



Volume 101
Number 1
February 2012

Published quarterly
by the
American Psychological
Association

ISSN: 0096-3445

Journal of Experimental Psychology: General

Editor
Julian J. Gottman

Associate Editors
Tom Curran
Klaus Fischer
Derek Griffin
Rajkumar Kulkarni
Michael Kubacki
Rebecca Lerner
Ira Markovits
Bob Rothbart
Sharon Thompson-Schill

www.apa.org/pubs/journals/xgp

Predicting Object Features Across Saccades: Evidence From Object Recognition and Visual Search

Arvid Herwig and Werner X. Schneider
Bielefeld University

When we move our eyes, we process objects in the visual field with different spatial resolution due to the nonhomogeneity of our visual system. In particular, peripheral objects are only coarsely represented, whereas they are represented with high acuity when foveated. To keep track of visual features of objects across eye movements, these changes in spatial resolution have to be taken into account. Here, we develop and test a new framework proposing a visual feature prediction mechanism based on past experience to deal with changes in spatial resolution accompanying saccadic eye movements. In 3 experiments, we first exposed participants to an altered visual stimulation where, unnoticed by participants, 1 object systematically changed visual features during saccades. Experiments 1 and 2 then demonstrate that feature prediction during peripheral object recognition is biased toward previously associated postsaccadic foveal input and that this effect is particularly associated with making saccades. Moreover, Experiment 3 shows that during visual search, feature prediction is biased toward previously associated presaccadic peripheral input. Together, these findings demonstrate that the visual system uses past experience to predict how peripheral objects will look in the fovea, and what foveal search templates should look like in the periphery. As such, they support our framework based on ideomotor theory and shed new light on the mystery of why we are most of the time unaware of acuity limitations in the periphery and of our ability to locate relevant objects in the periphery.

Keywords: eye movements, prediction, anticipation, ideomotor theory, peripheral vision

A striking characteristic of our visual system is its nonhomogeneity. On the retina, for instance, spatial resolution drops steeply toward the periphery to a 10th of its maximum value at an eccentricity of 20° (Land & Tatler, 2009). As a consequence, objects can be processed in detail only within an astonishingly small region of about 2° around the center of gaze corresponding to foveal vision. However, in stark contrast with this spatial inhomogeneity, the visual field seems, at least most of the time, to be uniformly detailed across a much larger visual angle than expected based on what is known about the nonhomogeneity of the visual system.¹ In fact, the impression of visual awareness of the environment in detail and high resolution is so strong that most people are unaware of how poor their visual acuity is in the periphery (Dennett, 1991, 2001).

Approaches to solve this “real” mystery of visual perception (O’Regan, 1992) have primarily focused on eye movements as a

tool to overcome acuity limitations (e.g., O’Regan, 1992; O’Regan & Noë, 2001). Because our eyes are in constant motion, any part of the scene can become the center of vision where perception of detail is possible. We first briefly review these approaches. We then introduce a theoretical framework based on ideomotor theory that focuses on the crucial role of feature prediction across eye movements. This framework assumes that predicting the perceptual consequences of eye movements allows recognition of peripheral objects to set in already prior to a saccadic eye movement, thus concealing acuity limitations in the periphery. Moreover, the framework suggests that predictions are used to anticipate not only how peripheral objects will look like in the fovea but also what foveal search templates should look like in the periphery. The latter factor, that is, predicting the peripheral appearance of objects, is assumed to be a critical factor in visual search. These new assumptions derived from the ideomotor framework are tested in three learning experiments.

This article was published Online First May 12, 2014.

Arvid Herwig and Werner X. Schneider, Department of Psychology and Cluster of Excellence, “Cognitive Interaction Technology,” Bielefeld University.

This work was supported by a grant from the Excellence Cluster “Cognitive Interaction Technology (CITEC),” awarded to Werner X. Schneider, and by German Research Council (Deutsche Forschungsgemeinschaft; DFG) Grant He6388/1-1, awarded to Arvid Herwig and Werner X. Schneider. We thank Katharina Weiß for her constructive and helpful comments on a previous version of this paper.

Correspondence concerning this article should be addressed to Arvid Herwig, Department of Psychology, Bielefeld University, P. O. Box 100131, D-33501 Bielefeld, Germany. E-mail: aherwig@uni-bielefeld.de

¹ It is known that we can easily break the impression of uniformity by testing, for example, our ability to read words in a text positioned just a few lines below our current center of gaze (e.g., Land & Tatler, 2009). However, there is some dispute in the literature of whether such active tests of peripheral vision are helpful in describing our daily impression of the visual field (e.g., Dennett, 2001; Noë, 2001). It is likely that these tests address access consciousness but not phenomenal consciousness (Block, 2012). To clarify this issue, we asked normal (i.e., naïve) perceivers about the rough extent of their visual field that seems highly detailed. The result of this informal survey revealed that the reported visual angle is much larger (around $\pm 20^\circ$) than what one would expect on the basis of the spatial inhomogeneity of the visual system.

In a nutshell, these experiments show how the mechanism of transsaccadic feature prediction derived from ideomotor theory can help to answer the question of why we are most of the time unaware of acuity limitations in the periphery. Moreover, this research sheds new light on primate's ability to locate relevant objects in the periphery. As such, it reconciles several seemingly separate fields, like object recognition, visual search, action control, and learning.

The Impression of Uniformity of the Visual Field

In general, two approaches to explain the impression of uniformity can be distinguished. The first class of approaches assumes that retinal nonhomogeneities are concealed by some kind of compensation mechanism working on internal representations. That is, in the course of visual perception, processing of visual information supplied via the retina leads to a detailed internal representation of the external world that gives rise to the experience of seeing a rich and detailed world. Although, for example, the existence of visual metamers (i.e., stimuli that differ physically but look the same; Freeman & Simoncelli, 2011) shows that such a representation cannot be pictorial, there is much evidence indicating the existence of detailed and sparse representations that are retained and combined across eye movements (cf. Henderson, 2008; Irwin, 1992).

The second class of approaches takes a different view, trying to avoid the question of how internal representations give rise to visual consciousness. According to the sensorimotor contingency theory of vision (O'Regan & Noë, 2001), seeing can be conceived as probing the external visual world by acting (e.g., moving the eyes). That is, the impression of seeing everything uniformly detailed comes into existence by the fact that checking this impression requires probing the external world by shifting attention in the first place. Thus, like the refrigerator light seems to be always on whenever one opens the door, visual detail seems to be uniformly distributed whenever one tries to check it by moving the eyes. As a consequence, the impression of uniformity is considered an illusion due to the immediate availability of detailed information in the external world (O'Regan, 1992). Importantly, in this framework, seeing without moving the eyes is a rare exception that cannot be considered as "seeing" . . . in the normal sense of the word" (O'Regan, & Noë, 2001, p. 947).

Although suggesting fundamentally different answers to the question, whether detailed information is represented internally or externally, both viewpoints stress the critical role of eye movements to build up the impression of uniformity. However, given human's tremendous ability to identify objects in target pictures at presentation rates shorter than the saccadic latency period (e.g., Potter, 1976; Thorpe, Fize, & Marlot, 1996), one might even wonder whether such an impression sets in already prior to saccadic eye movements, that is, before a given visual scene can be actively explored by moving the eyes. In the following section, we elaborate on prediction mechanisms in perception and action that we think are crucial in concealing acuity limitations in the periphery.

Predictive Mechanisms in Perception and Action

The past decades witnessed a great deal of research trying to understand how predictions guide perception and action (e.g., Bar,

2011; Hommel, Müsseler, Aschersleben, & Prinz, 2001; Hughes, Desantis, & Waszak, 2013). Interestingly, this increased interest in predictive mechanisms has surfaced in parallel in a number of seemingly independent fields of research. For instance, research on the fundamental question of why memory exists has led to the suggestion that memory's primary purpose is to generate predictions driving our perception and action (cf. Bar, 2011). Accordingly, memorized experiences are thought to enable a *proactive prediction* about the nature of the actual sensory input and, thus, constitute our perception of the world as much as it does incoming information. Likewise, predictions have been studied extensively to explain the experience of a stable visual world despite retinal image shifts accompanying eye movements (e.g., Duhamel, Colby, & Goldberg, 1992; McConkie & Currie, 1996; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011; Sommer & Wurtz, 2006). During the last two decades, this line of research was further boosted with the discovery of cells in retinotopically organized brain areas that increase their activity if a planned saccade is going to bring a stimulus into the cell's receptive field (Duhamel et al., 1992). This anticipatory activation has been explained differently, either as a shift of receptive fields (Duhamel et al., 1992; Melcher, 2007) or as a transfer of activation for attended targets (Cavanagh, Hunt, Afraz, & Rolfs, 2010; Rolfs et al., 2011). In general, such a *predictive remapping* process can help keep track of target *locations*. However, according to Krauzlis and Nummela (2011), "one of the main unanswered questions is whether these same types of mechanisms are involved in the stable perception of visual objects [or put differently] . . . whether similar remapping can keep track of object *identity*" [emphasis added](p. 131). To address this question, we think it is worthwhile to take a closer look at another line of research, that is, ideomotor theory, dealing with (identity) prediction in action selection and control (cf. Herwig, Beisert, & Prinz, 2013).

The ideomotor framework was proposed more than 150 years ago to answer the question of how voluntary action is possible at all (James, 1890; Lotze, 1852). In essence, ideomotor reasoning assumes that actions are cognitively represented by their sensory effects on the body and environment (for recent reviews, see Hommel, 2009; Nattkemper, Ziessler, & Frensch, 2010; Shin, Proctor, & Capaldi, 2010). As a consequence, action and perception share a common representational code (Prinz, 1990) and can be regarded in some sense as one and the same thing. Importantly, links between movements (m) and their sensory effects (e) are assumed to arise from learning. Once established, these movement–effect associations can become functional in two ways. First, associations allow predicting the outcome of given movements by means of forward computation (m→e). Second, these associations allow selection of appropriate movements given anticipatory effect representations by means of backward computation (e→m). Accordingly, the ideomotor framework states that voluntary actions are selected and controlled by a prediction or anticipatory activation of the action's perceptual consequences.

Up to now, the majority of studies supporting the ideomotor framework focused on manual actions like key presses or grasping movements (e.g., Elsner & Hommel, 2001; Herwig, Prinz, & Waszak, 2007; Herwig & Waszak, 2009, 2012; Kunde, 2001; Waszak & Herwig, 2007). However, manual movements are not the only kind of voluntary action, and there is no a priori reason why the ideomotor framework should be restricted to one specific

action modality. In fact, with an average of three to four saccades per second, eye movements are one of the most frequent primate movements under voluntary control. Moreover, eye movements, as a fundamental action as well as a perceptual device (Schneider, Einhäuser, & Horstmann, 2013), can be considered a prime candidate for investigating the ideomotor framework (Huestegge & Koch, 2010). Thus, according to the ideomotor framework, voluntary eye movements should also be selected and controlled by a prediction of their perceptual consequences or effects (for first theoretical considerations of eye movements in an ideomotor framework, see Wolff, 1984). Recent studies gathered first evidence for the idea of an effect-based control of eye movements (Herwig & Horstmann, 2011; Huestegge & Kreutzfeldt, 2012). For example, participants in the Herwig and Horstmann (2011) study were first required to saccade to the left or right to neutral faces, changing facial expression to happy or angry after the gaze fell on them. This acquisition phase was conducted to establish new movement–effect associations. In a subsequent test phase, happy and angry faces that had been previously presented as action effects served as imperative stimuli for a saccade to the left or right. Those participants who received a congruent mapping (e.g., who should saccade on the presentation of a happy face to the left side, if their previous saccades to the left triggered a happy face) were significantly faster, indicating that the perception of a learned effect activated the movement with which it was associated. Moreover, in the course of experiencing the saccade–effect relationship, saccades were directed more often to the mouth region of a neutral face about to change into a happy one and to the eyebrows regions of a neutral face about to change into an angry expression. Because the change in facial expression always followed the saccade, this latter result indicates that eye movements were guided by their predicted sensory effects on the environment.

One might object that when it comes to basic saccade control, effects on the environment are rather rare, which might thus render the effect-based control of eye movements an exceptional case. However, due to the visual system’s nonhomogeneity, each eye movement is accompanied by a direct perceptual effect on the retina. That is, prior to a saccade, peripheral objects are only coarsely represented, whereas objects are represented with high acuity when foveated (see Figure 1a). In the following, we suggest that it is exactly this perceptual effect of eye movements that should be the target of a predictive mechanism to control and select voluntary eye movements.

Feature and Identity Prediction Across Eye Movements

The nonhomogeneity of the visual system poses a number of challenges to the visual system. That is, while the eyes sample the environment via fast ballistic movements, the so-called saccades, the visual system has to keep track of relevant object locations as well as object features to assure stable and detailed perception. Our framework addresses this latter challenge by focusing on two prototypical scenarios (see Figure 1b).

