Intermittent regime of brain activity at the early, bias-guided stage of perceptual learning

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Perceptual learning improves visual performance. Among the plausible mechanisms of learning, reduction of perceptual bias has been studied the least. Perceptual bias may compensate for lack of stimulus information, but excessive reliance on bias diminishes visual discriminability. We investigated the time course of bias in a perceptual grouping task and studied the associated cortical dynamics in spontaneous and evoked EEG. Participants reported the perceived orientation of dot groupings in ambiguous dot lattices. Performance improved over a 1-hr period as indicated by the proportion of trials in which participants preferred dot groupings favored by dot proximity. The proximity-based responses were compromised by perceptual bias: Vertical groupings were sometimes preferred to horizontal ones, independent of dot proximity. In the evoked EEG activity, greater amplitude of the N1 component for horizontal than vertical responses indicated that the bias was most prominent in conditions of reduced visual discriminability. The prominence of bias decreased in the course of the experiment. Although the bias was still prominent, prestimulus activity was characterized by an intermittent regime of alternating modes of low and high alpha power. Responses were more biased in the former mode, indicating that perceptual bias was deployed actively to compensate for stimulus uncertainty. Thus, early stages of perceptual learning were characterized by episodes of greater reliance on prior visual preferences, alternating with episodes of receptivity to stimulus information. In the course of learning, the former episodes disappeared, and biases reappeared only infrequently.

Introduction

Perceptual skills improve with practice. This process, called perceptual learning, is observed in detection and discrimination tasks (De Valois, 1977; McKee & Westheimer, 1978). Perceptual learning could, in principle, be mediated by several mechanisms, including an increase in the number and strength of synaptic connections (Yotsumoto, Watanabe, & Sasaki, 2008), sharpening the neural code through sparsification (i.e., elimination of noise responses; (Hamame, Cosmelli, Henriquez, & Aboitiz, 2011) or increasing the task-specific attention (Ahissar & Hochstein, 2004). Another possibility is that perception improves because of a reduction in *bias* (Jones, Moore, Shub, & Amitay, 2015; Wenger & Rasche, 2006), in which case bias is understood as a systematic preference for a certain response category ("decision bias") or an attribute of stimulation ("perceptual bias").

In contrast to decision bias (Jones et al., 2015; Wenger & Rasche, 2006), perceptual biases (Albright, 2012; Allport, 1955; Chopin & Mamassian, 2011; Gepshtein & Kubovy, 2005; Harrison & Backus, 2010; van Dam & Ernst, 2010; Weiss, Simoncelli, & Adelson, 2002) are often entrenched in evolution. Many animals, for instance, prefer symmetric over asymmetric features in mates (Mller & Thornhill, 1998); human symmetry bias emerges early in infancy, around 4 months of age (Bornstein, Ferdinandsen, & Gross, 1981). Despite this,

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perceptual biases are modified by associative learning, such as classical conditioning (Haijiang, Saunders, Stone, & Backus, 2006; Harrison, Backus, & Jain, 2011). These observations prompted us to focus on how such bias changes during perceptual learning.

Perceptual biases often play an active role in visual information processing. For instance, orientation selectivity arises early in animal development under natural stimulation (Chapman, Gödecke, & Bonhoeffer, 1999; Coppola, Purves, McCoy, & Purves, 1998). Visual discrimination is generally better for horizontal than for vertical stimuli and better for vertical than oblique orientations: an effect that is manifested with simple stimuli, such as oriented contours (Appelle, 1972). However, in the naturally broadband stimulation, the *opposite* bias is observed (Essock, DeFord, Hansen, & Sinai, 2003). According to these studies, bias is deployed by the visual system actively to suppress the most common (and thus least informative) aspects of the stimulation. Thus, perceptual bias may have the role of compensating for imbalances in visual discrimination (Essock et al., 2003).

Perceptual bias and discriminability play complementary roles in the interpretation of visual stimuli. Among other things, perceptual biases help to determine the percept when the stimulation is ambiguous. Ambiguities are common in visual perception because stimulation is often fragmentary or incomplete due to occlusion (Balboa & Grzywacz, 2000) or because of uncertainties as to which parts of the stimulus should group to form an object (Geisler & Perry, 2009). Often, ambiguity is a matter of degree; rather than being equally probable, two alternatives can have the odds of, say, seven to three. Generally, the more ambiguous the stimulation the more prominent the role of perceptual bias (Chopin & Mamassian, 2011; Gepshtein & Kubovy, 2005). We expect this relationship to persist throughout perceptual learning.

Consider the ambiguity that characterizes perceptual grouping in dot lattices (Kubovy, 1994; Kubovy, Holcombe, & Wagemans, 1998). The dots are seen to group along one of several orientations. Most of the time, observers report the orientation with the shortest interdot distances, i.e., according to the principle of proximity. In this sense, grouping by proximity reflects observers' ability to discriminate interdot distances. The proportion of responses according to dot proximity is used as a measure of visual discrimination. Notably, in this task, observers sometimes reported seeing groupings different from those predicted by the proximity principle. Such reports reflect perceptual bias (Gepshtein & Kubovy, 2005). Here we define perceptual bias as the proportion of responses that favor a certain orientation regardless of dot proximity.

We used the grouping task to study how perceptual learning affects visual discrimination and bias in the course of a 1-hr experiment. We expected that observers' discrimination performance would increase, effectively making dot lattices less ambiguous. Correspondingly, the proportion of biased responses is expected to decrease.

Besides the time course of bias across the entire experiment, we were interested in the fluctuations in the strength of bias at a finer time scale. Participants make unbiased (i.e., proximity-based) responses in some trials and biased (i.e., orientation-based) responses in the others. The occurrence of a biased or unbiased response in one trial could, in principle, be independent of the next trial. Alternatively, the trial sequence could reveal a sequential effect. Gepshtein and Kubovy (2005) suggest that response preferences evolve slowly according to what they called "lasting brain states." In that case, we would expect persistency in the trial sequence, e.g., longer sequences of biased responses than expected by chance.

In studying the trial sequence, we focus on the relationship between perceptual bias and brain activity, which we monitor using EEG. Because learning involves an interaction between the incoming stimulus information and the ongoing brain activity (Gilbert & Sigman, 2007; Zanone & Kelso, 1992), the latter should be studied in a framework that takes into account not only stimulus-driven (evoked) processes but also the ongoing (spontaneous) processes that unfold in the brain at the moment of stimulus arrival (reviewed in Fiser, Berkes, Orban, & Lengyel, 2010; Gilbert & Sigman, 2007; Ringach, 2009).

Motivation of our EEG analyses

To the best of our knowledge, the relationship of perceptual bias to perceptual learning has not been previously studied in EEG. Careful consideration should therefore be given to the choice of particular event-related potential (ERP) components, EEG frequency bands, and analytical approaches used in our investigation based on what is known in the literature.

Association of perceptual bias with EEG activity

In evoked EEG activity, we focus on the early ERP components, such as P1 and N1. Both components reflect various aspects of perceptual grouping (Han, Jiang, Mao, Humphreys, & Qin, 2005; Khoe, Freeman, Woldorff, & Mangun, 2006). We previously used the current data to determine whether the P1 and N1 components were affected by participants' ability to discriminate dot proximity and found only an effect on P1 (Nikolaev, Gepshtein, Kubovy, & van Leeuwen, 2008). Here we will also consider the possible effect of bias on P1 and N1. The N1 component is larger in discrimination than detection tasks (Hopf, Vogel, Woodman, Heinze, & Luck, 2002; Ritter, Simson, Vaughan, & Friedman, 1979; Vogel & Luck, 2000). As a later visual component, N1 is more likely to reflect the dynamics of bias and discriminability than P1. The amplitude of the N1 component is likely to be increased for the proximity-driven, bias-independent responses as opposed to the biased (i.e., orientation-based) responses. We expect this effect to persist throughout the experiment for as long as biased responses continue to occur.

Spontaneous EEG activity in humans is dominated by the alpha rhythm, particularly over the visual cortical areas (Niedermeyer & Lopes da Silva, 2004). The alpha activity reflects top-down processes that set the state for optimal stimulus processing of sensory regions (Bonnefond & Jensen, 2012; Haegens, Handel, & Jensen, 2011; Handel, Haarmeier, & Jensen, 2011; Macdonald, Mathan, & Yeung, 2011; Mazaheri et al., 2014). These top-down processes operate via selective inhibition of task-irrelevant cortical areas and thus gate the flow of information in the cortex (Jensen, Bonnefond, & VanRullen, 2012; Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007; Mathewson et al., 2011).

Rather than bias, studies of ongoing alpha activity have focused on the relationship between prestimulus activity and *sensitivity* in simple detection and discrimination tasks (Ergenoglu et al., 2004; Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008; Wyart & Tallon-Baudry, 2009). Low sensitivity in such tasks was associated with high prestimulus alpha power. The latter may reflect a state of low attention or low cortical excitability due to overall detachment from the task.

For the relationship of alpha power and perceptual bias, we consider two alternative hypotheses. The first is that biased responses have the status of "default" perceptual states, which appear when attention is reduced. This would mean that the relationship of alpha power and bias is similar to that of alpha power and sensitivity. Biased responses should then be accompanied by *high* prestimulus alpha power. The second hypothesis is based on our consideration that the visual system imposes bias actively (Essock et al., 2003) in order to compensate for ambiguity. As an active process, bias deployment would be manifested as *low* prestimulus alpha power. We therefore ask whether biased perception involves increased or decreased alpha activity and how alpha activity is affected by learning.

Association of learning with EEG activity

Evidence for changes to P1 with learning is scarce. Some studies found such an effect (Wang et al., 2016; Zhang, Cong, Song, & Yu, 2013), and others did not (Song et al., 2005; Sterkin, Yehezkel, & Polat, 2012). By contrast, many previous studies reported changes of N1 in the course of training (Censor, Bonneh, Arieli, & Sagi, 2009; Qu, Song, & Ding, 2010; Scott, Tanaka, Sheinberg, & Curran, 2006; Song et al., 2010; Sterkin et al., 2012).

