly does not pose any behaviorally relevant cost such as a risk of injury, or a failure to obtain rewards. Hence, in line with the principle of least effort, in the absence of incentives, it may be advantageous to simply adapt in a purely bottom-up fashion. On the other hand, in somewhat higher-level visual memory and search tasks (e.g., Chun & Jiang, 1998; Fiser &

Aslin, 2001; Jiang, Swallow, Rosenbaum, & Herzig, 2013), learning of statistical structures of visual ensembles has been widely demonstrated to occur involuntarily and without incentives exceeding the compensation provided by our experiment.

It also remains possible that our contextual cues were not strong enough. That is, although participants generally noticed that we used three image categories in the surround of the adaptor sequences, their lack of awareness that these categories carried information about the orientation biases may have led to the visual system not using them to differentiate between contexts. As such, it is possible that a learning mechanism was engaged, but the failure to detect transitions between contexts prevented effective learning from taking place.

It is also possible that increases in adaptation strength over days were masked by perceptual learning whose effect was to *reduce* the perceptual consequences of adaptation, i.e. aftereffects. Specifically, although adaptation is behaviorally measured by quantifying aftereffects, it is important to remember that aftereffects reflect undesirable perceptual errors (i.e. the “coding catastrophe”; Schwartz, Hsu, & Dayan, 2007; Seriès, Stocker, & Simoncelli, 2009), and thus one conceivable goal of learning could be to correct these errors. As such, weakening aftereffects could be an indicator that later stages of visual processing are learning to reinterpret adaptation-induced shifts in population activity at earlier stages of processing, leading to error correction at the perceptual level. Weakening aftereffects over the course of multiple adapting sessions observed by Dong et al. (2016) could potentially be an example of such perceptual learning. Thus, although we observed neither strengthening nor weakening of TAE, this could potentially be a consequence of a balance of both an increase in adaptation rate *and* reduction in the susceptibility to perceptual aftereffects. While seemingly unlikely, it may be a fruitful future direction to test this possibility by

comparing simultaneously acquired measures of behavioral and neural effects of adaptation.

Our experiments demonstrate the viability of rapidly presenting samples from orientation distributions to induce robust, measurable behavioral aftereffects. While such stimuli have previously been used in electrophysiology (e.g., Benucci, Saleem, & Carandini, 2013; Zavitz, Yu, Rowe, Rosa, & Price, 2016), their use in human psychophysics is more limited (but see, e.g., McGovern, Roach, & Webb, 2014, for adapting to motion direction distributions). This type of stimulus allows for investigation of questions that would be difficult to study with the traditional approach that uses single grating adaptors. For example, using orientation distributions, one can assess how the width of the adaptor distribution, i.e. the stability, affects the adaptation dynamics. Using stimuli sampled from statistical distributions over a variety of visual features may, therefore, prove to be fruitful for future work.

Adaptation can be a rapid process and as such, characterization of the precise shape of its buildup and decay is non-trivial. We chose to use a trial-based orientation-matching task using a computer mouse to obtain relatively densely sampled measures of the current adaptation state. However, in practice our approach may not have been sensitive enough for quantifying changes in dynamics. Specifically, it is possible that neither the rate of trial completion (~10-12 sec on average), nor the amount of response variability (~1 deg mean absolute deviation) were sufficient to capture small changes in speed of buildup/decay or magnitude of TAE. Notably, the flat portions at the beginning of the TAE buildup and decay curves (Figs. 2.1.4, 2.1.6 2.2.2, 2.2.3) are artifacts arising from nearest-neighbor extrapolation from 0 sec to the time of the first trial completion, which often took ~10-12 sec. Consequently, the fine-grained patterns

of TAE buildup and decay at block start, which could potentially contain evidence for across-session changes in adaptation, were not captured by our paradigm.

An additional methodological change that could help the signal to noise of our experiments is spatial multiplexing of the adaptors. That is, under the assumption that adaptation builds up homogeneously across the retinotopic space, a task could be performed at one of multiple locations, while continuing to adapt at the others. allowing for a multi-fold increase in the amount of collected data per unit time. If the noise introduced by shifting participants' attention to multiple locations is small, then the reliability of the TAE estimates over time could be improved, allowing revelation of smaller changes in the shape of these functions.

Finally, it is also arguable that the incorporation of neural measures of adaptation, e.g. via EEG, could prove to be important for capturing changes in adaptation dynamics. Neural measurements are appealing because they directly capture the process of interest (i.e. neural adaptation) and thus eliminate the noise stemming from the task behavior. Moreover, the effects of adaptation could manifest in neural changes that are not straightforwardly reflected in behavioral measures (e.g. equalization or decorrelation across orientation channels, see Benucci, Saleem, and Carandini, 2013), but which could be apparent in neural changes. On the other hand, neural measures such as EEG come with noise of their own, and can require many or long trials (ERPs and SSVEPs, respectively) to allow for computing reliable estimates of neural activity. This is a methodological challenge when trying to measure experience-dependent changes like those investigated by our study, since increases in trial repetitions and duration both constitute experience. In other words, experience effects could already be contaminating the “pre-learning” measures, obscuring the effect of interest. Note, however, that this issue affects any paradigm that requires

multiple task repetitions for denoising purposes, which includes both of our behavioral experiments.

In sum, the two experiments discussed in this chapter showed that repeated adaptation to biased distributions of orientations induces robust TAE, but the dynamics of this effect are relatively unaffected by experience. It remains possible that stronger manipulations or more sensitive measures could still, in the future, find some evidence for these effects. However, our current data make clear that context effects in adaptation are not pervasive. Furthermore, we believe that our work may serve as a useful methodological lesson for both measuring dynamics of adaptation, and using statistical distributions as adaptors.

Chapter 3

Effects of repeated adaptation to biased orientation statistics in altered reality

Introduction

Our surroundings are composed of an array of distinct natural environments, each of which contains different structural regularities that translate into statistical regularities in the sensory inputs they generate (Torralba & Oliva, 2003). Knowledge of these regularities is potentially very useful, as it can guide one's expectations about what objects may be encountered in a given environment, or what actions may most likely lead to desirable outcomes. It also helps guide one's attention in the interaction with the environment. However, beyond these relatively high-level cognitive benefits, it is possible that environmental regularities could also be used to enhance the efficiency of early visual processing, by allowing it to more quickly adjust its neural sensitivities to match the statistics of the current environment.

Visual adaptation, the process through which the visual system calibrates itself to the current environment is a well-studied neural phenomenon (Chapter 1, see also reviews by Clifford et al., 2007; Webster, 2011; again, please forgive the overlap with previous chapters as this will facilitate publishing this chapter as a paper). However, the extent to which it is malleable by one's familiarity with the input statistics is presently unknown. Generally, adaptation is thought of as a "bottom-up" process whereby the sensitivity to a visual feature is adjusted based on the degree to which that feature is present in the visual input. For example, viewing a high-contrast vertical grating for a prolonged period leads to a reduction of perceptual sensitivity to orientations near vertical axis, while orientations around the horizontal axis remain relatively unaffected.

Knowledge of structural regularities present in real-world environments *could* be useful for aiding the visual system in selecting the appropriate feature sensitivities, making the adaptation process faster and/or more efficient. For example, the knowledge that forest environments contain large amounts of contrast at and around vertical orientations could be used by the visual system to reduce its vertical gain immediately upon entering a forest. It is possible that through repeated experience with the statistical regularities present in real world environments, the visual system may learn these regularities and exploit this knowledge to adapt more efficiently whenever that environment is re-encountered. In this chapter, we refer to distinct sets of input statistics as “contexts,” and the speeding of adaptation dynamics by knowledge of these statistics as “context-dependent adaptation.”

In the experiments described here, we test for such context-dependent adaptation. We did this by repeatedly exposing participants to a video feed of their surroundings that was filtered in real time to alter its orientation statistics, generating visual input with statistical regularities not previously experienced by our participants. Comparing behavioral measures of adaptation to these statistics across 3 successive days gave us a unique opportunity to quantify adaptation dynamics as a function of experience with the adapting statistics. We used these data to test whether experience can alter how we adapt.

Experiment 3.1: Speeded contrast adaptation following repeated viewing of vertically deprived visual input.

Introduction

In the first experiment, participants repeatedly viewed a video feed of their surroundings, which was filtered to remove the majority of contrast energy around the vertical orientation axis, for 2 hrs at a time on 3 consecutive days.

Prolonged viewing of visual input with this type of contrast deprivation has previously been shown to induce orientation-specific contrast adaptation; neurons tuned to the deprived orientation raise their gain as manifested through a robust tilt aftereffect (TAE, see Bao & Engel, 2012; Haak, Fast, Bao, Lee, & Engel, 2014). We tested whether the strength of TAE changed from day 1 to day 3 of the experiment. We hypothesized that the adaptation effects in the final session of the experiment should be stronger than effects in the initial session, if repeated experience with viewing novel statistical regularities can result in faster adaptation to those regularities.

Methods

Each participant ($n=12$, one excluded due to not showing reliable adaptation effects) completed three identical, two and a half hour long sessions of adapting to alterations in visual statistics with which they had no prior experience. Subjects viewed their surroundings via a head-mounted display (HMD; nVis Inc. nVisor SX60, 40 deg field of view) that presented them with a live video feed from a camera attached to the top of the HMD (640 x 480 resolution, 30 frames per second; Fig 3.1.1A). Each frame of the black-and-white video was filtered using a Butterworth filter to attenuate its contrast energy along the vertical axis (± 53.45 deg) by 99%, effectively removing vertical contours from the visual input (Fig 3.1.1B).

To maintain an engaged attentional state, participants watched videos of their choice on an online streaming platform. We restricted them to watching live-action content without subtitles, and encouraged watching videos with predominantly daylight scenes so as to keep contrast energy high.

We chose this adaptor, rather than traditional adaptation with high contrast gratings, for several reasons: First, adaptation to this type of filtered input is slower, leaving room for detectable experience-driven changes in adaptation dynamics. Secondly, the repeated, *long-duration* exposure to the filtered input may provide the visual system with evidence that the visual distortion introduced by the filter has long-term relevance, and is likely to be re-encountered at a later time. We reasoned that this would incentivize learning the input statistics, as this knowledge would be expected to be useful. Finally, the error signals introduced within the filtered natural input are semantically meaningful in that the objects do not appear the way they should, which may further push the visual system to adapt faster to correct the distortions.

