

Characterizing the effects of multidirectional motion adaptation

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Recent sensory experience can alter our perception and change the response characteristics of sensory neurons. These effects of sensory adaptation are a ubiquitous property of perceptual systems and are believed to be of fundamental importance to sensory coding. Yet we know little about how adaptation to stimulus ensembles affects our perception of the environment as most psychophysical experiments employ adaptation protocols that focus on prolonged exposure to a single visual attribute. Here, we investigate how concurrent adaptation to multiple directions of motion affects perception of subsequently presented motion using the direction aftereffect. In different conditions, observers adapted to a stimulus ensemble comprised of dot directions sampled from different distributions or to bidirectional motion. Increasing the variance of normally distributed directions reduced the magnitude of the peak direction aftereffect and broadened its tuning profile. Sampling of asymmetric Gaussian and uniform distributions resulted in shifts of direction aftereffect tuning profiles consistent with changes in the perceived global direction of the adapting stimulus. Adding dots in a direction opposite or orthogonal to a unidirectional adapting stimulus led to a pronounced reduction in the direction aftereffect. A simple population-coding model, in which adaptation selectively alters the responsivity of direction-selective neurons, can accommodate the effects of multidirectional adaptation on the perceived direction of motion.

Introduction

Our sensory systems are constantly adapting to their input to efficiently represent an ever-changing environment. This ongoing process of adaptation acts to alter the response properties of sensory neurons and affects perceptual experience. For instance, single-cell recordings in visual cortex show that adaptation leads to reduced firing rates in visual neurons as well as changes in their tuning and noise characteristics (see Kohn, 2007, for a review). These physiological changes modulate our sensory experience, leading to biases in the perception of certain stimulus attributes (Blakemore, Nachmias, & Sutton, 1970; Gibson & Radner, 1937; Mather, Verstraten, & Anstis, 1998) and changes in perceptual sensitivity (Hol & Treue, 2001; Phinney, Bowd, & Patterson, 1997; Regan & Beverley, 1983, 1985). For example, prolonged exposure to a stimulus moving in a particular direction causes the perceived direction of a subsequent stimulus to be repelled away from the adaptor (Levinson & Sekuler, 1976), and this direction aftereffect is often accompanied by a cost for discriminative accuracy (Hol & Treue, 2001).

Establishing clear quantitative links between the physiological and perceptual effects of adaptation represents a major challenge in understanding its role in sensory coding. Population-coding models are becoming increasingly important in bridging this gap between the effects of adaptation at neuronal and perceptual levels (e.g., Clifford, Wenderoth, & Spehar, 2000; Jin, Dragoi, Sur, & Seung, 2005; Price & Prescott, 2012; Series, Stocker, & Simoncelli, 2009). These models define a relationship between an observer's performance in a perceptual task and the underlying

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neurophysiology using an encoding–decoding framework. The encoding stage represents the transformation of sensory input into a pattern of activity across a population of neurons with different tuning preferences, and the decoding stage represents how the stimulus is “read out” from the neural responses for each experimental trial, allowing one to simulate observer performance on a given task. Within this population-coding framework, previous work has simulated the perceptual consequences of adaptation through a reduction in the gain or tuning bandwidth of neurons with similar tuning preferences to the adapting stimulus (Clifford et al., 2000; Kohn & Movshon, 2004; Series et al., 2009).

Although these advances represent a promising step toward a reconciled theory of adaptation, recent physiological findings suggest that adaptation can affect the encoding of sensory information in a larger variety of forms than previously thought. For instance, sensory neurons have been reported to adjust their responses to the mean, variance, and higher-order statistics of their sensory input to efficiently represent the surrounding environment (Dean, Harper, & McAlpine, 2005; Fairhall, Lewen, Bialek, & de Ruyter Van Steveninck, 2001; Wark, Lundstrom, & Fairhall, 2007). Linking the apparent dependency of neuronal responses on stimulus statistics to perceptual aftereffects is a challenge, not least because many static aspects of neuronal encoding (e.g., thresholds, nonlinear gain control) can themselves produce statistic-dependent neuronal effects (Bair & Movshon, 2004; Borst, Flanagin, & Sompolinsky, 2005; Yu & Lee, 2003). However, recent work in the auditory system suggests that the effects of stimulus statistics on the responses of neurons may manifest as perceptual aftereffects in human audition (Dahmen, Keating, Nodal, Schulz, & King, 2010). With the exception of some very recent work at brief timescales (Price & Prescott, 2012), very little is known about the effects of stimulus ensemble statistics on visual aftereffects. Moreover, it is unclear if standard population-coding models can accommodate the range of adaptation effects resulting from motion stimuli that vary along these dimensions.

Here we used the direction aftereffect to examine the magnitude and tuning of perceptual biases in perceived direction following adaptation to a stimulus comprised of dot directions sampled from custom-made probability distributions. We investigated how changes in the mean and variance of dot directions in the adapting stimulus affect our perceived direction of motion. In addition, we examined the effect of adapting to bidirectional motion using adapting stimuli containing motion in opposite or orthogonal directions to the adapting direction. To preempt our results, changing the variance, but not the mean, of motion directions

reduced the magnitude and broadened the tuning profile of the direction aftereffect. Changing the mean of the adapting stimulus shifted the tuning profile of the direction aftereffect in line with the perceived global direction of the adapting stimulus. For bidirectional adaptors, adding dots in opposite or orthogonal directions relative to the adapting motion led to a pronounced reduction in the direction aftereffect. A population-coding model, in which adaptation was modeled as a selective reduction in the gain of directionally tuned neurons, could account for the range of aftereffects observed across all conditions.

Methods

Subjects

Four human observers (all male) with normal vision participated in the study. Of these, three were authors (DPM, NWR, BSW) and one (DWM) was naive to the purpose of the experiments. All experiments adhered to the tenets of the Declaration of Helsinki.

Stimuli

The adaptor and test stimuli were random dot kinematograms (RDKs), generated on a Macintosh G5 computer using the PsychoPy stimulus generation library (Peirce, 2007). Stimuli were presented on an Iiyama Vision Master Pro 514 with a resolution of 1280×1024 pixels, a refresh rate of 75 Hz and a viewing distance of 76.3 cm. Each stimulus consisted of 350 dots (unless otherwise stated) and was presented within a circular aperture (6° diameter) on a uniform luminance background. Dot diameter and density were 0.1° and $\sim 10/\text{deg}^2$ (with the exception of experiments that manipulate dot number), respectively. In the first frame of motion, the dots were randomly positioned in the circular window and were displaced at $5^\circ/\text{s}$. Dots that moved outside the circular window were wrapped to the opposite side of the window.