The first scenario is about *object recognition*, or the question: Which objects are in the periphery? This question is, for example, important whenever objects appear in the periphery. In such a situation, the visual system has to make a decision whether to look at one of the objects or not. To assure a task-dependent guidance

of eye movements (e.g., Land & Tatler, 2009), this decision should be based on a first guess about the object’s identity. Crucial for determining object identity, for recognizing an object, are visual features. Low- and midlevel visual features are extracted in the ventral stream of the human and monkey brain prior to the determination of object identity (e.g., DiCarlo, Zoccolan, & Rust, 2012; Liu et al., 2013; Rousset, Thorpe, & Fabre-Thorpe, 2004). There is already good evidence that recognition of peripheral objects starts prior to saccades (e.g., Demeyer, De Graef, Wagemans, & Verfaillie, 2009; Kotowicz, Rutishauser, & Koch, 2010; Nuthmann, 2014). For instance, postsaccadic object identification is faster and more accurate, if the object’s identity does not change across the saccade—an effect known as the *preview benefit* (Rayner, McConkie, & Zola, 1980). How might this first guess about the identity of peripheral objects be achieved? Our approach assumes that peripheral object recognition is achieved by a *trans-saccadic feature and identity prediction*² mechanism (see Figure 1b, Phase 2, upper section). That is, before the eyes actually move, the visual system makes a prediction about what the peripheral object will look like in the fovea after saccade execution. Importantly, “look like” implies to predict not only object identity in the classical sense of the term (i.e., assigning objects to high-level categories) but also predict perceived visual features of the object. The computation of features seems to be a necessary requisite of object recognition (e.g., DiCarlo et al., 2012; Liu et al., 2013; Rousset, Thorpe, & Fabre-Thorpe, 2004). In other words, the attentionally selected presaccadic coarse peripheral information (saccade target) is used for predicting the much more precise postsaccadic foveal feature and identity information. First supporting evidence for this claim comes from studies investigating the predated effect (Deubel, Irwin, & Schneider, 1999; Hunt & Cavanagh, 2009). Here, participants believe 40–200 ms prior to the movement of the eye that they have already moved their gaze to the periphery. This might indicate that the predicted foveal perceptual pattern prior to saccade execution is confused with the actual visual impression—a sharper and clearer visual foveal image—after the saccade leading to a temporal misperception.

The second scenario in which the visual system needs to take nonhomogeneity into account is *visual search*, or the question: Where are relevant objects in the periphery? While searching for a particular object, like, for example, a pair of shoes, we typically have a more or less detailed representation about what our shoes look like. This idea, namely, that visual search is based on a foveal search template, is also reflected in current computational models addressing the role of eye movements during visual search (e.g., Zelinsky, 2008). However, if search templates reflect foveal target representations, the question arises of how the visual system can find target objects in the periphery where spatial resolution is poor. We suggest that visual search is based, once again, on a prediction mechanism. But in this second scenario visual search performance is based on predictions about how a foveal search template should look in the periphery (see Figure 1b, Phase 2, lower section). That

² We use the term *identity prediction* in the sense of Hughes et al.’s (2013) term “motor identity prediction,” which “refers to prediction of the identity of a sensory event based on an action performed by the participant” (p. 135). Because one may also consider object identity as a high-level feature of an object (e.g., computed in IT cortex), we are going to use *feature prediction* as the broader and more neutral term hereafter.

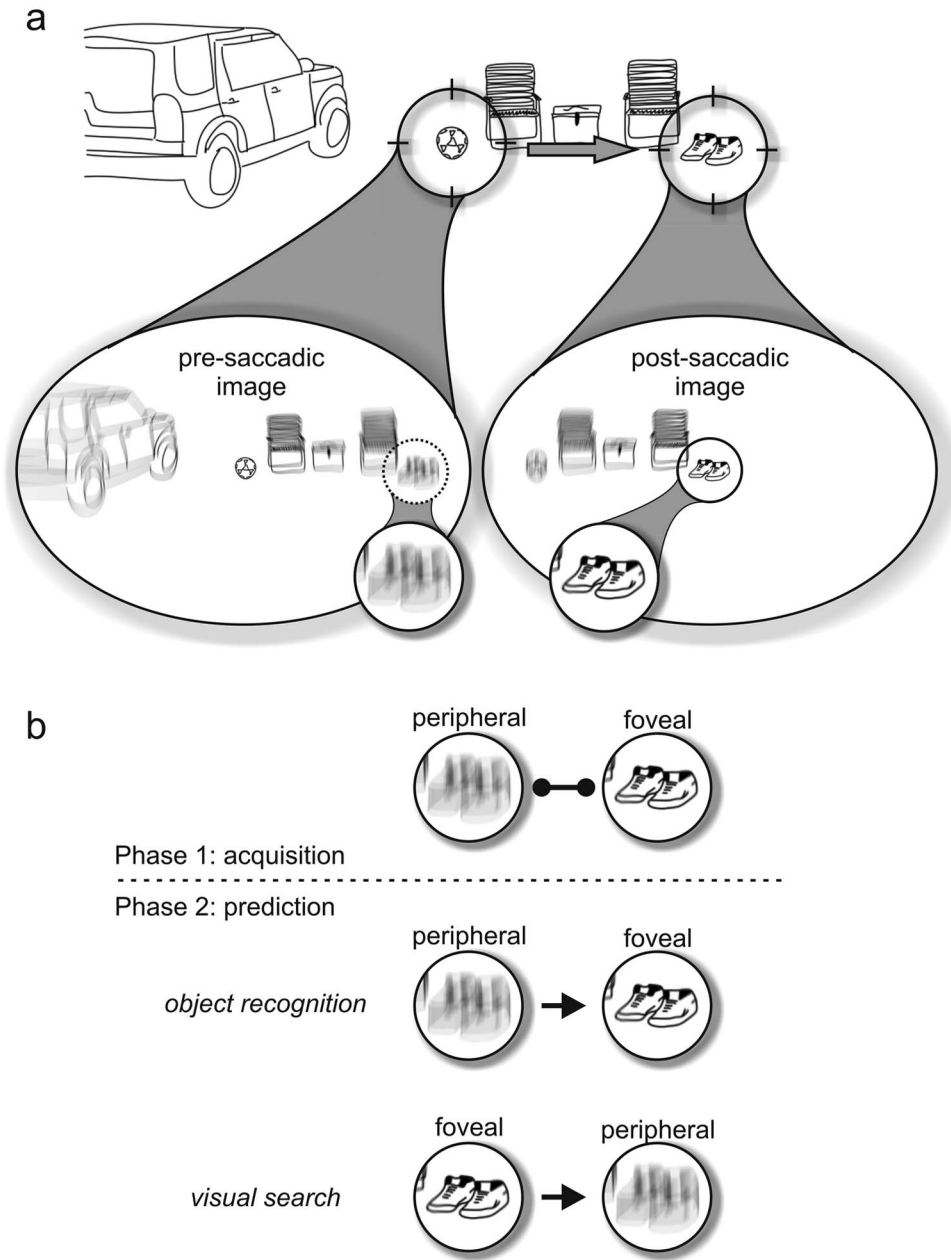


Figure 1. a: Due to the nonhomogeneity of the visual system, pre- and postsaccadic information of the saccade target object differ in acuity. b: The two-phase model of transsaccadic feature prediction. At Phase 1, pre- and postsaccadic information of the saccade target object is associated. At Phase 2, these associations are used to predict the foveal appearance of peripheral objects (peripheral object recognition) and the peripheral appearance of foveal search templates (visual search).

way, target candidates can be located when comparing such peripheral predictions with the actual visual input.

How is it possible to predict foveal information on the basis of peripheral information, or vice versa, as suggested here to solve the problem of peripheral object recognition and visual search? Building on the ideomotor framework, predictions should be made possible by associative learning. The underlying idea is that at first, the visual system learns during thousands of saccades to

associate attentionally selected pre- and postsaccadic information, that is, learns to associate for which saccadic eye movement which peripheral input pattern leads to which foveal pattern (see Figure 1b, Phase 1). A basic premise of this first phase is the storage of object features across the saccade, that is, transsaccadic memory (Deubel, Schneider, & Bridgeman, 1996, 2002). Support for associations of pre- and postsaccadic input, that is, transsaccadic learning, can be drawn from human (e.g., Cox, Meier, Oertelt, &

DiCarlo, 2005; Herwig & Horstmann, 2011) as well as monkey studies (Li & DiCarlo, 2008). For example, investigating the formation of invariant object representations, Li and DiCarlo (2008) found that the object selectivity of neurons from monkey's inferior temporal cortex (IT) was decreased after a brief learning phase of just 1 hr in which objects changed identity during the saccade. Likewise, human participants in the study of Cox et al. (2005) were more likely to confuse object pairs at retinal positions where objects during a learning phase slightly changed their features in midsaccade. Together, these studies thus support the assumption of a learning mechanism constantly associating neural activity patterns representing peripheral and foveal information of saccade target objects across eye movements. We suggest that once established, these transsaccadic associations can then be used for feature prediction (see Figure 1b, Phase 2).

The Present Study

We conducted three experiments to test whether peripheral object recognition and visual search is actually based on feature prediction across eye movements. The rationale underlying these experiments was as follows: If feature prediction is based on associations linking peripheral and foveal information, as suggested by our framework, it should be possible to bias this prediction mechanism by creating new and unfamiliar associations of peripheral and foveal patterns in the first place (i.e., in Phase 1). In the present study, we established such unfamiliar associations using the fact that during saccades, humans are effectively blind (for a related procedure, see Cox et al., 2005). Specifically, all experiments comprised an acquisition and a test phase in which eye position was monitored in real time. During acquisition, we presented participants with two different objects, one of which always changed one feature³ (i.e., its spatial frequency) as soon as the eyes started to move toward it. Thus, for this swapped object, pre- and postsaccadic feature information differed; that is, one spatial frequency was presented to the peripheral retina, and a different frequency was presented to the central retina. For almost all participants, this intrasaccadic object change remained unnoticed, a phenomenon known as *transsaccadic change blindness* (Grimes, 1996). The other object during acquisition served as a control condition and did not change its spatial frequency.

The test phases of our experiments separately addressed the scenarios of peripheral object recognition (Experiments 1 and 2) and visual search (Experiment 3). More specifically, in Experiments 1 and 2, we tested whether the prediction of foveal feature appearance, which is suggested to underlie peripheral object recognition, is biased for previously swapped objects. In Experiment 1, participants were required to judge the spatial frequency of a peripheral saccade target object by matching the frequency of a foveally presented test object following the saccade. We predicted that peripheral feature-based object recognition should be biased for previously swapped objects in the direction of the previously associated foveal pattern. That is, if the swapped object during acquisition changed its spatial frequency from low in the periphery to high in the fovea (Experiment 1a), during test, one and the same peripheral frequency should be judged higher for previously swapped objects compared with previously unswapped objects. Likewise, if the swapped object previously changed frequency from high in the periphery to low in the fovea (Experiment 1b), the

peripheral frequency of previously swapped objects should be judged lower than the frequency of previously unswapped objects. In Experiment 2, we tested whether the prediction of foveal appearance depends critically on the execution of a saccade. Here, participants experienced precisely the same perceptual events as in Experiment 1, but without any motor component to the task. Following the ideomotor framework, we predicted that biasing peripheral object recognition should be stronger in Experiment 1 than in Experiment 2. Finally, in Experiment 3, we tested whether also the prediction of peripheral feature appearance, which is suggested to underlie visual search, is biased for previously swapped objects. Here, we presented participants with a foveal search template on each trial and asked them to search and saccade to this target in the periphery. Importantly, the spatial frequency of the peripheral target object could physically either match or mismatch the frequency of the foveal search template. We predicted that the match and mismatch condition should affect visual search performance differently for previously swapped and unswapped objects. That is, for the unswapped object, visual search should be better for the matching condition because there were no transsaccadic changes in frequency during learning. However, for the swapped object, visual search should be better for the physical mismatching frequency because a mismatching frequency should be predicted on the basis of the new established associations.

Experiment 1

We conducted Experiment 1 to test feature prediction in peripheral object recognition. In our framework, we suggested that transsaccadic associations of pre- and postsaccadic feature information are used to predict the foveal appearance of peripheral objects. Thus, in Experiment 1, we tested whether this feature prediction can be biased by creating new and unfamiliar transsaccadic associations.

Method

Participants. Sixteen participants, whose ages were between 20 and 32 years, took part in Experiment 1. Eleven of the participants were female. For half the participants (Subgroup 1a), unfamiliar associations were established by changing one object's frequency from *low to high*. For the other half of participants (Subgroup 1b), one object changed its frequency from *high to low*. All participants reported normal or corrected-to-normal vision and were naïve with respect to the aim of the study.

Apparatus and stimuli. Participants performed the experiment in a dimly lit room and viewed the 19-in. (48-cm) display monitor running at 100 Hz from a distance of 71 cm. The screen's resolution was set to 1024 × 768 pixels, which corresponded to physical dimensions of 36 cm (width) × 27 cm (height). A video-based tower-mounted eye tracker (Eye Link1000, SR Research, Ontario, Canada) with a sampling rate of 1000 Hz was used for recording eye movements, and the right eye was monitored in all participants. The participants' head was stabilized by a chin and

³ Note that the processing of object identity in the ventral pathway can be studied at different levels of complexity (e.g., Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013; Rousselet et al., 2004). We return to this issue in the General Discussion.

a forehead rest. The central fixation stimulus was a black “plus” character ($0.3^\circ \times 0.3^\circ$, line width 2 pixels). Triangular and circular objects (1.5° edge length or diameter, respectively) filled with sinusoidal gratings of different spatial frequency (2.45 or 3.95 cpd, orientation 0°) served as potential saccade targets in the learning and test phase. In the test phase, the test objects could be filled with spatial frequencies of 1.7 , 2.45 , 3.2 , 3.95 , and 4.7 cpd. All stimuli were presented on a gray background with a mean luminance of 30 cd/m². Examples of the actual stimuli used in the experiment are shown in Figure 2c.