Previous studies of the relationship between alpha activity and perceptual learning have remained inconclusive. The power of alpha activity has been found to grow during learning (Fairclough, Venables, & Tattersall, 2005; Maclin et al., 2011; Smith, McEvoy, & Gevins, 1999). But this finding may reflect side effects of the learning process, including reduction in vigilance or mental effort during the long, monotonous experimental sessions. Therefore, such alpha effect may not be specific to learning.

More complex relationships between alpha power and learning have been reported. Hamame et al. (2011) found that the time course of alpha power during perceptual learning had a U-shaped profile, suggesting a two-stage process. In this view, neuronal ensembles are increasingly recruited for encoding new information in the early stage, but they decrease due to enhanced specificity and sparsification of encoding in the later stage. These stages last for thousands of trials, observed over several consecutive days. These effects are beyond our focus on the learning-related changes of ongoing alpha activity in single trials.

We propose that changes in the trial-by-trial fluctuations of alpha activity could reflect the relationship between learning and perceptual bias. In the following, we monitor alpha activity during a 1-s interval preceding stimuli onset, looking for a neural marker of orientation bias, and we study how this marker changes in the course of perceptual learning.

Change of bias and EEG activity across time in the course of learning

Gepshtein and Kubovy (2005) proposed that fluctuations in perceptual bias occur because of lasting brain states. Trial-by-trial analysis may reveal sequential effects in behavioral responses and spontaneous EEG activity. These could be understood as dynamical patterns (or "modes"). We expect corresponding modes to appear in behavior and EEG. Specifically, such modes can be characterized by their persistence. "Biased" modes are expected to be interleaved with "unbiased" modes, each with their own characteristic pattern of EEG. If the biased mode is a passive "default" state, we will expect alpha power to be higher in the biased than in the unbiased mode. If the biased mode is an active compensation for ambiguity, we expect the opposite: lower alpha power in the biased than unbiased mode.

To reveal the dynamical structure and persistence of these modes, we analyze serial dependencies in perceptual grouping and in single-trial alpha power. Serial dependencies can be revealed with the Lempel-Ziv complexity measure (Lempel & Ziv, 1976). This measure evaluates randomness of binary time series by computing the number of distinct patterns in the series. The lower the magnitude of Lempel-Ziv complexity, the more strongly it indicates that the underlying process is deterministic rather than random. Persistence of these modes can be measured in terms of the lengths of sequences of the same responses (biased or unbiased) and in terms of the associated alpha power.

Learning is characterized by transitions between different dynamical regimes, manifested in both behavior and brain activity (Kelso, 2012). If the relationship between bias and alpha activity changes in the course of learning, we expect this to be reflected in the dynamics of alpha activity. We may therefore observe a transition in dynamical regime in the course of perceptual learning during our experiment.

Materials and methods

Participants

Seventeen healthy participants (ages 19–36, median age 22, nine female) took part in the experiment. All participants gave informed consent in writing. The study conformed to the World Medical Association Declaration of Helsinki and was approved by the Research Ethics Committee of RIKEN Brain Science Institute (Wako-shi, Japan), where we conducted the experiment. Four participants were excluded from the analysis: two due to EEG artifacts and two because they were unable to perform the task as evidenced in their behavioral responses by absence of grouping according to proximity (Nikolaev et al., 2008).

Stimuli

We used rectangular dot lattices: multistable stimuli that are spontaneously grouped perceptually in equidistant, parallel strips of dots along one of four possible orientations. Perceptual grouping in these stimuli follows the principle of proximity (Kubovy, 1994). The shorter the distance between the dots in a certain direction, the more likely are the dots to be perceptually grouped along that direction. In Figure 1A, the four orientations that correspond to possible groupings are labeled a, b, c, and d. We will refer to reports of perceptual groupings along these orientations as *a*, *b*, *c*, and *d*, respectively. Grouping according to the principle of proximity is described quantitatively by the pure distance law (Kubovy et al., 1998). This law specifies the likelihood of each grouping as a function of stimulus aspect ratio (AR), with AR = $[b]/[a]$, the ratio of the second shortest and the shortest interdot distances in the b and a directions, respectively (with the square brackets indicating distance). We used four values of AR: 1.0, 1.1, 1.2, and 1.3. In all displays, the diameter of the dots was 0.2° of visual angle. The dots were presented with above-threshold detectability within an area of 6.9° of visual angle in diameter and

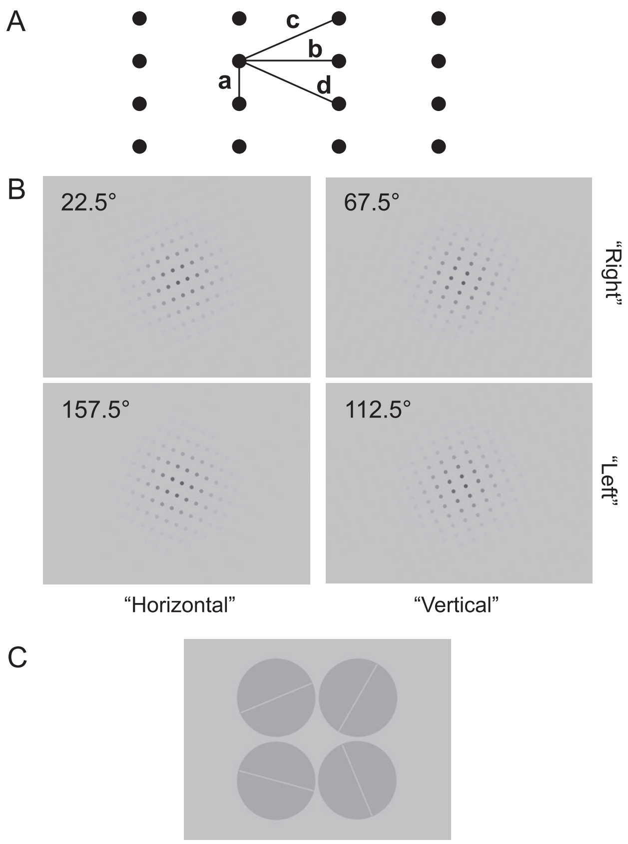

Figure 1. Perceptual grouping in dot lattices. (A) The perceived grouping depends on the *AR* of the dot lattice, which is the ratio of the two shortest interdot distances: along *a* (the shortest distance) and along *b* (the second shortest), $|b|/|a|$. The AR determines how often grouping along *a* is preferred over grouping along *b*. (B) Four dot lattices with AR 1.3 are displayed at four orientations. (C) Response screen. Participants were asked to click on the icon that corresponded to the orientation of the perceived grouping in the preceding stimulus. Positions of the response alternatives in the response screen varied randomly between trials.

with a circular shape in order to minimize the effect of the screen's edges. The distances between dot centers at AR = 1.0 were 0.6° of visual angle.

The lattices were presented in four oblique orientations, which were characterized by *a* being oriented 22.5°, 67.5°, 112.5°, or 157.5° counterclockwise from the horizontal (Figure 1B). The orientations can be classified according to whether orientation *a* is closer to the horizontal or to the vertical. Orientations of $a =$ 22.5° or 157.5° are near horizontal (henceforth labeled "horizontal"), and orientations 67.5° and 112.5° are near vertical (labeled "vertical"). Also, orientations 22.5° and 67.5° correspond to the right tilt whereas orientations 112.5° and 157.5° correspond to the left tilt. (As we find in the section Behavioral results, perceptual biases depended on the vertical/horizontal classification and not on the left/right classification. We therefore concentrate on the vertical/horizontal classification in the following.)

Regardless of AR, in half of the lattices, *a* was oriented horizontally, and in the other half *a* was vertical. Whereas usually responses are averaged across orientations when studying the way perceptual groupings depend on AR (Kubovy et al., 1998), orientation effects are the focus of our current investigation. Hence, we distinguish responses according to vertical or horizontal orientation of the perceived grouping reported. Our design thus allowed us to separate effects of orientation bias from effects of AR.

Procedure

Participants were seated 1.15 m from the screen in a dimly lit room. The stimuli were presented on a 17-in. CRT display (Eizo FlexScan T566) with an 85 Hz (noninterlaced) refresh rate using E-Prime (Psychology Software Tools, Inc., Sharpsburg, PA).

Each trial consisted of a sequence of four presentations: fixation, stimulus, blank screen, and response screen. During the fixation period, at the center of an otherwise empty screen, a small circle (0.2° in diameter) was presented on which participants had been instructed to fixate their gaze. The duration of the fixation period varied randomly according to a uniform distribution from 1200 to 1500 ms. EEG recorded during this fixation period was used in the further analyses of the prestimulus activity. The dot lattices were presented for 300 ms. The subsequent blank screen also lasted 300 ms. Next, the response screen was presented, which lasted until a response was received. The intertrial interval varied randomly from 1000 to 2000 ms according to a uniform distribution.

Participants reported the perceived grouping of the lattice by selecting one of four alternatives from the response screen (Figure 1C). The screen consisted of four circles ("response icons"), each cut in half by a line parallel to grouping *a*, *b*, *c*, or *d* of the lattice. Each of the response alternatives was located in one of the four quadrants of the response screen; their locations were assigned randomly for each trial. Participants responded by clicking on one of the response icons. We had asked participants to report the first orientation they perceived after stimulus onset and explained to them that the task had no correct or incorrect answer.

The four AR and four orientations yielded 16 different stimuli. Within each block of trials in the experiment, each of the 16 stimuli was presented 10 times in random order. Four blocks were presented to each participant (640 trials in total), which took about 1 hr on average, including three short (2–5 min) breaks between the blocks.

Behavioral data analysis

We evaluated grouping responses by calculating the probabilities of *a* and *b* responses for each response orientation (22.5°, 67.5°, 112.5°, or 157.5°). Groupings along *c* and *d* were seldom reported and therefore were not included in the analysis. To assess perceptual learning and to trace its evolution in the course of the experiment, we calculated two proximity discriminability and two orientation bias measures.