Procedure

A schematic of the general task procedure is illustrated in Figure 1a. Observers were required to fixate on a small dot at the center of the screen while adapting to a unidirectional or multidirectional RDK. The adaptation period lasted for 60 s in the first trial, with 5-s “top ups” at the beginning of each trial thereafter. Following adaptation, observers judged whether a unidirectional field of dots moved in a

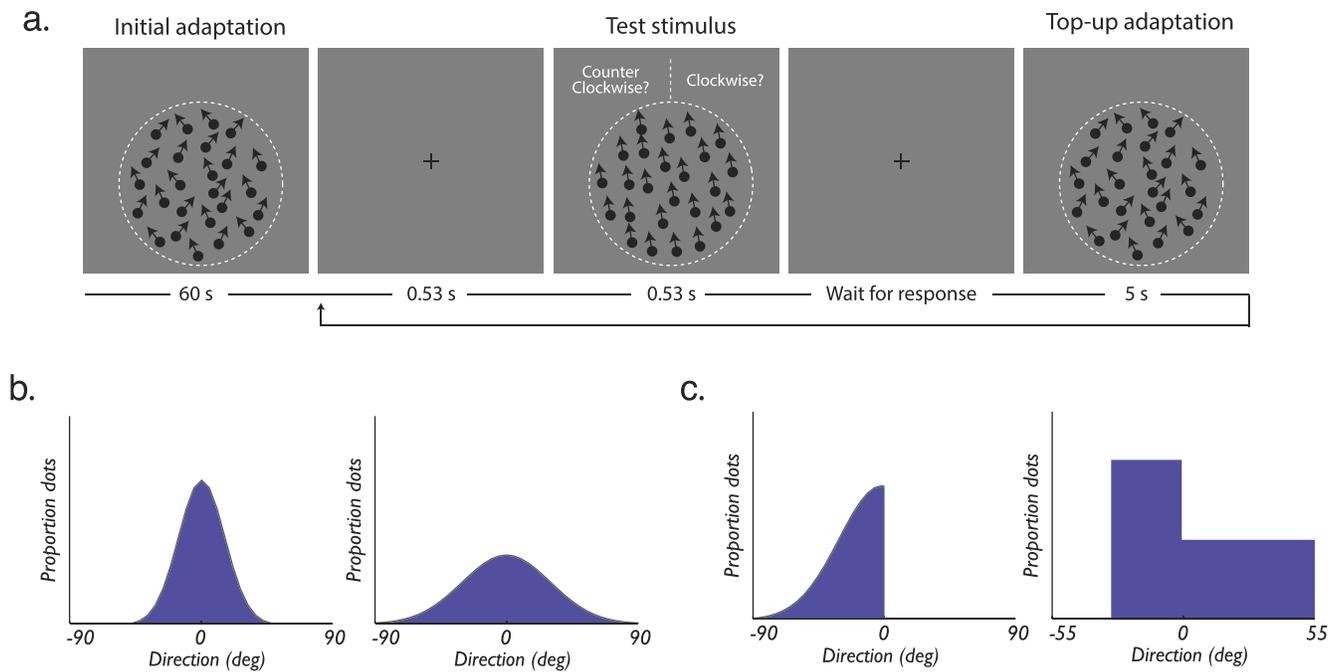


Figure 1. Schematic diagram of adaptation procedure and probability distributions from which adaptor dot directions were sampled. (a) Adaptation procedure. After an initial adaptation period of 60 s, participants were presented with a unidirectional field of dots for 0.53 s and were required to judge whether they moved clockwise or counterclockwise or upward. This was followed by a 5-s “top up” adaptation period before the presentation of another test stimulus. In different conditions, the composition of the adaptor stimulus varied according to one of four probability distributions. In two of these conditions, (b) the mean direction of the dots was kept constant, but the variance of the dot directions was varied. In the other conditions, (c) the adapting pattern was comprised of directions drawn from an asymmetric distribution with distinct measures of central tendency.

direction that was clockwise or counterclockwise from upward. The direction of the test stimulus was chosen at random from nine directions using the method of constant stimuli. The step size between successive directions was fixed for each observer whereas the entire range of directions could be offset by a fixed amount depending on the adapting condition, to capture the full psychometric function. Test stimuli were presented for 0.53 s and were separated by a 0.53-s interval containing a fixation dot on a background of mean luminance. Different conditions (i.e., different adapting directions or adaptor dot numbers) were tested in separate runs and were separated by at least 10 min (and typically much longer) to avoid cross-contamination of adaptation effects between conditions.

In Experiment 1, we measured direction aftereffect tuning profiles following adaptation to unidirectional and multidirectional dot patterns. In multidirectional conditions, adaptors were composed of dots sampled, with replacement, from a Gaussian distribution. Gaussian distributions with standard deviations of 15° and 30° were used to generate the adaptors (see Figure 1b). Estimates of the direction aftereffect were measured for adapting directions ranging between 0°

(upward) and $\pm 180^\circ$, and this value was chosen at random at the beginning of a run. In multidirectional conditions, the adaptor direction refers to the modal direction of the Gaussian distribution.

The procedure in Experiment 2 was identical to Experiment 1 with the exception that the multidirectional adapting patterns were generated through sampling of asymmetric Gaussian and uniform distributions (Figure 1c, see also Webb, Ledgeway, & McGraw, 2007; Webb, Ledgeway, & Rocchi, 2011). For the asymmetric Gaussian distribution, we independently assigned each half of the Gaussian (i.e., directions clockwise and counterclockwise to the modal direction) a different standard deviation. The standard deviation of the counterclockwise half of the distribution was 30°, and the corresponding value for the clockwise half was 0°. As in the preceding experiment, we manipulated the modal direction across the full $\pm 180^\circ$ range. For the uniform distribution, we assigned each half of the distribution (i.e., directions clockwise and counterclockwise to the median direction) a different range and sampling density. Dot directions were sampled for the counterclockwise half of the distribution at 5° intervals over a range of 55°, and the corresponding sampling density and range for the

clockwise half was 3° and 35°, respectively. Because the uniform distribution does not have a single modal direction, for this condition, we used the median to summarize the adaptor direction.

In Experiment 3, we measured the direction aftereffect with a unidirectional adaptor fixed at 30° clockwise from upward and systematically varied the amount of dots it contained on separate runs. The adapting stimulus contained either one, four, 16, 64, 256, or 512 dots. We also tested conditions with bidirectional adapting stimuli, in which additional dots moving in a second direction were added to the stimulus. The second direction moved in an opposing (150° counterclockwise from upward) or orthogonal (120° clockwise from upward) direction to the first direction and consisted of 64 or 256 dots. As in Experiments 1 and 2, the test stimulus contained 350 unidirectional dots.

