

Using ambiguous plaid stimuli to investigate the influence of immediate prior experience on perception

Olivia Carter · Joel S. Snyder · Sandy Fung · Nava Rubin

Published online: 8 October 2013
© Psychonomic Society, Inc. 2013

Abstract In a series of three experiments, we used an ambiguous plaid motion stimulus to explore the behavioral and electrophysiological effects of prior stimulus exposures and perceptual states on current awareness. The results showed that prior exposure to a stimulus biased toward one percept led to subsequent suppression of that percept. In contrast, in the absence of stimulus bias, prior perceptual experience can have a facilitative influence. The suppressive effects caused by the prior stimulus were found to transfer to an ambiguous plaid test stimulus rotated 180° relative to the adaptation stimulus, but were abolished if (1) the ambiguous test stimulus was only rotated 90° relative to the adaptation stimulus or (2) the adaptation stimulus was heavily biased toward the component grating percept. Event-related potential recordings were consistent with the involvement of visual cortical areas and suggested that the influence of recent stimulus exposure may involve recruitment of additional brain processes beyond those responsible for initial stimulus encoding. In contrast, the effects of prior and current perceptual experience appeared

to depend on similar brain processes. Although the data presented here focus on vision, the work is discussed within the context of data from a parallel series of experiments in audition.

Keywords Multistability · Vision · Audition · Motion · Rivalry · Electroencephalography

How the brain generates a perceptual experience from the current sensory input remains a great mystery of science. To investigate this question many researchers use ambiguous stimuli that are perceptually bistable. The term “bistable” means that an observer experiences continual switches in perceptual state, despite observing an unchanging stimulus (Leopold & Logothetis, 1999; Long & Toppino, 2004). Importantly, the balance between the relative dominance of the different perceptual interpretations is not fixed. Rather the observer’s perceptual state appears to depend heavily on the combined influence of the current stimulus properties (Long & Toppino, 2004) and temporal context in which it is experienced, both in respect to previous stimulus exposure (Brascamp, Knapen, Kanai, van Ee, & van den Berg, 2007; Kanai & Verstraten, 2005; Maloney, Dal Martello, Sahn, & Spillmann, 2005) and perceptual history (for a review, see Pearson & Brascamp, 2008). These effects of prior stimulus exposure and prior perceptual interpretations provide valuable insights into the mechanisms that determine one’s current conscious experience.

In a series of experiments, we used the auditory stream segregation paradigm to explore the influence of past experience on an observer’s subsequent perceptual grouping in audition (Snyder, Carter, Hannon, & Alain, 2009; Snyder, Carter, Lee, Hannon, & Alain, 2008; Snyder, Holder, Weintraub, Carter, & Alain, 2009). This paradigm involves the presentation of low tones (A), high tones (B), and silences (–) in a repeating ABA-pattern (Bregman & Campbell, 1971; Van Noorden, 1975). Listeners are more likely to report a single coherent ABA-

Electronic supplementary material The online version of this article (doi:10.3758/s13414-013-0547-5) contains supplementary material, which is available to authorized users.

O. Carter (✉)
School of Psychological Sciences, Faculty of Medicine, Dentistry & Health Sciences, Melbourne University, Melbourne 3010, Victoria, Australia
e-mail: ocarter@unimelb.edu.au

J. S. Snyder · S. Fung
Department of Psychology, University of Nevada Las Vegas,
Las Vegas, NV, USA

N. Rubin
Center of Neural Science, New York University, New York, NY,
USA

N. Rubin
ICREA and DTIC, Universitat Pompeu Fabra, Barcelona, Spain

“galloping” sound in the first few repetitions of a continual presentation of the auditory pattern. The coherent percept is also more commonly experienced when the frequency difference between A and B is small. With larger frequency differences, listeners generally begin to report two segregated streams of tones, each in a metronome-like rhythm (i.e., A-A-A-A- . . . and -B-B- . . .; audio demos are available as [online supplemental materials](#)). The repeating ABA- pattern is bistable, with perception alternating between interpretations of one coherent stream or two segregated streams, even when the stimulus is biased toward one of the two interpretations (Denham & Winkler, 2006; Pressnitzer & Hupé, 2006). By presenting a series of these auditory stream sequences in succession, we demonstrated robust effects of exposure to prior stimulus features that lasted up to tens of seconds. Specifically, we found that prior exposure to stimuli biased listeners toward either the coherent or segregated stream percepts in a *suppressive* fashion, increasing the likelihood of the alternative percept being experienced during the subsequent trial (Snyder et al., 2008). A separate *facilitative* influence of the prior percept was also found if the stimulus sequences were ambiguous and not biased toward one of the two percepts. These effects are consistent with adaptation effects reported previously in numerous vision studies (Carlson, 1953; Harris, 1980; Pearson & Brascamp, 2008). They were, however, novel in the context of the auditory streaming paradigm and provided important support for the influence of long-lasting memories for high-level auditory features (i.e., frequency difference and perceptual interpretation) on perception of streaming. The fact that equivalent *suppressive* and *facilitative* effects have now also been shown in the tactile domain (Carter, Konkle, Wang, Hayward, & Moore, 2008) provides strong evidence that these opposing influences of prior stimulus and perceptual history may be mediated by similar mechanisms and/or brain regions, independent of the sensory domain. The principal goal of the present study was to better understand the effects of prior experience in vision and to compare them to related findings in audition.

To investigate this question we selected the plaid stimulus (Wallach, 1935; English translation in Wuerger, Shapley, & Rubin, 1996) as it shares a number of analogous features with the auditory streaming paradigm used previously—most notably the switch between a single coherent percept to one consisting of two segregated stimulus elements (tones or gratings). Furthermore, the plaid stimulus has been demonstrated to show many of the traditional hallmarks of perceptual rivalry induced by bistable stimuli (Hupé & Rubin, 2003; von Grünau & Dubé, 1993). The plaid stimulus consists of two superimposed gratings moving at the same speed but in different directions. The stimulus is viewed through an aperture and is typically first perceived as a single moving plaid, but after prolonged viewing the gratings can be perceived as two segregated gratings moving past each other (Hupé & Rubin, 2003; von Grünau & Dubé, 1993; Wallach, 1976). One aspect

of the plaid stimulus that was of particular interest to us is that an observer’s percept can be biased toward the single coherent plaid or toward two segregated grating textures, by increasing or decreasing the angle (α) between the directions of movement of the two gratings (Hupé & Rubin, 2003; see Fig. 1). This sensitivity to α parallels the biasing of perception in the auditory streaming paradigm that can be achieved by varying the difference in frequency between the individual tone elements. In the three experiments described below, we used α to test whether the effects of prior stimulus that we had previously demonstrated in the auditory domain also exist in the visual domain. By combining psychophysics and electroencephalography (EEG), we systematically explored the levels of processing that likely underlie the effects of prior stimulus and perceptual context.

Experiment 1

In audition, a clear *suppressive* effect was caused by adaptation to an auditory sequence that was biased toward either the coherent or the segregated percept (Snyder et al., 2008). As an initial step here, we needed first to determine whether the same effect would be seen in vision. To assess this, four versions of the plaid stimulus with varying α values were presented in a sequence of 17 trials (Fig. 1), such that each successive trial acted as both the prior and current stimulus within the testing block (16 prior–current trial pairs per block). This procedure mirrored that used in a parallel auditory study (see Exp. 3 of Snyder et al., 2008). It should be noted that whereas numerous other studies have used adaptation to unambiguous stimuli to investigate the effects of different stimulus elements on the perception of ambiguous stimuli (Harris, 1980; Long & Toppino, 2004; von Grünau & Dubé, 1993), few studies—and none using the plaid stimulus—have used biased versions of the same ambiguous stimuli for both the adaptation and test stimulus periods to demonstrate suppressive effects of prior adaptation (cf. Maloney et al., 2005). Therefore, Experiment 1 had three principal aims: (1) to determine whether suppressive effects could indeed be induced by biased ambiguous plaid stimuli; (2) to compare the effects across a range of stimulus bias, to determine whether suppressive effects were limited to stimuli that were truly ambiguous, or whether effects were strong enough to overcome inherent biases within the test stimulus; and (3) to assess the temporal persistence of any observed effects by comparing conditions with interstimulus intervals (ISIs) of 1 or 10 s.

Method

Participants Six participants took part (one female, five male; 26–32 years of age). All were trained psychophysical observers from Harvard University Vision Sciences Laboratory, reporting

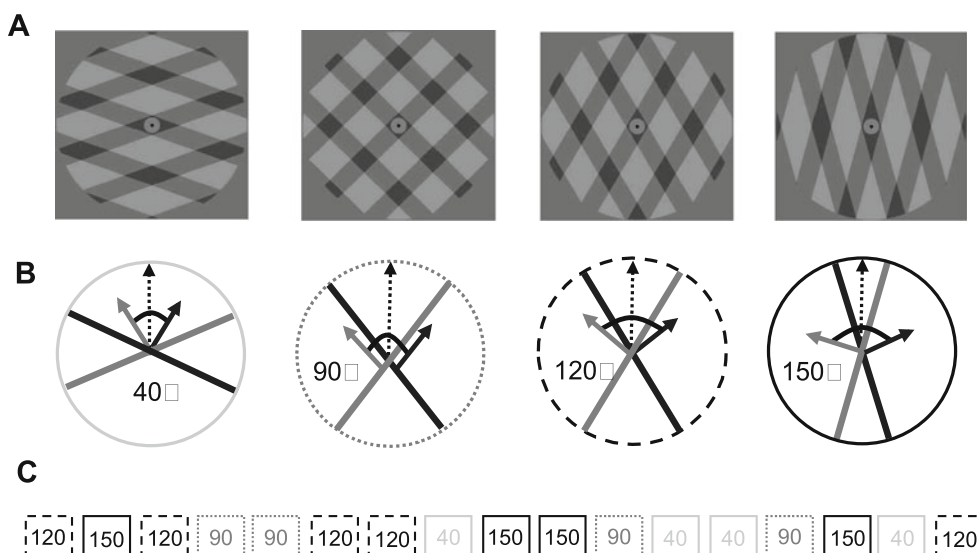


Fig. 1 Plaid stimulus used in Experiment 1. **a** The four versions of the plaid stimulus were composed of transparent moving gratings within a circular aperture (α values = 40°, 90°, 120°, and 150°). These stimuli are generally perceived as either a coherent plaid moving up or two segregated surfaces that are seen as diagonal gratings sliding past each other toward the left or right side of screen. **b** In order to bias the relative dominance of the coherent or segregated percept, the angle of the gratings

was altered. The larger the angle (α) between the directions of motion of the two grating components, the more likely the plaid will be segregated into the percept of two sliding gratings. **c** The 17 trials in each block of Experiment 1 were ordered to ensure that all possible pairs of two consecutive plaid stimuli occurred exactly once. Note that both the box style and number indicate the same α , as described in the caption for Fig. 2

normal or corrected-to-normal vision. Apart from authors O.C. and J.S.S., all other participants were naïve to the aims of the experiment. The experiment was approved by the Harvard University Committee on the Use of Human Subjects in Research.