The first proximity discriminability measure quantifies the degree to which responses distinguish *a* and *b*, the most prominent proximities in the stimulus. The measure consists of the difference between $N(a)$ and $N(b)$, the number of reports consistent (responses *a*) and inconsistent (responses *b*) with the proximity principle, converted to probabilities. The second measure registers how strongly preference for one proximity response over another is affected by AR. To obtain the required measure, we first compute proximity log odds for each AR:

$$L_{prox} = \log\left(\frac{N(b) + \frac{1}{6}}{N(a) + \frac{1}{6}}\right) \quad (1)$$

The arbitrary term of 1/6 is added to avoid division by zero (Tukey, 1977). Log odds as observed depend linearly on AR (Kubovy et al., 1998). We used the slope of the linear fit to the proximity log odds over AR (also known as the "attraction function") as a measure of participants' ability to discriminate dot proximity (Kubovy et al., 1998): The *steeper* the slope the *higher* the discriminability.

The other two measures register orientation bias. The first one measures the degree to which responses favor one orientation rather than another. The measure

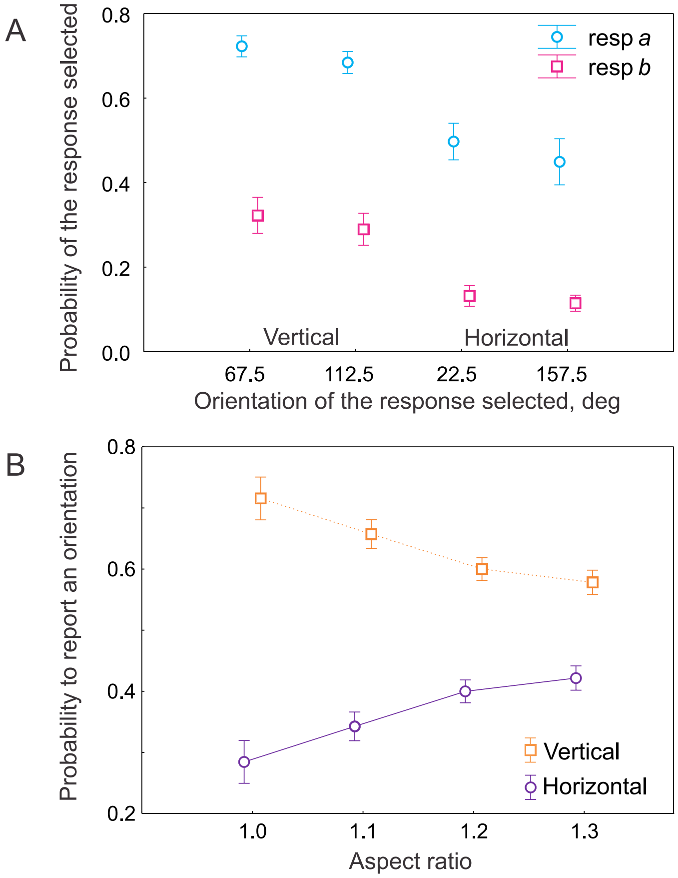

Figure 2. Preference for vertical orientations. (A) The probabilities of responses consistent and inconsistent with the proximity principle ("resp *a*" and "resp *b*," respectively) collapsed over AR. The groupings parallel to the vertical are reported more often than the groupings parallel to the horizontal. (B) Probabilities of the "vertical" and "horizontal" responses are separated for each AR. The preference for vertical is largest for the AR of 1.0, at which the stimuli are most ambiguous, and decreases as the AR increases. Data points are the means, and error bars are the standard errors across participants.

consists of the difference between $N(H)$, the count of "horizontal" reports, and $N(V)$, the count of "vertical" reports, converted to probabilities. The second measure registers how strongly the preference for one orientation over another depends on AR. To obtain this measure, we first divided the responses by their orientations to "vertical" and "horizontal" and computed orientation log odds:

$$L_{orient} = \log\left(\frac{N(H)+\frac{1}{6}}{N(V)+\frac{1}{6}}\right) \quad (2)$$

We then used the slope of the linear fit to the log odds as a function of AR. The steeper the slope, the more orientation preference is elicited as stimuli become more ambiguous and thus, according to this measure, the stronger the bias.

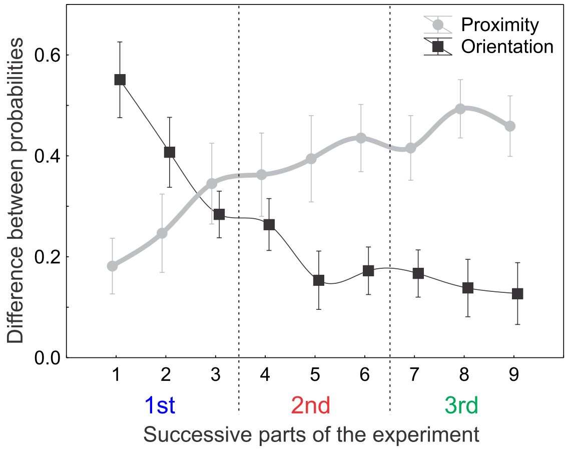

Figure 3. Evolution of orientation and proximity responses across the 1-hr duration of the experiment. Error bars represent standard errors across participants. The curve "Proximity" represents the difference between two probabilities: that of responses consistent (*a*) and that of responses inconsistent (*b*) with the proximity principle. This difference reflects the degree to which perceptual reports reflect the principle of proximity. The curve "Orientation" represents the difference between vertical and horizontal response probabilities. It reflects the degree to which the responses depended on preference for vertical orientations. The two factors traded off in the course of the experiment, reflecting an improvement in visual discriminability of small differences in interdot distances: an outcome of perceptual learning along with a corresponding decline in orientation-biased responses. On initial analyses, the course of the experiment was divided into nine successive episodes; these were subsequently grouped together into three larger parts, labeled "first, second, third" at the lower *x*-axis.

Electrophysiological recording

EEG was recorded using a 256-channel Geodesic Sensor Net (EGI, Eugene, OR). This sensor net includes electrodes for recording the vertical and horizontal electrooculogram (EOG). Data were digitized at 250 Hz. EEG was recorded relative to the vertex electrode (Cz) and was rereferenced to the average reference for the analyses. Impedance was kept below 50 kOhm. All channels were preprocessed online using 0.1-Hz high-pass and 100-Hz low-pass filtering.

ERP analysis

EEG data were preprocessed using BrainVision Analyzer (Brain Products GmbH, Gilching, Germany) and MATLAB (The MathWorks, Natick, MA). For analysis of the poststimulus evoked activity (ERPs), the EEG signal was filtered with a Butterworth zero-phase filter with a low cutoff frequency of 0.3 Hz and a high cutoff frequency of 25 Hz; the filter slope for both cutoffs was 48 dB/oct. The preprocessed EEG was segmented into trials that included 100 ms before and 400 ms after stimulus onset.

From 256 electrodes, we excluded 81 electrodes on the lower part of the head (mainly on cheeks and neck) that were subject to frequent muscle artifacts. For the remaining 175 electrodes, we ran an automatic artifact detection procedure implemented in BrainVision Analyzer using the recording reference electrode Cz. We excluded trials in which the absolute voltage difference exceeded 50 μV between two neighboring sampling points, the amplitude was outside +100 or −100 μV, or the amplitude was lower than 0.5 μV during more than 100 ms in any channel. Two participants who had more than 33% artifact trials were excluded from further analysis. In the remaining participants, on average, 2.3% of trials per participant were rejected because of artifacts. The average number of "good" trials per participant were for responses consistent with the proximity principle (responses *a*) 427 ($SD = 75$) and for responses inconsistent with the proximity principle (responses *b*) 147 ($SD = 32$), for responses according to the vertical orientation 366 ($SD = 60$) and for responses according to the horizontal orientation 208 ($SD = 45$).

Because we were interested in the effect of learning on perception of the ambiguous stimuli, we focused on the perceptual ERP components P1 and N1. We selected 19 electrodes over the occipital region around electrodes O1 and O2 (Figure 6A), where the maximal amplitude of these components is typically observed (Hillyard & Anllo-Vento, 1998; Luck, 2005) and averaged ERPs across these electrodes. We averaged ERPs across trials and corrected to a baseline obtained from a 100-ms interval before stimulus onset. Based on the grand-averaged ERP plots, we defined the intervals for extraction of the component amplitudes: 80–150 ms after stimulus onset for P1 and 150–200 ms for N1. The amplitude was extracted as the mean of the interval.