Data analysis

For each condition described above, observers completed one to two runs of 90 trials. Data were expressed as the proportion of trials in which an observer judged the test direction to be clockwise from upward. These data points were subsequently fitted with a logistic function of the form

$$p(\text{clockwise}) = \frac{1}{\left(1 + e^{\frac{\text{PSE} - x}{\text{JND}}}\right)} \quad (1)$$

where the point of subjective equality (PSE) is the stimulus level that leads to equal proportions of clockwise and counterclockwise responses and represents an estimate of the direction aftereffect. The JND is an estimate of the participant's threshold for discriminating the direction of motion. Direction aftereffect (DAE) magnitude was calculated by subtracting the PSE estimate for baseline (unadapted) trials from the PSE derived from each adaptation condition.

To quantify the tuning of the DAE as a function of direction for each of the adapting conditions in Experiments 1 and 2, we fit the DAE estimates with a Gaussian derivative of the form

$$DAE = \frac{d}{dx} a e^{\left(\frac{-(x-b)^2}{2c^2}\right)} \quad (2)$$

where x is the adaptor direction (mode or median), and a , b , and c are the amplitude, mean, and standard deviation of the underlying Gaussian, respectively. The best fitting values of b and c were taken as measures of the center of tuning and breadth of the tuning function. However, because the amplitude of the function (i.e., peak DAE magnitude) is not solely dependent on a , we defined amplitude as the maximum DAE obtained

across all adaptor directions for the best-fitting set of parameters; 95% confidence intervals (CIs) were constructed for each summary measure using non-parametric bootstrapping.

To quantify the dependency of the DAE on the number of dots in the adapting direction in Experiment 3, we fit the data with a simplified Naka-Rushton equation (Naka & Rushton, 1966) of the form

$$DAE = \frac{R_{\max} D}{D + D_{50}} \quad (3)$$

where D is the number of dots in the adapting direction, R_{\max} is the maximum saturating DAE, and D_{50} is the amount of adaptor dots required to evoke 50% of R_{\max} . Separate functions were fit for each condition in which the number of dots moving in an opposite or orthogonal direction was added to the adapting stimulus.

Modeling

To model adaptation-induced biases in perceived direction, we employed a population-coding framework in which (a) adaptation selectively alters the responsivity properties of direction-selective neurons and (b) mechanisms tasked with decoding population activity fail to compensate for these changes (Series et al., 2009). Our aim was to find the simplest formulation from this family of models that could simultaneously account for the patterns of DAEs observed across all experimental manipulations.

The population comprised 128 motion-sensitive neurons with direction preferences that were uniformly distributed across all possible directions. Each had a wrapped-Gaussian direction-tuning function; the response of the i th neuron to a dot moving in direction θ was given by

$$f_i(\theta) = \exp\left(-\frac{(\theta - \theta_1)^2}{2\sigma^2}\right) \quad (4)$$

where θ_1 is the neuron's preferred direction, and σ is the standard deviation of the tuning function. For all simulations, σ was fixed at 20° (47.1° full width at half height), which falls within the range of direction-tuning bandwidths previously reported in macaque middle temporal (MT) area (e.g., Albright, 1984). It is worth noting, however, that the findings reported here are not tightly coupled to the number or bandwidth of neurons chosen for the model population.

The mean response of a neuron to a distribution of n dots was obtained by summing the responses to each individual dot and normalizing the result to the summed response across the entire population:

$$R_i = \frac{K_i \sum_{j=1}^n f_i(\theta_j)}{\sum_{i=1}^m \sum_{j=1}^n f_i(\theta_j) + S_i} \quad (5)$$

K_i and S_i determine the peak response and semi-saturation level of the neuron, respectively. The baseline (i.e., nonadapted) values of these parameters were fixed for all neurons so as to produce similar dependencies on the number of dots moving in preferred and antipreferred directions as reported for single unit responses in monkey MT (Snowden, Treue, Ericksen, & Andersen, 1991).

Adaptation was modeled as a simple reduction in response gain, the most robust and commonly reported effect in physiological studies of motion adaptation (e.g., Kohn & Movshon, 2003; Krekelberg, van Wezel, & Albright, 2006; Yang & Lisberger, 2009). The magnitude of the gain reduction was proportional to the time-averaged (i.e., noise-free) response of a given neuron to the adapting stimulus:

$$K_i = K_0 \left(1 - \alpha \frac{R_i}{R_{\max}}\right) \quad (6)$$

where K_0 is the baseline response gain (fixed), and α is a free parameter controlling the maximum reduction in responsiveness. According to this formulation, adaptation produced the largest effect when the response of the neuron to the adapting stimulus R_i was equivalent to its maximum possible response (R_{\max} , defined as the average response to a set of 512 dots moving in the preferred direction). Note, we could have simulated adaptation as a shift in the semisaturation point of the neuron (i.e., increase of S_i), which would have produced comparable results.

For each of the experimental manipulations, we ran a trial-by-trial simulation, substituting the human observer with the model output. Population responses to each unidirectional test stimulus were corrupted by Poisson noise, such that the probability of a neuron producing response r_i given a mean response of R_i was given by

$$p(r_i | R_i) = \frac{R_i^{r_i}}{r_i!} e^{-R_i} \quad (7)$$

We implemented a range of decoders to derive a direction-discrimination decision from the noisy population response, including maximum likelihood, winner takes all, and vector average. However, as all decoders produced highly similar results, only the results for the maximum likelihood approach are shown here. The log-likelihood of each direction of motion θ was computed by

$$\log L(\theta) = \sum_{i=1}^m r_i \log f_i(\theta) \quad (8)$$

where r_i is the noisy response of the i th neuron (see Jazayeri & Movshon, 2006, for a detailed derivation). Binary decisions were determined by comparing the likelihood of directions clockwise ($0^\circ < \theta < 180^\circ$) and counterclockwise ($-180^\circ < \theta < 0^\circ$) of upward. Model psychometric functions were constructed for both adapted and unadapted conditions and analyzed in the same manner as described for the experimental data.

To fit the model to the data, we allowed the adaptation parameter α to vary and minimized the mean square error between the observer-averaged empirical and simulated DAEs across all stimulus manipulations.