Procedure and design. The experiment was divided into an acquisition phase and a test phase (see Figures 2 and 3 for an overview), which were run in a single session of about 45 min. Prior to each phase, a 9-point grid calibration procedure was applied. Each trial of the acquisition phase started (following a variable fixation interval of 500–1,000 ms) with the presentation of a triangular and a circular object. Objects were presented at 6° to the left and right of the screen’s center at random. Participants were instructed to freely saccade to the triangular or circular object, depending on their own choice, but to foveate each object

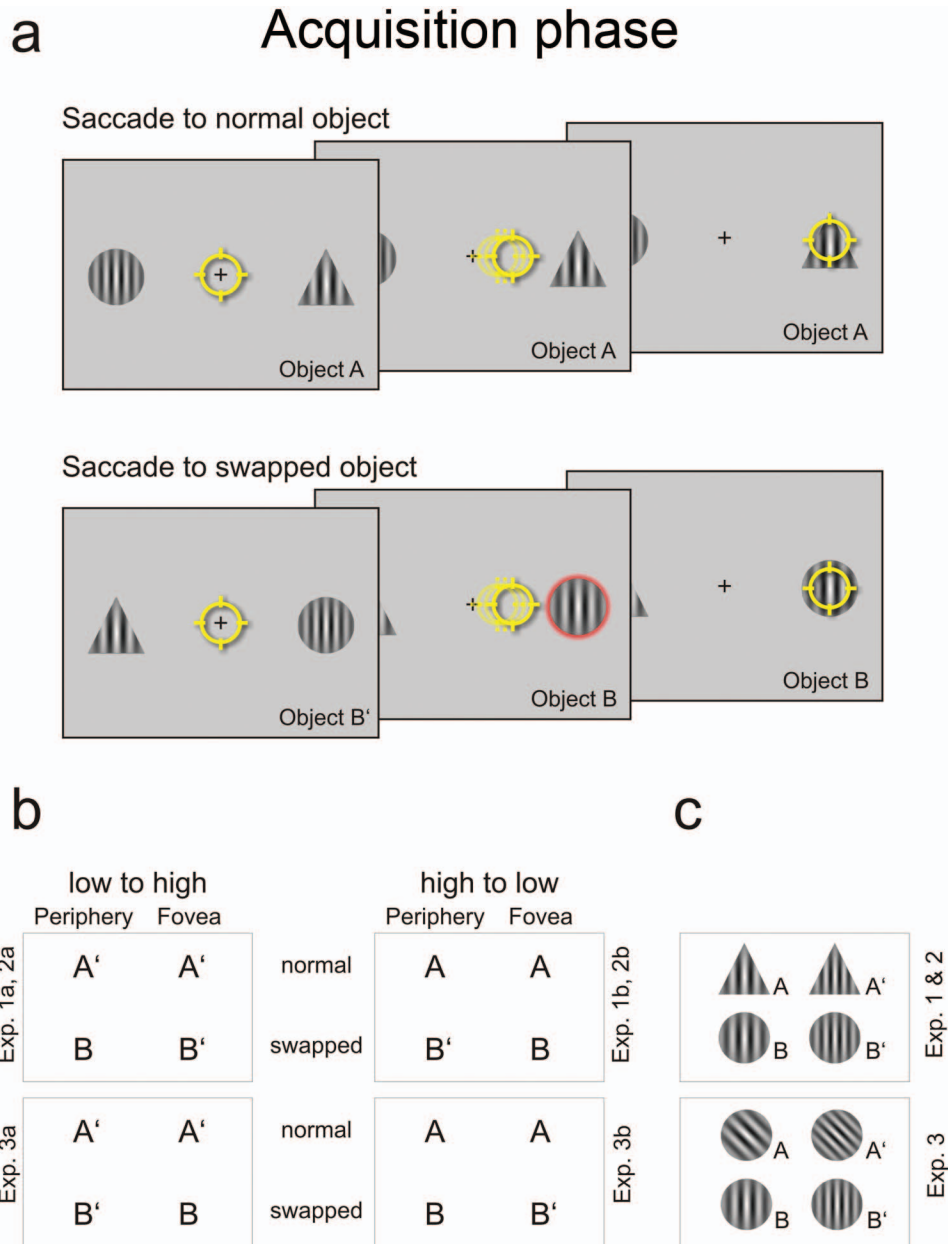


Figure 2. a: Trial structure of the acquisition phase in Experiments 1–3. Participants freely decided to saccade to one out of two objects. The “normal” object did not change spatial frequency during the saccade, whereas the “swapped” object changed spatial frequency. b: A schematic representation of the object combinations used in the acquisition phase of Experiments 1–3. c: Objects used in the acquisition phase of Experiments 1–3. See the online article for the color version of this figure.

Test phase: object recognition

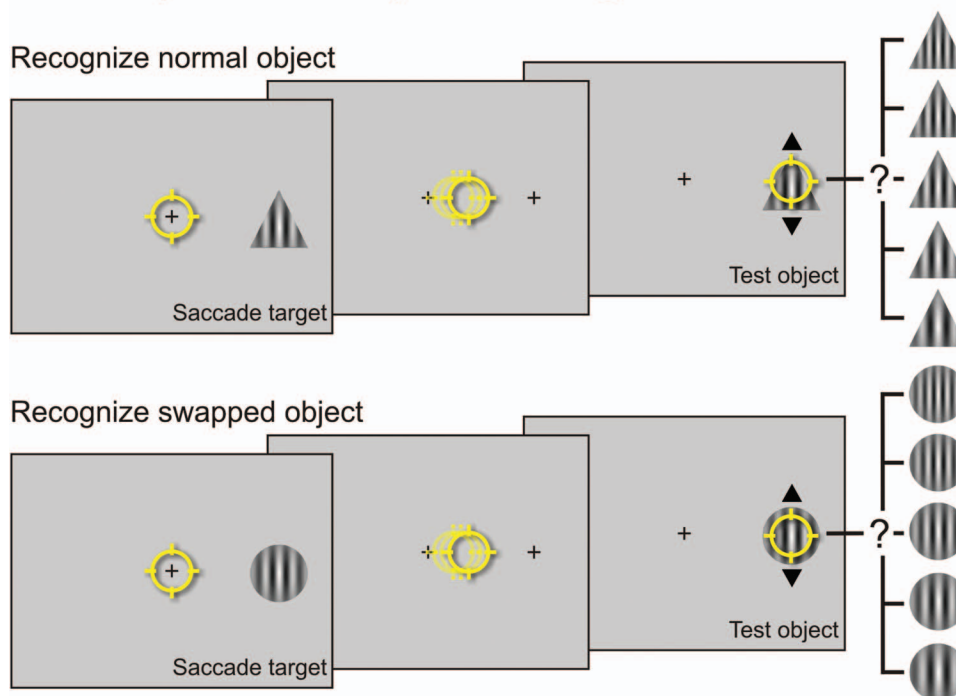


Figure 3. Trial structure of the test phase in Experiment 1. Participants were required to saccade to a peripheral saccade target, which disappeared as soon as the eyes started to move. Following the saccade, a test object was presented to the fovea, and participants had to match the frequency of the test object to the frequency of the presaccadic saccade target. See the online article for the color version of this figure.

about equally often and in a random order (i.e., to avoid fixed sequences, see also, Herwig & Horstmann, 2011). Feedback regarding the number of saccades to each object was provided every 48 trials. One of the two peripheral objects had a high-spatial frequency of 3.95 cpd, whereas the other peripheral object had a low-spatial frequency of 2.45 cpd. The mapping of peripheral frequency (high vs. low) and object shape (circular vs. triangular) was counterbalanced across participants. Importantly, for *Subgroup 1a*, we replaced the object with the low-spatial frequency by an object of similar shape with a high-spatial frequency of 3.95 cpd. Because this replacement occurred during the short time it takes to complete a saccade, different spatial frequencies of this particular object (swapped object, hereafter) were presented to the presaccadic peripheral and postsaccadic foveal retina. Thus, for Subgroup 1a, the swapped object changed its frequency from *low to high*. Conversely, for *Subgroup 1b*, we replaced the object with the high-spatial frequency by an object of similar shape with a low-spatial frequency of 2.45 cpd. Thus, for Subgroup 1b, the swapped object changed its frequency from *high to low* (see Figure 2b). For both subgroups, saccades to the peripheral object with the other spatial frequency (normal object, hereafter) did not lead to a replacement. In this case, the same spatial frequency was presented to the presaccadic peripheral and postsaccadic foveal retina. Following the saccade, both objects were presented for 250 ms and then replaced by a blank screen of 1,500 ms duration. With this manipulation, we could ensure that participants always foveated

triangular and circular objects filled with the same spatial frequency. The frequency of the swapped and the normal object only differed prior to the saccade in the periphery. The acquisition phase consisted of 240 trials, which were run in five blocks of 48 trials.

After completing the acquisition phase, participants received an on-screen instruction of the two subtasks of the test phase (see Figure 3). The first subtask was to saccade as fast and accurately as possible to one target object, which appeared 6° to the left or right of the fixation stimulus after a variable fixation interval of 500–1,000 ms. The target object could be a triangular or circular object filled with either a high-spatial frequency of 3.95 cpd or a low-spatial frequency of 2.45 cpd irrespective of its shape. As soon as the eyes started to move, the target object was replaced by a fixation stimulus, so that each saccade target was only presented to the peripheral retina. When no saccade was made within 350 ms after target onset, the trial was aborted and participants received an error message asking them to execute the eye movement faster. The second subtask started 500 ms after completion of the saccade with the presentation of a test object at the previous (and now foveated) saccade target location. Participants were required to match the spatial frequency of this foveally presented test object to the frequency of the presaccadic peripheral target object. The spatial frequency of the test object was chosen at random, but could be incrementally changed in steps of 0.75 cpd by pressing the up- or downward pointing arrow keys on the keyboard. Press-

ing the *enter* key, once the supposed frequency was found, terminated the trial. The test phase comprised 192 trials, which were run in four blocks of 48 trials. Each block was composed of a factorial combination of two target locations (6° to the left vs. right), two target shapes (triangular vs. circular), two spatial frequencies (2.45 vs. 3.95 cpd), and six repetitions of each combination, presented in random order. At the end of the experiment, we further asked participants in a debriefing (see the [Appendix](#)) whether they had seen objects change or appear otherwise unusual during the acquisition phase.

Data analysis. Saccade onsets were detected using a velocity criterion of 30°/s. *Saccade latency* was defined as the interval between the onset of the target and the initiation of a saccadic eye movement. We excluded trials in the acquisition and test phase if (a) saccades were anticipatory (latency < 100 ms), (b) gaze deviated by more than 1° from the display center at the time of saccade onset, (c) saccadic landing position deviated by more than 2° from the target position, or (d) saccadic latency was longer than 1,000 ms during acquisition or 350 ms during test. With these criteria, 11.3% of all acquisition trials and 11.4% of all test trials were discarded from analysis. The significance criterion was set to $p < .05$ for all analyses. Statistical t tests are two-sided unless otherwise stated.

Results

Acquisition phase. During acquisition, participants looked at the to-be-swapped object and the normal object about equally often (50.5 vs. 49.5%, respectively), $t(15) = 0.655$, $p > .523$. Moreover, they did not take longer to saccade to the to-be-swapped object ($M = 286$ ms), $t(15) = 0.220$, $p > .829$. Swapping occurred during the saccade (mean delay after saccade onset [$\pm SD$] was 29.1 (± 3.7) ms; mean saccade duration [$\pm SD$] was 43.5 [± 6.3] ms).

Test phase. Frequency judgments and saccadic latencies of the test phase were analyzed as a function of the within-subjects factor's spatial frequency of the presaccadic target object (2.45 vs. 3.95 cpd) and the object's status during acquisition (normal vs. swapped), as well as the between-subjects factor change direction (low to high vs. high to low), all of which are summarized in [Table](#)

1. Because preliminary analysis revealed no effect of target position (left vs. right), we collapsed the data across this factor and ran a 2 (frequency) \times 2 (status) \times 2 (direction) mixed analysis of variance (ANOVA) on judgment and latency data.

As expected, the analysis of frequency judgments revealed a significant main effect of frequency, $F(1, 14) = 307.734$, $p < .001$, $\eta_p^2 = .96$, confirming that participants judged the frequency to be lower for peripheral objects with a low (mean judgment = 2.92 cpd) than with a high frequency (mean judgment = 4.10 cpd). More importantly, there was also a significant interaction of status and direction, $F(1, 14) = 17.961$, $p < .001$, $\eta_p^2 = .56$, which is depicted in [Figure 4](#). As can be seen in this figure and as was corroborated by separate ANOVAs for each direction subgroup, participants of Subgroup 1a judged the spatial frequency of peripheral objects that were swapped during acquisition from low to high to be 0.15 cpd higher than that of objects that were not swapped during acquisition, $F(1, 7) = 18.836$, $p = .003$, $\eta_p^2 = .73$. Conversely, participants of Subgroup 1b judged the spatial frequency of peripheral objects that were swapped during acquisition from high to low to be 0.17 cpd lower than that of objects that were not swapped during acquisition, $F(1, 7) = 6.41$, $p = .039$, $\eta_p^2 = .48$. No other effect was significant: status, $F(1, 14) = 0.069$, $p = .797$, $\eta_p^2 = .01$; direction, $F(1, 14) = 0.001$, $p = .978$, $\eta_p^2 = .00$; Frequency \times Status, $F(1, 14) = 1.065$, $p = .320$, $\eta_p^2 = .07$; Frequency \times Direction, $F(1, 14) = 0.015$, $p = .904$, $\eta_p^2 = .00$; Frequency \times Status \times Direction, $F(1, 14) = 2.204$, $p = .160$, $\eta_p^2 = .14$. The analysis of latencies showed no significant effects ($ps > .10$).