Stimulus The plaid stimulus was composed of rectangular-wave gratings with a duty cycle of 0.33 (one third dark gray [14 cd/m²], two thirds light gray [22 cd/m²]), with each dark–light period spanning 1° of visual angle (Fig. 1a). The dark gratings moved at a speed of 2°/s. The intersecting regions of the dark gray gratings were visibly darker (7 cd/m²), consistent with the phenomenal impression of a single bound plaid surface or two transparent gratings with either the rightward- or leftward-tilting gratings sitting on top. This plaid pattern was presented within a circular aperture (13° diameter) with a gray background outside the aperture (14 cd/m²). A red 0.2° fixation dot was presented centrally within a dark gray 9-cd/m² exclusion zone with a 1° diameter. Each trial consisted of a 20-s presentation of the dynamic plaid stimulus. Between trials, the plaid gratings were removed from the screen, but the remaining stimulus features were kept constant (fixation point and dark gray aperture).

In each trial, the stimulus was oriented with the coherent plaid moving upward, and the angle between the directions of motion for the two gratings (α) was 40°, 90°, 120°, or 150° (corresponding to the two gratings being tilted to the left and right from a vertical orientation by 20°, 45°, 60°, or 75°, respectively) (see Fig. 1a and b).

The stimulus was generated using MATLAB and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and was presented on a 16-in. monitor (85 Hz, 768 × 1,024 resolution).

Procedure The plaid stimuli were presented over two separate sessions, each consisting of five blocks of 17 trials, each trial lasting 20 s. In each block, the trials were pseudorandomized using an algorithm that ensured that each of the 16 possible pairs of two consecutive plaid stimuli occurred exactly once. Because the first trial was not preceded by any stimulus, 17 trials were needed to achieve the 16 prior–current pair combinations (Fig. 1c). In the two sessions, trials were separated by an ISI of either 1 or 10 s. The sessions were either completed on separate days or after a break of at least 1 h, and the presentation order of the two sessions was counterbalanced across observers.

Participants were asked to maintain fixation throughout the experiment and to press (and hold down) the *down arrow* key when they perceived a coherent plaid. If the stimulus was perceived as two overlaying gratings sliding past each other, the *right arrow* key was pressed. Both keys were held down during periods of confusion and were released during the blank ISIs between each trial. Participants’ button response data were recorded every 200 ms throughout the 20-s duration of each trial. Head position was maintained at 57 cm using a chin rest and the experiments were conducted in a dimly lit room.

Results

For all effects, our main measure of interest was the average percentage of dominance of the segregated percept over the 20-s trial. A three-way analysis of variance (ANOVA) was run with prior- α , ISI, and current- α as the three factors.

The time course of perceptual bias during the prior trial for the 1-s and 10-s ISI conditions is illustrated in the left panels of Fig. 2a and c, respectively (these data are averaged across all participants as a function of prior- α for illustration purposes only). During the adaptation period, increasing α from 40° to 150° led to a systematic increase in predominance of the segregated percept, $F(3, 3) = 59.44$, $p < .001$, $\eta^2 = .983$ (power = 1.0) (left panels: Fig. 2a and b). After a 1-s ISI, adaptation to biased stimuli in the prior trial lead to a clear *suppressive* effect on the current trial (the right panel of Fig. 2a illustrates this effect for all trials with a current- α of 90°). Specifically, if the prior trial was biased toward increased dominance of the segregated percept, this percept was *less* likely to be reported during the current trial as indicated by a main effect of prior- α , $F(3, 3) = 22.32$, $p < .025$, $\eta^2 = .957$ (power = .926). This effect of prior- α on the predominance of

the segregated percept was clearly seen after an ISI of 1 s at current- α 90° and current- α 120° (Fig. 2b, right panel). Although this effect of prior- α was visibly reduced at the extreme values of current- α (40°- α or 150°- α), the interaction between current- α and prior- α was not testable due to insufficient residual degrees of freedom.

After a 10-s ISI, the effect of prior- α on current perception was still observed; however, the magnitude of the effect was reduced, as was suggested by a marginal interaction between ISI and prior- α , $F(3, 3) = 7.83$, $p = .062$, $\eta^2 = .887$ (power = .557) (Fig. 2c and d, right panel).

Simple effects of α were calculated by running independent one-way repeated measures ANOVAs for each of the four current- α conditions. Using the Bonferroni correction for repeated analysis, significant effects of prior- α were seen after an ISI of 1 s at current- α 90° and current- α 120° ($p < .01$, Fig. 2b). With a 10-s ISI, prior- α only had a significant effect on the predominance of the segregated percept on the 120° current- α condition ($p < .01$, Fig. 2d). At the extreme values of current- α (40°- α or 150°- α), the effect of prior- α was clearly reduced and never reached significance for either the 1-s or the 10-s ISI.

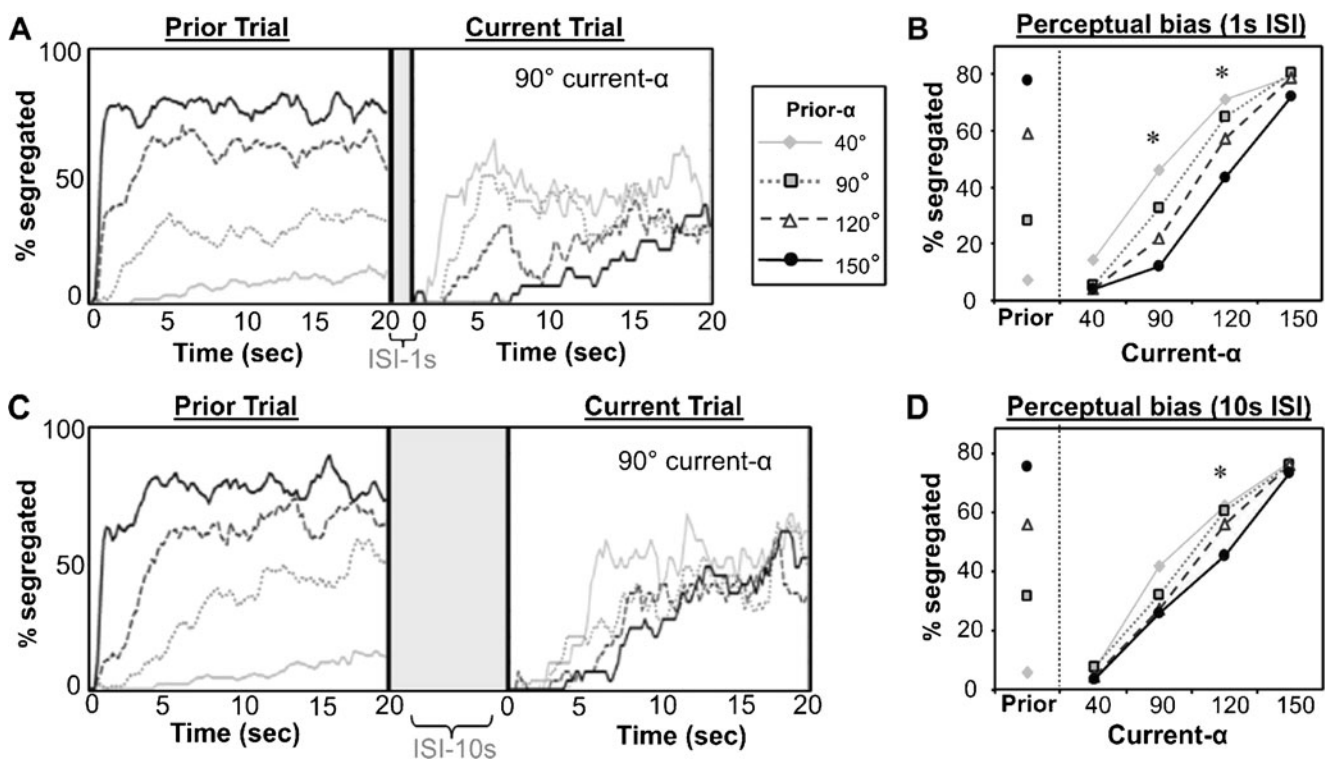


Fig. 2 Experiment 1 results. **a** The left panel shows the data from the 1-s interstimulus interval (ISI) condition. For illustration purposes only, this panel shows the average data from all trials for the four prior- α stimuli (40°- α , light gray solid line; 90°- α , dotted gray line; 120°- α , dashed dark gray line; 150°- α , solid black line). The right portion of the figure shows data from only those trials with a current- α of 90°. The *suppressive* effect of the prior stimulus is reflected by the inverted order of the curves during the prior and current trials. **b** The left panel illustrates the overall effect of

α on the predominance of the segregated percept during the prior trial, averaged over *all* prior trials. The right panel shows the main effect of prior- α on current- α : The larger the prior- α , the less the segregated percept dominates in the current trial. **(c and d)** These panels depict the corresponding data from the trials separated by a 10-s ISI. *Bonferroni-corrected significant effect of prior- α on perception for a particular current- α , $p < .01$

Discussion

Experiment 1 showed that the ambiguous plaid stimulus could be reliably used to demonstrate and investigate the influence of prior experience on one's current perceptual state in a way that is analogous to earlier studies in audition (Snyder et al., 2008). By systematically biasing perception toward either the coherent or segregated percepts (Hupé & Rubin, 2003, 2004), a clear *suppressive* effect of prior stimulus was shown (i.e., participants were less likely to report the segregated percept if their perception had been previously biased toward this percept). The *suppressive* effects were greatest when the current stimulus was only moderately biased itself, suggesting that prior stimulus exposure was not sufficient to overcome strong stimulus-driven biases.