Results

Experiment 1: Adaptation to direction variance broadens the tuning of the DAE

For comparison with multidirectional adaptation conditions, we first measured DAE tuning profiles following adaptation to unidirectional motion. Estimates of the DAE were obtained for adapting directions ranging between 0° and $\pm 180^\circ$. The white symbols in Figure 2 plot the magnitude of the DAE as a function of a single adaptor direction for four observers. Similar to previous studies, we observe the largest perceived shifts in motion direction following adaptation to adaptors 20° – 30° (hereafter referred to as the “peak DAE”) away from the test direction (Levinson & Sekuler, 1976; Schrater & Simoncelli, 1998). There was a clear tuning for the adaptor direction, and the DAE gradually declined as the difference between adaptor and test was made greater than 30° with little or no adaptation effects for differences over 120° . Additionally, two observers (DPM & DWM) showed a slight attractive bias for adapting directions greater than 120° (see also Clifford et al., 2000).

To determine the effects of direction variance in the adapting distribution on perceived direction, we measured DAEs in conditions in which adapting dots were normally distributed around a mean direction. Increasing the variance of dot directions led to a marked reduction in peak DAEs, along with smaller decreases in adaptation strength for near-peak adaptor directions (Figure 2, blue & red symbols). These reductions were accompanied by a broadening of DAE tuning profiles, which became more pronounced as adaptor variance was increased. This broadening of the DAE tuning profile is likely due to a broader range of direction-selective neurons responding to the adaptors with high directional variance while, at the same time, these adaptors are less effective at driving those

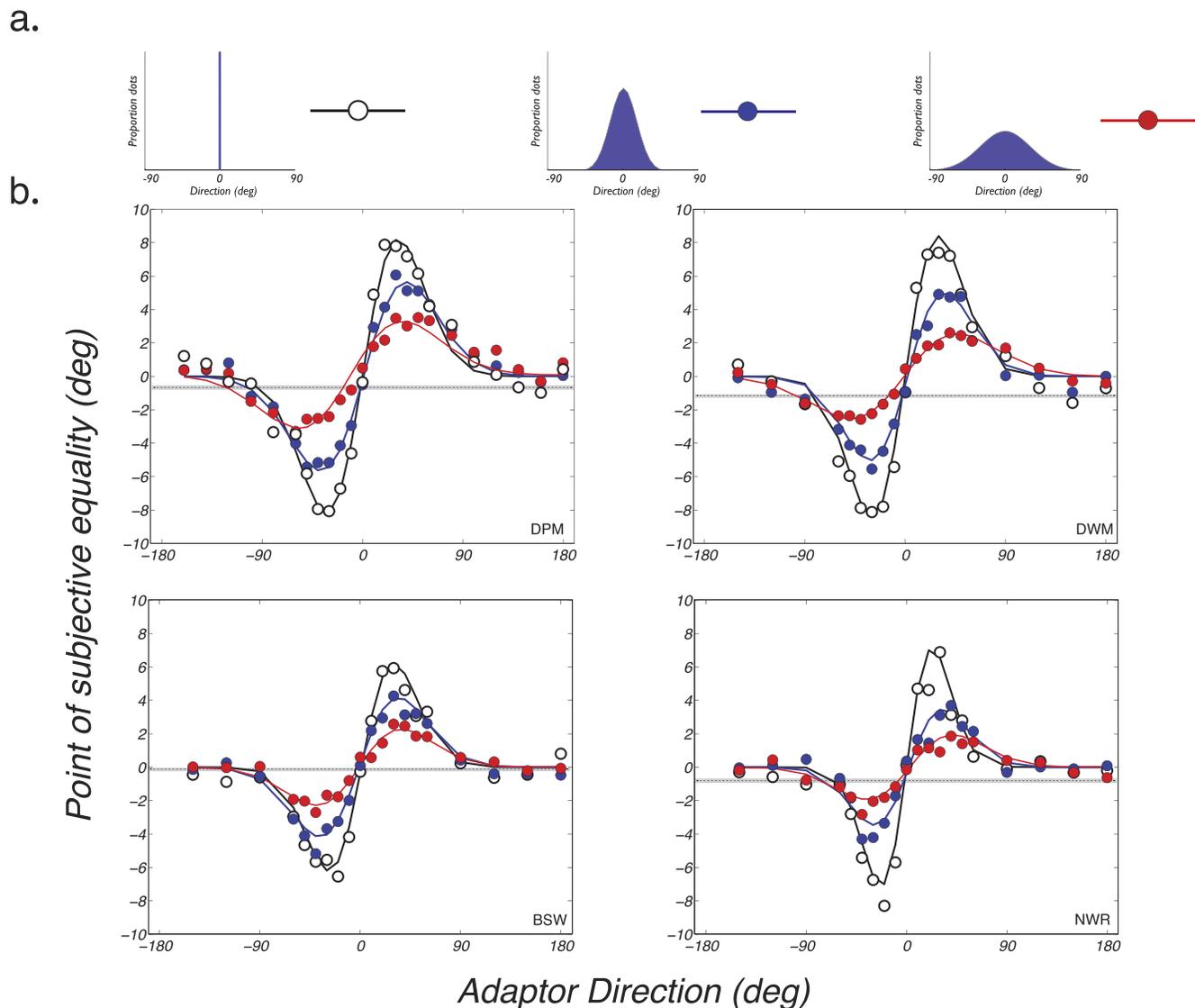


Figure 2. Adaptation to direction variance. (a) Probability distributions from which adaptor directions were drawn in Experiment 1. The mean of the distribution was kept constant across conditions, and direction variance was varied. (b) Increasing the variance of normally distributed directions in the adaptor caused a reduction in the peak DAE as well as a broadening of DAE tuning profiles. Solid lines show best-fitting Gaussian derivative function. Dashed lines and gray shaded area represent unadapted (baseline) PSEs \pm 1 SEM.

neurons selective for directions near the mean of the distribution, leading to smaller peak effects.

To quantify these effects, we fit the data with a first derivative of a Gaussian function as defined in Equation 2. Fitting this function to the data provides us with measures of the peak amplitude, the breadth of the tuning profile, and the overall shift along the x -axis required to fit each individual's data (see Methods). Although increasing the variance of adaptor dot directions was expected to affect both the peak amplitude and standard deviation of the fitted function, the center point of the tuning profile was expected to remain unchanged given the symmetrical nature of the adaptor. Figure 3 summarizes the best-fit parameter

values for the amplitude (Figure 3a), standard deviation (Figure 3b), and center point (Figure 3c) of the Gaussian function for each observer. Relative to the unidirectional condition, all four observers showed a substantial decrease in the amplitude of the function with an approximately fourfold reduction in its peak for the condition with the highest directional variance (Figure 3a). Large increases in the standard deviation of the function were also seen in this condition with three out of four observers demonstrating a 60% broadening in their tuning profile although observer BSW showed a 30% increase (Figure 3b). No systematic changes were observed in the center point of the Gaussian functions (Figure 3c).