Postsession debriefing. In the debriefing (see the [Appendix](#)), 14 participants explicitly reported that they noticed none of the objects to change frequency across saccades during the acquisition phase at all. The remaining two participants (see open diamonds in [Figure 4](#)), although not confident, were able to specify the object and frequency change direction. The results were still robust if those participants were eliminated from analysis.

Discussion

Our goal in Experiment 1 was to investigate feature prediction across eye movements as an important factor underlying peripheral

Table 1
Judgment and Latency Data as a Function of Object Status During Acquisition and Frequency During Test

Variable	Normal object				Swapped object			
	Low 2.45		High 3.95		Low 2.45		High 3.95	
	<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>
Exp. 1a								
judgment (cpd)	2.84	0.11	4.02	0.10	3.00	0.10	4.16	0.07
latency (ms)	174	10	177	10	173	9	176	8
Exp. 1b								
judgment (cpd)	3.03	0.14	4.15	0.03	2.79	0.14	4.04	0.07
latency (ms)	182	9	189	9	185	8	186	11
Exp. 2a								
judgment (cpd)	2.91	0.19	4.17	0.08	3.00	0.19	4.25	0.08
Exp. 2b								
judgment (cpd)	2.64	0.10	3.90	0.05	2.49	0.09	3.87	0.10

Note. Exp. = Experiment.

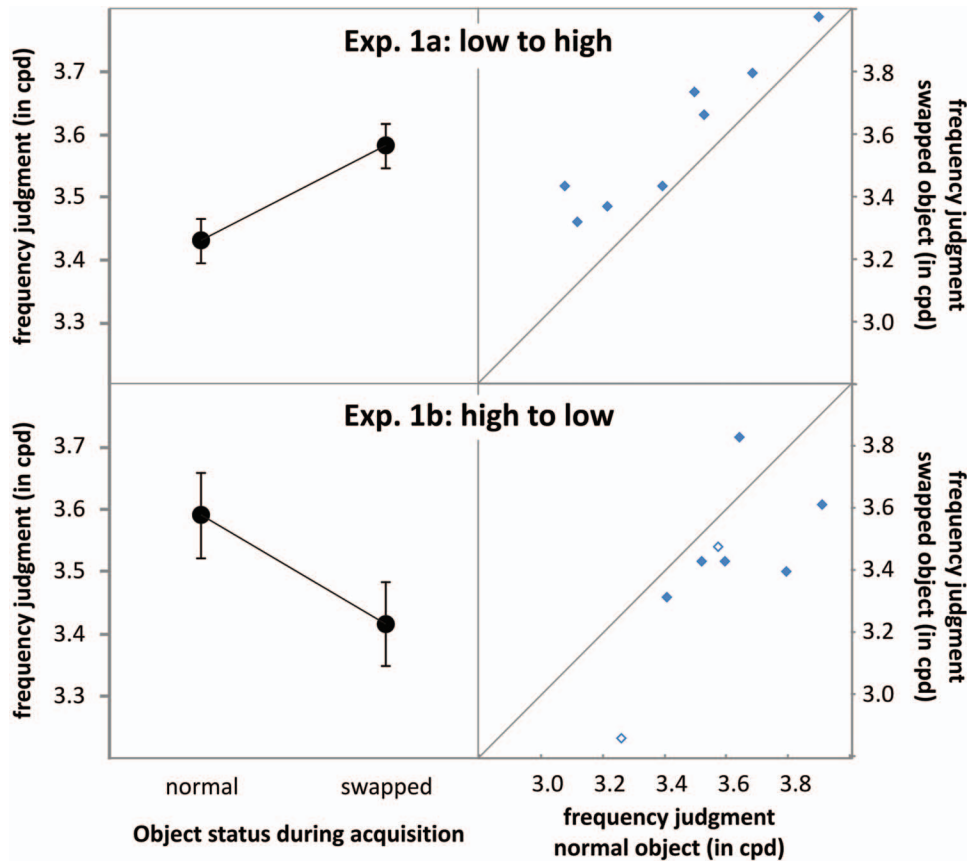


Figure 4. Mean frequency judgments of peripheral saccade targets in the test phase of Experiment 1 as a function of the object's status during acquisition (left side) and mean frequency judgments of the normal and swapped object for each participant (right side). Open diamonds represent participants who could specify the change direction during acquisition in a postsession debriefing (see the Appendix). Error bars represent within-subject standard errors of the mean (Loftus & Masson, 1994). See the online article for the color version of this figure.

object recognition. Experiment 1 provided clear evidence supporting this hypothesis. Participants judged one and the same spatial frequency presented in the periphery differently, depending on their past experience. That is, for objects that previously changed frequency intrasaccadically from low to high, participants judged the peripheral frequency to be higher than that of objects that were not swapped. In contrast, for objects that previously changed frequency from high to low, participants judged the peripheral frequency to be lower than the frequency of previously unswapped objects. Importantly, this latter result rules out one alternative explanation of the effect demonstrated in Subgroup 1a. Recent studies have shown an increase in perceived spatial frequencies for attended objects compared with unattended objects (Abrams, Barbot, & Carrasco, 2010; Gobell & Carrasco, 2005), which has been linked to changes in receptive field size at the neuronal level (e.g., Anton-Erxleben & Carrasco, 2013). One might thus object that the effect demonstrated in Subgroup 1a is actually due to differences in attention toward previously swapped and unswapped objects. That is, previously swapped objects might simply receive more attentional prioritization, which should lead to an increase in perceived spatial frequencies. However, such an alternative explanation

cannot hold for the effect demonstrated in Subgroup 1b, where the frequency of previously swapped objects has been judged lower than the frequency of unswapped objects. Instead, the present finding of peripheral object recognition biased toward previously associated postsaccadic foveal input supports our assumption of transsaccadic feature prediction based on past experience.

Interestingly, transsaccadic predictions were changed after a relatively brief experience (< 30 min) of altered statistics across saccades, even though almost all participants were unaware of this change. Moreover, there was no indication that biasing was different for previously presented and not presented peripheral frequencies of the swapped object, as suggested by the missing interaction effect (see also Table 1). This observation might indicate that past experience quickly generalizes from one stimulus to another, not actually experienced stimulus from the same category. Generalization of this sort is probably crucial for predicting postsaccadic foveal appearance of new stimuli not yet encountered.

Experiment 1 clearly supported our hypothesis that predictions are based on learning the associations between the peripheral and subsequent foveal information of one object. However, a further

critical assumption of the two-phase model of transsaccadic feature prediction, namely, that learning and predicting are particularly associated with making saccades, still needs to be tested. This second assumption is mainly based on ideomotor theory, which focuses on the critical role of action planning and execution on basic processes like learning and prediction (Herwig et al., 2007; Hommel et al., 2001; Hughes et al., 2013; Shin et al., 2010). However, an alternative view would be that learning and predicting, as demonstrated in Experiment 1, are not particularly associated with making saccades but reflect a more general mechanism of associating peripheral information with foveal information. If this latter alternative account is true, participants in Experiment 2 should show comparable effects on frequency judgments when they experience the same spatiotemporal patterns of peripheral and foveal information without any motor component. However, if learning and predicting are particularly associated with making saccades, as suggested by the two-phase model of transsaccadic feature prediction, then the effects in Experiment 1 should be pronounced as compared with the effects in Experiment 2.

Experiment 2

We conducted Experiment 2 to test whether the observed effect on frequency judgments in Experiment 1 depends critically on the execution of a saccade, as opposed to spatiotemporal experience of peripheral and foveal information without any planning and execution component. To this end, the participants of Experiment 2 were each paired with one of the 16 participants in Experiment 1 and received retinal exposure that was matched, trial for trial, to their counterpart in Experiment 1 (for a related procedure, see Cox et al., 2005).

Method

Sixteen new participants, whose ages were between 18 and 34 years, took part in Experiment 2. Thirteen of the participants were female. Each participant was paired with one of the participants of Experiment 1, so that half the participants (Subgroup 2a) were exposed to a frequency change of the swapped object from *low to high*, whereas the other half of the participants (Subgroup 2b) were exposed to a frequency change from *high to low*. All participants reported normal or corrected-to-normal vision and were naïve with respect to the aim of the study.

During acquisition, we instructed participants to fixate at the center of the monitor throughout the trial and to carefully attend to the cued object appearing first in the periphery, and then at the center of gaze. The timing as well as the decision of which of the peripheral objects appeared in the fovea was generated from the saccades made by their counterpart participant in Experiment 1 (yoked control design). More specifically, peripheral objects that later appeared at the center of gaze were cued in advance by presenting a horizontal line (0.34°, line width 2 pixels) to the left or right of the fixation cross together with both peripheral objects. The screen was left blank for the duration of the saccade of the counterpart participant in Experiment 1 to simulate the lack of detailed vision while the eyes are moving at high velocity. Comparable to Experiment 1, one of the peripheral objects always changed its spatial frequency (swapped object) when presented at the fovea, whereas the other object (normal object) did not change spatial frequency.

Failures to maintain fixation resulted in the trial being aborted and rerun. Due to problems in maintaining fixation, one of the participants had to be replaced. The test phase of Experiment 2 was a replication of the test phase of Experiment 1, with the only exception that no saccades were required. That is, a target object appeared 6° to the left or right of fixation for the duration of the saccadic latency of the counterpart participant in Experiment 1. Following a 500-ms blank, the test object was presented at the center, and participants had to match the spatial frequency of the foveal test object to the frequency of the peripheral target object.

Results

Test phase. Frequency judgments of the test phase are summarized in Table 1 and depicted in Figure 5. Once again, a 2 (frequency) × 2 (status) × 2 (direction) mixed ANOVA was conducted. The analysis revealed a significant main effect of frequency, $F(1, 14) = 259.546, p < .001, \eta_p^2 = .95$, confirming that participants judged the frequency to be lower for peripheral objects with a low (mean judgment = 2.76 cpd) than with a high frequency (mean judgment = 4.05 cpd). Moreover, the main effect of direction reached significance, $F(1, 14) = 6.769, p = .021, \eta_p^2 = .33$, reflecting that participants of Subgroup 2a, who foveated objects with a high-spatial frequency during acquisition, judged the frequency of peripheral objects during test overall higher (3.58 cpd) than participants of Subgroup 2b (3.22 cpd), who foveated objects with a low-spatial frequency during acquisition. More importantly, no other effect was significant: status, $F(1, 14) = 0.006, p = .942, \eta_p^2 = .00$; Status × Direction, $F(1, 14) = 3.191, p = .096, \eta_p^2 = .19$; Frequency × Status, $F(1, 14) = 0.626, p = .442, \eta_p^2 = .04$; Frequency × Direction, $F(1, 14) = 0.149, p = .706, \eta_p^2 = .01$; Frequency × Status × Direction, $F(1, 14) = 1.074, p = .318, \eta_p^2 = .07$.

It has to be noted that even though the Status × Direction interaction failed to reach significance, the descriptive pattern of results resembles the learning effect observed in Experiment 1. That is, participants of Subgroups 2a and 2b judged the spatial frequency of peripheral objects to be 0.08 cpd higher and 0.09 cpd lower, respectively, than that of objects that were not swapped during acquisition (see Figure 5). Thus, to test our prediction that the effect in Experiment 1 was actually stronger than the effect in Experiment 2, we calculated the learning effect as the difference between judgments for the normal and swapped object separately for each participant of Experiments 1 and 2. Differences were signed so that a positive value indicated a judgment shift in the direction of previously associated foveal input, whereas a negative value indicated a judgment shift in the reverse direction. A paired sample *t* test revealed that participants in Experiment 1 showed a significant stronger learning effect than participants in Experiment 2, $t(15) = 1.797, p = .046$, one-tailed; see Figure 6. In fact, the learning effect after performing saccades in Experiment 1 was twice as high (0.16 cpd) as the learning effect in Experiment 2 (0.08 cpd) without saccades.