When interpreting the data from both auditory streaming and visual plaid rivalry, it is important to be aware that the initial percept induced by both stimuli is strongly—often exclusively—biased toward the coherent percept (Hupé & Rubin, 2003; Pressnitzer & Hupé, 2006). After the initial dominance period the relative bias of the two percepts becomes more balanced. This distinction between the initial dominance period at stimulus onset and the subsequent perceptual alterations is also seen in binocular rivalry and a variety of other ambiguous stimuli (for a review, see Stanley, Forte, Cavanagh, & Carter, 2011). One consequence of this extreme bias toward the coherent percept is that the *identity* of the first percept is less informative about the effect of prior experience than it can be using other more balanced examples of rivalry (Brascamp, Pearson, Blake, & van den Berg, 2009; Chopin & Mamassian, 2010; de Jong, Knapen, & van Ee, 2012). Although this may cause us to miss some of the more subtle effects of prior stimulus adaptation, the fact that effects of prior stimulus are seen on the average perceptual dominance over the 20-s trial is testament to the strength of the effects reported (the relative persistence of the effects over the 20-s trial interval can also be seen in the time course data illustrated in Fig. 2a and c). One alternative measure of the initial dominance period, that does show strong effects of prior exposure is the *duration* of the initial dominance period (the latency to first switch). In Experiments 1 and 2 presented here, the change in latency to first switch showed the same pattern as the change in overall dominance reported (i.e., conditions with greater proportion of the segregated percept also had shorter latency to the first switch toward the segregated percept). However, as the two aspects of data are nonindependent and effectively describe the same overall result, the data on latency of first switch has not been reported.

The results here are consistent with *suppressive* effects of prior experience seen in our earlier auditory experiments (Snyder, Carter, et al., 2009; Snyder et al., 2008). However, one point of difference between the visual and auditory experiments is that the effects were shown to persist for up to

30 s in audition (Snyder et al., 2008; see also Snyder & Weintraub, 2013). In contrast, the influence of prior- α is unlikely to persist for such long durations given that the effects on the plaid were substantially reduced after a 10-s ISI.

Experiment 2

After demonstrating a robust *suppressive* effect of prior stimulus adaptation, we next explored the relative contribution of low- and high-level processes in the observed effects. In audition, *suppressive* effects of prior stimulus were surprisingly found to transfer to auditory stimuli constructed with tones from a different frequency range (i.e., containing nonoverlapping low-level features) but only partially to stimuli with different rhythmic structure (Snyder, Carter, et al., 2009; Snyder & Weintraub, 2011). In addition, *facilitative* effects of prior percept were also seen when non-biased stimuli were used in successive trials. Together, these results were not explainable by low-level (i.e., frequency-specific) neural populations coding the individual tone elements, which had previously been thought to be sufficient to explain auditory segregation of pure tone patterns (Hartmann & Johnson, 1991; Moore & Gockel, 2002; Snyder & Alain, 2007). Rather the results suggested a *suppressive* contribution of neural populations coding the “difference” in frequencies between the individual tone elements and a *facilitative* contribution of the percept-level representation of “coherence” versus “segregation” (Snyder, Carter, et al., 2009).

Experiment 2 investigated the involvement of similar higher-level processes in vision. Specifically, we tested whether *suppressive* effects could transfer across plaid stimuli rotated either 90° or 180° (i.e., motion vectors for the two gratings or the diamond-like plaid intersections within adaptation and test stimulus would be nonoverlapping, while all other stimulus properties would be held constant). We also assessed the effect of prior perceptual state, in the absence of any stimulus change.

Method

Ten participants took part (three female, seven male; 24–32 years of age), including five from Experiment 1. Apart from authors O.C. and J.S.S., all other participants were naïve to the aims of the experiment.

Five blocks of 16 trials were presented. Each trial consisted of a 15-s adaptation period and a 15-s test period, separated by a 1-s ISI. During the adaptation period, the plaid region was either blank or contained a plaid with α values of 50°, 105°, or 150°. The ambiguous 105°- α plaid was always used as the test. On each trial, the orientation of the adaptation plaid was randomly selected from among coherent motion being seen as up, down, to the left, or to the right. The motion direction of

the test plaid was either consistent with the adaptation stimulus or rotated $\pm 90^\circ$ or 180° . Note that the effect of rotation was only assessed in respect to adaptation to the biased 150° and 50° stimuli; consequently, the 105° – 105° adaptation–test pair was only assessed in a condition of no rotation. Each adaptation–test pair was separated by a 5-s interval and only presented once per block. During these intervals and the “blank” adaptation period, a uniform gray field was presented in place of the plaid.

In all other respects, the stimulus and instructions were identical to those described for Experiment 1.

Results

The same pattern of results was observed, regardless of the absolute motion direction of the adaptation plaid. The data, therefore, were grouped across the four adaptation motion directions and were analyzed only on the basis of relative rotation between the adaptation and test periods.

Consistent with Experiment 1, after 0° rotation, adaptation- α had a significant *suppressive* effect on the overall dominance of the segregated percept during the test, $F(1, 9) = 22.72$, $p < .0025$, $\eta^2 = .716$ (power = .988; see Fig. 3a). Interestingly,

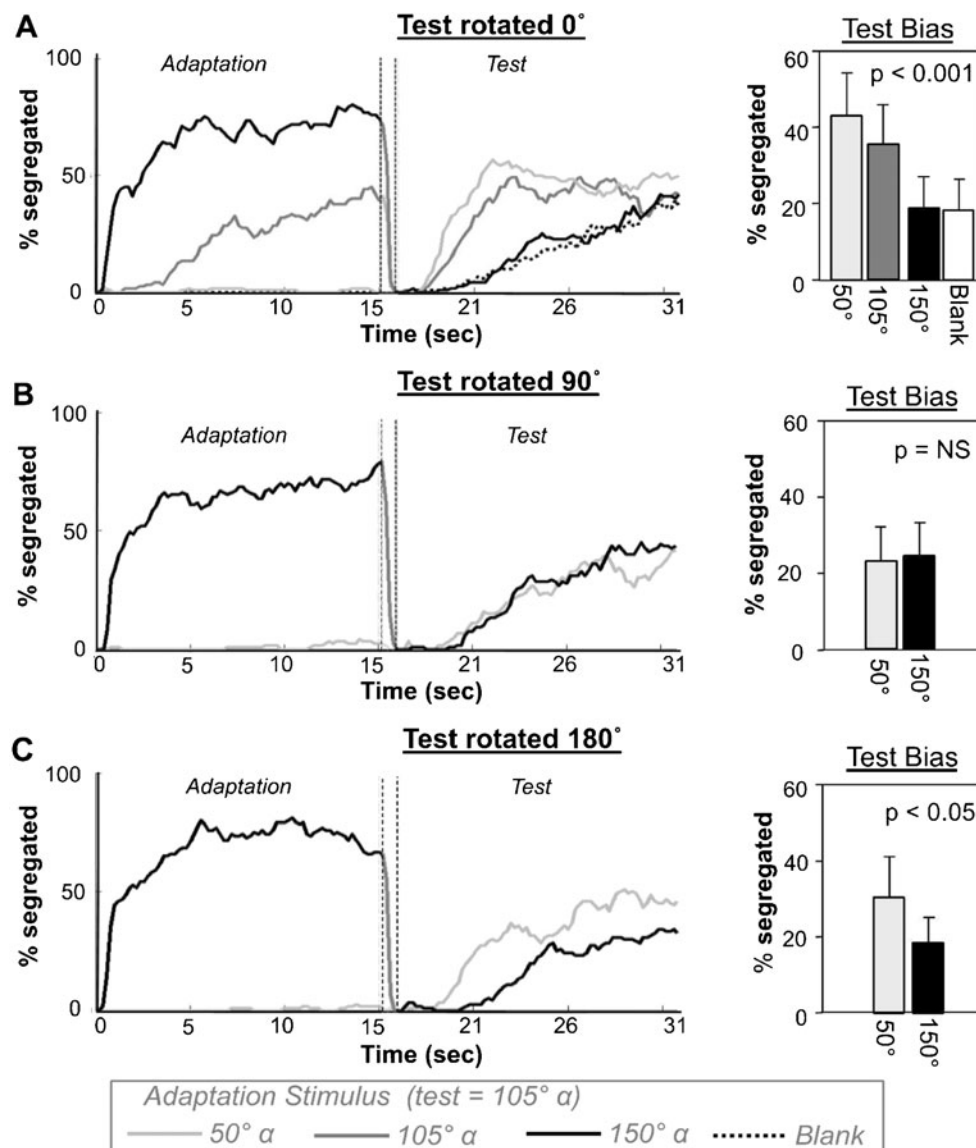


Fig. 3 Results from Experiment 2. The time-course data are shown on the left side of each row, whereas the overall effect of adaptation- α on the percent dominance of the segregated bias during the test period is shown in each corresponding right panel. Error bars represent 95 % confidence intervals. **a** After 0° rotation, clear suppressive effects were seen when the test stimulus followed one of the two biased adaptation stimuli, relative to

trials following the ambiguous 105° - α plaid. The dotted black line shows the effect of adaptation to a blank stimulus. **b** When the test stimulus was rotated 90° relative to the adaptation stimulus, we observed no effect of prior exposure to the biased 50° - α or 150° - α plaid stimuli. **c** Adaptation effects returned in trials on which the test stimulus was rotated 180° relative to the adaptation stimulus

trials preceded by the $150^\circ\text{-}\alpha$ plaid were indistinguishable from those preceded by a blank interval.