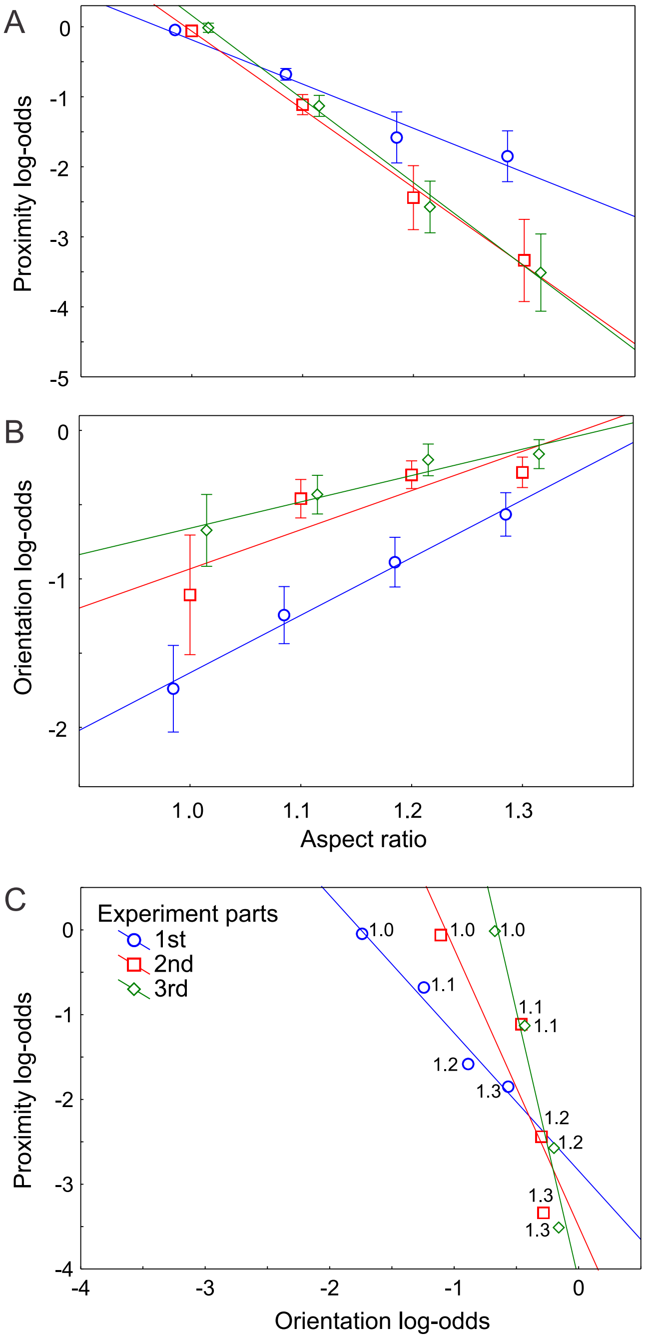

Figure 4. Evolution of grouping by proximity across three session parts. (A) Proximity discriminability. Proximity log odds (Equation 1) reflect the degree to which responses were consistent with the proximity principle. Response log odds are plotted against stimulus AR separately for the three successive parts of the experiment. The lines are linear-regression fits; their slopes correspond to participants' ability for perceptual grouping, which we call "discriminability of proximity." (B) Orientation bias. Orientation log odds (Equation 2) reflect the degree to which responses depend on orientation. Orientation log odds are plotted against stimulus AR separately for the three successive parts of the experiment. The lines are linear-regression fits; their slopes correspond to the degree the preference for a vertical orientation increases as the stimulus becomes more ambiguous. These slopes are taken as a measure of orientation bias. Data points are the means and error bars are the standard errors across participants. (C) Response log odds from panels A and B are plotted against one another, illustrating the trade-off between orientation bias and proximity discriminability. The steeper the slope of the linear fits, the more proximity discriminability prevails over orientation bias. Thus the increasing steepness of the slope across the experiment reflects the transition from perception that primarily depends on the generic orientation bias to perception that primarily depends on stimulus-specific proximity over the course of the experiment. This trend reflects perceptual learning.

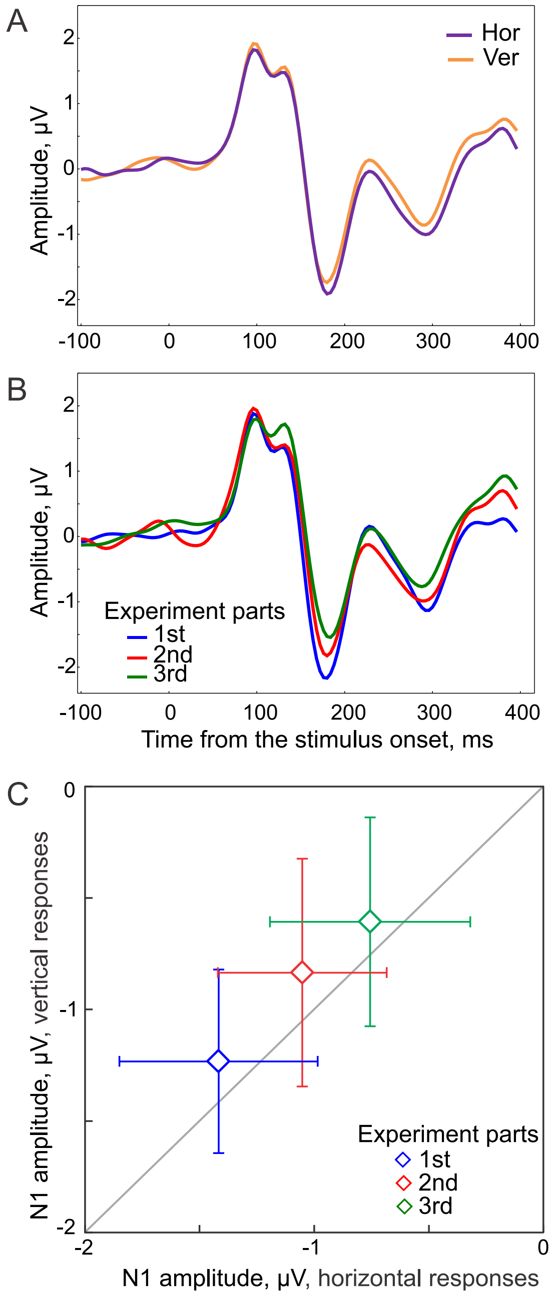

Figure 5. Effect of orientation bias on event-related potentials. (A) Grand-averaged ERPs over 19 occipital electrodes for horizontal and vertical responses. The amplitude of the ERP components N1 about 180 ms after stimulus onset is larger for horizontal than vertical responses. (B) The same for three successive parts of the experiment. The N1 amplitude decreases in the course of the experiment. (C) Mean-error plots of N1 amplitude for horizontal and vertical responses across the three parts of the experiment.

Control for possible effect of microsaccades

We considered whether microsaccades during the prestimulus interval might explain the difference in alpha power between biased and unbiased responses. This could, in principle, occur for the following reasons. The microsaccadic lambda responses, i.e., the potentials evoked in about 100 ms after the saccade offsets over the occipital areas, could be translated to the increased spectral power in the alpha band (Dimigen, Valsecchi, Sommer, & Kliegl, 2009). Microsaccades help resolve perceptual ambiguities (reviewed in Rolfs, 2009). Moreover, Laubrock, Engbert, and Kliegl (2008) showed that the direction of microsaccades *before* onset of ambiguous apparent motion is systematically related to the direction of motion that will subsequently be perceived. Despite our participants being instructed to fixate on the fixation cross during the 1-s prestimulus interval, it cannot be excluded that their microsaccade rate was increased and/or their microsaccade direction was biased toward one or another resolution of the subsequent ambiguous percept. Difference in the number of spontaneous microsaccades could be associated with orientation bias. Microsaccadic lambda responses overlapping with the spontaneous alpha activity could have a systematic effect on the total alpha power. To exclude this possibility, we counted the amount of microsaccades and compared it between conditions (see Supplementary Materials for the method of microsaccade detection in EOG and for the results in Table S1).

Frequency analysis

For analysis of the prestimulus activity, we segmented the EEG into trials that included 1000-ms intervals before stimulus onset. Such intervals corresponded to the period when participants looked at the fixation circle waiting for stimulus presentation.

Previous studies showed that alpha activity is most prominent over parieto-occipital sites; its sources have been localized in the parieto-occipital cortex (Capotosto, Babiloni, Romani, & Corbetta, 2009; van Dijk et al., 2008; Vanni, Revonsuo, & Hari, 1997). We selected 59 electrodes over the parieto-occipital regions for our analysis of alpha activity (Figure 6A). We applied the artifact detection procedure with the same criteria as in the ERP analysis. On average, 0.9% of trials per participant were rejected, and the number of "good" trials per participant were for responses consistent with the proximity principle (responses *a*) 433 ($SD = 74$) and for responses inconsistent with the proximity principle (responses *b*) 150 ($SD = 31$), for responses according to the vertical orientation 371 ($SD = 58$) and for responses according to the horizontal orientation 212 ($SD = 45$).

To evaluate the relationship of prestimulus alpha activity and learning, we applied the fast Fourier transform to extract alpha power from the 1-s prestimulus interval. The Fourier transform was used