Postsession debriefing. In the debriefing, 13 participants explicitly reported that they did not notice one of the objects to change frequency across different retinal positions during the acquisition phase at all. The remaining three participants (see open diamonds in Figure 5) were able to specify the object and

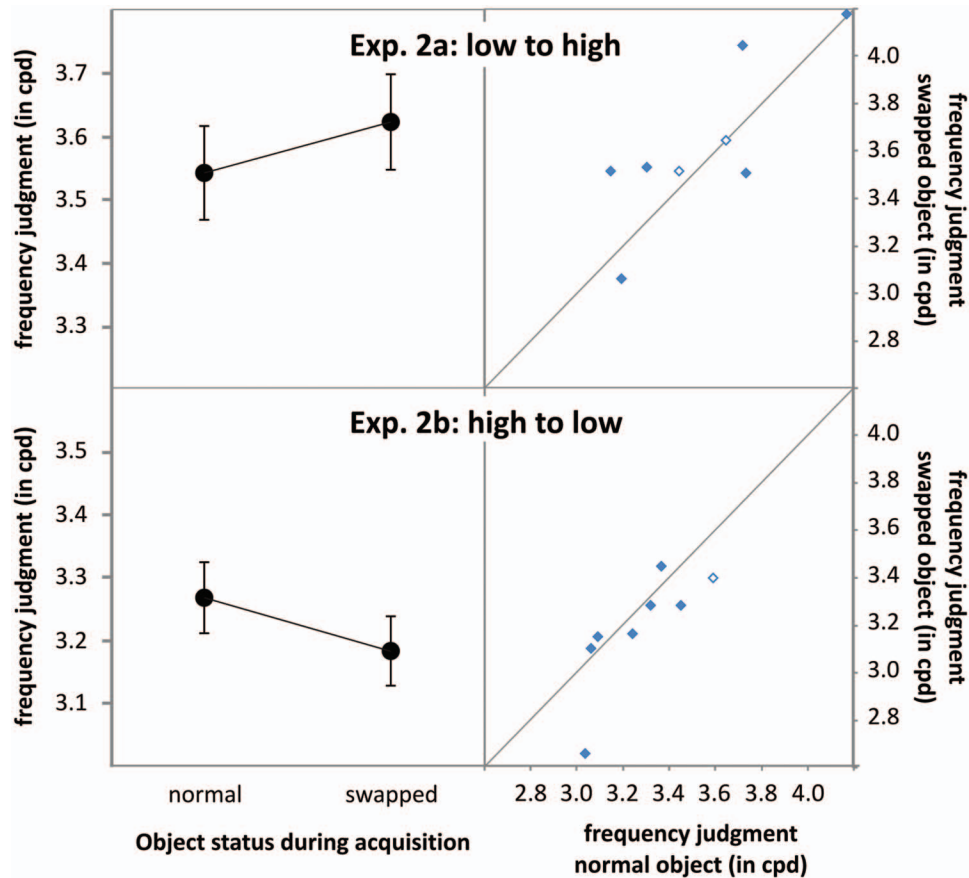


Figure 5. Mean frequency judgments of peripheral saccade targets in the test phase of Experiment 2 as a function of the object's status during acquisition (left side) and mean frequency judgments of the normal and swapped object for each participant (right side). Open diamonds represent participants who could specify the change direction during acquisition in a postsession debriefing (see the Appendix). Error bars represent within-subject standard errors of the mean (Loftus & Masson, 1994). See the online article for the color version of this figure.

frequency change direction. Once again, the pattern of results was the same if those participants were eliminated from analysis.

Discussion

In Experiment 2, we tested whether the effect reported in Experiment 1 is particularly associated with making saccades, as opposed to spatiotemporal experience alone. Importantly, participants in this second experiment experienced precisely the same perceptual events as in Experiment 1, but without any motor component to the task. That is, the retinal positions and timing of object exposure were replayed for each participant from the saccades made by their counterpart participant in Experiment 1. However, in contrast to Experiment 1, participants in Experiment 2 showed no significant effect of anomalous exposure during acquisition on their frequency judgments during test. Moreover, a comparison between both experiments revealed that participants in Experiment 1 showed a significantly stronger, and numerically twice as high, learning effect than participants in Experiment 2. This result is in line with

ideomotor theory, which emphasizes the critical role of action planning and execution on basic processes like learning and prediction (Hommel et al., 2001).

It has to be noted, however, that this result should not be taken to indicate that nonmotor associations and predictions play no role at all. First, there is no doubt that learning also takes place without the involvement of movements, as it is evident, for example, from perceptual learning (Fahle, 2009), and the build-up of associations between different co-occurring visual objects (Chun & Turk-Browne, 2008). The same holds true for prediction mechanisms, which are also strongly used outside the motor system (Bar, 2009; Bubic, von Cramon, & Schubotz, 2010). Second, although not significant, the descriptive pattern of results in Experiment 2 resembles the learning effect observed in Experiment 1. This latter observation might point to the additional involvement of nonmotor learning and prediction mechanisms. However, the finding of a pronounced effect when participants actively make saccades clearly points to a specific contribution of action planning and execution to the kind of learning and prediction observed in Experiment 1.

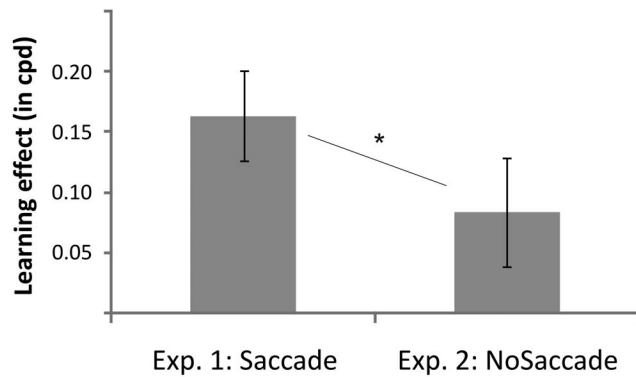


Figure 6. Comparison of the learning effect computed as the signed difference between the frequency judgments of normal and swapped objects in Experiment 1 (with saccade) and Experiment 2 (without saccade). See text for more details. Error bars represent standard errors of the mean.

Experiment 3

Experiment 3 was conducted to test feature prediction in visual search. In this second scenario, in which the visual system needs to take nonhomogeneity into account, the challenge is to find a peripheral target object with poor spatial resolution based on a foveal high-resolution search template. In our framework, we suggested that transsaccadic associations of pre- and postsaccadic information can also be used the other way around, that is, to predict the peripheral appearance of foveal search templates. Thus, in Experiment 3, we tested whether the prediction of peripheral appearance can be biased by creating new and unfamiliar transsaccadic associations.

Method

Participants and stimuli. Sixteen new participants, whose ages were between 16 and 31 years, were tested in Experiment 3. Eleven of the participants were female. Half the participants (Subgroup 3a) were exposed to a frequency change of the swapped object from *low to high*, whereas the other half of the participants (Subgroup 3b) were exposed to a frequency change from *high to low*. All reported normal or corrected-to-normal vision and were naïve with respect to the aim of the study.

Preliminary tests revealed that triangular and circular objects could be found very easily. To increase search difficulty, we used only circular objects (1.5° diameter) as potential saccade targets, which differed in orientation of the sinusoidal gratings (0° vs. 45°). Like in Experiments 1 and 2, objects could be filled with different spatial frequencies (2.45 or 3.95 cpd). Examples of the stimuli used in Experiment 3 are shown in Figure 2c.

Procedure and design. Experiment 3 was divided into an acquisition phase and a test phase, which were run in a single session of about 45 min. The acquisition phase was similar to Experiments 1 and 2 with the following modifications: We instructed participants to freely saccade to the vertical or tilted object, depending on their own choice. When presented in the periphery, both objects had the same spatial frequency of 2.45 cpd for Subgroup 3a or 3.95 cpd for Subgroup 3b. For one half of the participants, the peripheral vertical object changed its spatial fre-

quency either to 3.95 (Subgroup 3a) or to 2.45 cpd (Subgroup 3b) as soon as a targeting saccade was detected (swapped object), whereas the tilted object did not change its spatial frequency when foveated (normal object). For the other half of the participants, the mapping of orientation and frequency change was reversed. With this manipulation, we could ensure that participants always observed vertical and tilted objects of the same spatial frequency in the periphery. The frequency of the swapped and the normal object only differed postsaccadically when the object was foveated.

After completing the acquisition phase, participants received an on-screen instruction for the search task of the test phase (see Figure 7). Each test trial started with the central presentation of the search target for 100 ms. The search target was varied within blocks and was either the foveal version of the previously swapped object (e.g., vertical object) or the foveal version of the previously normal object (e.g., tilted object). Participants were instructed to search for and saccade as fast as possible to the object with the same orientation in the search display. The search display appeared with an interstimulus interval of 900 ms and comprised a vertical and a tilted object, which were randomly presented horizontally 6° to the left or right of fixation.⁴ The spatial frequency of each object was chosen from 2.45 and 3.95 cpd at random. Thus, the spatial frequency of the target (and independently, the spatial frequency of the distractor) could physically either match or mismatch the task-irrelevant spatial frequency of the previously presented search target.

Importantly, based on the object's status during acquisition (normal vs. swapped), frequency matches and mismatches could be both, congruent and incongruent to the experience during acquisition. That is, when participants of Subgroup 3a (or Subgroup 3b, respectively) had to search for the normal object, a peripheral target with a low- (or high-, respectively) spatial frequency of 2.45 (or 3.95, respectively) cpd matched the frequency of the previously presented search target. Moreover, this match was also congruent with the experience during acquisition where the normal object had the same spatial frequency in peripheral and foveal vision. On the contrary, a peripheral target with a high- (or low-, respectively) spatial frequency of 3.95 (or 2.45, respectively) cpd mismatched the frequency of the previously presented search target and was at the same time incongruent with the experience during acquisition. However, when participants had to search for the swapped object, the reverse was true. Here, a match of spatial frequency was now incongruent with the experience during acquisition, whereas a mismatch was now congruent. This is because during acquisition, the swapped object had different spatial frequencies in peripheral and foveal vision (see Figure 7).

As soon as the eyes started to move, both objects were removed to prevent new transsaccadic learning. When no saccade was made within 1,000 ms after search display's onset, the trial was aborted and participants received an error message asking them to execute the eye movement faster. The test phase comprised 192 trials, which were run in four blocks of 48 trials. Each block was composed of a factorial combination of two possible search targets

⁴ Admittedly, using only two stimuli in the search display is a more or less rudimentary version of a standard visual search task. However, given seminal studies on visual search with set sizes of two stimuli and eye movements as the dependent variable (e.g., Chelazzi et al., 1993, 1998), we think it is acceptable to call this task a visual search task.

Test phase: visual search

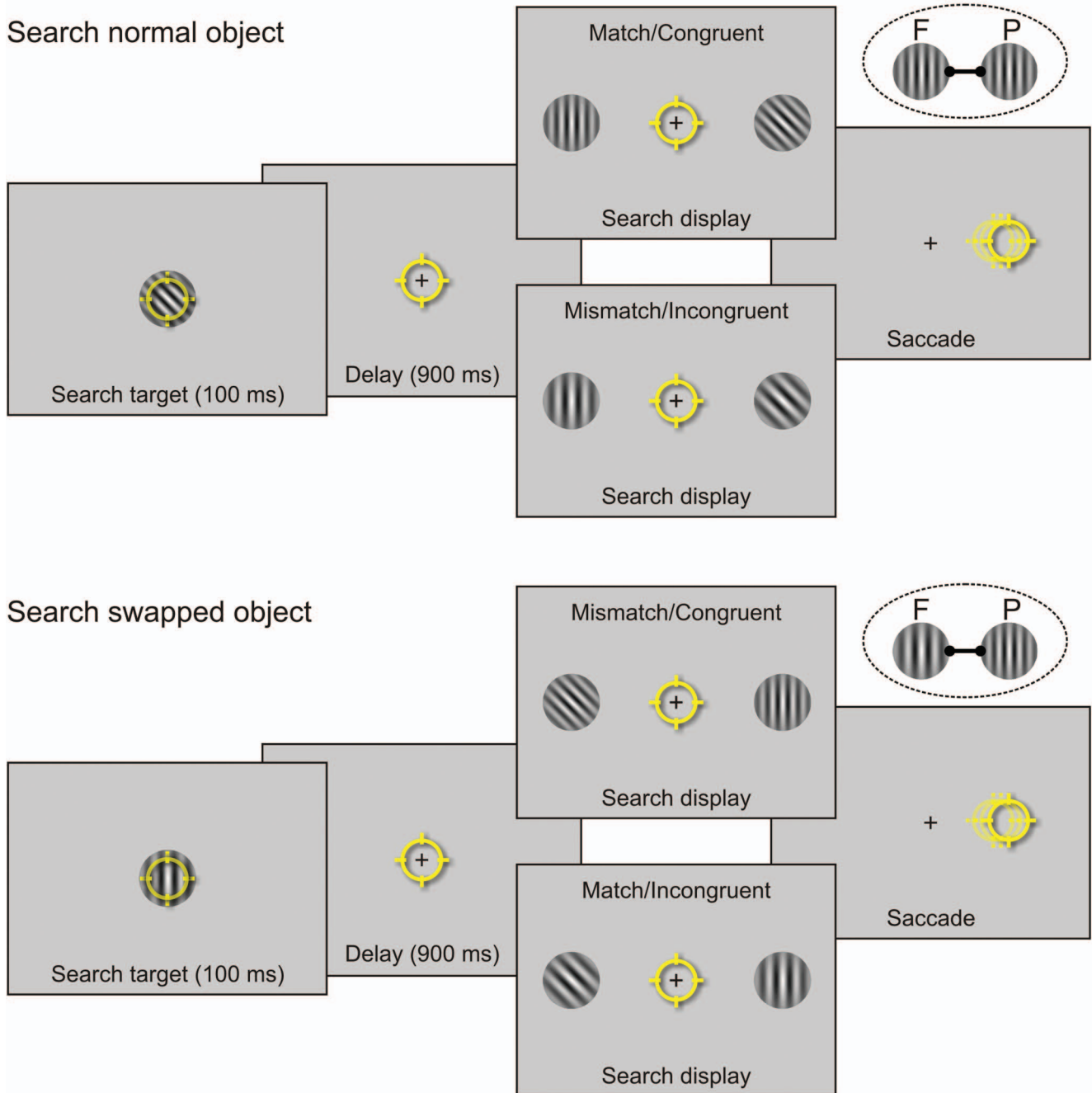


Figure 7. Trial structure of the test phase in Experiment 3. Each trial started with the central presentation of a search target. Participants were required to search for and saccade as fast as possible to the object with the same orientation in the search display. The spatial frequency of the target could physically either match or mismatch the spatial frequency of the previously presented search target. On the basis of the learning history, frequency matches and mismatches could be both, congruent and incongruent with the experience during acquisition. F = foveal; P = peripheral. See the online article for the color version of this figure.