When the test was rotated $\pm 90^\circ$, the effect of adaptation- α was abolished, $F(1, 9) = 0.52$, n.s. (Fig. 3b). Surprisingly, when the test was rotated by 180° between the adaptation and test stimuli, a clear suppressive effect of prior- α was present (though weaker than that seen in the 0° -rotation condition), $F(1, 9) = 8.52$, $p < .05$ (Fig. 3c). This pattern of results was reflected by an interaction between adaptation- α and rotation, $F(2, 8) = 36.87$, $p < .001$, $\eta^2 = .902$ (power = 1.0).

To assess the effect of prior perception, we reanalyzed the data from trials in which the $105^\circ\text{-}\alpha$ stimulus was presented in both the adaptation and test periods. After first sorting all trials on the basis of whether the final percept during the adaptation period was coherent or segregated, we found no effect of prior perceptual state on the perceptual dominance during the subsequent test period, $F(1, 9) = 0.14$, $p = .717$, $\eta^2 = .015$ (power = .063).

Discussion

A previous study by von Grünau and Dubé (1993) demonstrated that adaptation to unambiguous versions of the coherent or segregated plaid stimuli (or selected elements of the stimuli such as a single grating) lead to clear *suppressive* effects on subsequent viewing of an ambiguous (transparent) plaid stimulus (von Grünau & Dubé, 1993). Consistent with this study, and with our results from Experiment 1, we also found a suppressive effect of adaptation to “coherence” using our novel biased stimuli in the no-rotation condition.

In direct contrast, however, we found no effect of adaptation to a stimulus biased toward segregation (the $150^\circ\text{-}\alpha$ stimulus) relative to the trials in which a blank gray screen was presented during the adaptation period (Fig. 3a, dotted line). Our contradictory “segregation adaptation” results likely reflect the fact that we used adaptation to an intact ambiguous plaid that was heavily biased toward the segregated percept, rather than using the individual grating elements that make up the ambiguous plaid stimuli (von Grünau & Dubé, 1993). Together, these results suggest that adaptation to the individual motion vectors of the identical grating components is sufficient to induce *suppressive* effects (von Grünau & Dubé, 1993). However, adaptation to pattern “segregation” per se is not sufficient to cause *suppressive* effects of the segregated percept. Our results also provide a cautionary warning that contradictory results can be seen when comparing adaptation to biased ambiguous stimuli with adaptation to nonambiguous stimuli.

In audition, not only were *suppressive* effects seen for both segregated and coherent percepts, but these effects of prior stimulus transferred to subsequent test stimuli that did not share low-level stimulus features (i.e., tones sampled from nonoverlapping frequency ranges; Snyder, Carter, et al., 2009). This result was consistent with the proposed involvement of higher-level neural populations in distinguishing

between coherence/binding and segregation with complex auditory stimuli (Snyder & Alain, 2007). Using the plaid motion stimulus, the present study was unable to identify an analogous degree of transference in vision. Indeed, the influence of prior stimulus exposure was totally abolished when the stimulus was rotated by 90° , such that the component motion vectors from the adaptation and test plaid stimuli did not overlap. In further contrast to our auditory experiments, we found no effect of prior perception. However, it is difficult to draw strong conclusions from this prior-perception result, as we had data from only ten trials (for each of the ten participants) in which the same $105^\circ\text{-}\alpha$ stimulus was presented in both the adaptation and test periods.

The second surprising result was that despite all *suppressive* effects being abolished after 90° rotation, they nevertheless reappeared (though at reduced levels) when the test stimulus was rotated 180° relative to the adapting stimulus. Together, our results suggest that the primary driver of our observed *suppressive* effect may be sustained adaptation of the neural population selective for the axis, but not the absolute direction, of motion of the dominant percept(s). In the case of the coherent plaid, the axis of motion of the dominant percept was consistent with the diamond intersections. In the case in which the segregated gratings dominated perception, the diamond intersections still followed the same motion axis; however, they appeared to be insufficient to cause *suppressive* effects when they were not perceptually salient.

Although it is difficult to speculate as to the neural locus of this “axis-of-motion” effect, some neurons in primary visual cortex (V1) are known to respond (generally at a reduced capacity) to motion traveling along the same axis, but in the opposite direction to the neuron’s “preferred” direction (Hubel & Wiesel, 1962, 1968). In contrast, neurons in the motion-sensitive medial temporal (MT) area generally showed greater direction selectivity and no response to motion 180° from the preferred direction (Dubner & Zeki, 1971). It may also be that the orientation of the gratings (also likely represented in V1) could be playing a role as they are close to horizontal for both the upward and downward motion. Alternatively, adaptation to the strongly biased plaid stimuli may have led to “priming” of a higher-level representation of a coherent plaid percept that is direction specific and is expressed as a suppressive effect on plaids moving in the opposite direction. Although further research will be needed to tease apart the effects observed here, the plaid provides a useful stimulus to better understand the effects of prior exposure to visual motion and its effect on perceptual dominance.

Experiment 3

The final experiment was designed to parallel our previous study that had used an EEG protocol to investigate the

physiological correlates of the effects of prior auditory experience on the auditory streaming paradigm. In that study, we were able to dissociate the pattern of neural modulation associated with the initial encoding of the current stimulus from the influence of previous stimulus exposure (Snyder, Holder, et al., 2009). Here, we aimed to measure the neural populations involved in both the encoding of the current stimulus and stimulus-driven adaptation for the visual plaid.

An additional aim of Experiment 3 was to further explore any evidence of a *facilitative* effect of prior percept. Such *facilitative* effects of prior percept have now been seen using a range of ambiguous stimuli in the visual (Brascamp et al., 2008; Leopold, Wilke, Maier, & Logothetis, 2002; Maier, Wilke, Logothetis, & Leopold, 2003), and tactile domains (Carter et al., 2008). Using the auditory streaming paradigm we were also able to demonstrate *facilitative* effects of prior percept (Snyder, Carter, et al., 2009; Snyder, Holder, et al., 2009). In Experiment 2 above, we were unable to detect a significant *facilitative* effect of prior percept; however, this may have been due to a lack of power (data were limited to only ten trials for each of the ten participants). To maximize the number of trials obtained for analysis, we tested more people in our final experiment and only considered the three no-rotation conditions from Experiment 2.

Methods

Participants A group of 32 participants (19 women, 13 male; 18–42 years of age) with normal or corrected-to-normal vision from the University of Nevada, Las Vegas, community participated after giving written informed consent according to guidelines at the University of Nevada, Las Vegas. Five additional participants took part but did not complete the experiment due to technical problems (three), abnormal pattern of perception during adaptation (one), or withdrawal from the experiment due to physical discomfort (one).

Materials and procedure All stimulus parameters were the same as described above in Experiment 2. The only difference was that the size of the adaptation and test plaid pattern was increased (to maximize the EEG responses) with a diameter of 21.4° and a black 0.2° fixation dot was presented centrally within a dark gray exclusion zone of 1.8° diameter.

The plaid pattern moved upward smoothly for six frames (100 ms), followed by six blank gray frames (100 ms) and then reappeared as if it had been moving throughout the blank period, giving an impression of smooth movement with a 5-Hz flicker. The resulting motion onsets, separated by a 200-ms interonset interval, were used to time lock the EEG responses.

Each trial consisted of an 8-s adaptation period (40 onsets), a 1.5-s ISI, and an 8-s test period (40 onsets) (see Fig. 4a). Five blocks of 30 trials were presented (ten for each of the three adaptation- α values). Thus, each adaptation- α was presented

50 times, resulting in 2,000 onsets for each participant per condition. Three practice trials (one of each type) were presented prior to beginning the experiment. Stimuli were presented on a 19-in. monitor (60 Hz, $1,680 \times 1,050$) using a custom program written with Presentation software.

Participants sat in a comfortable chair in a dimly lit room and rested their heads against the back of the chair at a viewing distance of 80 cm. Participants were asked to fixate on the central point during electrophysiological recording and to remain still while the stimuli were presented. At the end of each adaptation and test period, the participants used their right hand to indicate on a button box whether they perceived (1) a coherent upward moving plaid pattern for the entire sequence or (2) two sliding gratings moving diagonally toward the upper left and upper right, respectively, at any point during the sequence. EEG signals were digitized continuously (512-Hz sampling rate and a 104-Hz bandwidth) using a 72-channel Biosemi ActiveTwo system. For more details on the EEG setup, see Snyder, Holder, et al. (2009).

Data analysis A repeated measures ANOVA was used to test for the effect of adaptation- α (50° , 105° , 150°) on the proportions of trials that participants reported the segregated percept during the adaptation and test periods individually.

All offline ERP analyses were performed using the Brain Electrical Source Analysis software (BESA), except for baseline correction and amplitude measurements, which were performed by custom scripts in MATLAB. Noisy electrodes were noted during the recording and were interpolated prior to analysis. Ocular artifacts (blinks, saccades, and smooth movements) were first corrected automatically within BESA using a spatial-filtering based method (Ille, Berg, & Scherg, 2002). Epochs contaminated by any remaining artifacts (amplitude $> 150 \mu\text{V}$, gradient $> 75 \mu\text{V}$, low signal $< 0.10 \mu\text{V}$) were automatically rejected before averaging. EEG epochs were averaged separately across all nonartifact trials for each of the three stimulus conditions, for the adaptation and test sequences, and for each electrode site, and re-referenced to the average of all electrodes not adjacent to the eyes. Epochs were digitally bandpass filtered to attenuate frequencies below 3 Hz (6-dB/octave attenuation, forward) and above 30 Hz (24-dB/octave attenuation, symmetrical).