Each of the three experimental sessions began with a baseline period during which subjects viewed 5 min of unfiltered videos and then completed a behavioral task block to measure a baseline level of contrast adaptation. Afterwards, participants began viewing filtered input, and the strength of adaptation was measured twice, after 30 min and 2 hours of adaptation.

A. Apparatus



B. Vertical contrast deprivation



C. Plaid task

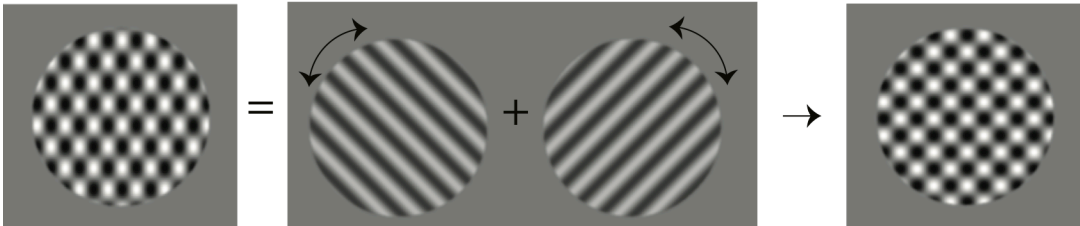


Figure 3.1.1 Experimental setup

(A) Participants wore a head-mounted display with an attached camera. (B) The video feed from the camera was filtered in real time to remove 99% of contrast energy along the vertical orientation axis. Prolonged viewing of this input induced contrast adaptation measured behaviorally with the TAE. (C) The magnitude of TAE was measured using a plaid task. Stimuli were checkerboard patterns consisting of two sinusoidal gratings mirror-symmetric around vertical axis. Participants judged the appearance of the plaid pattern and adjusted the orientation of the component gratings to maximize perceived “squareness” of the pattern.

We quantified adaptation by measuring the TAE using the “plaid task” (Fig 3.1.1C; adapted from Meese & Georgeson, 1996). In each trial, participants viewed brief presentations (200 ms with 2000 ms ISI) of 5 deg plaid patterns consisting of two superimposed 25% contrast, 1.5 cpd sine wave gratings, each tilted by the same amount clockwise and counter-clockwise from vertical. Subjects pressed arrow keys to increase or decrease the tilt of the component gratings in 0.5 or 1 deg steps until the subjective appearance of the pattern corresponded to a square checkerboard (as opposed to one with horizontally or vertically elongated rectangles). Once this percept was reached, subjects confirmed their response by pressing the space bar, triggering the start of the next trial with new, randomized component angles. Blocks of TAE measurement lasted 150 sec each, during which time participants completed as many trials as they could.

Because deprivation of vertical contrast induces gain increases in vertically-tuned neurons in the visual cortex (Bao & Engel, 2012; Haak et al., 2014), neural population responses to the plaid patterns in our task changed systematically with subjects' adaptation state. Specifically, whenever one views, e.g., a ± 45 deg plaid, this generates a pattern of activation across orientation-tuned neurons, which is thought to be interpreted by later stages of visual processing to estimate the pattern's orientations (see, e.g., Schwartz, Hsu, & Dayan, 2007). In an unadapted state, the two components of a plaid should elicit peak responses in neurons tuned to the component orientations, i.e., $+45$ deg and -45 deg, and systematically weaker responses in neurons with dissimilar tuning. This leads to veridical orientations estimates for the component gratings, and hence a square appearance of the plaid pattern. However, following adaptation to vertically-deprived input, vertically-tuned neurons respond more strongly to a ± 45 deg plaid, shifting the distribution of the activation pattern slightly closer towards vertical (e.g. ± 43 deg). This results in a percept of orientations closer to vertical, and so checks that are slightly taller than they are wide. Since the goal in our plaid task is to adjust the plaid to appear square, the participant in this case, would likely move the physical orientation of the plaid components towards horizontal (e.g. to ± 47 deg) to bring the peak activation back to ± 45 deg tuned neurons, achieving a square percept.

In order to minimize response variability unrelated to adaptation, all subjects completed several practice sessions consisting of 5 task blocks with no preceding adaptation. Participants qualified for the main experimental sessions if they were able to complete 10 or more trials per block, their mean task responses varied by less than 1 degree across blocks, and their within-block mean absolute deviations did not exceed one degree. Most participants met these criteria within 4-5 practice sessions.

To test whether any change in adaptation dynamics occurred, we first generated TAE decay curves for each participant by taking each day's raw data for both the 30 and 120 min test times and subtracting that day's mean baseline response. Afterwards, we computed the difference in the decay curves between days 1 and 3, and binned these timecourses into three 50-second bins for statistical analysis. Finally, we used a one-sample t-test to determine whether the data in each time bin came from a distribution centered at 0 (i.e. no difference in TAE between days).

To more completely test the nature of the hypothesized changes in adaptation dynamics, we performed alternative analyses where we fit exponential functions to the timecourses. For these tests, we used bootstrapping methods, since individual curves were too noisy to achieve satisfactory fits. We resampled our data pool with replacement in 1000 iterations. For each iteration, we fitted the mean TAE decay curves of each day with an exponential decay function augmented with a vertical offset term (3 parameters):

$$(1) \quad y(t) = Ae^{-Bt} + C$$

Here the A term corresponds to the peak TAE at the start of the decay function, B is the time constant of the decay, representing the rate of decay, and C is a vertical offset from 0. The C parameter was needed due to occasional observation of TAE reaching an asymptotic state with an opposite sign than the initial peak. Although this type of undershoot was not expected to occur in Exp 3.1, it can be observed, for example, if the internal template for square percept shifts over the course of the experiment. Because of this, we quantified the peak TAE as the difference between the A and C parameters, rather than as just the A

parameter alone. Finally, we also computed the total TAE as the integral over the entire decay function.

For each iteration of the resampling analysis, we computed the change of these fitted quantities between days 1 and 3, and afterwards examined whether the distribution of these differences was reliably different from 0 (i.e. whether 95% of the values had the same sign). Note that this analysis performed group level (as opposed to single subject) fitting, which allowed us to overcome the noisiness of single subject TAE decay curves.

Results

Viewing of vertically deprived video content induced a robust TAE at all test times and sessions (Fig 3.1.2). Over the course of each block, the TAE was initially stronger, and then decayed over time, reflecting deadaptation from the repeated viewing of the test plaid patterns. We tested the strength of TAE at both 30 and 120 min test times by splitting the decay curves into three 50 sec wide time bins, and computed statistics on these bins.

The initial peak strength of the TAE (first bin) was higher at 120 min than 30 min, as adaptation slowly grew in strength ($P < 0.05$, 0.1-0.66 deg increase 95% CI). However, we did not observe growth in the residual TAE at the middle and tail end of the test block ($P > 0.14$ and $P > 0.9$, respectively).

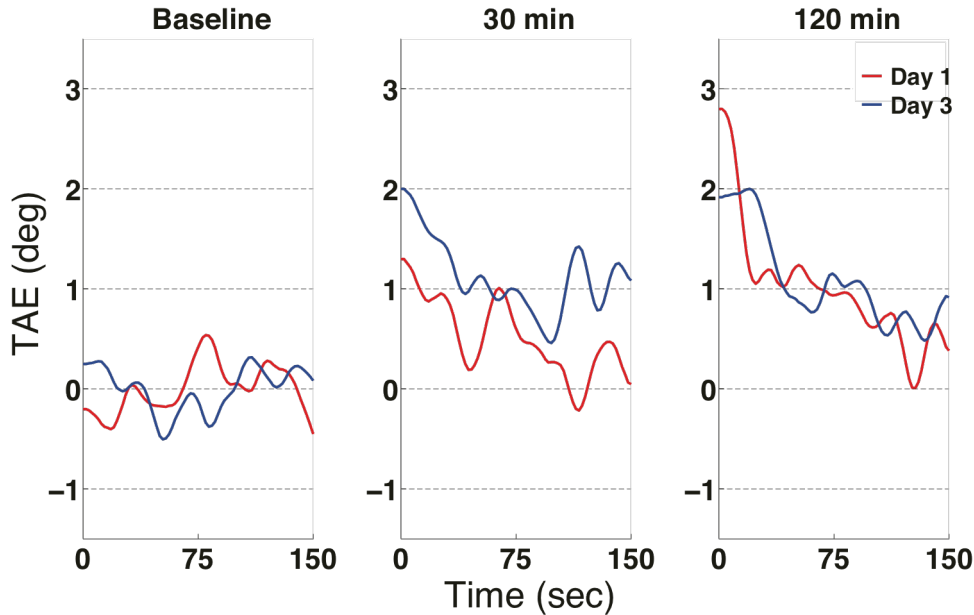


Figure 3.1.2. TAE decay over days

Plots depict average TAE decay at the three within-session test points (sub-plots), for day 1 and day 3 (red vs blue curves) of the experiment. At both 30 min and 120 min test times, we observed robust TAE.

We tested for changes in adaptation dynamics by comparing the decay curves from sessions 1 and 3 (Fig 3.1.3). We observed a significant increase in TAE at the 30 min, but not 120 min time point (Fig 3.1.3, blue vs green line). This difference was significant in 2 out of 3 time bins for the former test time ($P < 0.05$), and none for the latter (all bins $P > 0.4$). Furthermore, although the TAE in the first 50 sec bin grew reliably from 30 min to 120 min on day 1 ($P < 0.05$, right-tailed), this difference was no longer significant on day 3 ($P > 0.22$). This suggests that experience with vertically deprived visual input allowed the visual system to approach an asymptotic state of adaptation at a faster rate.