(vertical vs. tilted), two target locations (6° to the left vs. right), two target frequencies (2.45 vs. 3.95), two distractor frequencies (2.45 vs. 3.95 cpd), and three repetitions of each combination, presented in random order. At the end of the experiment, we further asked participants in a debriefing whether they had seen objects change or appear otherwise unusual during the acquisition phase (see the [Appendix](#)).

Data analysis. Trials in the acquisition and test phase were excluded from analysis if (a) saccades were anticipatory (latency < 100 ms), (b) gaze deviated by more than 1° from the display center at the time of saccade onset, (c) saccadic landing position deviated by more than 2° from the target or distractor position, or (d) saccadic latency was longer than 1,000 ms. With these criteria, 12.7% of all acquisition trials and 15.3% of all test trials were discarded from analysis.

Results

Acquisition phase. In the acquisition phase, the results were similar to the previous experiments: Participants looked at the to-be-swapped object and the normal object equally often (50.2 vs 49.8%, respectively), $t(15) = 0.495$, $p > .628$. Moreover, they did not take longer to saccade to the to-be-swapped object ($M = 280$ ms), $t(15) = 1.685$, $p > .113$. Once again, swapping occurred during the saccade (mean delay after saccade onset [\pm *SD*] was 27.6 [\pm 3.6] ms; mean saccade duration [\pm *SD*] was 46.1 [\pm 7.3] ms).

Test phase. In the test phase, search performance was indistinguishable for trials with distractor matches and mismatches, which were thus combined for analysis. [Table 2](#) summarizes the percentage of correct first saccades (i.e., directed to the target instead of distractor) and saccadic latencies of correct first saccades as a function of the within-subjects factors target frequency match (match vs. mismatch), acquisition congruency (congruent vs. incongruent), and the between-subjects factor change direction (low to high vs. high to low).

The 2 (match) \times 2 (congruency) \times 2 (direction) mixed ANOVA on the percentage correct data revealed a significant main effect of acquisition congruency, $F(1, 14) = 37.061$, $p < .001$, $\eta_p^2 = .73$. As can be seen in [Figure 8](#), for almost all participants, search performance was better for acquisition-congruent combinations of peripheral and foveal objects as compared with acquisition-incongruent combinations. Neither the main effects of

match, $F(1, 14) = 2.188$, $p = .161$, $\eta_p^2 = .13$; and direction, $F(1, 14) = 0.678$, $p = .424$, $\eta_p^2 = .05$; nor the interactions of match and congruency, $F(1, 14) = 0.433$, $p = .521$, $\eta_p^2 = .03$; as well as match, congruency, and direction, $F(1, 14) = 0.053$, $p = .822$, $\eta_p^2 = .00$, reached statistical significance. The analysis of latencies showed, besides a marginal significant effect of congruency, $F(1, 14) = 4.080$, $p = .063$, $\eta_p^2 = .23$ (congruent: 304 ms, incongruent: 312 ms), no effects ($ps > .456$). Suffice it to say that latencies did not counteract the percent correct data, and thus a speed-accuracy trade-off can be excluded.

Postsession debriefing. In the debriefing, 15 participants explicitly reported that they noticed none of the objects to change frequency across saccades during acquisition. The results were still robust if the participant who was able to specify the change direction (see the open diamond in [Figure 8](#)) was eliminated from analysis.

Discussion

Our aim in Experiment 3 was to investigate feature prediction in visual search where peripheral target objects need to be found on the basis of foveal search templates. Due to the visual system's nonhomogeneity, visual search requires that differences in spatial resolution of potential target objects and search templates are taken into account ([Zelinsky, 2008](#)). We suggested that this challenge is tackled by predicting the peripheral appearance of foveal search templates on the basis of transsaccadic associations of pre- and postsaccadic information. As a consequence, it should be possible to bias the prediction mechanism in visual search by past experience.

The results of Experiment 3 corroborate our hypothesis. Search performance, as indicated by the percent of first saccades directed to the target, was indeed better for acquisition-congruent combinations of peripheral and foveal objects. That is, participants found the peripheral target more frequently if it matched their feature prediction. Thus, visual search is mainly determined by a prediction mechanism based on associations acquired during the short learning phase of about 30 min, whereas the actual physical match or mismatch during test seems to be less important.

General Discussion

The notion of prediction recently received increased interest as a fundamental mechanism to explain the working of the human

Table 2
Proportion of Correct Saccades and Latency Data as a Function of Frequency Match and Acquisition Congruency

Variable	Frequency match				Frequency mismatch			
	Congruent		Incongruent		Congruent		Incongruent	
	<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>
Exp. 3a								
correct sac. (%)	86.33	3.98	79.81	6.88	82.24	4.54	73.33	4.08
latency (ms)	289	28	298	28	292	28	296	33
Exp. 3b								
correct sac. (%)	77.73	6.09	74.56	4.28	78.63	3.99	70.51	5.68
latency (ms)	319	38	323	38	316	37	333	45

Note. Exp. = Experiment; sac. = saccade.

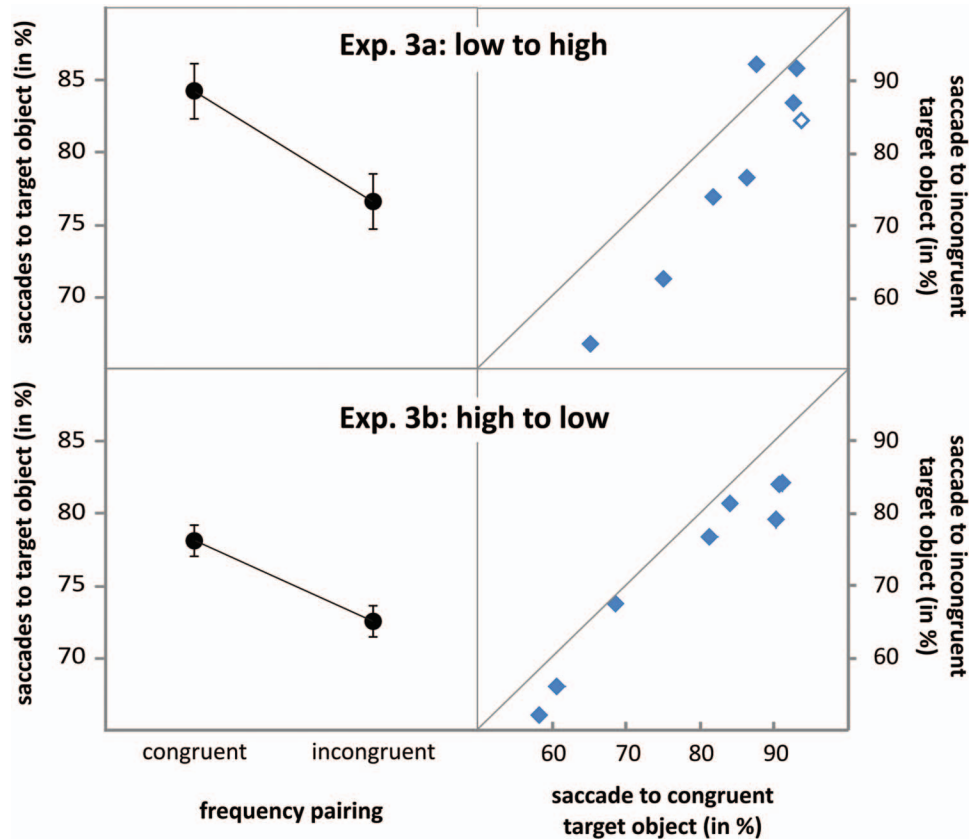


Figure 8. Mean proportion of correct saccades in the test phase of Experiment 3 as a function of the congruency of the frequency pairing (left side) and proportion of correct saccades to the congruent and incongruent target object for each participant (right side). Open diamonds represent participants who could specify the change direction during acquisition in a postsession debriefing (see the Appendix). Error bars represent within-subject standard errors of the mean (Loftus & Masson, 1994). See the online article for the color version of this figure.

mind and brain (cf. Bar, 2009, 2011; Bubic et al., 2010; Clark, 2013; Friston, 2005). Although most of this previous work focused on the question of how predictions help the mind and brain to cope with an uncertain future, in the present research, we investigated a further predictive mechanism that is thought to enable peripheral object recognition and visual search in face of the visual system's nonhomogeneity. In particular, we investigated the mechanism of transsaccadic feature prediction derived from ideomotor theory in three learning experiments. In Experiment 1, we showed that feature prediction can be biased by past experience so that objects, which, in an acquisition phase, intrasaccadically changed their spatial frequency from low (in the periphery) to high (in the fovea), are later on judged to be higher when they appear in the periphery. Likewise, objects that previously changed frequency from high (in the periphery) to low (in the fovea) are later on judged to be lower, which rules out an alternative explanation of the effect based on attentional prioritization of the swapped object. Together, these results thus demonstrate that feature prediction during peripheral object recognition is biased toward previously associated postsaccadic foveal input. In Experiment 2, we tested whether the prediction of foveal appearance depends critically on the execution of a saccade. Although participants experienced precisely the same

perceptual events as in Experiment 1, the exclusion of the motor component reduced the effect substantially. This finding is in line with our two-phase model of transsaccadic feature prediction derived from the ideomotor framework, which assumes that learning and predicting are particularly associated with making saccades. Finally, Experiment 3 showed that transsaccadic associations of pre- and postsaccadic information are also used the other way around to predict the peripheral feature appearance of foveal search templates. That is, during visual search, feature prediction is biased toward previously associated presaccadic peripheral input. Before we delve into the question of how feature and location prediction might be related, in the following sections of the General Discussion, we first elaborate on transsaccadic feature prediction in object recognition and visual search in further detail.

Feature Prediction in Object Recognition

Despite the nonhomogeneity of the visual system, human's ability to recognize objects irrespective of where they fall on the retina is quite astonishing. In general, such an invariance points to the crucial role of memory processes in object perception (Palmeri & Tarr, 2008), which fits well with the idea that perception depends in large

measure on memorized experiences enabling predictions about the nature of incoming information (Bar, 2011). Although typically movements of the eyes assure that the high-resolution foveal region is brought to interesting spots of the visual field for detailed visual sampling, there is also evidence that object recognition already starts in the periphery, so that recognition of foveal objects takes into account presaccadic visual input (Demeyer et al., 2009; Henderson, 1994; Kotowicz et al., 2010; Rayner et al., 1980). However, the question remains of how exactly highly degraded and imprecise peripheral information can be used for object recognition. In the introduction, we suggested a mechanism termed *transsaccadic feature prediction* to solve this problem. In particular, transsaccadic feature prediction means that presaccadic coarse peripheral information is used for predicting the much more precise postsaccadic foveal information. Consistent with ideomotor theory, this prediction mechanism is thought to be based on past experience in the form of associations linking pre- and postsaccadic object information. The findings from our first two experiments clearly support this idea. By creating new and unfamiliar associations of pre- and postsaccadic object information in the first place, peripheral object recognition was biased toward the predicted postsaccadic foveal input. Importantly, even when directly asked for frequency changes during acquisition (see the Appendix), almost all participants reported being unaware that one of the objects had changed. Although such self-reports should be interpreted carefully, this finding makes it very unlikely that our participants used explicit knowledge to solve peripheral object recognition. Rather, it suggests that feature prediction is based on implicit knowledge about the perceptual effects of saccadic eye movements.

The magnitude of biasing feature prediction was about 0.16 cpd in Experiment 1. Compared with the actual frequency change of 1.5 cpd during acquisition, this seems rather small. However, given the short acquisition phase of about 30 min pitted against a lifetime of previous learning in an unaltered visual environment, the small magnitude is not surprising. Finding biasing effects of feature predictions at all after such a brief exposure to altered visual statistics shows rather the plasticity of visual representations and suggests that associating pre- and postsaccadic object information can be considered a default option of the visual system not restricted to early visual learning. This interpretation is also supported by other recent studies of transsaccadic learning in adults reporting associations after relatively short acquisition phases (Cox et al., 2005; Herwig & Horstmann, 2011).

Furthermore, the present finding of biasing feature prediction by past experience fits well with other recent results pointing to an effect-based control of eye movements. For example, Huestegge and Kreutzfeldt (2012) recently showed that saccades to peripheral objects could be initiated more quickly if the same target object (compared with neutral or incongruent objects) was presented foveally prior to the imperative auditory stimulus. This result is in line with ideomotor theory assuming that actions (e.g., saccadic eye movements) are selected and controlled by an anticipation or prediction of their perceptual effects (e.g., foveation of the target object). The present findings extend this and other data (Herwig & Horstmann, 2011) by showing that such an effect-based control can be easily altered by past experience even if this alteration does not reach awareness. Moreover, they clearly indicate that transsaccadic associations can be used in both directions, that is, to predict how peripheral objects will look in the fovea and what foveal target templates should look like in the periphery.