To examine the effects of adaptation- α on the onset-evoked ERPs, trial epochs with Time 0 at each onset were segmented with a 400-ms pretrigger baseline period and a 400-ms posttrigger active period (corresponding to four onset cycles). ERPs were baseline corrected by subtracting the mean of the -20 - to 0 -ms portion of the epoch (20 ms preceding an onset) from each point in the epoch.

To examine the effects of perception during adaptation on α -related activity, EEG epochs were processed as described above, using only those epochs with an adaptation- α of 105° , and were divided according to perception reported during the

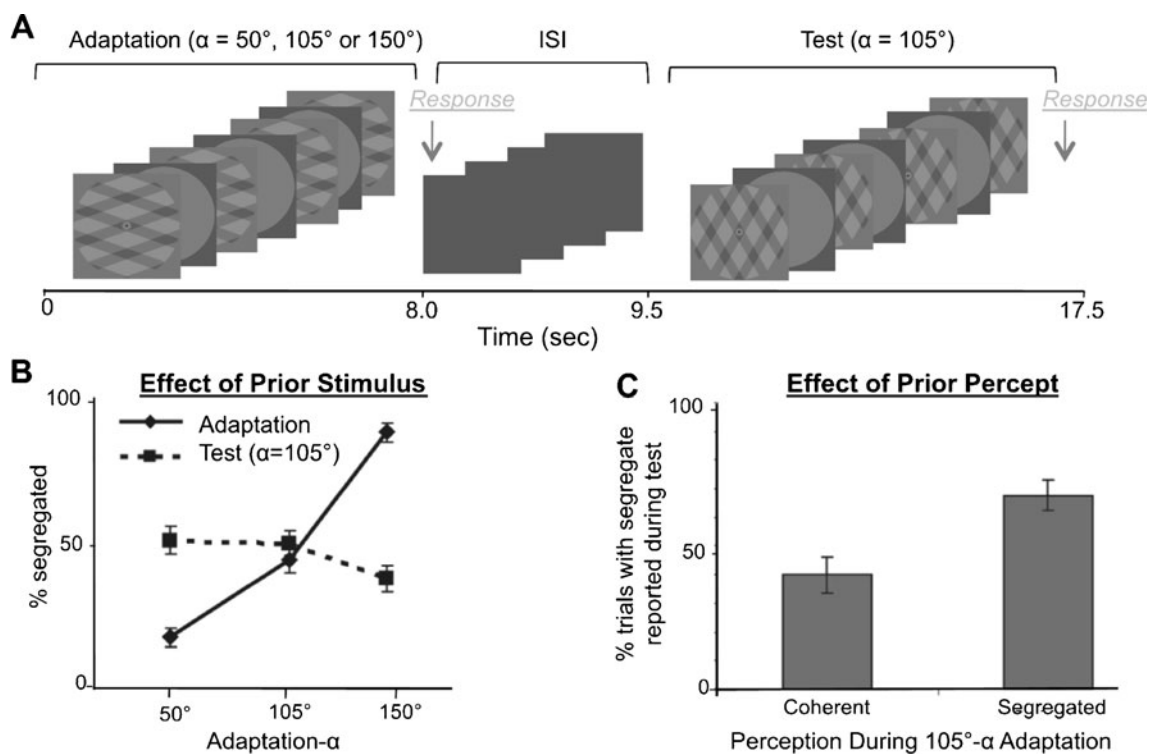


Fig. 4 Stimuli and behavioral results in Experiment 3. **a** The plaid was presented intermittently to evoke event-related potential (ERP) responses, moving smoothly for 100 ms at a time, followed by a 100-ms blank. Each trial started with adaptation to the 50° - α , the 105° - α , or the 150° - α plaid. After a 1.5-s ISI with a blank screen, an ambiguous 105° - α plaid was presented for the test period. **b** Behavioral data averaged across all participants ($\pm SE$) show that larger adaptation- α values resulted in more

reports of segregated gratings during adaptation (solid line, filled diamonds), but this same percept was *suppressed* during the ambiguous 105° - α test (dotted line, filled squares). **c** Grouping data on the basis of the prior percept from the 105° - α adaptation trials show that perceiving the segregated percept during the adaptation period *facilitated* this segregated percept when the same, ambiguous 105° - α stimulus was used for the test period ($\pm SE$)

adaptation sequence. We reaveraged the data for 31 participants who had at least 100 nonartifact epochs for each percept in the adaptation and test periods.

All epochs corresponding to either adaptation- α or perception were further sorted into four time bins (t_1, t_2, t_3, t_4 , corresponding to the 1st, 2nd, 3rd, and 4th quarters of a trial, respectively) to examine how effects of adaptation- α or perception changed during the course of the adaptation and test sequences.

To visualize and identify the time ranges and electrodes expressing maximal differences, we first calculated difference waves from the grand-averaged original waveforms between conditions of interest. The mean event-related potential (ERP) amplitudes were then calculated from the original waveforms for the identified time ranges and electrodes expressing maximal differences. The difference waves were not used for statistical analysis; rather, the original waveforms were used, as they typically have better signal-to-noise ratios. Note that mean amplitude values can reflect both changes in amplitude and latency of neuronal sources and are less susceptible to noisy data than are peak amplitude/latency measurements (Picton et al., 2000). Mean amplitudes were averaged across electrode sites for each participant and submitted to ANOVAs.

Results

Behavior Consistent with the *suppressive* effects seen in Experiments 1 and 2, adaptation to larger α values biased observers toward the segregated percept during the adaptation period, $F(2, 30) = 84.23, p < .001, \eta^2 = .849$ (power = 1.0) (Fig. 4b, solid line) and reduced reports of the segregated percept during subsequent presentation of the ambiguous 105° - α test, $F(2, 30) = 21.95, p < .001, \eta^2 = .594$ (power = 1.0). This significant *suppressive* effect reflects a relative increase in the segregated percept after 50° - α and 105° - α adaptation, as compared to periods of adaptation to the 150° - α plaids (Fig. 4b, dashed line).

To assess the effect of prior perception, data from all trials with the ambiguous 105° - α presented during the adaptation and test periods were divided on the basis of whether or not participants experienced the segregated percept at any point during the adaptation period. One participant was excluded for always perceiving the adaptation in the same way, whereas all other participants reported both percepts at the end of different adaptation trials. Prior perception was found to have a *facilitative* effect, such that participants perceiving segregated gratings during adaptation periods were more likely to report the

same perceptual state during the ambiguous test, $F(1, 30) = 33.69, p < .001, \eta^2 = .529$ (power = 1.0) (Fig. 4c).

Electrophysiology ERPs time-locked to motion onsets occurred with maximal amplitude at 108 ms in midline-occipital and lateral-temporal electrodes. This peak is somewhat earlier than previous reports of motion-related ERPs. This is likely to be due to the quasi-steady-state nature of the 5-Hz stimulus presentation rate and/or the fact that this early response may represent an onset response, rather than a motion-specific response (Ahlfors et al., 1999; Aspell, Tanskanen, & Hurlbert, 2005; Bundo et al., 2000; Probst, Plendl, Paulus, Wist, & Scherg, 1993). However, some early motion-specific responses have been identified (e.g., Ffytche, Guy, & Zeki, 1995; Uusitalo, Virsu, Salenius, Nasanen, & Hari, 1997).

The visually identified electrodes showing maximal α -related modulations during the adaptation period were based on difference waves taken between the most extreme α levels (150° – 50°). As is shown in Fig. 5a and b, separate difference waves were taken for each of four 2-s time bins (t1–t4) of the trial (each bin contained ten onset-evoked responses per trial that were averaged together). Significant negative increases of ERP amplitude were quantified in the original waveforms and occurred from 30 to 60 ms and from 125 to 170 ms following the onset at Oz, $F_s(2, 30) = 42.51$ and $22.33, p_s < .001, \eta^2_s = .739$ and $.598$ (power = 1.0 and 1.0), and these differences became larger throughout the course of the trial (i.e., from t1 to t4), especially for the largest α , as indicated by a main effect of time, $F_s(3, 29) = 0.04$ and $6.00, p_s < .005, \eta^2_s = .510$ and $.383$ (power = .995 and .929), and an interaction between α and time bin, $F_s(6, 26) = 4.38$ and $6.04, p_s < .01, \eta^2_s = .503$ and $.582$ (power = .949 and .991).

Modulations during the test period due to adaptation- α were visually identified by calculating difference waves between trials preceded by 50° - α and 150° - α , respectively. Note that this subtraction is in the opposite direction than was used for the adaptation- α calculations, in line with the opposite/suppressive effects of adaptation- α seen on perception during the adaptation and test period. As shown in Fig. 5a (bottom) and Fig. 5b (right), adaptation- α -related difference waves were present throughout the test sequence, with an increase from t1 to t2 and subsequent decreases at t3 and t4 from 10 to 60 ms at Oz (as quantified in the original waveforms), as indicated by a significant linear trend for α , $F_s(2, 30) = 7.04, p < .005, \eta^2 = .319$ (power = .901), and significant linear and quadratic trends for time, $F_s(3, 93) = 17.42$ and $37.31, p_s < .001, \eta^2_s = .360$ and $.546$ (power = .981 and 1.0). Some of the changes in amplitude observed in the waveform may have resulted in part from changes in latencies of components, as in the adaptation data. Correlations between the effects of α (150° – 50°) on ERPs during adaptation (at 30–60 and 125–170 ms) and the effect of α on ERPs during the test

(at 10–60 ms) were small [$r(30) = .385, p < .05$, and $r(30) = .043, p = .82$, respectively], meaning that individuals with large α -related modulations during the adaptation did not necessarily have large modulations during the test due to adaptation- α .