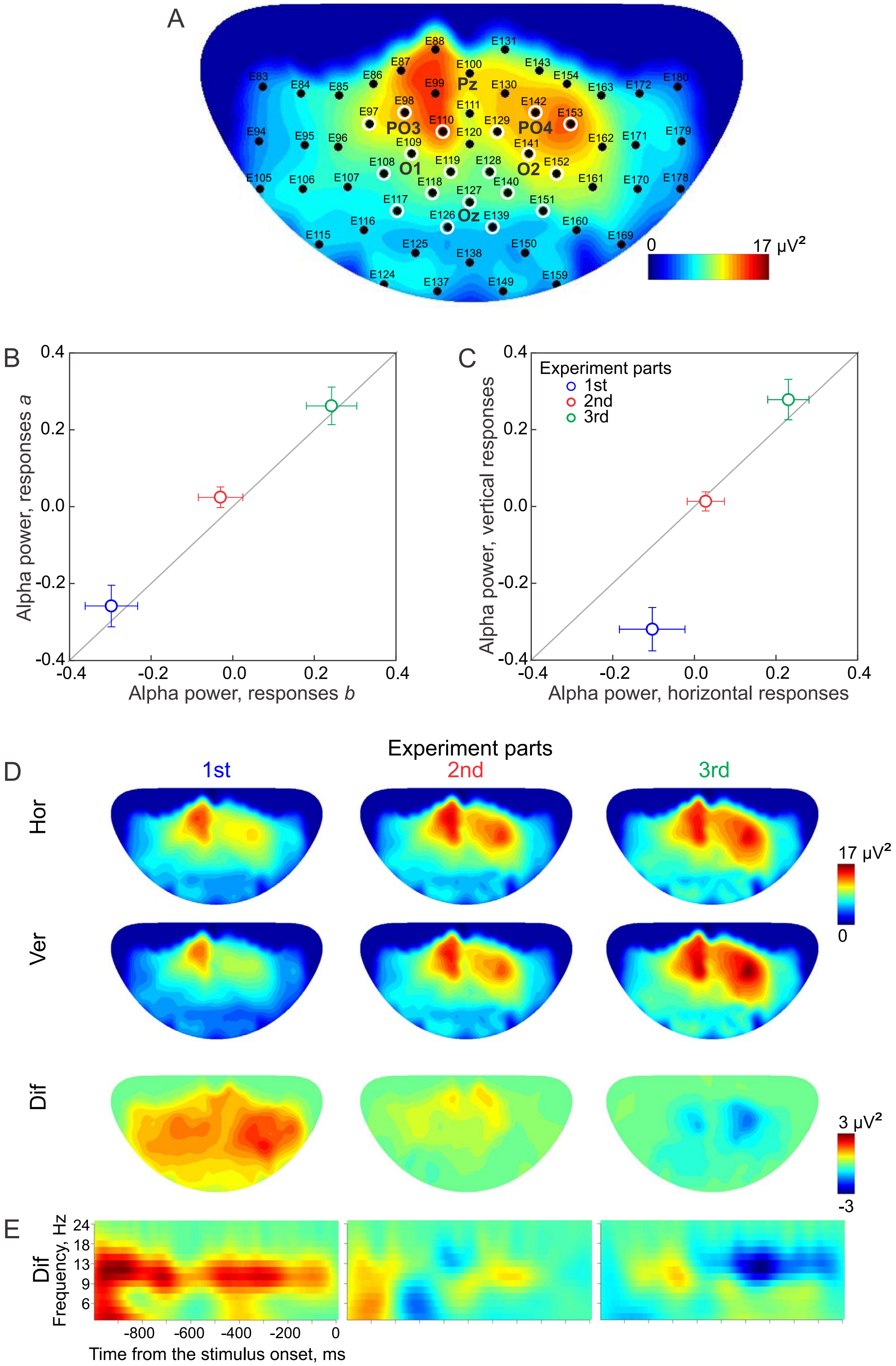

Figure 6. Prestimulus alpha power in three parts of the experiment. (A) The topography of prestimulus alpha power averaged across all participants and conditions over the parieto-occipital areas. The numbers following the label "E" are the electrode numbers of the geodesic sensor net. Some of the landmark electrodes that correspond to the international 10–20 system of electrode placement are labeled in bold (Pz, O2, etc.). Electrodes used in the ERP analysis are circled. (B) Prestimulus alpha power associated with responses *a* (consistent with the proximity principle) and with responses *b* (inconsistent with the proximity principle) is shown for three successive parts of the experiment. (C) Prestimulus alpha power associated with horizontal and vertical responses is shown for three successive parts of the experiment. In panels B and C, alpha power was log transformed and standardized; the data points are the means of alpha power, and the error bars are the standard errors across participants. (D) The topography of prestimulus alpha power associated with horizontal (top row) and vertical (middle row) responses and the difference between them (bottom row) for three successive parts of the experiment. (E) Time–frequency plots of prestimulus alpha power. Differences between "horizontal" and "vertical" responses are shown for three parts of the experiment.

to obtain the power spectrum with a resolution of 1 Hz after applying a Hanning window of 10% of the segment length. We extracted the power in the alpha band by summing spectral lines between 8 and 13 Hz. To approximate the normal distribution, we computed the natural logarithm of the power values. Values were transformed into standard scores for trials over the entire experiment. To validate that the expected effects occur in the alpha frequency band, we produced time–frequency plots using a wavelet transform. A complex Morlet wavelet of three-cycle length was employed for extraction of the instantaneous power values at the frequencies from 4 to 25 Hz in 15 logarithmic steps. The wavelets were normalized to have unit scale power to sample rate.

Complexity analysis

We predicted that the time series of responses and their corresponding prestimulus alpha power show a dynamical structure, involving serial persistence. To test this prediction, we computed their Lempel-Ziv complexity (Lempel & Ziv, 1976). This measure evaluates randomness of binary time series by computing the number of distinct patterns in the series. The lower the magnitude of Lempel-Ziv complexity, the stronger it indicates that the underlying process is deterministic rather than random. We scored individual trial series for each third of the experiment according to which response was given, resulting in binary response series (e.g., …VHHHVVVHVV…), and calculated their Lempel-Ziv complexity. We used a normalized measure of Lempel-Ziv complexity suggested by Kaspar and Schuster (1987) that is independent of series length as implemented by Faul (2005). The algorithm scans series of the same symbols incrementally while increasing the complexity count every time a new subseries of symbols is encountered, followed by normalization.

In order to investigate the Lempel-Ziv complexity of prestimulus alpha activity, we converted magnitudes of alpha power in trial sequences to binary series. For each experiment part, the mean alpha power across all trials was computed, and each trial was coded as zero or one according to whether its alpha power was, respectively, below or above the mean. We compared the complexity in the actual and surrogate data. To obtain the latter, we shuffled the trial order. We repeated the shuffling procedure 1,000 times and computed the 95% confidence intervals of the mean Lempel-Ziv complexity distributions of the shuffled series. The confidence intervals were corrected for bootstrap bias using the accelerated bootstrap method (Efron, 1987). We used only the lower bound of the confidence interval because we were interested in the cases in which complexity was lower than random.

For statistical analysis, we used an ANOVA with the Huynh-Feldt correction (ε) of p values to compensate for violation of sphericity if the number of degrees of freedom was two or more. For post hoc analysis we used Tukey's honestly significant difference test.

The EEG data set analyzed in the current study was previously used for investigating association between perceptual ambiguity and the poststimulus activity evoked by dot lattices (Nikolaev, Gepshtein, Gong, & van Leeuwen, 2010; Nikolaev et al., 2008).

Results

Behavioral results

The probabilities of responses *a* and *b* are plotted separately for each response orientation in Figure 2A. To test possible orientation biases in participants' responses, we ran two repeated-measures ANOVAs on the response probability with a factor of response type (*a* vs. *b*) and with a factor of response orientation: either vertical–horizontal orientation (vertical: 67.5° or 112.5° vs. horizontal: 22.5° or 157.5°) or right–left orientation (right: 22.5° or 67.5° vs. left: 112.5° or 157.5°). We found higher probability of responses *a* than *b*, $F(1, 12) = 158.1$, $p < 0.001$, and of vertical than horizontal responses, $F(1, 12) = 65.0$, $p < 0.001$, but no effect of right–left orientation. Vertical responses *a* were more frequent than horizontal responses *b* as was indicated by an interaction between response type and vertical–horizontal orientation, $F(1, 12) = 9.1$, $p = 0.01$. No other interactions were observed. Preferences for responses *a* versus *b* were in overall accordance with the principle of grouping by proximity (Kubovy et al., 1998). In addition, for both responses *a* and *b*, orientations near the vertical were more frequent than near the horizontal. Based on these observations, we use dot proximity as a parameter that controls stimulus-driven processes, and we use orientation (horizontal–vertical but not left–right) as a parameter that controls the degree to which responses depend on intrinsic factors.

Perception of ambiguous stimuli can be viewed as the result of a compromise between factors intrinsic and extrinsic to the brain (Chopin & Mamassian, 2011; Gepshtein & Kubovy, 2005). Intrinsic factors will be more prominent when the stimulus is weak. Indeed, the preference for vertical orientations was more prominent in the more ambiguous stimuli, i.e., when the aspect ratio of dot lattice was close to unity and the competing dot groupings were equally likely or near equally likely (Figure 2B).

To capture response trends over the course of the experiment, we divided the entire trial sequence into nine successive episodes of about 70 trials each (Figure 3). Bins of this size allowed us to approach the evolution of perceptual interpretations at a short time scale but do not contain enough trials for reliable EEG analyses. Within every bin, we measured proximity discriminability as a difference between the probabilities of responses *a* and *b* and orientation bias as the difference between the probabilities of vertical and horizontal responses. We found that, over the course of the experiment, perceptual reports became more dependent on proximity, $F(8, 96) = 9.2$, $p < 0.001$, $\varepsilon = 0.96$, and less on orientation, $F(8, 96) = 8.8$, $p < 0.001$, $\varepsilon = 0.45$. In other words, the two factors traded off, and the trade-off shifted in favor of proximity over the course of the experiment.

To study the effect of these trends on EEG, we need larger bin sizes. Figure 3 shows that the "proximity" and "orientation" curves change abruptly in the first three of nine episodes. Indeed, the proximity probabilities' difference was significantly higher (post hoc $p = 0.02$) and the orientation probabilities' difference was significantly lower (post hoc $p = 0.006$) in the third than first episode. After that, the opposite trends are preserved, but they become much less prominent (no post hoc differences). This indicates that perceptual interpretations evolve differently in the first three episodes than afterward. Accordingly, for our subsequent analyses, we joined the first, second, and third three bins into three successive parts of about 200 trials each as indicated at the lower *x*-axis of Figure 3.

For three successive parts of the experiment, we calculated proximity and orientation log odds according to Equations 1 and 2. In Figure 4A, we plot proximity log odds as a function of AR separately for three parts of the experiment. Repeated-measures ANOVA on the proximity log odds with factors of experiment parts (three parts) and aspect ratio (four levels) revealed effects of experiment parts, $F(2, 24) = 12.9$, $p < 0.001$, $\varepsilon = 1.0$, aspect ratio, $F(3, 36) = 30.2$, $p < 0.001$, $\varepsilon = 0.54$, and their interaction, $F(6, 72) = 7.1$, $p < 0.001$, $\varepsilon = 0.68$. Post hoc tests showed that proximity log odds were larger in the first than the second and third parts (all *p*s < 0.002) of the experiment and that there was no difference between the second and third parts ($p = 0.91$). The main effect of experiment parts corresponds to Figure 3 in showing that the preferences according to the principle of proximity increased after the first part of the experiment. The interaction is due to an increase in slope from the first to the second part. This indicates that the proximity discriminability increased between the first and the second part of the experiment. The increased discriminability is a main indicator of perceptual learning.

In Figure 4B, we plot the orientation log odds as a function of AR separately for the three parts of the experiment. An ANOVA on orientation log odds revealed effects of experiment parts (three parts), $F(2, 24) = 11.1$, $p < 0.001$, $\varepsilon = 0.95$, aspect ratio (four levels), $F(3, 36) = 7.6$, $p = 0.01$, $\varepsilon = 0.39$, and their interaction, $F(6, 72) = 2.8$, $p = 0.04$, $\varepsilon = 0.61$. The orientation log odds were smaller in the first than in the remaining two thirds of the experiment (all post hoc *p*s < 0.006). There was no difference between the second and third parts ($p = 0.56$). The main effect of experiment parts corresponds to the result of Figure 3: proximity was a weaker determinant of the response in the first part than afterward. The interaction is due to a decrease in the slope between the first and later parts of the experiments. This implies that orientation bias is weakened after the first 200 trials.