In an alternative, bootstrapping analysis, we resampled our data 1000 times and fitted the average curve of each sample with an exponential decay function (see Eq. 1 in methods above). While peak TAE and decay time parameters at the 30 min time point both showed trends towards larger values on day 3 (vs day 1),

neither of these trends reached statistical significance. However, the total TAE over the course of the decay curve (i.e. the area under the curve) was reliably larger on day 3 than day 1; this increase was visible in 97.9% of resamplings. We, again, only found such a change for the 30 min, but not 120 min time point. In other words, while there was no evidence for any one specific parameter of the exponential decay function changing at the 30 min time point, the overall *pattern* of the decay function suggests a reliably stronger TAE on day 3 than day 1.

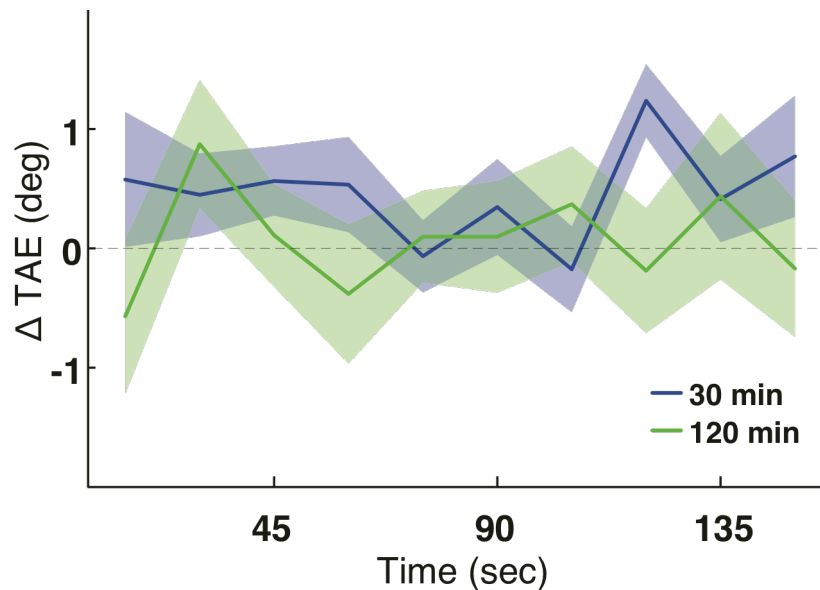


Figure 3.1.3 TAE on day 1 vs 3

The curves depict the average difference between day 3 and 1 of the experiment binned into 10 time bins (15 sec each) for the 30 and 120 min test times (green vs blue). Positive difference reflects stronger TAE on day 3. The error bar depicts ± 1 SE. We found significantly stronger TAE at 30 min time point during the first and last 50 sec of the decay curve. For illustration purposes, the timecourse is divided into 15 sec bins, while statistics were computed using coarser 50 sec bins.

Discussion

In this experiment, we observed that repeatedly adapting to vertically deprived visual input over the course of 3 sessions strengthened adaptation. This difference manifested itself at our earlier, 30 min time point, suggesting that the visual system may have learned to reach an asymptotic state of adaptation

faster. However, since we only tested at the 30 and 120 min points, it is unclear *how much quicker* the visual system actually adapted.

Furthermore, because participants always adapted to vertically deprived input, it is unclear whether our results reflect genuine learning, or slow decay of *temporally-tuned* mechanisms observed in previous work (Bao & Engel, 2012; Bao, Fast, Mesik, & Engel, 2013; Mesik et al., 2013). These studies have shown that prolonged adaptation engages multiple mechanisms tuned to different timescales of adaptation, allowing the visual system to remain adapted to slow-changing input regularities via a mechanism with long time constant, while also compensating for transient changes in input statistics using a mechanism with short time constant. One possible reason why we may have found seemingly faster adaptation on day 3 compared to day 1 is that a slow adaptation mechanism became strongly adapted during the initial session, and remained partially adapted across sessions. As such, the faster adaptation may have resulted from the summed effect of the already adapted slow mechanism and a quickly adapting fast mechanism. While this residual adaptation may predict systematic changes in the performance in the baseline plaid task (which we did not observe in our data), this is complicated by the fact that a fast mechanism can be adapted in opposite direction from the slow mechanism, making their effect cancel out and produce seemingly unadapted behavior.

Although we cannot rule out this account for our results completely, it is relatively unlikely. First, relative to the ~22 hour inter-session interval, the 2 hr session duration is relatively short, making it difficult for effects to last between sessions. Presumably, a 2 hr adaptation period should be unlikely to engage a mechanism with a decay time constant that's an order of magnitude greater than the induction period. Furthermore, the slow mechanism should become re-engaged by the natural, non-deprived input that the participants experience between

sessions (although one could argue that the chromatic differences in the input could cause different neural populations to be engaged by the input during the experiment vs between sessions).

Overall, our results suggest that repeatedly adapting to stereotypical orientation statistics can lead to increased speed of adaptation, although our design does not allow us to determine the magnitude of the speed change.

Experiment 3.2: No changes in contrast adaptation dynamics following repeated adaptation to multiple sets of biased orientation statistics in altered reality

Introduction

Exp 3.1 did not provide the strongest test of the hypothesis that the visual system extracts environmental statistics and re-applies this knowledge when the same environment is later re-encountered. This is because it is possible that the increase in adaptation speed that we observed was due to lingering adaptation effects from previous sessions, as described above (albeit we note that that this possibility is unlikely).

To eliminate this possibility, we designed a pair of followup experiments with *two* contexts that caused *opposite* gain changes in the same orientation-selective neural populations. During each session of these experiments, participants gained experience within both contexts by switching back and forth between them in regular intervals. Under these circumstances, it should be impossible to produce faster adaptation to both contexts that could be explained by lingering effects in long-term mechanisms. This is because lingering gain changes from one context would actually interfere with adaptation to the other context. Increases in adaptation strength for both contexts would, therefore, constitute strong evidence for *context-dependent* adaptation

Methods: Experiment 3.2A

Participants (n=9, one excluded due to not showing reliable adaptation effects) viewed video content in three sessions on consecutive days, as in experiment 3.1. Two adapting contexts were presented at different points in the session: In one context, visual input was deprived of vertical content while the contrast of horizontal content was simultaneously enhanced. In the second context the filtering was reversed such that the horizontal content was deprived while verticals were enhanced (see Fig 3.2.1, left for example images). In both contrast deprivation and enhancement, the contrast energy was reduced/increased by 99% in a ± 25 deg bandwidth around the affected orientation axis.

We chose to use this type of orientation filter for three reasons: First, simultaneous deprivation around one orientation axis and enhancement around the orthogonal axis should, in theory, magnify the TAE since the responses of both the vertically-tuned and horizontally-tuned populations should congruently shift in the same direction after adaptation. For example, deprivation along vertical orientation axis should lead to an *increase* in vertical gain, attracting the peak in the population-level responses elicited by oblique orientations (e.g. ± 45 deg plaid) *towards* vertical. Similarly, contrast enhancement around horizontal orientations should lead to a gain *decrease* along horizontal orientations, pushing the peak in the population level responses to oblique orientations *away from* horizontal. Together, then, these effects synergistically shift population response peak in the same overall direction, leading to theoretically more reliable and possibly stronger TAE.

Second, our filter choice allowed us to better balance the adapting contexts such that the adaptors were similarly strong in both contexts. If we only altered contrast along one axis with contrast reduction in one context and enhancement

in the other context, it is unclear that adaptation to the input generated by the two filters would affect the gain with similar strength. This is particularly an issue because with our naturalistic input contrast enhancement often produced a “clipping” distortion whereby the intended contrast was impossible to display due to exceeding the maximum display luminance, thus preventing the images from accurately reflecting our filter design.

Finally, our two contexts affected the same populations of neurons, but in opposite directions, ensuring that if we found changes in adaptation dynamics, they would not be attributable to lingering adaptation in long-term mechanisms. Specifically, since the second context affects the neural gain in opposite direction to the first context and the durations of exposure were matched, any previous adaptation within long-term mechanisms should be eliminated during adaptation to the next context.

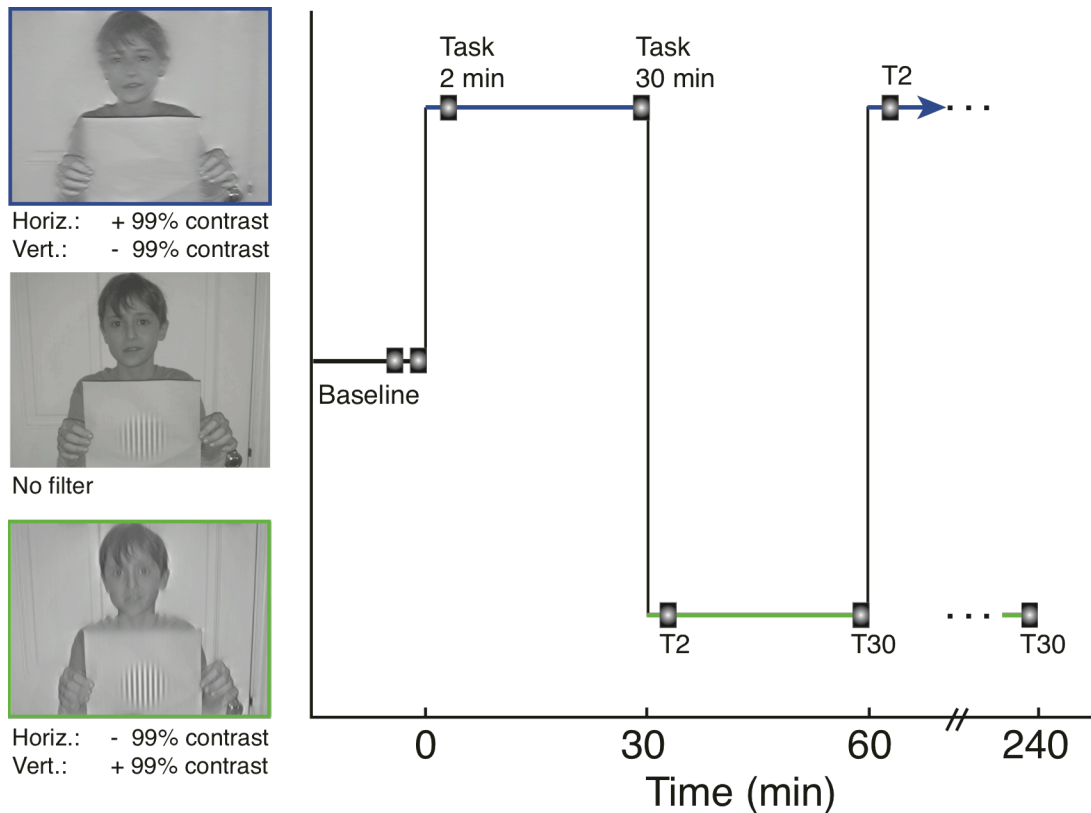


Figure 3.2.1 Experiment structure

Each session began with participants viewing 5 minutes of unfiltered video, followed by a pair of baseline blocks. Afterwards, video frames were filtered using one of two filters that altered vertical and horizontal energy in opposite directions (see example images on the left). Adaptation contexts alternated every 31 min, and TAE was always tested at 2 min and 30 min time points (circular markers on the timeline).