To identify brain activity specific to the individual's perceptual state, the data from the trials in which the ambiguous 105° - α plaid was presented during both the adaptation and test period were sorted on the basis of whether a coherent plaid or segregated gratings was perceived during the adaptation period. For ERPs corresponding to the adaptation and test periods, a perception-related modulation peaking around 90 ms was maximal at Oz (Fig. 5c–d), with more positive activity when participants perceived segregated gratings rather than the coherent plaid (quantified in the original waveforms from 75 to 100 and from 75 to 115 ms, for adaptation and test, respectively), although the modulation was only significant during adaptation, $F(1, 30) = 4.86, p < .05, \eta^2 = .139$ (power = .569), but not during the test, $F(1, 30) = 1.784, p = .19, \eta^2 = .056$ (power = .253).

A separate modulation also occurred during the adaptation and test with more positive activity when participants perceived two gratings at right lateral electrodes (quantified in the original waveforms at PO7 and PO8 from 160 to 185 and 140 to 175 ms for adaptation and test, respectively), resulting in a significant hemisphere by perception interaction, $F(1, 30) = 9.48, p < .005, \eta^2 = .240$ (power = .846) and $F(1, 30) = 6.23, p < .025, \eta^2 = .172$ (power = .676).

In contrast to the effects of adaptation- α , correlations between effects of perception (segregated – coherent) on ERPs indicated substantial similarity between the perception-related brain activity during adaptation and test [Oz effect, $r(29) = .752, p < .001$; PO8 effect, $r(29) = .422, p < .025$].

Discussion

The α -related difference waves were present throughout the adaptation sequence (even during t1), with maximum amplitude at occipital electrodes, and increased amplitude over time (Fig. 5a and b, left), possibly reflecting the increasing occurrence of the segregated percept as viewing duration increased (Hupé & Rubin, 2003; Pressnitzer & Hupé, 2006). The apparent difference in scalp topographies during the adaptation and the test, in addition to the low correlations between the adaptation and test α -related modulations, suggest that (at least partially) distinct neural populations underlie the stimulus adaptation effects and encoding of the current stimulus.

We were able to show a *facilitative* effect of prior percept in this final experiment consisting of 50 105° - α adaptation/test trials per person, which mirrors our results in audition (Snyder, Carter, et al., 2009; Snyder, Holder, et al., 2009) and is consistent with previous reports of perceptual

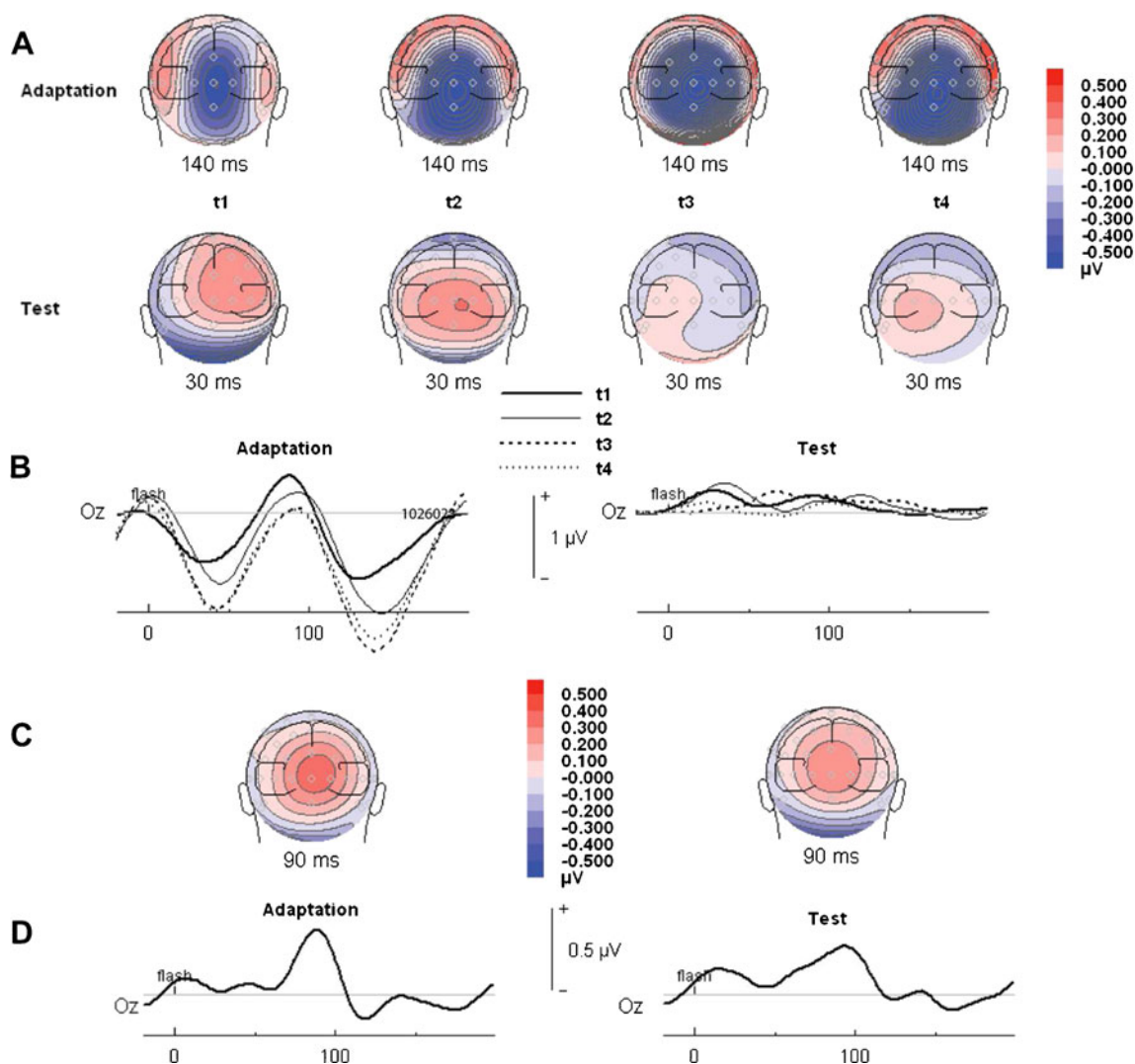


Fig. 5 Grand-average difference waves ($150^\circ - 50^\circ$ for adaptation and $50^\circ - 150^\circ$ for test) showing modulations due to adaptation- α . **a** Scalp topographical patterns of voltage at the largest peak of difference waves during adaptation and test (140 and 30 ms after onset, respectively). In both cases, the maximum difference was seen at midline occipital electrodes. **b** Difference wave traces for adaptation ($150^\circ - 50^\circ$) and test ($50^\circ - 150^\circ$): Evolution of difference waves over time, shown for four time bins (t1–t4) at electrode Oz during the adaptation and test periods. The effect of α increases over time during adaptation and decreases over time during test, indicative of a decaying effect of adaptation- α . **c** Grand-average

effects of perception on event-related potentials (ERPs) at the midline occipital electrode. When segregation rather than coherence was perceived during adaptation, the ERPs showed similar modulations during adaptation and test. Scalp voltage patterns are for difference waves (segregation – coherence for both adaptation and test). The largest peaks of difference waves during adaptation and test showed the maximum difference at midline occipital electrodes. **d** Difference wave traces (segregation – coherence for both adaptation and test). The maximum difference due to current and prior perception occurred around 90 ms

facilitation or *stabilization* in vision (for a review, see Pearson & Brascamp, 2008). However, to avoid movement artifacts in the EEG analysis, participants did not report their perceptual state throughout the duration of the trial (in contrast to Exps. 1 and 2), but rather had to indicate at the end of the trial whether or not they had experienced the segregated percept during the trial. Therefore, on trials in which participants selected the response that “the segregated percept was never experienced during the entire trial duration” we can be confident that the coherent percept was dominant at the trial’s end. But we have

no way of determining which trials finished with the segregated percept dominating.

ERPs during adaptation and test were modulated by the perceptual state as reported at the end of the adaptation. Importantly the distinct time courses and polarities of modulations as a result of perceptual state, relative to modulations due to α and prior- α , suggest that the α -related modulations described above were not simply due to effects of perception on the ERPs. Another notable finding was the similar and correlated effects of perceptual state at the end of adaptation

on ERPs during adaptation and test, suggesting similar neural generators for these two effects.

General discussion

This study used the ambiguous plaid stimulus to explore the effects of prior experience on current visual perception. Combining psychophysics and EEG, both prior stimulus properties and perceptual state were found to influence current perception in distinct ways.

Investigating the effect of prior stimulus and perceptual experience using psychophysics

The present experiments paralleled a recent series of auditory studies using ambiguous stimuli that investigated the perceptual consequence of prior adaptation to biased stimuli (Snyder, Carter, et al., 2009; Snyder et al., 2008; Snyder, Holder, et al., 2009). Both the present visual experiments and the previous auditory studies follow an extensive tradition of using adaptation to investigate a range of different aspects of perceptual processing in visual (Addams, 1834; Gibson & Radner, 1937), auditory (Holt, 2005; Shu, Swindale, & Cynader, 1993), tactile (Thalman, 1922; Watanabe, Hayashi, Kajimoto, Tachi, & Nishida, 2007), gustatory (Filipello, 1956), and olfactory (Cheesman & Mayne, 1953) domains.

Experiment 1 provided an initial demonstration (1) that it is possible to reliably bias the perception of the ambiguous plaid stimulus toward either the coherent or segregated percept by decreasing or increasing α , respectively, and (2) that the biased stimuli could induce *suppressive* effects on subsequently presented ambiguous plaid stimuli. This initial demonstration of *suppressive* effects with the plaid stimulus were consistent with those seen in our related auditory study (Snyder, Carter, et al., 2009; Snyder et al., 2008) and an additional study using ambiguous tactile stimuli (Carter et al., 2008).