Combining the results of Figure 4A and B, in Figure 4C, we plot orientation log odds against proximity log odds over the course of the experiment. Figure 4C makes it clear that the decline in orientation bias co-occurs with an increase in proximity discriminability. We conclude that perceptual learning is characterized by a transition from predominance of orientation bias to stimulus-specific discrimination over the course of the experiment.

Event-related potentials

To investigate perceptual and postperceptual processes associated with proximity and orientation, we compared event-related activity for responses consistent versus inconsistent with the proximity principle (responses *a* vs. *b*) as well as for responses consistent versus inconsistent with the orientation preference (vertical vs. horizontal). To consider the effect of learning, we analyzed the activity evoked by the presentation of the dot lattices in three parts of the experiment separately.

We applied repeated-measures ANOVAs with either proximity response (*a* vs. *b*) or orientation response (horizontal vs. vertical) as first factor and experiment parts (three parts) as a second factor on the amplitude of the component P1 and N1. For proximity response, P1 amplitude was larger for *a* than *b* responses, $F(1, 12) = 7.6$, $p = 0.02$ (Figure S1A, B in Supplementary Materials). There was neither an effect of experiment parts nor an interaction. There was no orientation response effect on P1.

The P1 component showed a double peak: the first one about 100 ms and the second one about 140 ms after stimulus onset (Figure 5A, B). The bimodality occurred because P1 was obtained by averaging the evoked activity over 19 electrodes including lateral (around O1 and O2) as well as central (around Oz) locations. Figure

S1A and B shows that the early peak at 100 ms had a maximum at the lateral locations whereas the late peak at 140 ms had a maximum at the central locations.

We found a larger (more negative) N1 amplitude associated with horizontal than with vertical responses, $F(1, 12) = 6.9$, $p = 0.02$ (Figures 5A and S1C). We also found a decrease in N1 with experiment parts for both proximity response, $F(2, 24) = 3.9$, $p = 0.045$, $\varepsilon = 0.79$, and orientation response, $F(2, 24) = 5.6$, $p = 0.02$, $\varepsilon = 0.8$ (Figure 5B). An analysis with polynomial linear contrast over the three parts of the experiment indicated that the decrease of N1 amplitude showed a linear trend for both response factors, $F(1, 12) = 5.3$, $p = 0.04$ and $F(1, 12) = 6.9$, $p = 0.02$, respectively (Figure 5C). There were no interactions between experiment parts and proximity or orientation response.

In sum, the effect of proximity was manifested in the ERP component P1 with a peak latency of around 100 ms from stimulus onset. The effect of orientation started affecting ERP from the following component N1 with a peak latency of around 180 ms. Both effects remained constant in the course of the experiment even though the N1 linearly decreased.

Prestimulus alpha power

We investigated the association of proximity and orientation responses with the alpha power over the 1-s interval before stimulus presentation. Figure 6A illustrates the topographical distribution of alpha power over the parieto-occipital areas averaged across all participants and conditions. For the statistical analysis, we averaged the power across 59 parieto-occipital electrodes. Two ANOVAs on the alpha power with factors of experiment parts (three parts) and proximity response (*a* vs. *b*) or orientation response (horizontal vs. vertical) showed that alpha power increased toward the end of the experiment, $F(2, 24) = 15.4$, $p < 0.001$, $\varepsilon = 0.8$ and $F(2, 24) = 19.6$, $p < 0.001$, $\varepsilon = 0.9$, respectively (Figure 6B through D).

We found neither a main effect of proximity response nor an interaction with experiment part (Figure 6B). In contrast, we found a prominent interaction between experiment part and orientation response (horizontal vs. vertical), $F(2, 24) = 15.7$, $p = 0.0004$, $\varepsilon = 1.0$. Alpha power was larger for horizontal than vertical orientation responses in the first part of the experiment (post hoc $p < 0.001$) but not in the second and third parts (all ps > 0.74) (Figure 6C, D). The time–frequency plots (Figure 6E) indicate that the difference between horizontal and vertical responses occurred almost exclusively in the alpha band. We found no difference in the amount of microsaccades between horizontal and vertical responses (see Table S1 in Supplementary Materials), indicating that microsaccadic lambda responses overlapping with the spontaneous alpha activity could not explain the alpha effect observed in the first part of the experiment. Thus, alpha power was associated with bias rather than with proximity. This association, however, lasted only as long as the bias remained a predominant factor in response choice.

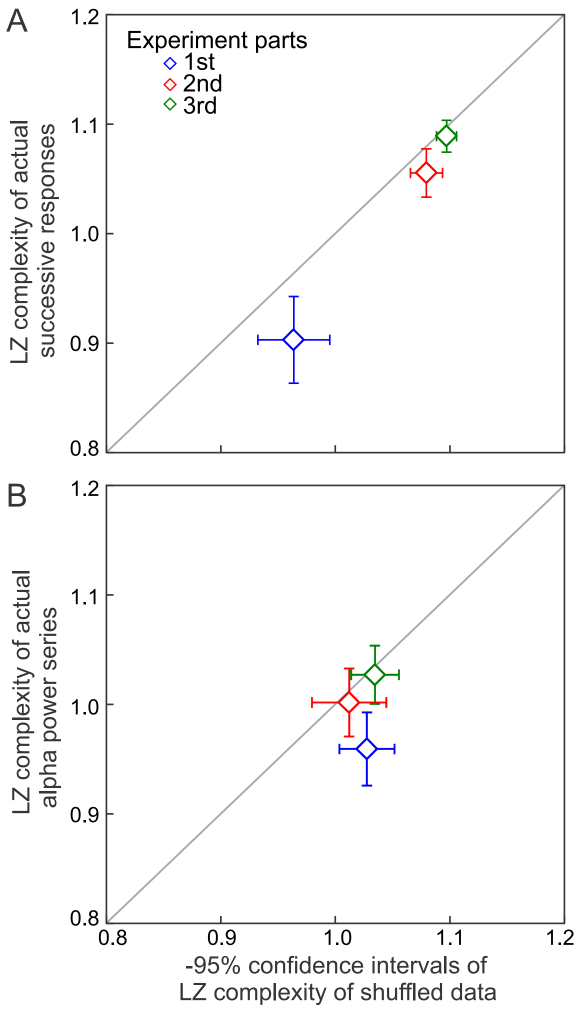

Figure 7. (A) Lempel-Ziv (LZ) complexity for successive horizontal and vertical responses. (B) LZ complexity of prestimulus alpha power in successive trials. In both panels, LZ complexity of actual data is plotted against the lower bound of the confidence interval of mean LZ complexity in distributions of shuffled data for three parts of the experiment. In the first part of the experiment, LZ complexity of the actual data is lower than the complexity of the corresponding shuffled series. The error bars are the standard errors across participants.

Serial dependencies in behavioral responses and prestimulus alpha power

To reveal the dynamic structure of responses and corresponding prestimulus alpha power, we computed the Lempel-Ziv complexity of their time series. We found that the Lempel-Ziv complexity was different between the actual and surrogate data in responses when distinguished according to orientation (horizontal or vertical responses) but not when according to proximity (responses *a* or *b*). The effect occurred only in the first part of the experiment (Figure 7A). For responses distinguished according to orientation, an ANOVA on complexity with factors data (actual vs. the lower bound of the confidence interval of shuffled series) and experiment parts (three parts) revealed an effect of data: The complexity of the actual data was lower than shuffled, $F(1, 12) = 8.3$, $p = 0.01$. The complexity prominently increased with experiment parts, $F(2, 24) = 19.2$, $p < 0.001$, $\varepsilon = 0.73$: The complexity in the first part was lower than in the second and third parts (both post hoc ps < 0.001), and the complexity in the second and third parts did not differ from one another ($p = 0.6$). An interaction tendency was found between data and experiment parts, $F(2, 24) = 2.96$, $p = 0.07$, $\varepsilon = 1.0$. Even though the interaction only approached significance, Figure 7A indicates a large difference between actual and shuffled data in the first part of our experiment. Therefore, we used the post hoc test to explore this effect. Indeed, the complexity in the first experiment part was lower than that of the shuffled data (post hoc $p < 0.009$). The results of this exploration are therefore in accordance with the prediction of serial dependency in orientation preference during the first part of the experiment.

For responses distinguished according to proximity, the ANOVA did not reveal a difference between actual and shuffled data. This indicates that proximity responses simply follow the random order of stimulus presentation.

We estimated the Lempel-Ziv complexity of prestimulus alpha power series as above. The complexity was found to be different between the actual and the surrogate data only in the first part of the experiment (Figure 7B). The ANOVA revealed an effect of data: Complexity of the actual data was lower than that of the shuffled data, $F(1, 12) = 10.5$, $p = 0.007$, and an interaction between data and experiment parts, $F(2, 24) = 3.99$, $p = 0.045$, $\varepsilon = 0.77$. Again, complexity of actual data was lower than complexity of the shuffled data only in the first part of the experiment (post hoc $p < 0.007$). The low-complexity alpha power series in the first part of the experiment is in accordance with the predicted serial dependencies in their temporal structure.

We then correlated the Lempel-Ziv complexity of response series distinguished according to orientation bias (horizontal vs. vertical) with that of alpha power series. A correlation was obtained only in the first part of the experiment ($r = 0.57$, $p = 0.04$). These findings indicate that in the initial stage of perceptual learning a common underlying dynamic regime is consistently manifesting itself both in behavior and alpha activity.

In sum, whereas proximity responses followed the random ordering of the trials, orientation responses in the first part of the experiment showed sequential dependencies. The same is true for the time series of the prestimulus alpha signal. Both series were correlated, suggesting a common underlying dynamic. The initial stage of perceptual learning, therefore, is characterized by dynamic brain states capable of generating biased responses to the visual stimulus.