The procedures were the same as in experiment 3.1, with several notable differences (Fig 3.2.1):

1. Each experimental session lasted 4.5 hours instead of 2.
2. Each adapting context was experienced for 31 min at a time before changing to the other adapting context. Contexts reversed back and forth in this A-B-A-B fashion for the entire 4.5-hour period, such that each context was seen 4 times for a total of ~2 hours.

3. The magnitude of TAE was measured at the 2 min and 30 min time points in each context to quantify both rapid and slower adaptation.
4. Following the 30 min task block, participants remained in the current context for an extra minute so that the contextual transition would occur after the participant resumed watching video. We did this, along with verbal announcement that we were changing the “distortion,” to make the context change more salient.
5. Prior to each task block, participants viewed a 1-minute video clip, which was identical for all subjects and blocks. This was done as an attempt to reduce response variability due to differences in adaptation to movie brightness, stemming from participants viewing different video content from one another (since they were able to pick their own movies to watch). Although differences in light adaptation may not predict different levels of TAE, noise may arise, for example, due to differences in the visibility of the plaids.
6. The controls of the plaid task were changed so that lateral mouse movements controlled the orientation of the component gratings. This was done in an attempt to speed up the task by allowing participants to quickly zero in on the square percept by making large movements at the start of the trials.
7. The plaid task was done on a background consisting of a screenshot of the filtered world (as opposed to gray background used in the previous experiment), with image contrast under the plaid stimulus removed using a Gaussian window. This was done in order to provide subjects with a

contextual cue suggesting that the task is still taking place in the same environment as the free-viewing portion of the experiment.

8. A sound cue was added to the task to provide feedback about orientation changes. Specifically, for each half-degree of orientation change, a brief click sound was played, giving the task an added sense of continuity even during the ISIs when the plaids were not seen.
9. The Butterworth filter used for contrast attenuation and enhancement was adjusted to have a narrower orientation bandwidth (from ± 53.4 deg to ± 25 deg), and lower order (from 6 to 3; making its cutoffs less sharp). The purpose of the former change was to prevent overlap in the attenuating and enhancing components of the filter, while the latter change was to reduce image artifacts (e.g. x-shaped artifacts on object corners, etc.).

Results

Consistent with the previous experiment, filtered visual input statistics induced robust TAE in both adapting contexts (Fig 3.2.2). As expected, these effects were opposite in sign for the two contexts. Noting the comparable TAE decay curves for the two adapting contexts, we collapsed the results across contexts (flipping the sign of the second context to align the TAE decay curves), while keeping 2 min and 30 min test times separate. The average TAE across the decay curve was detectable at both the 2 min and 30 min time points (all sessions, $P < 0.05$ for 2 min, and $P < 0.001$ for 30 min, uncorrected).

To test for effects of adapting time generally, we compared the decay time courses for 2 min and 30 min test times. We divided the time courses into three 50 sec bins, averaged the TAE within each bin, and performed statistics on the differences between corresponding bins at the two test times. We found that

following 30 min of adaptation TAE was both stronger and longer-lasting, with significantly higher TAE for the 30 minute test time across the entire time course ($P < 0.01$ in all 3 bins, uncorrected).

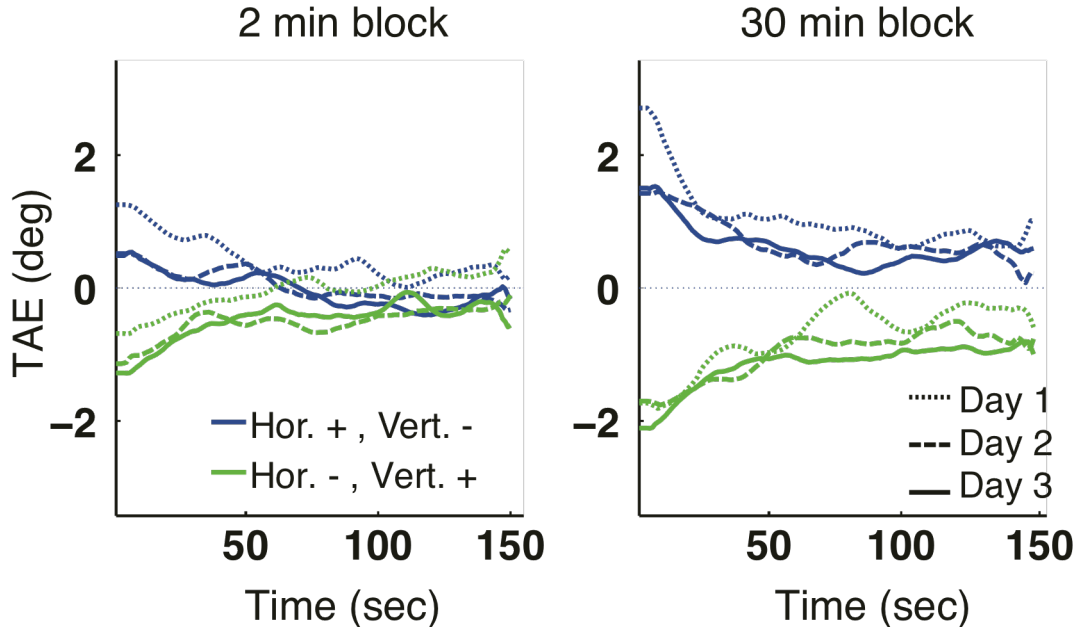


Figure 3.2.2 TAE decay curves

Curves depict TAE decay on all 3 days (see line style legend on the right) in both contexts (see line color legend on the left) at both testing times (2 min on the left and 30 min on the right panel). The aftereffect grew stronger and longer lasting with increased adaptation duration.

To examine the effect of experience on adaptation dynamics, we again quantified changes in adaptation over days by subtracting the Day 1 curve from the Day 3 curve (Fig 3.2.3). However, unlike our original results from Experiment 3.1, we observed no changes in the induced TAE decay curve for either test time across days. That is, the difference between the decay curves from Day 1 and 3 did not significantly differ from 0 at any part of the TAE decay function, suggesting that repeatedly adapting within our two contexts had no effect on the adaptation dynamics (all bins $P > 0.25$, uncorrected). These results were confirmed using a resampling analysis (see Exp 2.1 methods), where none of our measures of

adaptation dynamics (peak, decay rate, and total TAE) showed a reliable change across days.

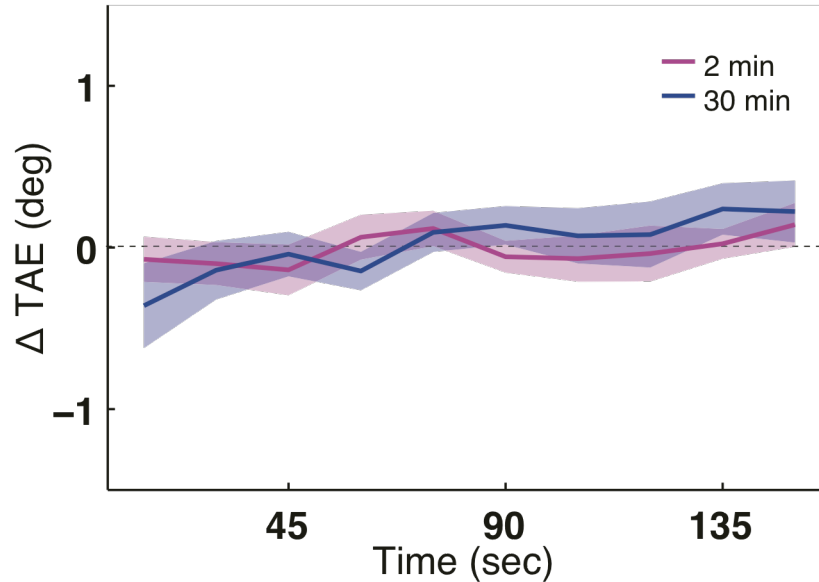


Figure 3.2.3 No changes in TAE across days

The curves depict the average difference between day 3 and 1 of the experiment binned into 10 time bins for the two conditions (pink vs blue). Positive difference reflects stronger TAE on day 3. The error bar depicts ± 1 SE. All time points show no difference from 0 ($P > 0.25$, uncorrected). For illustration purposes, the timecourse is divided into 15 sec bins, while statistics were computed using coarser 50 sec wide bins.

Discussion

In experiment 3.2A, we failed to observe changes in adaptation dynamics akin to those seen in experiment 3.1. Although there are many possible explanations (see General Discussion at the end of this chapter), one major difference between the two experiments was the duration for which each context was experienced continuously. In experiment 3.1, the single adapting context was seen for 2 hours, while in experiment 3.2A, contexts alternated every 31 minutes. As such, one major possibility for why we failed to observe changes in adaptation dynamics was that the rate at which contexts switched was too fast for the visual system to engage its learning mechanisms.

Introduction: Experiment 3.2B

In experiment 3.2B, we decided to re-run the dual-context experiment with timing parameters closely matched to those used in our initial single-context experiment 3.1, allowing the visual system to experience each context continuously for two hours.