One of the most surprising findings from our auditory studies was that adaptation effects transferred to other stimuli with nonoverlapping low-level stimulus elements (i.e., the test stimulus consisted of tones from a frequency range that was completely nonoverlapping with the adaptation stimulus). These results were unexpected, as it suggested an involvement of neurons coding the magnitude of separation between tone elements. This was in direct contrast to the commonly held view that the principal determinants of whether an auditory tone sequence is perceived as a single coherent percept, or as two segregated tone streams, is the relative activity of the neurons coding the frequency of individual tone elements (Micheyl et al., 2007). Because of the noted similarities between the auditory streaming and the visual plaid paradigms, which both alternate between segregated and coherent percepts (Hupé, Joffo, & Pressnitzer, 2008), we were interested to

explore whether an analogous effect of magnitude of difference between component motion direction (α) could be identified in the plaid stimulus. To assess whether our *suppressive* effects of prior adaptation could transfer to stimuli with nonoverlapping component features (i.e., motion vectors), in Experiment 2 we investigated the effect of stimulus rotation. In contrast to the transference seen in audition, *suppressive* effects of the plaid stimulus did not survive a 90° rotation. Although this result may suggest greater involvement of the low-level stimulus features in this visual paradigm relative to the auditory streaming paradigm, it is possible that greater transference would have been seen if other stimulus features such as spatial frequency were varied instead of orientation. More research is needed to draw firm conclusions about the underlying mechanisms. However, the finding that *suppressive* effects returned when the test stimulus was rotated 180° provides some evidence of the involvement of neural populations sensitive to component grating orientation or with bidirectional motion responses.

To test the effects of prior perceptual state on the perception of subsequent ambiguous stimuli, data from the ambiguous 105°- α adaptation were sorted on the basis of prior perception during the adaptation period. Although the present experiments were not optimized to investigate this effect of prior percept, both Experiments 2 and 3 contained trials suitable for this analysis. In Experiment 2, we found no effects of prior percept; however, this may have been due to the limited numbers of trials available in the analysis. In Experiment 3, prior perception was found to have a *facilitative* effect: If participants perceived two segregated gratings during the adaptation period, they were more likely to report the same perceptual state during the test period. This result is consistent with similar findings using a variety of other ambiguous visual (Brascamp et al., 2008; Leopold et al., 2002; Maier et al., 2003), auditory (Snyder, Carter, et al., 2009; Snyder, Holder, et al., 2009), and tactile (Carter et al., 2008) stimuli. However, the present data need to be interpreted with caution, since participants were not able to report their perceptual state throughout the duration of the trial.

Taken together, these results suggest that both the *suppressive* and *facilitative* effects demonstrated here using the plaid represent a general characteristic of ambiguous stimuli that exists across sensory modalities. The greater degree of transference of adaptation in the auditory studies suggests a relatively greater influence of low-level sensory areas in vision than audition. However, more work is still required to fully understand these effects as a number of factors remain to be explored. For example, it is likely that effects will depend heavily on stimulus presentation times as it has previously been shown that changing the duration of presentation time, or inter-stimulus interval, can cause the effects of previous stimulus/percept to completely reverse from *facilitation* to *suppression* (Brascamp et al., 2007; Kanai & Verstraten, 2005).

Using EEG to investigate the suppressive and facilitative effects of the plaid

The ERP results from Experiment 3 showed modulations due to α during the adaptation and test at occipital electrode sites. These results are consistent with earlier proposals that the biasing effects of α result from activation of motion-direction-selective neurons such as those that are present in V1 and MT (Hubel & Wiesel, 1962, 1968; Huk & Heeger, 2002; Serences & Boynton, 2007).

Looking at the adaptation period in isolation, the modulations of ERPs peaked around 40 and 140 ms following onset of the motion stimuli and became larger in amplitude as time progressed throughout the adaptation period. Although continuous behavioral judgments were not collected in the present study, to minimize motor artifacts, we can infer from Experiments 1 and 2 that the incidence of the segregated percept would have likely increased over the duration of the trial. It is therefore possible that this increase in amplitude of α -related ERPs at occipital electrodes is related to the increased likelihood of the segregated percept after initial dominance of the coherent percept in the plaid paradigm. The increased amplitude over time could reflect the engagement of two distinct neural populations representing the two segregated gratings, as compared to the single neural network required to represent the coherent plaid pattern moving in a single direction. Although speculative, this possibility is consistent with current theories about the neural mechanisms underlying the segregation of analogous auditory tone patterns (Micheyl et al., 2007; Snyder & Alain, 2007).

During the test, modulation of the ERP as a function of adaptation- α was seen at 30 ms following the onset of the plaid stimuli. This modulation was present for the first half of the test period but markedly diminished during the second half of the test period, possibly reflecting the fading of neural adaptation underlying the *suppressive* adaptation- α effect. The different topographies and the low correlations between α -related modulations during the adaptation and test suggest that, at least partially distinct neural populations are modulated by prior stimuli, relative to the neural populations that were activated by the initial processing of the stimuli.

This issue deserves further exploration in future studies to address whether the effects of prior stimuli and prior percepts can truly be dissociated. For example, it would be important to manipulate the prior stimulus without also changing the prior perception and *visa versa*. Since in the present experiment we used extreme alpha values to reliably bias perception, more subtle differences in alpha would be needed to generate enough trials dominated by each of the alternative percepts. It might then also be possible to sort trials on the basis of ERP amplitude (rather than stimulus or percept values) during adaptation to see if the brain activity in time ranges we identified as being important are actually sufficient by themselves to modulate later perception during the test. In addition, simple replications

and extensions of the ERP effects would be important to carry out because the present ERP experiment was exploratory by necessity. The identified ERP modulations are not routinely associated with known motion-specific responses and would therefore benefit from modification of the paradigm used in the present study. For example, using longer delays between stimulus flicker would enable clearer identification of the time course of ERP modulations to individual stimulus onsets than was possible in the present study, which used more of a steady-state-like ERP paradigm.

For trials in which the ambiguous 105°- α was used for both the adaptation and test stimulus, the present study identified perception-related ERP modulations that occurred at midline electrodes at 90 ms and lateral occipital electrodes at 160 ms in response to the onset of motion stimuli during both the adaptation and test. Significant correlations across individuals between the amplitude of perception-related modulations during the adaptation and test periods suggests that common neural populations may be involved in both representation of current percepts and the maintenance of a memory trace reflecting prior perceptual states. Given that one recent study identified brain activity in face-specific brain areas during storage of prior perception of face stimuli during binocular rivalry (Sterzer & Rees, 2008), it follows that the motion-specific brain areas responsible for determining the observers' current percept may be the same brain areas that maintain a representation of recent perceptual states induced by the plaid. Although future research will be required in order to identify the specific brain regions involved, the present data are consistent with a number of previous studies implicating superficial occipital cortex along with medial temporal and parietal areas specifically in coding ambiguous motion perception (Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996; Brouwer & van Ee, 2007; Dodd, Krug, Cumming, & Parker, 2001; Grunewald, Bradley, & Andersen, 2002; Moutoussis & Zeki, 2008; Serences & Boynton, 2007; Williams, Elfar, Eskandar, Toth, & Assad, 2003).

Conclusion

Here we have shown that the *suppressive* effects of prior stimulus bias and the *facilitative* effects of prior perceptual state previously seen using auditory and tactile stimuli can also be demonstrated using the ambiguous plaid motion stimulus. The fact that these results mirror findings of a parallel series of studies using the auditory streaming paradigm (Snyder, Carter, et al., 2009; Snyder et al., 2008; Snyder, Holder, et al., 2009) suggests that a full understanding of the neural factors responsible for generating one's current experience may require consideration of prior adaptation effects across all modalities.

Author note This work was supported by the College of Liberal Arts at University of Nevada, Las Vegas, a Clinical Research Training Program fellowship (No. T32 MH16259-28) from the National Institutes of

Health, and National Science Foundation Grant No. BCS1026023 (to J.S.S.), as well as by research fellowships from the Australian National Health and Medical Research Council (Nos. 368525 and 628590, to O.C.). The authors thank David Weintraub for help performing data entry and Ken Nakayama for helpful discussions about the project.