Feature Prediction in Visual Search

Beside peripheral object recognition, our framework also addressed feature prediction in visual search. Specifically, Experiment 3 showed that search performance, as indicated by the percent of first saccades directed to the target, was indeed better if the peripheral target matched the participant's prediction of the peripheral appearance of the previously presented foveal search template. That is, feature prediction in visual search was biased toward previously associated presaccadic peripheral input.

In the majority of classical studies investigating visual search, the nonhomogeneity of the visual system is not considered (e.g., Treisman & Gelade, 1980; Wolfe, 1994; Wolfe & Horowitz, 2004; for a few exceptions, see Meinecke, 1989; Wolfe, O'Neill, & Bennett, 1998). Furthermore, the role of eye movements during visual search tended to be sidelined (for exceptions, see Findlay, 1997; Geisler & Chou, 1995; Zelinsky, 1996; Zelinsky & Sheinberg, 1997), which, however, changed recently with progress in eye tracking technology and computational modeling of visual search performance (e.g., Nuthmann, 2014; Wischnewski, Belardinelli, Schneider, & Steil, 2010; Zelinsky, 2008). To date, initial saccade direction can even be "considered to be a gold standard of search guidance" (Zelinsky, Adeli, Peng, & Samaras, 2013, p. 1). In general, these models assume that eye movements in visual search are guided by a combination of visual features derived from retinal input and information about the target stored in memory. In particular, the computational target acquisition model (TAM) of Zelinsky (2008) first transforms the search image so that it reflects the visual acuity limitations of the human visual system. Following a feature decomposition stage, a foveal search template is next compared with the transformed search image to produce a target map indicating visual similarity between each pixel of the search image and the foveal search template. Where to look next is then determined by the geometric average of the activity on the target map. In contrast to the framework suggested in the introduction, TAM does not incorporate a learning mechanism linking foveal and peripheral object representations so that the construction of the target map cannot be modified by past experience. Consequently, the finding of Experiment 3 that predicted similarity seems to be more important than actual physical similarity cannot easily be explained on the basis of TAM.

The work of Wischnewski and colleagues (2010) provides a further computational model that might be suited to incorporate the mechanism of feature prediction based on past experience. By taking into account the visual system's nonhomogeneity, their model combines static and dynamic-processing streams at the level of visual proto-objects. Proto-objects are conceived as ellipsoidal visual units with additional medium-level features (i.e., position, size, shape, and orientation of the principal axis). Importantly, for each proto-object, attentional priorities in the form of attentional weights are computed according to Bundesen's (1990) theory of visual attention. Where to look next is then determined by the proto-object with the highest weight according to a given search task (see also Schneider, 2013). Because this model also allows computing a second postsaccadic proto-object map, transsaccadic learning (i.e., associating pre- and postsaccadic proto-object representations) could be easily implemented. On the basis of the current framework, such an extension would allow searching for foveal search templates represented on a proto-object level based on past experience.

Interplay of Location and Feature Prediction

Although our research clearly shows that feature prediction across saccades can be altered by a relatively brief exposure to new and unfamiliar combinations of pre- and postsaccadic information, the question remains open of how feature prediction is related to location prediction across saccades. Location prediction has been shown at the neural as well as the behavioral level. For example, cells in retinotopically organized brain areas increase their activity if a planned saccade will bring a stimulus into the cell's receptive field (Duhamel et al., 1992). Likewise, discrimination performance increases around 75 ms before a saccade at the fovea, which is the future retinotopic location of the saccade target (Rolfs et al., 2011, Experiment 4). There is no doubt that at some point in visual processing, location and feature prediction need to be integrated to perceive a stable and detailed world (Cavanagh et al., 2010; Irwin, 1992; Krauzlis & Nummela, 2011; Melcher & Colby, 2008). Although an exhaustive debate over possible integration mechanisms is beyond the scope of the present article, a brief overview of neural networks involved in location prediction and feature processing might help to derive some possible constraints on this integration.

Neurons that are involved in location prediction prior to saccadic eye movements have been found mainly in areas relevant in eye movement and attention control like the lateral intraparietal area (LIP), the frontal eye fields (FEF), and the superior colliculus (Duhamel et al., 1992; Umeno & Goldberg, 1997; Walker, Fitzgibbon, & Goldberg, 1995). Although LIP and FEF have been recently suggested to be ideal areas for the implementation of transsaccadic memory (Wurtz, Joiner, & Berman, 2011), their relative lack of stimulus specificity might render them not as suitable for visual feature prediction. Indeed, the processing of object features occurs in the ventral pathway through numerous levels in a recurrent network from primary visual cortex (V1) to the IT or (TE) cortex (e.g., Kravitz et al., 2013; Rousselet et al., 2004). Interestingly, predictive remapping has also been reported for cells in the extrastriate area V3A (and much less also in V3 and V2; Nakamura & Colby, 2002). Because area V3A is currently debated to be part of the ventral pathway (Kravitz et al., 2013), this result might indicate that the integration of location and feature prediction perhaps takes place at intermediate levels of visual processing, that is, at a level of early object representations (or proto-objects). This idea would fit well with theoretical as well as computational models assuming a crucial role of such medium-level visual features in the control of saccadic eye movements (Schneider, 2013; Wischnewski et al., 2010). Alternatively, the interplay of location and feature prediction could be established by the maintenance of a coupling between areas involved in location prediction and feature processing (Cavanagh et al., 2010; for bidirectional connections between LIP and TE, see, e.g., Webster et al., 1994). Such a coupling could rely on object-based "pointers" of a visual working memory map that are linked with visual feature maps (Schneider, 2013). If so, then associative learning of foveal and peripheral appearances should be considered as a "postattentive" process that presupposes working memory representations of the associated stimulus representations.

What is obvious is that at the neural level, the hypotheses about the interplay of location and feature prediction are currently just sketches of possibilities. However, we hope that the present framework of feature prediction in object recognition and visual search

might provide a new opportunity to investigate the interplay of location and feature prediction in future research.

Summary and Conclusions

In summary, the results of the present study suggest that the visual system actually uses transsaccadic association of pre- and postsaccadic object information for feature prediction across eye movements. The mechanism of feature prediction thus allows predicting how peripheral objects will look in the fovea and how foveal search templates should appear in the periphery. The first aspect is relevant for peripheral object recognition in the face of the visual system's nonhomogeneity, whereas the latter aspect is assumed to be a critical factor underlying visual search. Well in line with ideomotor theory, the present results thus highlight the importance of past experience for an effect-based control of eye movements.

As suggested in the introduction, transsaccadic feature prediction probably also contributes to our impression to see the visual field uniformly detailed. That is, before we actually move our eyes, the prediction of precise postsaccadic foveal information for objects of interest might conceal acuity limitations in the periphery (Deubel et al., 1999). Another important factor in combination with such a prediction mechanism of single objects is probably our ability to grasp the general meaning, or gist of scene at a single glance, which certainly adds to the feeling of seeing everything (e.g., Oliva & Torralba, 2006).

References

- Abrams, J., Barbot, A., & Carrasco, M. (2010). Voluntary attention increases perceived spatial frequency. *Attention, Perception & Psychophysics*, *72*, 1510–1521. doi:10.3758/APP.72.6.1510
- Anton-Erxleben, K., & Carrasco, M. (2013). Attentional enhancement of spatial resolution: Linking behavioural and neurophysiological evidence. *Nature Reviews Neuroscience*, *14*, 188–200. doi:10.1038/nrn3443
- Bar, M. (2009). The proactive brain: Memory for predictions. *Philosophical Transactions of the Royal Society B*, *364*, 1235–1243. doi:10.1098/rstb.2008.0310
- Bar, M. (Ed.). (2011). *Predictions in the brain: Using our past to generate a future*. New York, NY: Oxford University Press. doi:10.1093/acprof:oso/9780195395518.001.0001
- Block, N. (2012). The grain of vision and the grain of attention. *Thought: A Journal of Philosophy*, *1*, 170–184.
- Bubic, A., von Cramon, D. Y., & Schubotz, R. I. (2010). Prediction, cognition and the brain. *Frontiers in Human Neuroscience*, *4*, 1–15. doi:10.3389/fnhum.2010.00025
- Bundesden, C. (1990). A theory of visual attention. *Psychological Review*, *97*, 523–547. doi:10.1037/0033-295X.97.4.523
- Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences*, *14*, 147–153. doi:10.1016/j.tics.2010.01.007
- Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *Journal of Neurophysiology*, *80*, 2918–2940.
- Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature*, *363*, 345–347. doi:10.1038/363345a0
- Chun, M. M., & Turk-Browne, N. B. (2008). Associative learning mechanisms in vision. In S. J. Luck & A. R. Hollingworth (Eds.), *Visual memory* (pp. 209–245). Oxford, England: Oxford University Press. doi:10.1093/acprof:oso/9780195305487.003.0007

- Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behavioral and Brain Sciences*, *36*, 181–253. doi:10.1017/S0140525X12000477
- Cox, D., Meier, P., Oertelt, N., & DiCarlo, J. (2005). Breaking position-invariant object recognition. *Nature Neuroscience*, *8*, 1145–1147. doi:10.1038/nn1519
- Demeyer, M., De Graef, P., Wagemans, J., & Verfaillie, K. (2009). Transsaccadic identification of highly similar artificial shapes. *Journal of Vision*, *9*, 1–14.
- Dennett, D. C. (1991). *Consciousness explained*. Boston, MA: Little, Brown.
- Dennett, D. C. (2001). Surprise, surprise. *Behavioral and Brain Sciences*, *24*, 982–982. doi:10.1017/S0140525X01320113
- Deubel, H., Irwin, D. E., & Schneider, W. X. (1999). The subjective direction of gaze shifts long before the saccade. In W. Becker, H. Deubel, & T. Mergner (Eds.), *Current oculomotor research: Physiological and psychological aspects* (pp. 65–70). New York, NY: Plenum Press. doi:10.1007/978-1-4757-3054-8_8
- Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Research*, *36*, 985–996. doi:10.1016/0042-6989(95)00203-0
- Deubel, H., Schneider, W. X., & Bridgeman, B. (2002). Transsaccadic memory of position and form. *Progress in Brain Research*, *140*, 165–180. doi:10.1016/S0079-6123(02)40049-0
- DiCarlo, J. J., Zoccolan, D., & Rust, N. C. (2012). How does the brain solve visual object recognition? *Neuron*, *73*, 415–434. doi:10.1016/j.neuron.2012.01.010
- Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, *255*, 90–92. doi:10.1126/science.1553535
- Elsner, B., & Hommel, B. (2001). Effect anticipation and action control. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 229–240. doi:10.1037/0096-1523.27.1.229
- Fahle, M. (2009). Perceptual learning and sensory plasticity. In L. Squire (Ed.), *Encyclopedia of neuroscience* (pp. 523–533). Amsterdam, the Netherlands: Academic Press. doi:10.1016/B978-008045046-9.00230-8
- Findlay, J. M. (1997). Saccade target selection during visual search. *Vision Research*, *37*, 617–631. doi:10.1016/S0042-6989(96)00218-0
- Freeman, J., & Simoncelli, E. P. (2011). Metamers of the ventral stream. *Nature Neuroscience*, *14*, 1195–1201. doi:10.1038/nn.2889
- Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society of London B*, *360*, 815–836. doi:10.1098/rstb.2005.1622
- Geisler, W. S., & Chou, K. (1995). Separation of low-level and high-level factors in complex tasks: Visual search. *Psychological Review*, *102*, 356–378. doi:10.1037/0033-295X.102.2.356
- Gobell, J., & Carrasco, M. (2005). Attention alters the appearance of spatial frequency and gap size. *Psychological Science*, *16*, 644–651. doi:10.1111/j.1467-9280.2005.01588.x
- Grimes, J. (1996). On the failure to detect changes in scenes across saccades. In K. A. Akins (Ed.), *Perception. Vancouver studies in cognitive science*, Vol. 5 (pp. 89–110). New York, NY: Oxford University Press.
- Henderson, J. M. (1994). Two representational systems in dynamic visual identification. *Journal of Experimental Psychology: General*, *123*, 410–426. doi:10.1037/0096-3445.123.4.410
- Henderson, J. M. (2008). Eye movements and scene memory. In S. J. Luck & A. Hollingworth (Eds.), *Visual memory* (pp. 87–121). Oxford, England: Oxford University Press. doi:10.1093/acprof:oso/9780195305487.003.0004
- Herwig, A., Beisert, M., & Prinz, W. (2013). Action science emerging: Introduction and leitmotifs. In W. Prinz, M. Beisert, & A. Herwig (Eds.), *Action science: Foundations of an emerging discipline* (pp. 1–33). Cambridge, MA: MIT Press. doi:10.7551/mitpress/9780262018555.003.0001
- Herwig, A., & Horstmann, G. (2011). Action-effect associations revealed by eye movements. *Psychonomic Bulletin & Review*, *18*, 531–537. doi:10.3758/s13423-011-0063-3
- Herwig, A., Prinz, W., & Waszak, F. (2007). Two modes of sensorimotor integration in intention-based and stimulus-based actions. *Quarterly Journal of Experimental Psychology*, *60*, 1540–1554. doi:10.1080/17470210601119134
- Herwig, A., & Waszak, F. (2009). Intention and attention in ideomotor learning. *Quarterly Journal of Experimental Psychology*, *62*, 219–227. doi:10.1080/17470210802373290
- Herwig, A., & Waszak, F. (2012). Action-effect bindings and ideomotor learning in intention- and stimulus-based actions. *Frontiers in Psychology*, *3*, 1–18. doi:10.3389/fpsyg.2012.00444
- Hommel, B. (2009). Action control according to TEC (theory of event coding). *Psychological Research*, *73*, 512–526. doi:10.1007/s00426-009-0234-2
- Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, *24*, 849–878. doi:10.1017/S0140525X01000103
- Huestegge, L., & Koch, I. (2010). Fixation disengagement enhances peripheral perceptual processing: Evidence for a perceptual gap effect. *Experimental Brain Research*, *201*, 631–640. doi:10.1007/s00221-009-2080-2
- Huestegge, L., & Kreuzfeldt, M. (2012). Action effects in saccade control. *Psychonomic Bulletin & Review*, *19*, 198–203. doi:10.3758/s13423-011-0215-5
- Hughes, G., Desantis, A., & Waszak, F. (2013). Mechanisms of intentional binding and sensory attenuation: The role of temporal prediction, temporal control, identity prediction, and motor prediction. *Psychological Bulletin*, *139*, 133–151. doi:10.1037/a0028566
- Hunt, A. R., & Cavanagh, P. (2009). Looking ahead: The perceived direction of gaze shifts before the eyes move. *Journal of Vision*, *9*, 1–7.
- Irwin, D. E. (1992). Memory for position and identity across eye movements. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *18*, 307–317. doi:10.1037/0278-7393.18.2.307
- James, W. (1890). *The principles of psychology*. New York, NY: Dover. doi:10.1037/11059-000
- Kotowicz, A., Rutishauser, U., & Koch, C. (2010). Time course of target recognition in visual search. *Frontiers in Human Neuroscience*, *4*, 1–11.
- Krauzlis, R. J., & Nummela, S. U. (2011). Attention points to the future. *Nature Neuroscience*, *14*, 130–131. doi:10.1038/nn0211-130
- Kravitz, D. J., Saleem, K. S., Baker, C. I., Ungerleider, L. G., & Mishkin, M. (2013). The ventral visual pathway: An expanded neural framework for the processing of object quality. *Trends in Cognitive Sciences*, *17*, 26–49. doi:10.1016/j.tics.2012.10.011
- Kunde, W. (2001). Response-effect compatibility in manual choice reaction tasks. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 387–394. doi:10.1037/0096-1523.27.2.387
- Land, M. F., & Tatler, B. W. (2009). *Looking and acting: Vision and action in natural behaviour*. Oxford, England: Oxford University Press.
- Li, N., & DiCarlo, J. J. (2008). Unsupervised natural experience rapidly alters invariant object representation in visual cortex. *Science*, *321*, 1502–1507. doi:10.1126/science.1160028
- Liu, N., Kriegeskorte, N., Mur, M., Hadj-Bouziane, F., Luh, W.-M., Tootell, R. B. H., & Ungerleider, L. G. (2013). Intrinsic structure of visual exemplar and category representations in macaque brain. *Journal of Neuroscience*, *33*, 11346–11360. doi:10.1523/JNEUROSCI.4180-12.2013
- Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review*, *1*, 476–490. doi:10.3758/BF03210951