Methods: Experiment 3.2B

We ran another 8 participants in an alternative version of experiment 3.2A. One participant's data was excluded due to a failure to observe reliable adaptation effects. All procedures were the same as in the previous experiment, except that participants remained in each context for a period of 2 hours before switching conditions. During this period, we measured the strength of TAE at the 2 min, 30 min, and 120 min time points. At the conclusion of exposure to the 2nd context, participants re-entered the initial context for 2 minutes to allow for an additional test of within-session re-adaptation.

Results

Consistent with our previous results, our manipulation of orientation statistics induced robust TAE (Fig 3.2.4, $P < 0.005$ at all test times except "2 min end", uncorrected), and over the session these effects grew stronger and longer lasting. This growth was significant for the 2 vs 30 min and 2 vs 120 min comparisons, but not between 30 and 120 min. These duration scaling effects were somewhat less reliable than in Exp 3.1 ($P < 0.05$ in 1/3 time bins for 30 vs 2 min comparison (remaining two bins were $P < 0.09$), and 3/3 in 120 vs 2 min comparison), likely due to the number of daily repetitions per conditions being one quarter of the repetition count in Exp. 3.1, leading to noisier decay curves.

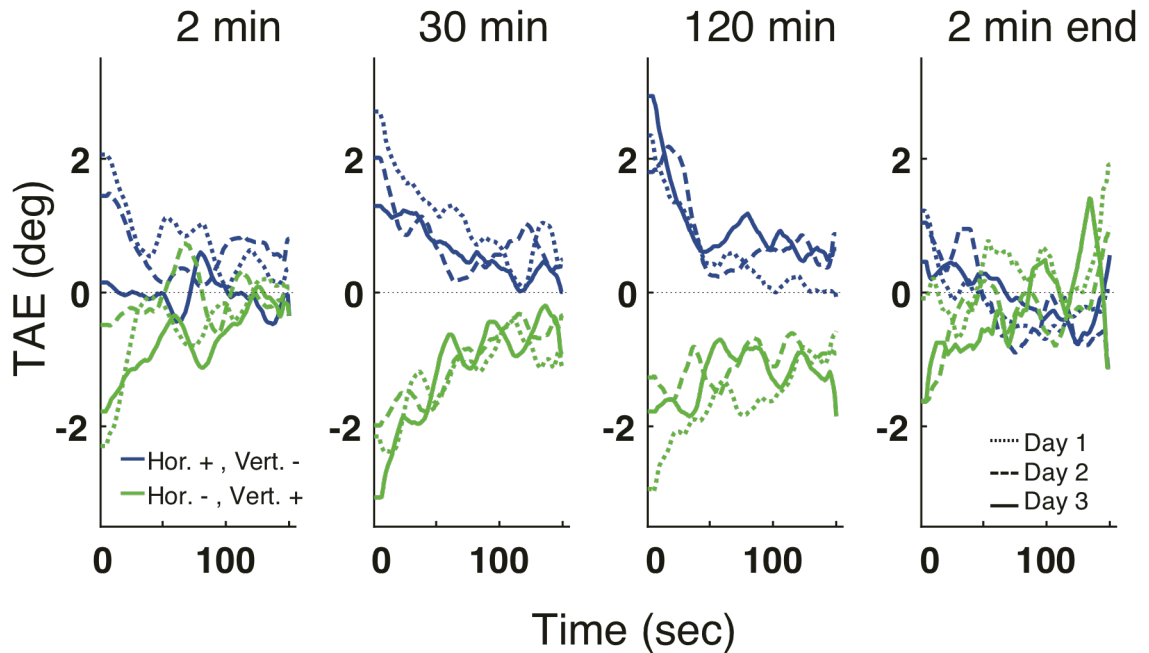


Figure 3.2.4 TAE decay curves

Curves depict TAE decay on all 3 days. The aftereffect grew stronger and longer lasting with increased adaptation duration.

However, as in experiment 3.2A, when we calculated changes in TAE across days (Fig 3.2.5) by subtracting Day 3 curves from Day 1 curves (after averaging the curves for the two contexts), we did not observe reliable changes in TAE across days at any of the test times ($P > 0.05$ in all cases, although the first bin of the 2 min comparison showed marginal significance at $P = 0.0585$, with day 3 showing *weaker* TAE than day 1). These results were generally confirmed with our resampling analysis with exponential fitting (again, see Exp 2.1 methods). We found both a reliably *lower* peak TAE and area under the decay curve on day 3 compared to day 1, consistent with the 3 bin analysis.

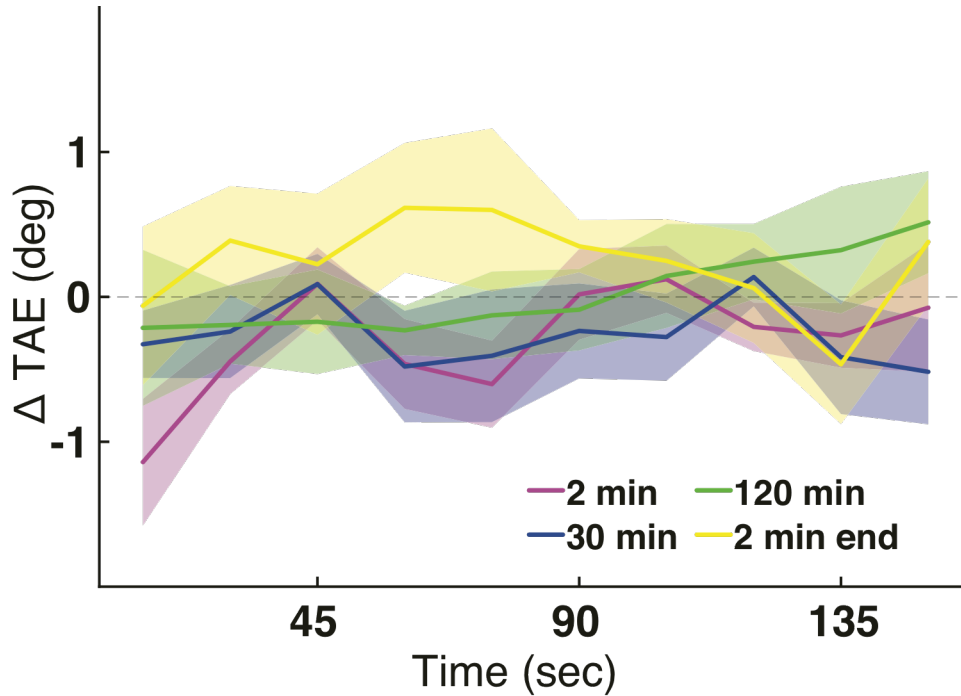


Figure 3.2.5 No changes in TAE across days

The curves depict the average difference between day 3 and 1 of the experiment binned into 10 time bins, with the two adaptation contexts collapsed together. The color depicts testing time. Positive difference reflects stronger TAE on day 3. The error bar depicts ± 1 SE. For illustration purposes, the timecourse is divided into 15 sec bins, while statistics were computed using coarser 50 sec wide bins.

These results thus indicate that perceptual experience may alter adaptation dynamics, although the time and direction at which we observed changes was inconsistent with our results in Exp 3.1.

Discussion

In experiment 3.2B, we observed a reduction of TAE at the 2 min time point on day 3 compared to day 1, in contrast to the absence of changes seen in Exp 3.2A. However, once again, changes at the 30 min time point seen in Exp 2.1 were not replicated.

What could be the reason for the weakening of TAE at the 2 min test time? One possibility is that the filtered input actually became a less potent adaptor, leading to a weaker aftereffect; such results have previously been observed (Dong, Gao, Lv, & Bao, 2016; see *General discussion* below for more details). However, it is unclear why adaptation would weaken on the very short time-scale, while remaining relatively unchanged in the remaining blocks.

Another possibility is that the strength of adaptation at the 2 min point did not, in fact, change, but instead the weaker effects may have resulted from the effects of the preceding 2 hours of adaptation becoming longer-lasting. In other words, on day 3, two hours of adaptation in the initial context may have been stronger than on day 1, making adaptation for two minutes in the second context insufficient to bring the TAE to the level seen on day 1. Although we did not observe any changes for the 2 hour test times, it is noteworthy that TAE decay has not reached 0 by the end of the test block, so it remains possible that the overall duration of decay could nevertheless differ between days 1 and 3.

While it remains unclear what caused the potentially interesting changes at the 2 min time point, we again failed to replicate changes in TAE strength at the 30 min time point seen in Exp 2.1. Together, the results of experiments 3.2A and 3.2B provide little to no evidence that repeated exposure to environments can engage mechanisms allowing the visual system to learn to increase its speed of adaptation.

Experiment 3.3: Replication of the initial single-context experiment

Introduction

Our failure to replicate changes in adaptation dynamics at the 30 min time point in our two-context experiments created a concern that the effect found in the

original experiment may have been spurious. As such, we decided to run an almost identical replication of the initial single-context finding.

Methods

In an attempt to replicate the result from experiment 3.1, we ran a nearly identical paradigm on 11 additional participants, of which 3 were excluded due to not showing reliable adaptation effects.

The paradigm differed from the original experiment in several respects:

1. In addition to testing the TAE strength after 30 min and 2 hrs of adaptation, we added a 3rd test time at the 2 min time point. This allowed us to test for changes in very rapid adaptation effects, and made the paradigm more similar to Exp. 3.2.
2. The paradigm included all task changes from experiments 3.2A-B, including the viewing of a fixed 1 minute pre-task video clip, mouse controls of the task, sound feedback during orientation adjustment, task embedding in the screenshot of participant's surrounding environment, and the use of narrower filter with ± 25 deg orientation bandwidth (vs the wider ± 53.4 deg filter).
3. Since our previous results showed that even at the end of the 150 sec task blocks the TAE was greater than zero, we prolonged the 2 hr testing block to 450 sec. This allowed us to more thoroughly test whether there were any changes in the TAE decay functions.