The length of sequences with the same responses

Having found serial dependencies in the orientation response series, we consider whether the dynamic structure is characterized by persistence. We scored same-response sequences according to their length, e.g., the sequence "HHH" was scored as a sequence of length three, ignoring subsequences of length two: "HH." We log transformed the scores and computed their geometric means for each participant in each part of the experiment. We then shuffled the trial order and obtained shuffled-sequence length scores. We repeated this procedure 1,000 times and computed the 95% confidence interval of the mean for the shuffled-sequence distribution. The confidence interval was corrected for bootstrap bias using an accelerated bootstrap method.

We found that sequence lengths of actual data differed from shuffled ones. An ANOVA on sequence length with factors data (actual vs. shuffled), orientation response (horizontal vs. vertical), and experiment parts (three parts) revealed that in the actual data, sequence lengths were longer than in the shuffled ones, $F(1, 12) = 20.8$, $p < 0.001$. Sequences of vertical responses (V-sequences) were longer than sequences of horizontal responses (H-sequences), $F(1, 12) = 23.7$, $p < 0.001$. There was an interaction between orientation response and experiment parts, $F(2, 24) = 9.1$, $p = 0.003$, $\varepsilon = 0.82$. The difference between lengths of H- and V-sequences was considerably larger in the first part of experiment (post hoc $p < 0.001$) than in the second ($p = 0.047$) and third ($p = 0.15$) parts (Figure 8A). In addition, V-sequences were significantly longer in the first than in the second ($p = 0.02$) and third ($p < 0.006$) part of the experiment whereas H-sequences did not vary significantly (all ps > 0.7). No interactions with data were observed. Thus, orientation responses show persistence everywhere throughout the experiment. This occurs even though the role of orientation bias decreases in the course of the experiment, which is marked by a decline in the length of V-sequences.

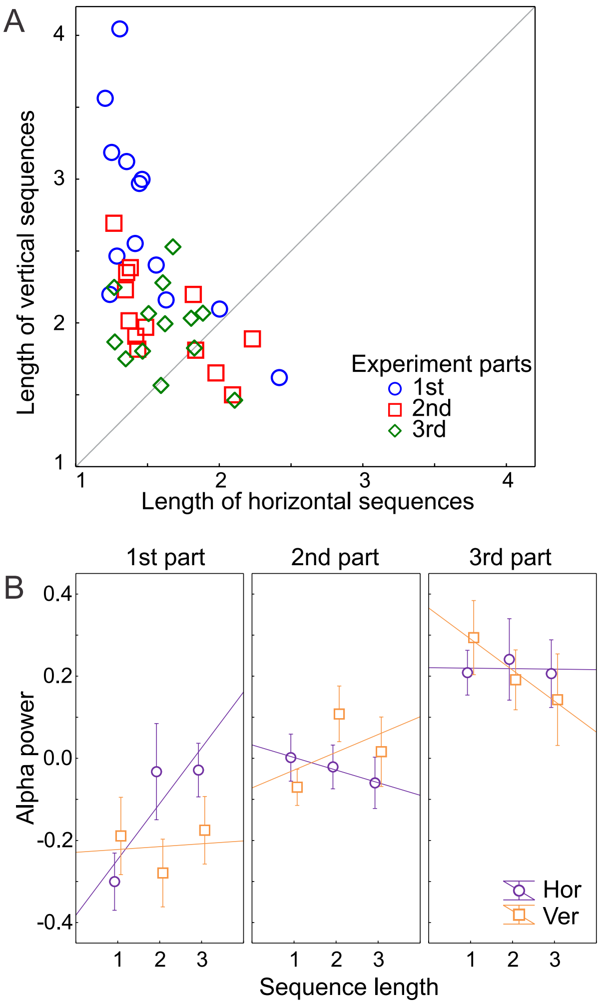

Figure 8. (A) Lengths of sequences of same responses (i.e., horizontal sequences or vertical sequences) are plotted for different parts of the experiment. Each data point represents one participant in one part of the experiment. In the first part, sequences of vertical responses are substantially longer than sequences of horizontal responses. (B) Prestimulus alpha power (standard scores) for different sequence lengths of successive vertical and horizontal responses in three parts of the experiment. Alpha power is larger for horizontal than vertical responses only for sequence lengths two and three (i.e., for periods of alpha activity longer than 3 s) in the first part of experiment. The lines are linear-regression fits. The error bars are the standard errors across participants.

Next, we evaluated the association of sequence length with prestimulus alpha power. We restricted this analysis to orientation-response sequences of lengths one, two, and three due to insufficient numbers of longer sequences. To obtain equal samples, we randomly selected sequences of lengths of one and two in numbers equal to that of length three sequences, resampling with replacement 1,000 times and computing averages. For each sequence, we calculated the average alpha power across its trials. The difference of alpha power between horizontal and vertical orientations appears to depend on sequence length (Figure 8B). An ANOVA with factors of experiment parts (three parts), sequence length (three levels), and orientation response (horizontal vs. vertical) showed that power increased over parts of the experiment, $F(2, 24) = 11.2$, $p = 0.001$, $\varepsilon = 0.83$, as we already observed. In addition, there was an interaction between experiment part, sequence length, and orientation response, $F(4, 48) = 2.8$, $p = 0.04$, $\varepsilon = 0.99$. We found linear trends over H-sequences for the first, $F(1, 12) = 10.2$, $p = 0.008$, part of the experiment but not for any other parts nor for V-sequences, all $Fs(1, 12) < 1.4$, $p > 0.27$. Thus, increased alpha power for horizontal responses in the first part of the experiment (Figure 6C) arises when the unbiased responses persist across trials (Figure 8B).

In sum, the dynamics in the early part of the experiment are shown to consist of two alternating modes: one characterized by persistence of low-power alpha activity in combination with responses in accordance with the orientation bias and the other by high-power alpha activity associated with unbiased responses. The alternating modes constitute the specific regime of behavior and alpha activity in the early stage of perceptual learning.

Discussion

Observers viewed ambiguous dot lattices and reported the orientations of perceived dot groupings. As in the previous studies, the orientation of perceptual grouping was a function of the ratio of distances between the dots in agreement with the principle of spatial proximity (Kubovy et al., 1998; also see Nikolaev et al., 2008). Observers' ability to consistently perform a perceptual task according to a stimulus parameter reflects a measure of their visual discriminability.

Besides the stimulus factor of proximity, responses are also affected by observers' perceptual bias: a preference for the vertical orientation (Figure 2A). Because dot lattices are broadband stimuli, the bias for vertical over horizontal orientations is not surprising (Essock et al., 2003). It is surprising, however, that orientation bias persisted during the experiment whereas in Gepshtein and Kubovy (2005) it changed from trial to trial. The persistence of bias facilitated our further analyses. In line with previous observations, the perceptual bias had a larger impact in the more ambiguous stimuli (Chopin & Mamassian, 2011; Gepshtein & Kubovy, 2005).

The plot of proximity log odds (called "attraction function" by Kubovy et al., 1998) in Figure 4A describes how the probabilities of reporting the two most likely dot groupings depend on the AR of the lattices. We used the slope of the attraction function as a measure of visual discriminability. Similarly, the plot of orientation log odds in Figure 4B describes how the probabilities of perceiving the orientation of the lattice depend on the aspect ratio. We used the slope of the latter function as a measure of orientation bias.

We used these measures to determine how the trade-off of bias and discriminability evolves over the course of a 1-hr experiment. Orientation bias was predominant in the first third of the experiment, but its role declined in favor of discriminability afterward (Figure 4C). We interpret this result as a manifestation of *perceptual learning*: an improvement in discrimination of the spatial structure of the stimulus. This result shows that perceptual learning involves more than improving the discrimination to stimulus features. To an equal extent, perceptual learning is accompanied by reduction of stimulus-independent preferences (biases). Because such biases are significant in perception of ambiguous stimuli, the effect of learning is stronger for ambiguous than unambiguous stimuli (Harrison & Backus, 2010; van Dam & Ernst, 2010). Accordingly, we found a greater reduction in bias in the course of the experiment in the more ambiguous stimuli (Figure 4B).

Even though perceptual bias declined considerably from its initial prominence over the course of the experiment (Figure 4C), the bias did not disappear. Throughout the experiment, the bias kept a large role in the perception of the more ambiguous stimuli (Figure 4B). Thus, perceptual bias does not only play a role in the early stage of learning, but it maintains its role in compensating for the remaining ambiguity.

Evoked potentials and prestimulus alpha activity in the course of learning

To study the neural mechanisms involved in this behavior, we analyzed evoked potentials and prestimulus alpha activity. In the evoked potentials, we found no change of P1 in the course of the experiment, in line with some (Song et al., 2005; Sterkin et al., 2012) but not other (Wang et al., 2016; Zhang et al., 2013) previous studies of the effect of learning on P1. In contrast, the N1 amplitude gradually decreased (Figure 5B, C), and the prestimulus alpha power gradually increased (Figure 6B, C) in the course of the experiment. These trends are consistent with perceptual learning. However, they might also indicate other phenomena: Decreasing N1 amplitude with repetition of stimuli (Verbaten, Roelofs, Sjouw, & Slangen, 1986) could be attributed to reduction of attention (Song et al., 2010) or habituation (Carretié, Hinojosa, & Mercado, 2003; Qu et al., 2010). Likewise, the gradual increase in alpha power (Figure 6B, C) may reflect a reduction of vigilance during the experiment (Fairclough et al., 2005; Maclin et al., 2011; Smith et al., 1999).

Because we anticipated that these analyses could be inconclusive and because we were interested in the dynamics of trade-off of perceptual bias and discriminability, we studied the relationship between EEG measures and orientation bias in greater detail. The analysis of evoked potentials revealed that, throughout the experiment, perceptual responses according to proximity were related to the P1 component, which is consistent with previous reports of the association between P1 and perceptual grouping (Han et al., 2005; Nikolaev et al., 2008). The orientation bias was reflected in the subsequent N1 component. N1 amplitude was larger for unbiased than biased responses (Figure 5A, C). Depending on the stimulus and the task, the N1 component may indicate several perceptual processes of which visual attention is a main factor (Hillyard & Anllo-Vento, 1998). In the focus of attention, N1 reflects visual discrimination performance (Hopf et al., 2002; Ritter et al., 1979; Vogel & Luck, 2000). The larger N1 amplitude for unbiased trials than for biased ones, therefore, is consistent with greater discriminability in the former than in the latter. The result is still inconclusive, however, as to whether biased responses occur because of lacking attention or are actively imposed.