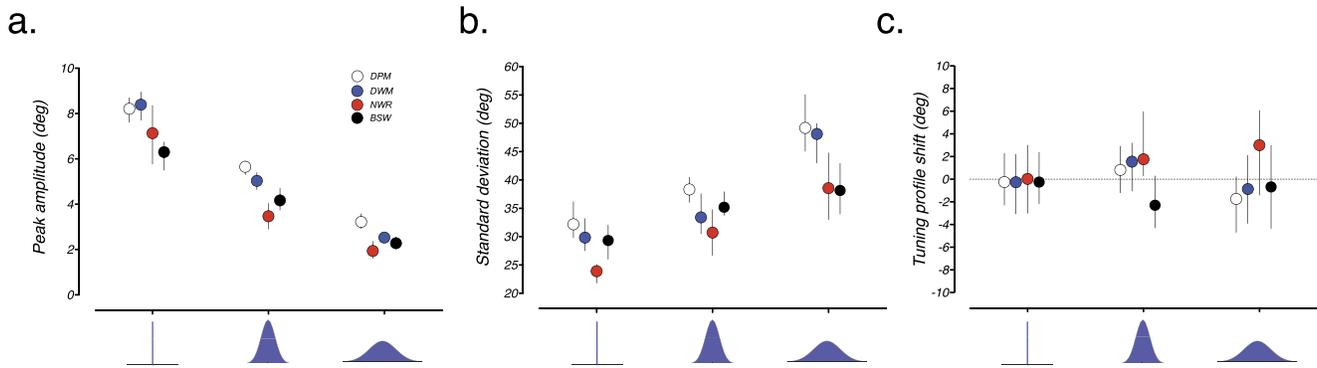


Figure 3. Individual parameter values from Gaussian derivative fits to data from Experiment 1. As the direction variance of the adaptor is increased, the peak amplitude of the DAE tuning function decreases (a), and the standard deviation increases (b). No systematic changes were observed in the center position of the Gaussian function (c). Error bars represent bootstrapped 95% CIs.

Experiment 2: Adaptation to asymmetric distributions of directions shifts the peak DAE

We were also interested in whether adapting to asymmetric directions of motion would shift the adapting direction, leading to the largest misperception of motion to the perceived direction of the stimulus ensemble. This was, in part, motivated by our previous work investigating whether stimulus motion statistics or the stimulus motion readout from a population of directionally tuned neurons provide a better indicator of the perceived direction of a global motion stimulus (Webb et al., 2007; Webb et al., 2011). To test these alternatives, observers had to judge the perceived global direction of a dot field whose local directions were sampled from asymmetric distributions with distinct measures of central tendency. A maximum-likelihood readout of stimulus motion was shown to predict the perceived direction better than any central tendency stimulus direction (Webb et al., 2007). To determine if DAEs correspond to the perceived direction of the adapting motion, we chose two of the most diagnostic distributions from our previous work and used them to generate our adapting directions.

Adaptation to dot motion sampled from a skewed Gaussian distribution (Figure 4a) resulted in a large lateral shift in DAE tuning profiles (Figure 4b). As in Experiment 1, fitting a first derivative of a Gaussian function to the plotted data allowed us to quantify these effects. Figure 5 plots the shift in the position of the peak of the function along the x -axis required to adequately fit the data. There is an average positive shift across all participants of 17.07° , and this figure is consistent with the perceived global direction of the adapting stimulus (Webb et al., 2007). Asymmetric sampling from a rectangular distribution caused a negative shift in the peak DAE for three of the four observers with observer DWM showing no shift in either direction. The average shift of these three

observers is -3.23° , which is again in close correspondence with the perceived direction of the adapting stimulus and the prediction of a maximum-likelihood decoder that reads out from a population of direction-selective neurons (Webb et al., 2007).

Experiment 3: Adaptation to bidirectional motion reduces the magnitude of the DAE

Extracellular recordings in visual area MT show that neurons rapidly increase their firing rate as the density of a random dot pattern moving in the neuron's preferred direction is increased, reaching asymptote at relatively low dot densities (Snowden et al., 1991). However, when dots moving in the antipreferred direction of the neuron are added to the stimulus, a more gradual rise in spiking activity is observed with greater amounts of dots in the antipreferred direction leading to increasingly shallow slopes (Snowden et al., 1991). These changes in neural responses are believed to arise through division-like inhibition between neurons tuned to opposite directions of motion (e.g., Simoncelli & Heeger, 1998). We wondered whether these changes in the response characteristics of visual neurons would be reflected in human perception. Using the DAE, we carried out an analogous psychophysical experiment in which we systematically increased the amount of adaptor dots moving 30° clockwise from upward. In subsequent conditions, we investigated how adding dots in directions opposite or orthogonal to the adapting direction affected the magnitude of the DAE.

Figure 6 plots the magnitude of the DAE as a function of the number of dots in the adapting RDK. In unidirectional conditions, the magnitude of the DAE grew steadily as the number of adaptor dots increased. This effect reached asymptote between 256 and 512 dots for most observers. Adding dots in directions opposite to the adapting motion (Figure 6a) led to a