Results

The average decay curves for each testing time point are plotted in Fig 3.3.1. As in the original experiment, viewing vertically-deprived visual input induced TAE,

although the magnitude was substantially smaller than in the previous experiments (~1 deg vs 2 deg in first 15 sec of the decay curve). The TAE averaged across days and all times within testing blocks was only reliably greater than zero at 120 min ($P < 0.005$ in the initial 150 sec of decay), and marginally significant ($P < 0.057$) at 30 min. Statistics on binned time courses showed a significant TAE in 1/3, 1/3, and 5/9 bins for 2, 30, and 120 min, respectively. As before, the TAE strength exhibited duration scaling, although we only observed reliable increases in the comparison between 2 min and 120 min test times ($P < 0.05$ in all 3 bins). These weaker adaptation effects, and the absence of TAE in 3 excluded participants, are likely attributable to the narrower filter bandwidth compared to the initial experiment.

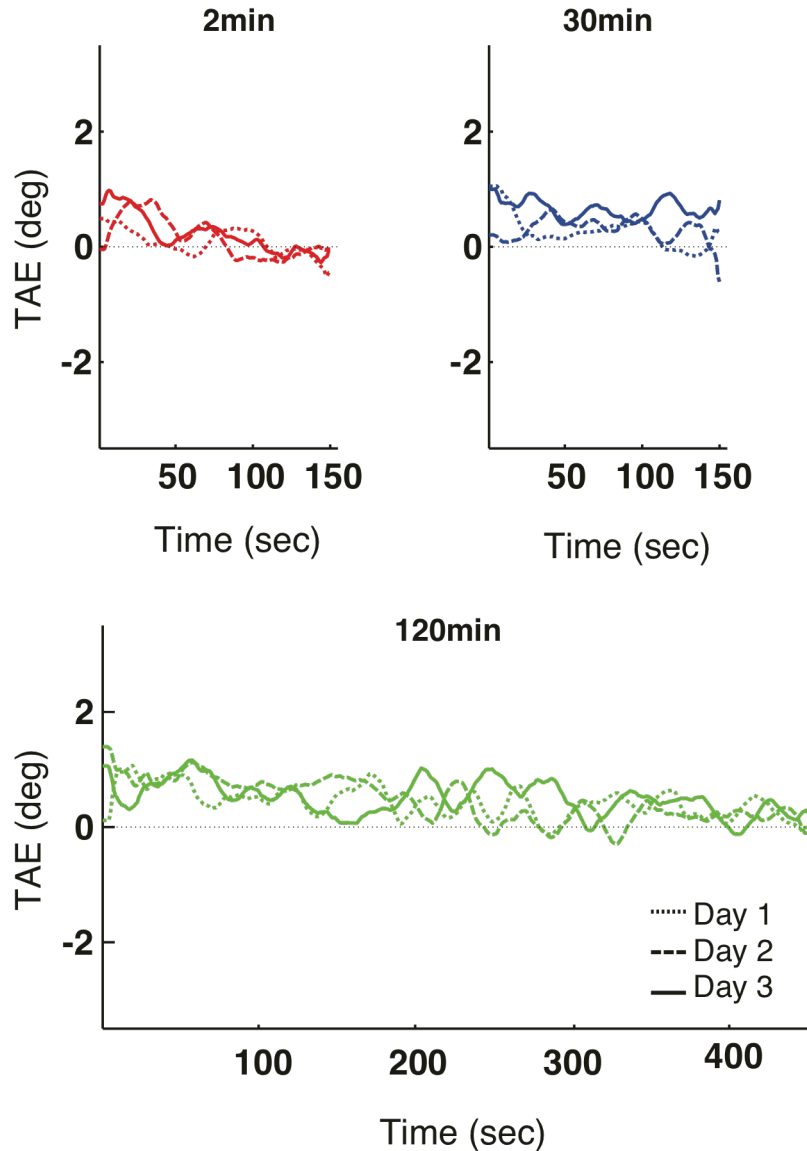


Figure 3.3.1: Average TAE decay curves
 Curves depict TAE decay on all 3 days. The aftereffect grew stronger and longer lasting with increased adaptation duration.

To test for across day changes in adaptation strength, we computed the Day 3 – Day 1 difference in TAE for all 3 time bins (each 50 sec wide, 9 bins for the 120 min block), and compared these against zero. Critically, we observed a slightly increased mean TAE on day 3 at the 30 min time point (Fig 3.3.2), significant in

the bin corresponding to the final 50 sec of decay ($P < 0.05$). While weaker, this result is consistent with those observed in Exp 2.1.

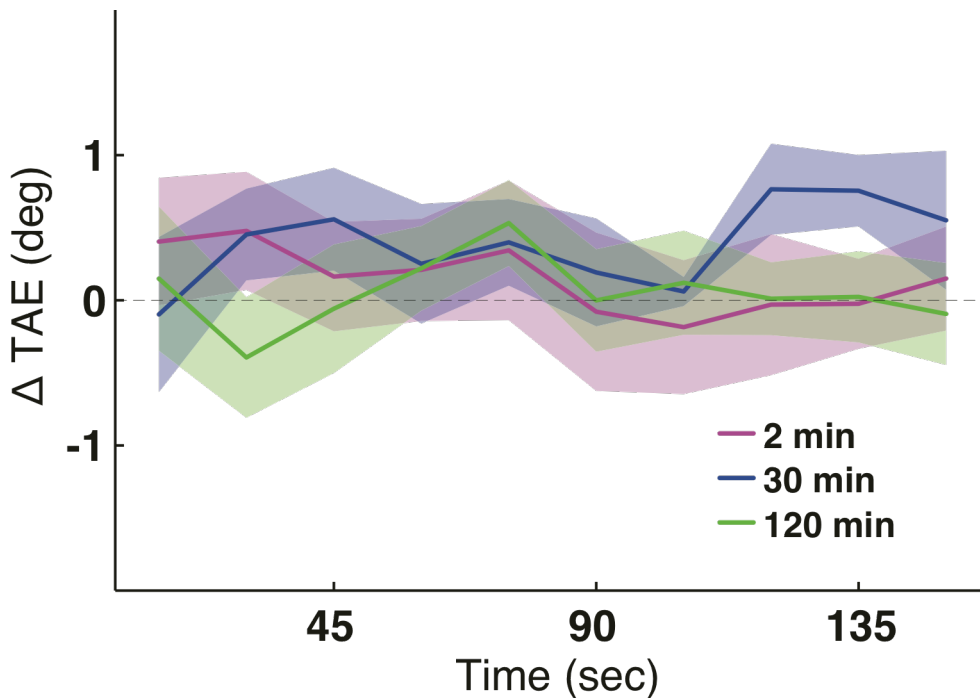


Figure 3.3.2 Slight changes in TAE across days

The curves depict the average difference between day 3 and 1 of the experiment binned into 10 time bins. The color depicts testing time. Positive difference reflects stronger TAE on day 3. The error bar depicts ± 1 SE. Results for 150-450 sec in the 120 min are not depicted, but were similar to the initial 150 sec. For illustration purposes, the timecourse is divided into 15 sec bins, while statistics were computed using coarser 50 sec wide bins.

Additionally, we repeated the day 1 vs 3 comparisons using resampling analyses combined with exponential function fitting (see Exp 2.1 methods). Consistent with results in Exp 2.1, we found no reliable changes in fit parameters corresponding to either the peak TAE strength or the rate of decay, but found significant increase in the total TAE (area under the curve) for the 30 min time point (97.7% of iterations exhibited such an increase in TAE).

Discussion

In this final experiment, we attempted to replicate our original finding that repeated adaptation to vertically-deprived, naturalistic input speeds adaptation

dynamics. Although our paradigm induced much weaker effects than Exp 2.1, we observed a small yet significant increase in TAE strength at the 30 min time point, consistent with our original result in Exp 2.1.

It is notable that the narrower orientation bandwidth of the filter used in the present experiment produced weaker TAE than the original experiment (compare Figs 3.1.2 and 3.3.1). This, in combination with the single-subject TAE decay curves being relatively noisy, and the subject sample size being smaller, likely translated into lower SNR of the present experiment, which may have played a role in a somewhat weaker effect in this replication (i.e., 1/3 vs 2/3 significant bins). It is possible that further replication attempts could find more reliable effects of experience if the filter bandwidth and sample size were matched to the original experiment.

Based on these results, we believe that repeatedly viewing visual input with low-level statistical regularities may induce small increases in the speed of contrast adaptation.

General discussion

In this study, we conducted four experiments testing how repeated exposure to natural visual input with particular orientation statistics influences adaptation dynamics. In three experiments we observed small, significant changes in adaptation dynamics over the course of three sessions, whereas one experiment showed no such changes. Taken together, these results suggest that under conditions created within our experiments, contrast adaptation may exhibit some experience-dependent malleability, albeit these changes appear to be relatively small.

Across the experiments, the key variable that seemed to matter in inducting experience-dependent changes was whether the experiment contained one or two adapting contexts. In both single-context experiments, we saw consistent changes at the 30 min test time, whereas in the dual-context experiments we only saw a significant change at the 2 min test time in one of the two experiments. Because of the inconsistent results in the dual-context experiments and the opposite direction of the one significant effect relative to our hypothesis, we are cautious in interpreting it as a successful demonstration of context-dependent adaptation. Nevertheless, further work may be warranted to investigate the reliability of the effect and its neural mechanisms.

In light of the null effects in dual-context experiments, what do our single context results mean? On the one hand, it remains possible that the effects found in the single-context experiments may have stemmed from changes in slowly decaying adaptation mechanisms lingering across days. The dual context experiments were designed to eliminate this possibility since each context caused opposite gain changes, making it impossible for one slowly decaying mechanism to facilitate next-day adaptation in both contexts. Our failure to observe context-dependent adaptation in these experiments means our initial concerns cannot be ruled out. On the other hand, there are several reasons why the lingering effects explanation seems unlikely (see discussion under Exp 3.1). Instead, we believe that our single-context results do, in fact, reflect a more profound change in how our participants adapted as they gained experience with the adapting environment.