- Lotze, R. H. (1852). *Medizinische Psychologie oder Physiologie der Seele* [Medical psychology or physiology of the soul]. Leipzig, Germany: Weidmannsche Buchhandlung.
- McConkie, G. W., & Currie, C. B. (1996). Visual stability across saccades while viewing complex pictures. *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 563–581. doi:10.1037/0096-1523.22.3.563
- Meinecke, C. (1989). Retinal eccentricity and the detection of targets. *Psychological Research*, *51*, 107–116. doi:10.1007/BF00309305
- Melcher, D. (2007). Predictive remapping of visual features precedes saccadic eye movements. *Nature Neuroscience*, *10*, 903–907. doi:10.1038/nn1917
- Melcher, D., & Colby, C. L. (2008). Trans-saccadic perception. *Trends in Cognitive Sciences*, *12*, 466–473. doi:10.1016/j.tics.2008.09.003
- Nakamura, K., & Colby, C. L. (2002). Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proceedings of the National Academy of Sciences*, *99*, 4026–4031. doi:10.1073/pnas.052379899
- Nattkemper, D., Ziessler, M., & Frensch, P. A. (2010). Binding in voluntary action control. *Neuroscience and Biobehavioral Reviews*, *34*, 1092–1101. doi:10.1016/j.neubiorev.2009.12.013
- Noë, A. (2001). Experience and the active mind. *Synthese*, *129*, 41–60. doi:10.1023/A:1012695023768
- Nuthmann, A. (2014). How do the regions of the visual field contribute to object search in real-world scenes? Evidence from eye movements. *Journal of Experimental Psychology: Human Perception and Performance*, *40*, 342–360. doi:10.1037/a0033854
- Oliva, A., & Torralba, A. (2006). Building the gist of a scene: The role of global image features in recognition. *Progress in Brain Research*, *155*, 23–36. doi:10.1016/S0079-6123(06)55002-2
- O'Regan, J. K. (1992). Solving the “real” mysteries of visual perception: The world as an outside memory. *Canadian Journal of Psychology*, *46*, 461–488. doi:10.1037/h0084327
- O'Regan, J. K., & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences*, *24*, 939–973. doi:10.1017/S0140525X01000115
- Palmer, T. J., & Tarr, M. J. (2008). Visual object perception and long-term memory. In S. J. Luck & A. Hollingworth (Eds.), *Visual memory* (pp. 163–207). Oxford, England: Oxford University Press. doi:10.1093/acprof:oso/9780195305487.003.0006
- Potter, M. C. (1976). Short-term conceptual memory for pictures. *Journal of Experimental Psychology: Human Learning and Memory*, *2*, 509–522. doi:10.1037/0278-7393.2.5.509
- Prinz, W. (1990). A common coding approach to perception and action. In O. Neumann & W. Prinz (Eds.), *Relationships between perception and action: Current approaches* (pp. 167–201). Berlin, Germany: Springer-Verlag. doi:10.1007/978-3-642-75348-0_7
- Rayner, K., McConkie, G. W., & Zola, D. (1980). Integrating information across eye movements. *Cognitive Psychology*, *12*, 206–226. doi:10.1016/0010-0285(80)90009-2
- Rolfs, M., Jonikaitis, D., Deubel, H., & Cavanagh, P. (2011). Predictive remapping of attention across eye movements. *Nature Neuroscience*, *14*, 252–256. doi:10.1038/nn.2711
- Roussellet, G. A., Thorpe, S. J., & Fabre-Thorpe, M. (2004). How parallel is visual processing in the ventral pathway? *Trends in Cognitive Sciences*, *8*, 363–370. doi:10.1016/j.tics.2004.06.003
- Schneider, W. X. (2013). Selective visual processing across competition episodes: A theory of task-driven visual attention and working memory. *Philosophical Transactions of the Royal Society of London B*, *368*, 1–13. doi:10.1098/rstb.2013.0060
- Schneider, W. X., Einhäuser, W., & Horstmann, G. (2013). Attentional selection in visual perception, memory and action: A quest for cross-domain integration. *Philosophical Transactions of the Royal Society B*, *368*, 1–7. doi:10.1098/rstb.2013.0053
- Shin, Y. K., Proctor, R. W., & Capaldi, E. J. (2010). A review of contemporary ideomotor theory. *Psychological Bulletin*, *136*, 943–974. doi:10.1037/a0020541
- Sommer, M. A., & Wurtz, R. H. (2006). Influence of the thalamus on spatial visual processing in frontal cortex. *Nature*, *444*, 374–377. doi:10.1038/nature05279
- Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature*, *381*, 520–522. doi:10.1038/381520a0
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*, 97–136. doi:10.1016/0010-0285(80)90005-5
- Umeno, M. M., & Goldberg, M. E. (1997). Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *Journal of Neurophysiology*, *78*, 1373–1383.
- Walker, M. F., Fitzgibbon, E. J., & Goldberg, M. E. (1995). Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *Journal of Neurophysiology*, *73*, 1988–2003.
- Waszak, F., & Herwig, A. (2007). Effect anticipation modulates deviance processing in the brain. *Brain Research*, *1183*, 74–82. doi:10.1016/j.brainres.2007.08.082
- Webster, M. J., Bachevalier, J., & Ungerleider, L. G. (1994). Connections of inferior temporal areas TEO and TE with parietal and frontal cortex in macaque monkeys. *Cerebral Cortex*, *4*, 470–483. doi:10.1093/cercor/4.5.470
- Wischniewski, M., Belardinelli, A., Schneider, W. X., & Steil, J. J. (2010). Where to look next? Combining static and dynamic proto-objects in a TVA-based model of visual attention. *Cognitive Computation*, *2*, 326–343. doi:10.1007/s12559-010-9080-1
- Wolfe, J. M. (1994). Guided search 2.0: A revised model of visual search. *Psychonomic Bulletin & Review*, *1*, 202–238. doi:10.3758/BF03200774
- Wolfe, J. M., & Horowitz, T. S. (2004). What attributes guide the deployment of visual attention and how do they do it? *Nature Reviews Neuroscience*, *5*, 495–501. doi:10.1038/nrn1411
- Wolfe, J. M., O'Neill, P., & Bennett, S. C. (1998). Why are there eccentricity effects in visual search? Visual and attentional hypotheses. *Perception & Psychophysics*, *60*, 140–156. doi:10.3758/BF03211924
- Wolff, P. (1984). Saccadic eye movements and visual stability: Preliminary considerations towards a cognitive approach. In W. Prinz & A. F. Sanders (Eds.), *Cognition and motor processes* (pp. 121–137). Berlin, Germany: Springer. doi:10.1007/978-3-642-69382-3_8
- Wurtz, R. H., Joiner, W. M., & Berman, R. A. (2011). Neuronal mechanisms for visual stability: Progress and problems. *Philosophical Transactions of the Royal Society of London Series B*, *366*, 492–503. doi:10.1098/rstb.2010.0186
- Zelinsky, G. J. (1996). Using eye saccades to assess the selectivity of search movements. *Vision Research*, *36*, 2177–2187. doi:10.1016/0042-6989(95)00300-2
- Zelinsky, G. J. (2008). A theory of eye movements during target acquisition. *Psychological Review*, *115*, 787–835. doi:10.1037/a0013118
- Zelinsky, G. J., Adeli, H., Peng, Y., & Samaras, D. (2013). Modelling eye movements in a categorical search task. *Philosophical Transactions of the Royal Society B*, *368*, 1–12. doi:10.1098/rstb.2013.0058
- Zelinsky, G. J., & Sheinberg, D. (1997). Eye movements during parallel-serial visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *23*, 244–262. doi:10.1037/0096-1523.23.1.244

(Appendix follows)

Appendix

Participants' Debriefing Questions

The postsession debriefing was conducted as an interview using the funnel method. That is, the interview started with the most abstract and open-ended questions and then funnelled down to the most specific and closed-ended questions. The following three questions were asked:

1. Was there anything strange in the course of the experiment? (If yes, during the first or second part of the experiment?)
2. Did the stimuli during the first part of the experiment abruptly change from time to time? (If yes, how did they change?)

3. Concerning the first part of the experiment: Did one stimulus abruptly change its frequency from time to time during the cascade? (If yes, which one and in which direction, from low to high or from high to low?)

Received October 23, 2013

Revision received February 5, 2014

Accepted April 4, 2014 ■

Members of Underrepresented Groups: Reviewers for Journal Manuscripts Wanted

If you are interested in reviewing manuscripts for APA journals, the APA Publications and Communications Board would like to invite your participation. Manuscript reviewers are vital to the publications process. As a reviewer, you would gain valuable experience in publishing. The P&C Board is particularly interested in encouraging members of underrepresented groups to participate more in this process.

If you are interested in reviewing manuscripts, please write APA Journals at Reviewers@apa.org. Please note the following important points:

- To be selected as a reviewer, you must have published articles in peer-reviewed journals. The experience of publishing provides a reviewer with the basis for preparing a thorough, objective review.
- To be selected, it is critical to be a regular reader of the five to six empirical journals that are most central to the area or journal for which you would like to review. Current knowledge of recently published research provides a reviewer with the knowledge base to evaluate a new submission within the context of existing research.
- To select the appropriate reviewers for each manuscript, the editor needs detailed information. Please include with your letter your vita. In the letter, please identify which APA journal(s) you are interested in, and describe your area of expertise. Be as specific as possible. For example, "social psychology" is not sufficient—you would need to specify "social cognition" or "attitude change" as well.
- Reviewing a manuscript takes time (1–4 hours per manuscript reviewed). If you are selected to review a manuscript, be prepared to invest the necessary time to evaluate the manuscript thoroughly.

APA now has an online video course that provides guidance in reviewing manuscripts. To learn more about the course and to access the video, visit <http://www.apa.org/pubs/authors/review-manuscript-ce-video.aspx>.