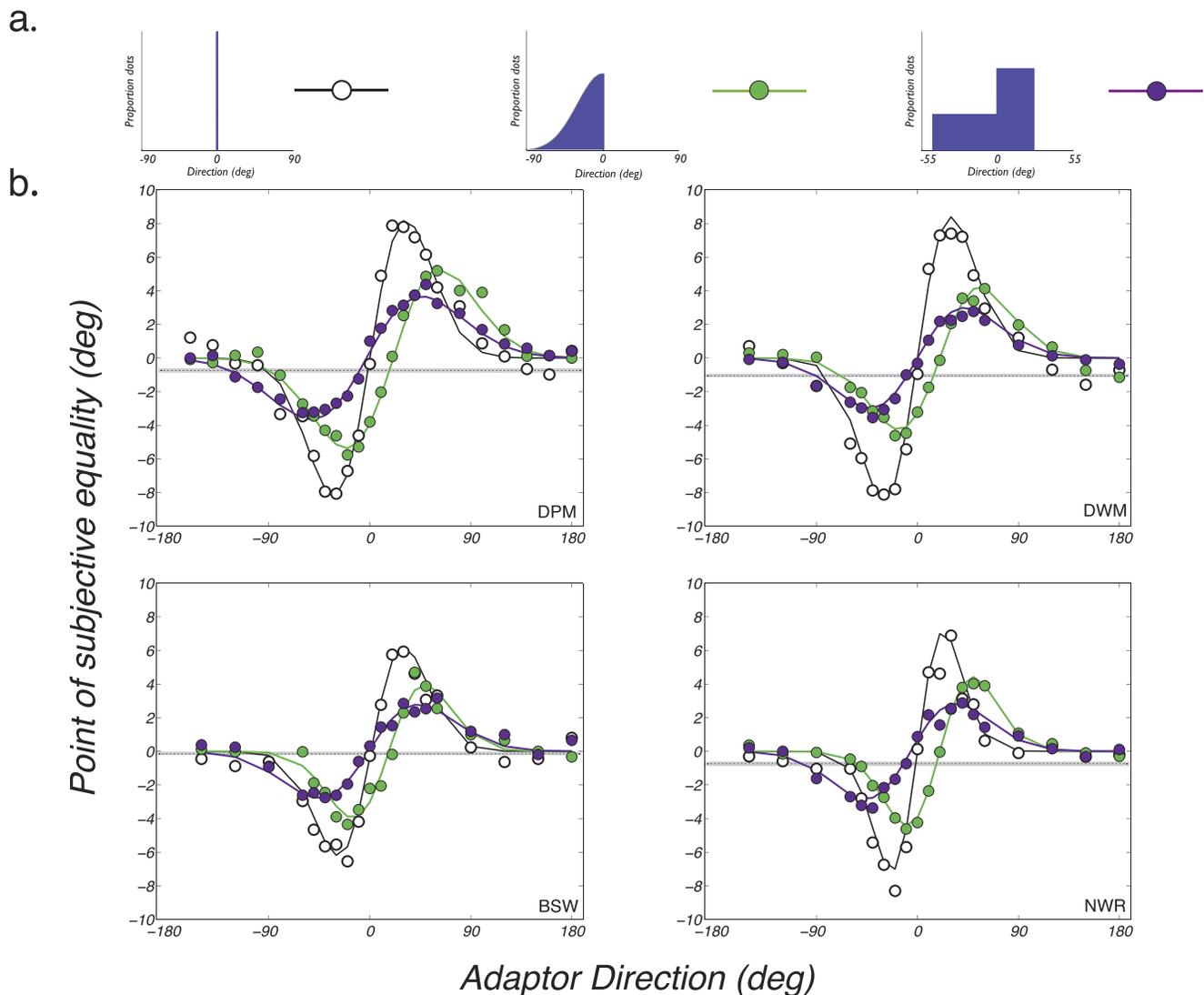


Figure 4. Adaptation to asymmetric distributions of directions. (a) Probability distributions from which adaptor directions were drawn in Experiment 2. (b) Adaptors comprised of asymmetric distributions of directions produced shifts in the DAE tuning profiles. Solid lines show best-fitting Gaussian derivative function. Dashed lines and gray shaded area represent unadapted (baseline) PSEs ± 1 SEM.

pronounced reduction in the DAE, and increasing their number caused further decreases in the size of the adaptation effect. Additionally, the size of the DAE continued to rise beyond the number of adapting dots that led to asymptotic DAEs in unidirectional conditions.

This pattern of results bears a strong resemblance to the physiological findings reported by Snowden et al. (1991), suggesting that the results may be mediated by division-like inhibitory interactions between neurons tuned to opposite directions as suggested by others (Curran & Lynn, 2009; Snowden et al., 1991). Based on our model simulations (see Modeling and below), this normalization process is likely to occur during the integration of motion signals prior to adaptation, affecting the responses of direction-selective neurons.

To test whether this suppression is related to specialized opponency mechanisms or reflects a more general suppressive effect, we repeated the experiment but substituted the opposite direction dots for dots moving in an orthogonal direction to the adaptor. Figure 6b shows that the pattern of results are almost identical to those attained with dots moving in the opposing direction to the adaptor, suggesting that these effects may arise via suppression from a broadly tuned normalization pool (Heeger, 1992).

To quantify the effects of adding antipreferred dots to the adapting stimulus, we fit the data in Figure 6a and b with Equation 3. This equation provides a good description of the effects of adding dots to the adaptor in the opposite and orthogonal directions (R^2 values ranged between 0.88 and 0.99). We have not summa-

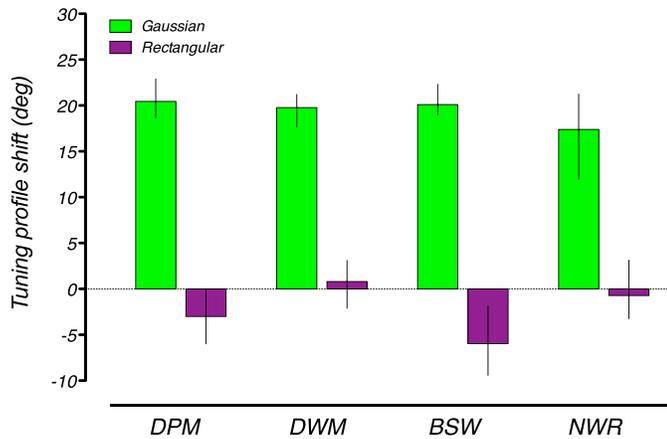


Figure 5. Individual estimates of the lateral shift of DAE tuning profiles in Experiment 2. Adaptation to dot motion sampled from a skewed Gaussian distribution (green bars) led to large positive shifts in DAE tuning profiles. Adaptation to directions sampled from the asymmetric rectangular distribution (purple bars) resulted in smaller negative shifts of the tuning profile for three out of four participants. Error bars represent bootstrapped 95% CIs.

alized the parameter values derived from these fits because in a number of cases (e.g., subject NWR in Figure 6a) they do not saturate, which produces unconstrained and therefore implausible semisaturation constants.

Model simulations

To examine whether aftereffects produced by adaptation to multidirectional stimuli can be accommodated within a population-coding framework, we fit a simple model simultaneously to data obtained in each of our psychophysical experiments. Figure 7 shows the output of the best-fitting model, which provides excellent agreement with the group-averaged data set plotted alongside it ($R^2 = 0.95$, normalized RMS error = 4.2%). The quality of the fit between data and model is notable here for a couple of reasons. First, the implementation of adaptation in the model is the simplest that we could envisage. Adaptation was simulated by a reduction of response gain, the magnitude of which was proportional to the neuron's response to the adapting stimulus. To account for the data, there was no need to build in more subtle adaptation-induced changes to neuronal response properties, such as change in the width of the direction-tuning function (Yang & Lisberger, 2009) or shift in preferred direction (Kohn & Movshon, 2003). Second, the fitting of the model involved a single free parameter (α , see Methods), controlling the maximum proportional gain reduction possible, which was common to all experimental manipulations.