While our experiments were designed to test for context-dependent adaptation, it is possible our significant results could reflect a context-independent changes in the adaptation rate. Specifically, rather than learning the orientation statistics, experience with the filtered visual input may have changed how much the visual

system was willing to adjust the gain based on the moment-to-moment error signals. Increased rate of adaptation may have resulted, for example, from learning that the statistics of the filtered input in the single context experiments were stable, and did not change unexpectedly. In contrast, the input statistics in the dual context experiments went through drastic changes in each session, potentially reinforcing the more “cautious” adaptation rate. This type of modulation of adaptation rate based on environmental consistency has previously been shown in motor adaptation (Gonzalez Castro, Hadjiosif, Hemphill, & Smith, 2014). However, if context stability was the key variable in our experiments, it is puzzling that we did not observe changes in adaptation rate in Exp 3.2B, where each context was observed for the same continuous duration as in Exp 3.1 and 3.2.

While this possibility is intriguing and deserves further attention, the rest of this chapter will discuss our results in light of our original hypothesis, i.e., that experience allows the visual system to adapt faster via context-dependent adaptation.

The significant single-context results we observed are promising; however there are a number of factors that could have played a role in our effects being relatively small and mostly absent in the dual-context experiments.

Insufficient learning incentives

One variable that may play an important role in contextual adaptation is the extent to which there are *incentives* to learn. It is possible that the visual system requires ample evidence that the adapting context has long-term relevance, and thus its learning mechanisms may be engaged only on a slower timescale than we were able to test in our experiments. In real life, visual contexts are often

encountered hundreds of times over the course of many months, and years. Compared to this, the three-day span of our experiment may have been far too short to induce learning (especially when having to simultaneously learn statistics of two contexts). Consistent with this idea, habitual wearers of colored lenses, with years of experience, have recently been shown to not experience chromatic aftereffects when taking their glasses off, whereas people without such prolonged experience show significantly slower aftereffect decay (Engel et al., 2016).

Another source of evidence that may be used by the visual system to decide whether to engage learning processes is the presence of behaviorally relevant error signals experienced during adaptation. Specifically, if the visual system is put in a situation where being unadapted is disadvantageous, perhaps because accomplishing one's behavioral goals becomes more difficult, then this may incentivize learning to more effectively adapt within that environment. Although our filtering distorted the appearances of objects in the video feed seen by subjects, this may not have provided very strong error signals, particularly because participants generally watched videos passively, and did not experience any obvious behavioral costs from slow adaptation. Consistent with this, recent work by Fulvio and Rokers (2017) shows that explicit feedback about one's behavioral performance in a 3D perceptual task is crucial for learning to use sensory cues embedded into the task. As such, a possible future direction may be to test whether the addition of stronger error signals into the experimental paradigm facilitates experience-dependent changes in adaptation. For example, participants could play video games, build puzzles, or do other tasks that induce meta-cognitive awareness of their impaired performance.

Interference in learning mechanisms

In our two context experiments (3.2A and B) we only observed small change at the 2 min block in Exp 3.2B, where adaptation showed an apparent weakening over days. The relatively weaker learning may have resulted from destructive interference between learning induced in each context. That is, even if the visual system has the capacity to create the kind of internal models of the environment that allow for rapid context-dependent adaptation, the system needs to know when to update each of these contextual models (Qian et al., 2012). If it fails to recognize contextual transitions, and hence continues updating a single model, then learning accumulated during one context will be eliminated by learning induced by the subsequent context.

Although we did explicitly announce contextual changes to our participants, it is possible that in the real world, contextual transitions arise in a way we could not mimic through these relatively unnatural announcements. For example, real world contexts likely generally correspond to different physical locations, and hence contextual transitions may be signaled through activity in location-selective populations engaged during physical transitions between environments, or simply through cognitive awareness that one is transitioning from one environment to another. If this were the case, then a more appropriate experimental paradigm would involve associating different input statistics (i.e. image filters) with different physical or virtual (e.g. different video games) locations.

Insensitive measures

It is possible that in both types of experiments, our behavioral effects may have been either too small or too noisy to capture changes in adaptation across days. To maximize our sensitivity to small adaptation effects, we trained our participants on the plaid task extensively, but the behavioral noise may nevertheless have remained large enough to obscure small changes in TAE

magnitude. Likewise, subtle changes in the decay rate may have also been obscured by relatively long period required to complete each trial (~10 sec). Indeed, individual TAE decay curves varied considerably in their shape and noisiness. As such, future work on this topic may benefit from new behavioral measures of TAE that are less noisy and faster-to-complete, as well as the use of other tools for quantifying adaptation effects, such as EEG or fMRI.

When is contextual-learning desirable?

A more general, theoretical consideration arising from this study is the question of the circumstances under which context-specific adaptation is desirable. Although familiar visual contexts are abundant in one's natural environment it may not be efficient for such knowledge to be used for contrast adaptation. For example, it is possible that the neural and energy costs associated with maintaining mechanisms for experience-dependent gain changes outweigh their benefit of slightly faster adaptation speed. After all, at the neural level, sensory adaptation is known to operate very quickly (e.g., Benucci, Saleem, & Carandini, 2013; Zavitz, Yu, Rowe, Rosa, & Price, 2016).

Additionally, even in highly structured visual environments, the dynamic nature of perception stemming from constant eye movements and navigation through the environment results in the moment-to-moment visual input falling onto any one receptive field being highly variable. As such, the benefits of using the knowledge of average input statistics to enhance adaptation efficiency may be negligible.

On the other hand, the intentional nature of perception, whereby one selects where to look based on the knowledge of the objects in the surroundings and one's behavioral *goals* may serve to be a much more powerful source of information for altering adaptation dynamics. For example, while navigating

around one's workplace while going to a meeting, the visual input is highly predictable due to the knowledge of the building layout, positioning of furniture, etc. The input stemming from this kind of active perception within familiar environments is often subject to less input stochasticity than more passive visual experience (e.g. watching an unfamiliar movie), and hence may benefit from contextual adaptation. Indeed, a number of recent studies show that top-down *expectations* have significant perceptual and neural consequences (e.g., Kok, Brouwer, van Gerven, & de Lange, 2013; Kok, Failing, & de Lange, 2014; Kok, Jehee, & de Lange, 2012), including in the facilitation of contrast adaptation (Pinchuk-Yacobi, Dekel, & Sagi, 2016).

While top-down expectations may control some contextual effects in adaptation, it is possible that the knowledge of statistical regularities in different environments may nevertheless be beneficial for adaptation of other visual features. Color (Engel et al., 2016), blur, optic flow, image texture statistics, frequency of different facial features, etc., may all be highly predictable in specific situations and/or environments, and thus may be good candidates for being subject to contextual adaptation. For example, the blur levels experienced when wearing spectacles versus not having them on are generally quite predictable, as are ambient light levels at different times of day. Thus spectacle-contingent blur adaptation and time-of-day-contingent luminance adaptation could both be fairly useful types of contextual adaptation.

Consistent with this, Yehezkel et al. (2010) found that following prolonged, 4 hr adaptation to anisotropic blur, participants showed no aftereffect when the blurring lens was removed, whereas a group adapting for just 2 hours experienced a robust aftereffect. Furthermore, when the 4-hr participants were brought in for 2 sessions, they showed a progressive increase in the adaptation effects across days. These results suggest that extended experience with a

predictable geometrical distortion may allow the visual system to learn to rapidly switch between functioning in distorted and undistorted contexts, perhaps through context-dependent adaptation.

On the other hand, contrast and motion, two arguably less predictable low-level features, have been shown to induce weakening adaptation effects as a function of repeated experience with them (Dong et al., 2016). It is unclear why our pattern of results (including those presented in Chapter 2), with the exception of the 2 min block in Exp 2.2B, differs from those of Dong et al., but one possibility is that the experimental paradigm of Dong et al. utilized considerably simpler and predictable adaptors, leading to different rates of learning. Specifically, their adaptors generally contained one level of coherent motion or one orientation at a set contrast level, making it easier for the visual system to learn the stimulus parameters. In both our grating and naturalistic input experiments, there was a much greater degree of stochasticity in the moment-to-moment input, making the visual system's structure learning difficulty significantly greater. Moreover, our dual-context experiments made the learning difficulty greater still by introducing the need to discriminate between contexts and updating appropriate internal models. Nevertheless, it is noteworthy that consistent with Dong et al., our dual-context experiment, 2.2B, showed weaker TAE at the 2 min time point on day 3 compared to day 1. As noted earlier, however, this apparent weakening could potentially be a consequence of *strengthened* TAE in the 120 min block of the preceding condition, rather than actual weakening of adaptation.

While the results of Dong et al. were highly robust, it is also notable that the direction of adaptation changes with experience was opposite to what one may expect if the visual system learns to adapt *faster*. In fact, their results may better be interpreted as the visual system learning to *correct* the coding catastrophe, i.e. learning to reinterpret adaptation-induced shifts in the patterns of population

activity in early visual areas. That is, one's visual system may be learning the correct mapping between physical features and the activities they generate under adapted conditions. Although this kind of *perceptual learning* may occur in tandem with actual changes in adaptation dynamics, disentangling how much of each phenomenon takes place is non-trivial. In fact, an apparent *no change* in behavioral effects across days can potentially occur if the adaptation dynamics changes and perceptual learning are balanced just right (i.e. stronger neural adaptation with partially corrected readout at higher level may appear as no change). It is possible that the relatively weak magnitude of the experience-dependent effects that we observed was, in part, due to this balance between adaptation and perceptual learning.

As a final note, it should be acknowledged that our relatively mild effects have a positive implication for a sizable body of already published literature. Specifically, many adaptation studies (e.g. on animal models) assume that tasks can be repeated over many blocks and sessions, and results then be averaged for noise-reduction purposes. If adaptation dynamics changed with experience, then learning effects could conceivably distort some of the conclusions drawn within these studies. The relatively small effects in our results provide evidence that perhaps there will not be a need to re-interpret results that rest upon the assumption that adaptation is a hard-wired process with fixed dynamics. On the other hand, much of animal work requires months of task training during which animals view the task stimuli orders of magnitude more frequently than our participants did. Our results do not apply to this body of work, as profound experience-dependent plasticity may very well be occurring at these very long timescales.

Chapter 4

Final thoughts

In this dissertation, I explored the hypothesis that the visual system can improve the efficiency of its adaptation processes by learning and utilizing the structural knowledge of commonly encountered environments, or contexts. Specifically, we hypothesized that repeated exposure to adapting contexts would lead to adaptation that's either faster or stronger.