The analysis of prestimulus alpha power did not reveal any association with visual discriminability. In particular, responses consistent and inconsistent with the proximity principle of grouping did not differ in alpha power (Figure 6B). Previous studies have shown that better detection and discrimination of stimulus features occurred when the prestimulus alpha power was low (Ergenoglu et al., 2004; Linkenkaer-Hansen et al., 2004; Thut et al., 2006; van Dijk et al., 2008; Wyart & Tallon-Baudry, 2009). Because responses according to proximity reflect visual discriminability, we might have expected that the responses consistent with proximity would follow a lower alpha power than the responses inconsistent to proximity. On the other hand, the null result offers a first hint as to which of the two processes, bias or discriminability, plays the more active role in their trade-off.

Biased responses were more prominent in the initial stage of the experiment (Figure 3). We observed that, as long as this was the case, prestimulus alpha power was associated with orientation bias. Prestimulus alpha power was reduced in the trials with biased responses (Figure 6C through E). This result is inconsistent with the hypothesis that biased responses appear by default when visual processes are suppressed. This hypothesis, which assumes that the biases constitute a passive consequence of sensory inhibition, was one of two possibilities. The evidence of low alpha power associated with biased responses favors the alternative hypothesis: that the visual system imposes bias actively. This mechanism could be understood as follows.

Perception of ambiguous stimuli depends on top-down signals that mediate biases, possibly reflecting prior expectations of the upcoming stimuli (Douglas & Martin, 2007; Nauhaus, Busse, Carandini, & Ringach, 2009) or reflecting prior visual representations against which the incoming stimuli are matched (Hesselmann, Kell, & Kleinschmidt, 2008). The biases may help to overcome stimulus uncertainty (Chopin & Mamassian, 2011; Harrison & Backus, 2010; van Dam & Ernst, 2010) or compensate for the lacking visual discriminability (Essock et al., 2003). Spontaneous brain activity reflects the top-down influences (Fiser et al., 2010; Gilbert & Sigman, 2007; Ringach, 2009) that are thought to play a central role in formation of perceptual biases (Harmelech & Malach, 2013). Because deployment of prior visual representations is accompanied by low prestimulus alpha power, the deployment of bias is an active process. In contrast, when prestimulus alpha power is high, perceptual interpretations are driven by the stimulus. This means that the trade-off between discriminability and bias is controlled by the bias.

To summarize, our findings suggest that early stages of perceptual learning are characterized by episodes in which the perception of ambiguous stimuli is driven by preexisting visual representations, or resident biases, rather than by fluctuations of visual discriminability.

Serial dependencies indicate a distinct regime in the early stage of learning

To further explore the role of the orientation bias in the initial stage of learning, we assumed that the bias and its signature in alpha activity reflect the dynamics of lasting brain states (Gepshtein & Kubovy, 2005). We tested this hypothesis by measuring serial dependencies in orientation responses and alpha power in the first third of the experiment.

We investigated the serial dependencies using Lempel-Ziv complexity: a measure of randomness in binary time series. We found that the complexity of orientation series was lower than in the shuffled data (Figure 7A), revealing a serial dependency. In contrast, we found no serial dependency in the (unbiased) responses that followed the proximity principle. Serial dependence was also observed in the time series of alpha power (Figure 7B), suggesting that orientation preferences and alpha power could be governed by the same intrinsic dynamics. Indeed, we found a positive correlation between the two time series, confirming the association of bias and alpha dynamics.

These results were observed in the first third of the experiment and not in its subsequent parts. In other words, the joint dynamics of bias and alpha activity occurred only during the early stage of perceptual learning. Sagi and Tanne (1994) described this initial process as a fast and saturating stage of learning, which may last for several hundreds of trials, compatible with the 200 trials in our initial part.

To further characterize the serial dependency uncovered in the analyses of Lempel-Ziv complexity, we studied repetitions of subsequent identical responses. These repetitions occurred in the first third of the experiment more frequently than expected from chance (Figure 8A). That is, the relationship between perceptual grouping and the attendant prestimulus alpha power was characterized by the persistence predicted by the hypothesis of lasting brain states (Gepshtein & Kubovy, 2005). A difference in alpha power between the trials with biased and unbiased responses (Figure 6C through E) was found only for sequences of two to three identical responses and not when the perceived orientation was switching from one trial to the next (Figure 8B). Unperturbed by the intervening evoked activity, prestimulus alpha power remained low during sequences of biased responses, and it remained high during sequences of unbiased responses.

This is evidence that, early in perceptual learning, alpha activity adheres to a *distinct dynamic regime*. This regime consists of two alternating modes of behavior and alpha activity. The first mode (which we call the “biased mode”) is characterized by biased responses, low power of the alpha activity, and low amplitude of the ERP component N1. The second mode (“visual discrimination mode”) is characterized by stimulus-driven, proximity-based responses, high power of the prestimulus alpha oscillations, and high amplitude of the ERP component N1. The biased mode is more persistent than the visual discrimination mode during the initial stage of learning (Figures 3, 7, and 8).

Intermittent brain dynamics may underlie the observed regime

The alternating modes showed persistency up to at least two sequential trials (Figure 8). Because each trial took about 3 s, the modes could last for 6 s or more. Alternations between modes at this time scale reflect the heterogeneity and complexity of the alpha rhythm (Stam, Pijn, Suffczynski, & Lopes da Silva, 1999), known as *intermittent dynamics* in spontaneous alpha activity (Breakspear, 2002; Bressler & Kelso, 2001; Freeman & Barrie, 2000; Gong, Nikolaev, & van Leeuwen, 2007; Nikolaev et al., 2010). In spontaneous alpha activity, intermittency leads to episodes of stable and unstable activity and to fast transitions between these episodes (Breakspear, Williams, & Stam, 2004; Freeman, Burke, & Holmes, 2003; Friston, 2000; Gong, Nikolaev, & van Leeuwen, 2003; Gong et al., 2007; Ito, Nikolaev, & van Leeuwen, 2005, 2007; Kaplan, Fingelkurts, Fingelkurts, Borisov, & Darkhovsky, 2005; Lehmann, Ozaki, & Pal, 1987; Stam et al., 1999).

Intermittent dynamics is generally characterized by spontaneous transitions between low-amplitude and high-amplitude oscillations (Breakspear & Terry, 2002; Freyer, Aquino, Robinson, Ritter, & Breakspear, 2009; Ito et al., 2007; Lopes da Silva, van Lierop, Schrijer, & Storm van Leeuwen, 1973). It is plausible that such intermittent dynamics reflects activation of the mechanisms that deploy perceptual biases and help to resolve sensory uncertainty. Specifically, intermittency can help neural systems to exit attractor states while ensuring the flexibility of perception needed for accommodating the great variety of stimulation (Bressler & Kelso, 2001; Friston, 1997; Kelso, 1995; Tognoli & Kelso, 2014; van Leeuwen, 1990, 2007). Intermittent dynamics allows the system to explore alternative interpretations of visual information, helping to overcome perceptual ambiguities (Braun & Mattia, 2010; van Leeuwen, 1990).

In particular, the alternation of two modes may help the visual system to balance effects of incoming stimulus information and internal processes (Zanone & Kelso, 1992). This may be needed to perform orientation judgment under uncertain stimulation in the initial stage of learning. The information about stimulus orientation gathered over several trials while the system dwells in the mode of visual discrimination may have to be loaded into visual working memory (Rideaux, Apthorp, & Edwards, 2015). If perceptual learning engages working memory in this fashion, then, according to a recent working memory model (Raffone, Srinivasan, & van Leeuwen, 2014; Simione et al., 2012), this process competes for central capacity with the uptake of incoming stimulus information (Meghanathan, van Leeuwen, & Nikolaev, 2015; Raffone, Srinivasan, & van Leeuwen, 2015). When memory loading absorbs the central capacity, this may result in reduced visual discrimination and hence in a weakening of grouping by proximity. Crucially, the competition for central capacity keeps intact the top-down influences on the early visual representations (represented in the model, according to Simione et al., 2012, by top-down activity from the "higher perceptual map"). In the present context, top-down activity corresponds to perceptual bias. According to this line of reasoning, the biased mode may thus be regarded as an intermission in the process of perceptual learning.

The resolution of the two-mode regime corresponds to the reduction of the biased state in the later parts of the experiment. During the transition from deterministic to random series of responses and alpha power values (reflected in Lempel-Ziv complexity, Figure 7) alpha power gradually increases over trials. This implies that the task is becoming less demanding of the system resources, including working memory and the processes of consolidation. The reduced demands are accompanied by an increase in the dimensionality of dynamics. This phenomenon has been previously observed in the analysis of reaction time series (Kelly, Heathcote, Heath, & Longstaff, 2001), and according to Figure 7, it also applies to orientation responses and electrical brain signals.

To summarize, perception and brain activity show the same dynamics during the early stages of perceptual learning. The dynamics are characterized by mode transitions: an inherent property of intermittency. Initial learning consists of switching between the visual discrimination mode (in which perception of external stimuli is accompanied by an intensive acquisition of the new sensory information) and the biased mode (which is guided by intrinsic, prelearning preferences). The process that projects biases top-down is in control, and it intermittently suppresses the flow of stimulus information for the periods of a few trials at a time in our experiment. A likely reason for the intermittent suppression is that the information gathered in the visual discrimination mode needs to be consolidated, thus occupying central resources. Eventually, the alternation of modes fades, giving way to a regime characterized by stable alpha activity and stimulus-driven perception, in which the role of bias is reduced to the role of compensating for stimulus uncertainty. The finding of a distinctive dynamic regime of brain function at the early stages of perceptual learning extends our understanding of the role of spontaneous brain states in learning. Manifestations of this regime in the dynamics of alpha activity offer a novel perspective on the role of alpha rhythms in perceptual learning.

Keywords: EEG, spontaneous alpha activity, perceptual learning

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