Discussion

Understanding how and why our sensory systems adapt to dynamic environments is a fundamental goal of sensory neuroscience. One theory posits that adaptation acts to adjust the response properties of sensory neurons in an attempt to match the distribution of stimuli found in the environment (Barlow, 1972; Laughlin, 1981). Although physiological studies have provided evidence that sensory neurons might display such efficient coding (see Wark et al., 2007, for a recent review), psychophysical support has been limited as the majority of studies have employed standard adapt-test protocols, in which a single visual attribute is adapted for a prolonged period. Here, we examined how adaptation to different stimulus ensembles, composed of distributions of local directions, affects subsequent motion perception. We have demonstrated three main psychophysical results. First, increasing the variance of dot directions comprising the adaptor caused a decrease in the magnitude of perceived shifts of motion along with a broadening of DAE tuning profiles. Second, asymmetric sampling of Gaussian and rectangular distributions resulted in shifts of DAE tuning profiles consistent with the perceived global direction of the adaptor stimulus. Finally, adding dots moving in opposite or orthogonal directions to the adapting motion led to a pronounced reduction in the magnitude of the DAE. Together, the results demonstrate that adaptation-induced perceptual biases are influenced in a variety of ways by the composition of the adapting stimulus, all of which can be captured within a population-coding framework in which adaptation is modeled as a reduction in neuronal gain. Here we relate our results to previous psychophysical and physiological findings.

Relationship to other studies

In light of the many physiological demonstrations of single cells adapting to the statistics of their environment (e.g., Baccus & Meister, 2002; Fairhall et al., 2001; Smirnakis, Berry, Warland, Bialek, & Meister, 1997), recent psychophysical results suggest that perceptual performance is also modulated by the statistics of recent sensory history (Chopin & Mamassian, 2012; Dahmen et al., 2010; Price & Prescott, 2012). Most relevant to the current study, Price and Prescott (2012) showed that direction discrimination thresholds could be increased or decreased following adaptation to different distributions of directions. Specifically, they showed that adaptation to an “All Flanks” adaptor, composed only of directions $\pm 30^\circ$ and $\pm 60^\circ$ from the category boundary (upward), led to an increase in discrimination thresholds compared to a uniform adapting condition in which all directions had an equal probability of presentation across time (see

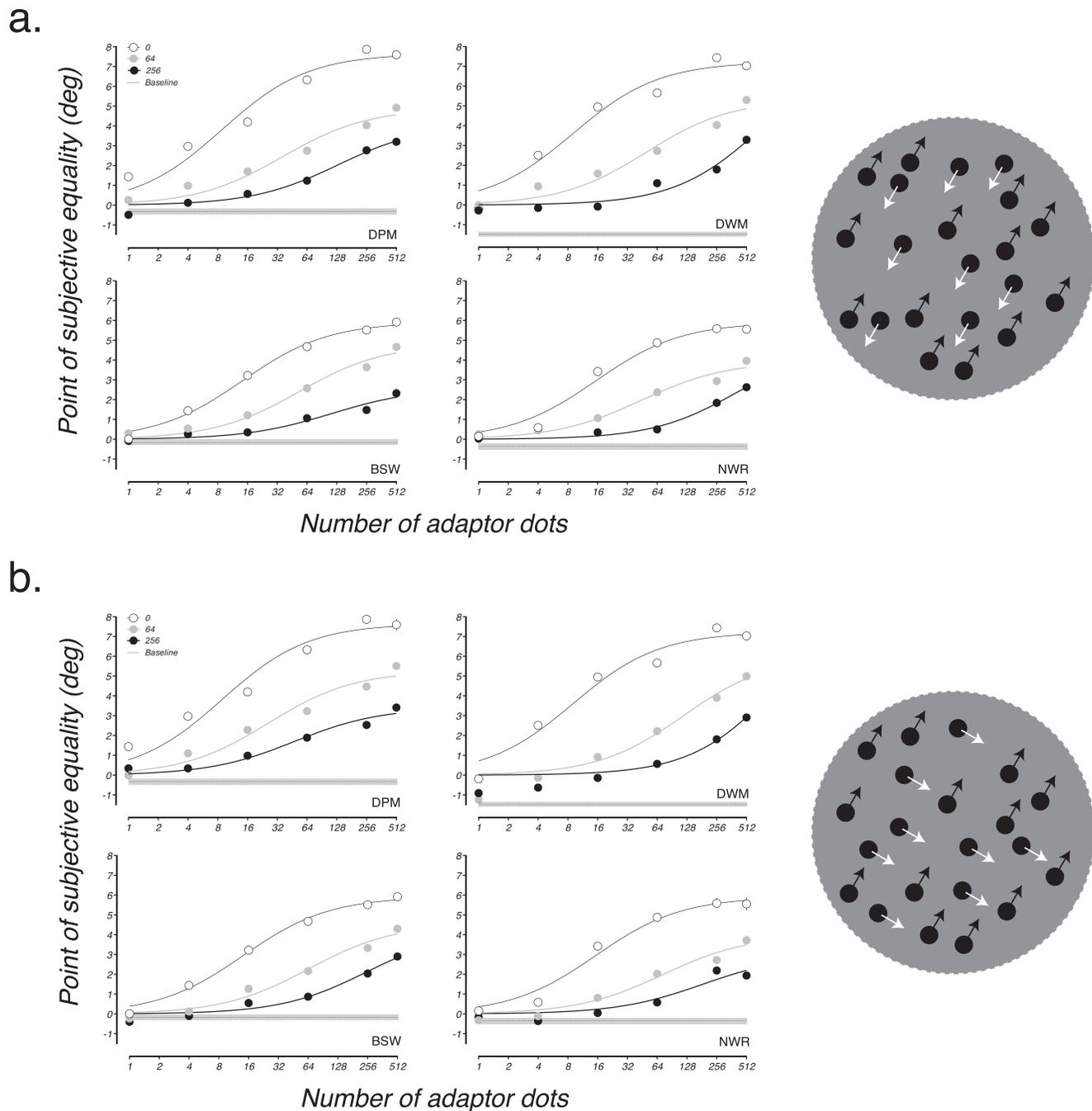


Figure 6. Adaptation to bidirectional motion. (a) Adding dots moving in the opposite direction to the adapting motion (30°) led to smaller adaptation effects along with shallower rises in the DAE as the number of dots in the adapting direction was increased. Increasing the number of dots moving in the opposite direction further decreased the magnitude of adaptation effects. (b) An almost identical pattern of results was observed when dots moving in an orthogonal direction to the adapting motion were added to the stimulus, suggesting the presence of broadly tuned suppression between direction-selective neurons. Dashed lines and gray shaded area represent unadapted (baseline) PSEs ± 1 SEM.

also Hol & Treue, 2001; McGovern, Roach, & Webb, 2012; Regan & Beverley, 1985). Additionally, when participants adapted to all directions other than those between $\pm 30^\circ$ and $\pm 60^\circ$ (“No Flanks” condition), adaptation led to an improvement in direction discrimination compared to either the uniform adapting

condition or the “All Flanks” condition although baseline measurements of direction discrimination were not reported. Similar to the current study, a standard population-coding model was sufficient to account for these changes in discrimination thresholds along with the concomitant changes in perceptual bias.