Although contextual-adaptation mechanisms appear intuitively useful, probing their existence experimentally is complicated. Not only is it difficult to capture rapid adaptation dynamics psychophysically (so as to be able to observe subtle changes due to experience), but given the relative scarcity of prior studies of contextual adaptation, the conditions under which its mechanisms become engaged (if they indeed exist) are poorly understood. In particular, there are plethora of variables such as the experiment duration, learning incentives, type of contextual cues used to indicate contextual changes, strength of behaviorally relevant error signals, and others that may be highly relevant to whether the visual system utilizes contextual adaptation. However, due to limited time and resources, it is impossible to test and optimize all of these parameters. Consequently, null results are difficult to interpret as they may simply reflect poor parameter choices. While one could rightly point out that this problem affects all behavioral science, it is particularly salient in cases where little prior work exists that could be used to constrain parameter choices for new experiments.

The work in this dissertation is a set of attempts to find evidence for context-specific adaptation while tackling the above issues.

Our single-context results in Chapter 3 provide novel evidence that contextual adaptation may indeed occur, and extend upon the previous work demonstrating interactions between experience and adaptation (Dong et al., 2016; Engel et al., 2016; Yehezkel et al., 2010). To our knowledge, our results are not predicted by current models of visual adaptation, which generally do not consider adaptation to be malleable through experience. At the same time, our unsuccessful attempts to produce similar results in our dual-context experiments make the interpretation of the single-context results somewhat complicated, as it is unclear whether the changes in adaptation rate across days reflects the kind of a learning mechanism outlined throughout this dissertation. In particular, we were not able to demonstrate that the visual system has the flexibility to discriminate between different statistical structures of environments and apply appropriate knowledge from previous experience. As such, one important goal for future work will be to further explore the nature of these experience-dependent changes, both behaviorally and through neuroimaging.

While the dual context experiments did not yield significant changes in adaptation dynamics (with the exception of the 2 min point in Expt 3.2.2), it may be informative to explore the reasons for this by comparing their paradigms.

The importance of contextual cues

As elaborated in discussion of both Chapter 2 and 3, the most likely theoretical lesson from the dual context experiments is that appropriate choice of *contextual cues* may be crucial for successful contextual learning. In our monitor experiments, we attempted to use both low level oriented cues that were embedded with statistical structures matching the adaptor sequences, as well as meaningful natural images with no statistical similarity to the adaptors. On the other hand, in the experiments utilizing filtered video, we did not build in explicit contextual cues other than a verbal announcement of “distortion” changing

whenever we switched the context. However, we reasoned that the stereotypical way in which the appearances of objects in participants' surrounding were distorted may have nevertheless served as a powerful cue.

Given that we obtained null results in the monitor experiments, we believe that the likely reason was that none of these cues captured the aspects of real world environments that the visual system utilizes for differentiating contexts. Consequently, contextual switches led to destructive interference with learning that may have occurred in the previous context, preventing context-specific adaptation from taking place (for detailed discussion, see Chapters 2 & 3). Indeed, as outlined in Chapter 1, for successful context-specific *motor* adaptation, the choice of contextual cues is crucially important (Howard et al., 2013).

Thus, in light of our results a key question is what cues may the visual system be able to utilize? To this end, examination of real world contexts may provide likely possibilities. For example, real world contexts generally occupy different physical locations, making it possible that signals associated with spatial navigation may be critical for context-specific adaptation. If this were true, then contextual adaptation effects may reveal themselves under conditions where participants move, either physically or virtually, to different locations, each associated with different adapting statistics.

Secondly, real world contexts are not only *meaningful* (e.g. forests, restaurants, parks, etc.), but they are also tightly linked to the statistical regularities in the visual input. That is, forests have high prevalence of near-vertical contrast energy *because* they contain a large quantity of trees. As such, the knowledge (from vision, or other senses) that one is in the vicinity of trees may be a powerful cue that the vertical gain should be reduced. This aspect of real environments was

not fully captured in any of our experiments. In the monitor experiment (2.2), associations between adaptors and image categories used as cues were arbitrary, violating the logic above. In the filtered video experiments, the objects in participants' surroundings were the vehicle of adaptation, as in the real world. However, unlike in the real world, the context identity could be inferred from the changes in the appearance of objects not the changes in the distribution of objects themselves (which were identical across contexts). As such, perhaps our contextual manipulation was implemented at a lower level of processing than it is in the real world. One way in which future work could address this hypothesis is by measuring effects of experience on adaptation within virtual environments where low-level biases in orientation, contrast, or color, would be generated through changes in the *distributions of objects* appearing in each context.

Timescales of contextual exposure

In addition to an appropriate choice of contexts and their cues, long duration and high frequency of exposure to visual contexts are likely also critical factors for inducing contextual adaptation. In real life, contexts are usually experienced repeatedly, and for long durations. We designed our experiments to include both of these features, but due to practical limitations, neither could be closely matched the real life experience. In our single context experiments, we saw significant changes with 2 hours of adaptation repeated 3 times, suggesting that 2 hours may be enough for inducing contextual adaptation. However, it is unclear if similar results could be obtained with shorter durations (e.g. 30 min). Across all the dual context experiments, we utilized 2 min, 30 min, and 2 hour adapting durations, but only found one significant effect for the 2 hour duration. Because the direction of this significant result was opposite from what we expected, it is unclear whether reflects a real phenomenon, or a false positive (but see discussion in Chapter 3 for a possible explanation that involves adaptation strengthening across days). If it indeed is a real effect, then these results can be

interpreted as longer adapting durations being important for contextual adaptation.

Unfortunately, although we *think* that long adapting durations are important, the fact that the contextual cues we used in dual-context experiments may have interfered with learning (see above) make it hard to draw strong conclusions. In fact, the durations and cues in the dual context experiments are confounded such that the cause of our null results could be attributed to either or both of them. As such, it is possible under appropriate conditions, contextual adaptation could arise even with relatively short timescales. Perhaps a more practical approach for future work, however, would be to assess the importance of longer timescales through attempting to replicate our *single*-context results with shorter adapting durations.

Need for methodological advances

Besides the more theoretical considerations, we believe that the work in this dissertation also taps into some methodological issues related to the measurement of adaptation effects. In particular, because adaptation is a rapid process that is modulated not only by the adaptor, but also by the test stimuli used for measurement, quantifying the dynamics of its buildup and decay is complicated. To get a single estimate of the current aftereffect magnitude, participants typically require several looks at the stimulus to refine their response. However, due to the dynamic nature of adaptation, the stimulus appearance often changes from moment to moment *within* a given trial, diminishing participants' confidence about their responses. This, paradoxically, leads to participants often needing *more* looks at the stimulus convince themselves that their response is accurate, which ultimately reduces the temporal resolution of the data even further.

In the case of our experiments, we were interested in comparing adaptation dynamics across days, and thus our goal was to create a procedure to measure the shape of its underlying function with dense temporal sampling. For this reason, we chose the plaid and orientation matching tasks to be controlled using a computer mouse, so that participants could intuitively make both large and fine adjustments very quickly. However, perhaps due to the logic outlined above, in practice neither of these tasks resulted in a trial completion rate that we hoped for (generally for low-noise baseline results, participants needed ~10 sec or more per trial).

Our struggle to obtain fast, fine-grained measure of adaptation using a matching task poses a question of whether a different task would be more appropriate? With their frequent use for measuring adaptation, staircase procedures may be the natural candidate (Cornsweet, 1962). In staircases, a perceptual state such as the magnitude of TAE is estimated through iterative, step-wise updating of the stimulus based on participant's perceptual judgments. On every trial, the stimulus appearance depends on the previous responses (e.g., if counter-clockwise response was given, then next stimulus is subjected to a clockwise orientation increment) and over time, the procedure converges on (and oscillates around) a behavioral threshold, e.g. orientation that subjectively appears vertical.

On one hand, it is undoubtedly true that given their built-in serial dependence, staircases should be more robust (than matching tasks) to perceptual fluctuations, which likely played a role in our experiment. As such, it is possible that staircases *may* be better suited for capturing small changes in the peak TAE strength. At the same time, staircases would arguably be a less trustworthy approach to capturing changes in the *shape* of buildup and decay, since the staircase state can only accurately track the true magnitude of an aftereffect if it is already near the actual aftereffect magnitude. This is problematic particularly

when the tracked process is rapid, like adaptation. Staircases could, nevertheless, still be viable for measuring the shape of adaptation if participants were provided with multiple step-size options well-matched to the magnitude of the measured effect, and the onset of the adaptation buildup or decay began only once the staircase caught up with the current perceptual state.

One goal for future work could be to develop better techniques for behavioral measures of adaptation dynamics. As discussed in Chapter 2, a possible extension of current techniques would be to utilize spatial multiplexing of adaptor and test stimuli, such that for each time point in the adaptation buildup or decay, multiple measurements are obtained at different locations in the visual field. This way, the aftereffect magnitude at each time point can be estimated with lower uncertainty, leading to higher fidelity measures of adaptation dynamics.

Another potentially useful goal would be to create novel approaches to analyze data from matching tasks (like those used in our experiments) in a way that utilizes not only the final response, but also the intermediate within-trial behavior. For example, given the stimulus parameters at the start of the trial, the initial direction of mouse movement puts an upper/lower bound constraint on the adaptation magnitude, as does every within-trial reversal in the stimulus adjustment direction. This data, which is generally discarded, could be combined in some weighted combination with the actual responses to, again, produce a more reliable estimate of the shape of aftereffect buildup and decay.

Conclusions

All in all, the work in this dissertation demonstrates that, at least under some conditions, the visual system has the flexibility to change its adaptation dynamics through experience. Although I did not demonstrate these experience driven-changes in multi-context experiments, I believe that further experimentation with

methodological adjustments, some of which are discussed above, may prove to be more successful.

Finally, as a more general note, this work was inspired by considerations of how vision operates in the real world and integrates bottom up signals with previous experience. I believe that although simpler experiments focused on purely bottom-up visual processing can be very informative, in the long run the above philosophy will be critical for generating hypotheses aimed at understanding the flexibility of the visual system.

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