References

- Addams, R. (1834). An account of a peculiar optical phenomenon seen after having looked at a moving body. *London and Edinburgh Philosophical Magazine and Journal of Science*, 5, 373–374.
- Ahlfors, S. P., Simpson, G. V., Dale, A. M., Belliveau, J. W., Liu, A. K., Korvenoja, A., & Ilmoniemi, R. J. (1999). Spatiotemporal activity of a cortical network for processing visual motion revealed by MEG and fMRI. *Journal of Neurophysiology*, 82, 2545–2555.
- Aspell, J. E., Tanskanen, T., & Hurlbert, A. C. (2005). Neuromagnetic correlates of visual motion coherence. *European Journal of Neuroscience*, 22, 2937–2945.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10, 433–436. doi:10.1163/156856897X00357
- Brascamp, J. W., Knapen, T. H., Kanai, R., Noest, A. J., van Ee, R., & van den Berg, A. V. (2008). Multi-timescale perceptual history resolves visual ambiguity. *PLoS ONE*, 3, e1497. doi:10.1371/journal.pone.0001497
- Brascamp, J., Knapen, T. H. J., Kanai, R., van Ee, R., & van den Berg, A. V. (2007). Flash suppression and flash facilitation in binocular rivalry. *Journal of Vision*, 7(12):12, 1–12. doi:10.1167/7.12.12
- Brascamp, J. W., Pearson, J., Blake, R., & van den Berg, A. V. (2009). Intermittent ambiguous stimuli: Implicit memory causes periodic perceptual alternations. *Journal of Vision*, 9(3):3, 1–23. doi:10.1167/9.3.3
- Bregman, A. S., & Campbell, J. (1971). Primary auditory stream segregation and perception of order in rapid sequences of tones. *Journal of Experimental Psychology: Human Perception and Performance*, 89, 244–249.
- Britten, K. H., Newsome, W. T., Shadlen, M. N., Celebrini, S., & Movshon, J. A. (1996). A relationship between behavioral choice and the visual responses of neurons in macaque MT. *Visual Neuroscience*, 13, 87–100.
- Brouwer, G. J., & van Ee, R. (2007). Visual cortex allows prediction of perceptual states during ambiguous structure-from-motion. *Journal of Neuroscience*, 27, 1015–1023.
- Bundo, M., Kaneoke, Y., Inao, S., Yoshida, J., Nakamura, A., & Kakigi, R. (2000). Human visual motion areas determined individually by magnetoencephalography and 3D magnetic resonance imaging. *Human Brain Mapping*, 11, 33–45.
- Carlson, V. R. (1953). Satiation in a reversible perspective figure. *Journal of Experimental Psychology: Human Perception and Performance*, 45, 442–444.
- Carter, O., Konkle, T., Wang, Q., Hayward, V., & Moore, C. (2008). Tactile rivalry demonstrated with an ambiguous apparent-motion quartet. *Current Biology*, 18, 1050–1054.
- Cheesman, G. H., & Mayne, S. (1953). The influence of adaptation on absolute threshold measurements for olfactory stimuli. *Quarterly Journal of Experimental Psychology*, 5, 22–30.
- Chopin, A., & Mamassian, P. (2010). Task usefulness affects perception of rivalrous images. *Psychological Sciences*, 21, 1886–1893.
- de Jong, M. C., Knapen, T., & van Ee, R. (2012). Opposite influence of perceptual memory on initial and prolonged perception of sensory ambiguity. *PLoS ONE*, 7, e30595. doi:10.1371/journal.pone.0030595
- Denham, S. L., & Winkler, I. (2006). The role of predictive models in the formation of auditory streams. *Journal of Physiology*, 100, 154–170.
- Dodd, J. V., Krug, K., Cumming, B. G., & Parker, A. J. (2001). Perceptually bistable three-dimensional figures evoke high choice probabilities in cortical area MT. *Journal of Neuroscience*, 21, 4809–4821.
- Dubner, R., & Zeki, S. M. (1971). Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus in the monkey. *Brain Research*, 35, 528–532.
- Ffytche, D. H., Guy, C. N., & Zeki, S. (1995). The parallel visual motion inputs into areas V1 and V5 of human cerebral cortex. *Brain*, 118, 1375–1394.
- Filipello, A. (1956). A critical comparison of the two-sample and triangle binomial design. *Food Research*, 21, 235–241.
- Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines: I. Quantitative studies. *Journal of Experimental Psychology*, 20, 453–467.
- Grunewald, A., Bradley, D. C., & Andersen, R. A. (2002). Neural correlates of structure-from-motion perception in macaque V1 and MT. *Journal of Neuroscience*, 22, 6195–6207.
- Harris, J. P. (1980). How does adaptation to disparity affect the perception of reversible figures? *American Journal of Psychology*, 93, 445–457.
- Hartmann, W. M., & Johnson, D. (1991). Stream segregation and peripheral channeling. *Music Perception*, 9, 155–184.
- Holt, L. L. (2005). Temporally nonadjacent nonlinguistic sounds affect speech categorization. *Psychological Science*, 16, 305–312.
- Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology*, 160, 106–154.
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, 195, 215–243.
- Huk, A. C., & Heeger, D. J. (2002). Pattern-motion responses in human visual cortex. *Nature Neuroscience*, 5, 72–75.
- Hupé, J.-M., Joffo, L.-M., & Pressnitzer, D. (2008). Bistability for audio-visual stimuli: Perceptual decision is modality specific. *Journal of Vision*, 8(7):1, 1–15. doi:10.1167/8.7.1
- Hupé, J.-M., & Rubin, N. (2003). The dynamics of bi-stable alternation in ambiguous motion displays: A fresh look at plaids. *Vision Research*, 43, 531–548.
- Hupé, J.-M., & Rubin, N. (2004). The oblique plaid effect. *Vision Research*, 44, 489–500.
- Ille, N., Berg, P., & Scherg, M. (2002). Artifact correction of the ongoing EEG using spatial filters based on artifact and brain signal topographies. *Clinical Neurophysiology*, 19, 113–124.
- Kanai, R., & Verstraten, F. A. J. (2005). Perceptual manifestations of fast neural plasticity: Motion priming, rapid motion aftereffect and perceptual sensitization. *Vision Research*, 45, 3109–3116.
- Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: Changing views in perception. *Trends in Cognitive Sciences*, 3, 254–264.
- Leopold, D., Wilke, M., Maier, A., & Logothetis, N. (2002). Stable perception of visually ambiguous patterns. *Nature Neuroscience*, 5, 605–609.
- Long, G. M., & Toppino, T. C. (2004). Enduring interest in perceptual ambiguity: Alternating views of reversible figures. *Psychological Bulletin*, 130, 748–768.
- Maier, A., Wilke, M., Logothetis, N. K., & Leopold, D. A. (2003). Perception of temporally interleaved ambiguous patterns. *Current Biology*, 13, 1076–1085.
- Maloney, L. T., Dal Martello, M. F., Sahn, C., & Spillmann, L. (2005). Past trials influence perception of ambiguous motion quartets through pattern completion. *Proceedings of the National Academy of Sciences*, 102, 3164–3169.
- Micheyl, C., Carlyon, R. P., Gutschalk, A., Melcher, J. R., Oxenham, A. J., Rauschecker, J. P., & Courtenay Wilson, E. (2007). The role of auditory cortex in the formation of auditory streams. *Hearing Research*, 229, 116–131.

- Moore, B. C. J., & Gockel, H. (2002). Factors influencing sequential stream segregation. *Acta Acustica United With Acustica*, 88, 320–333.
- Moutoussis, K., & Zeki, S. (2008). Motion processing, directional selectivity, and conscious visual perception in the human brain. *Proceedings of the National Academy of Sciences*, 105, 16362–16367.
- Pearson, J., & Brascamp, J. (2008). Sensory memory for ambiguous vision. *Trends in Cognitive Sciences*, 12, 334–341.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437–442. doi:10.1163/156856897X00366
- Picton, T. W., Bentin, S., Berg, P., Donchin, E., Hillyard, S. A., Johnson, R., Jr., & Taylor, M. J. (2000). Guidelines for using human event-related potentials to study cognition: recording standards and publication criteria. *Psychophysiology*, 37, 127–152. doi:10.1111/1469-8986.3720127
- Pressnitzer, D., & Hupé, J. M. (2006). Temporal dynamics of auditory and visual bistability reveal common principles of perceptual organization. *Current Biology*, 16, 1351–1357.
- Probst, T., Plendl, H., Paulus, W., Wist, E. R., & Scherg, M. (1993). Identification of the visual motion area (area V5) in the human brain by dipole source analysis. *Experimental Brain Research*, 93, 345–351.
- Serences, J. T., & Boynton, G. M. (2007). The representation of behavioral choice for motion in human visual cortex. *Journal of Neuroscience*, 27, 12893–12899.
- Shu, Z. J., Swindale, N. V., & Cynader, M. S. (1993). Spectral motion produces an auditory after-effect. *Nature*, 364, 721–723.
- Snyder, J. S., & Alain, C. (2007). Toward a neurophysiological theory of auditory stream segregation. *Psychological Bulletin*, 133, 780–799.
- Snyder, J. S., Carter, O. L., Hannon, E. E., & Alain, C. (2009a). Adaptation reveals multiple levels of representation in auditory stream segregation. *Journal of Experimental Psychology: Human Perception and Performance*, 35, 1232–1244.
- Snyder, J. S., Carter, O. L., Lee, S. K., Hannon, E. E., & Alain, C. (2008). Effects of context on auditory stream segregation. *Journal of Experimental Psychology: Human Perception and Performance*, 34, 1007–1016.
- Snyder, J. S., Holder, W. T., Weintraub, D. M., Carter, O. L., & Alain, C. (2009b). Effects of prior stimulus and prior perception on neural correlates of auditory stream segregation. *Psychophysiology*, 46, 1208–1215.
- Snyder, J. S., & Weintraub, D. M. (2011). Pattern specificity in the effect of prior Δf on auditory stream segregation. *Journal of Experimental Psychology: Human Perception and Performance*, 37, 1649–1656.
- Snyder, J. S., & Weintraub, D. M. (2013). Loss and persistence of implicit memory for sound: Evidence from auditory stream segregation context effects. *Attention, Perception, & Psychophysics*, 75, 1059–1074. doi:10.3758/s13414-013-0460-y
- Stanley, J., Forte, J. D., Cavanagh, P., & Carter, O. (2011). Onset rivalry: The initial dominance phase is independent of ongoing perceptual alternations. *Frontiers in Human Neuroscience*, 5(140), 1–9.
- Sterzer, P., & Rees, G. (2008). A neural basis for percept stabilization in binocular rivalry. *Journal of Cognitive Neuroscience*, 20, 389–399.
- Thalman, W. A. (1922). The after-effect of movement in the sense of touch. *American Journal of Psychology*, 33, 268–276.
- Uusitalo, M. A., Virsu, V., Salenius, S., Nasanen, R., & Hari, R. (1997). Activation of human V5 complex and rolandic regions in association with moving visual stimuli. *NeuroImage*, 5, 241–250.
- Van Noorden, L. P. A. S. (1975). *Temporal coherence in the perception of tone sequences*. Eindhoven: Eindhoven University of Technology. Unpublished doctoral dissertation.
- von Grünau, M., & Dubé, S. (1993). Ambiguous plaids: switching between coherence and transparency. *Spatial Vision*, 7, 199–211.
- Wallach, H. (1935). Über visuell wahrgenommene Bewegungsrichtung. *Psychologische Forschung*, 20, 325–380.
- Wallach, H. (1976). *On perception*. New York, NY: Quadrangle.
- Watanabe, J., Hayashi, S., Kajimoto, H., Tachi, S., & Nishida, S. (2007). Tactile motion aftereffects produced by appropriate presentation for mechanoreceptors. *Experimental Brain Research*, 180, 577–582.
- Williams, Z. M., Elfar, J. C., Eskandar, E. N., Toth, L. J., & Assad, J. A. (2003). Parietal activity and the perceived direction of ambiguous apparent motion. *Nature Neuroscience*, 6, 616–623.
- Wuerger, S., Shapley, R., & Rubin, N. (1996). On the visually perceived direction of motion by Hans Wallach: 60 years later. *Perception*, 25, 1317–1367.