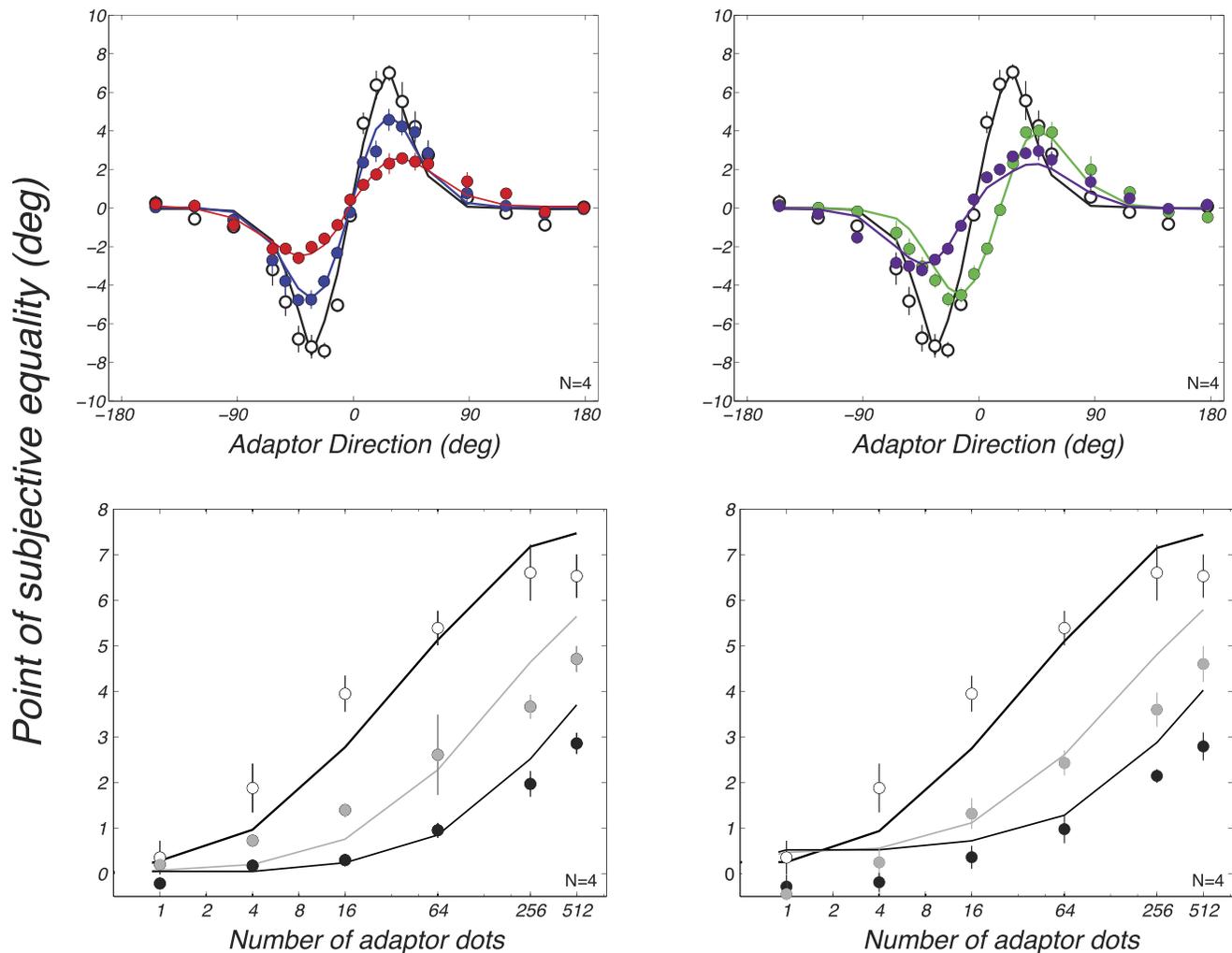


Figure 7. Group-averaged data for all experiments along with the best fitting model to the data. A population-coding model was simultaneously fit to the data from all three experiments (see text for further details). This model provided an excellent approximation of the data ($R^2 = 0.95$). Error bars represent ± 1 SEM between different participants.

In spite of the similarities, a number of differences exist between the two studies. Most notably, Price and Prescott's (2012) study was mainly concerned with how perception is affected following adaptation to dynamic stimuli that evolve across *time* whereas we were interested in how humans adapt to a stimulus in which the local dot directions are varied across *space*. Given that motion is differentially integrated across space and time, understanding the role of both dimensions is important for the development of a unified theory of adaptation. As noted by Price and Prescott, the two approaches are likely to lead to slightly different behavioral and neuronal effects, and each method has its advantages and disadvantages. For instance, whereas the adaptor in the current study allowed us to keep the energy of each direction roughly constant across time, thereby reducing the likelihood of nonuniform adaptation effects, we cannot rule out the influence of interactions between neurons tuned to different direc-

tions and/or spatial locations on our results. We do not view this as a major limitation of the study, however. Physiological studies have demonstrated that suppressive effects produced when nonpreferred stimuli are presented within the classical receptive field (e.g., Kohn & Movshon, 2003; Petersen, Baker, & Allman, 1985) or when stimuli are presented in the surround (e.g., Patterson, Wissig, & Kohn, 2013; Schwartz, Hsu, & Dayan, 2007; Webb, Dhruv, Solomon, Tailby, & Lennie, 2005; Wissig & Kohn, 2012) are themselves subject to the effects of adaptation, and we were interested in observing the psychophysical manifestations of these effects. Indeed, Experiment 3 was conducted to characterize the interplay between suppression and adaptation, and the resulting inclusion of divisive normalization to our model proved fundamental in simulating our psychophysical results. This experiment replicated an earlier study by Curran and Lynn (2009), who showed that adding dots moving in an

opposite direction to adapting motion reduces the magnitude of the DAE. We extended this finding by showing that a similar pattern of results can be seen by adding dots moving in any direction, indicative of broadly tuned suppression between direction-selective neurons (see also Simoncelli & Heeger, 1998).

Another key difference between Price and Prescott's (2012) study and the current one is the difference in adaptation duration. Whereas Price and Prescott had a constant adaptation period of 1.5 s, the current study had an initial adaptation period of 60 s with 5-s "top ups" in subsequent trials. It has long been recognized that the duration of adaptation impacts on the strength and length of perceptual aftereffects (Greenlee, Georgeson, Magnussen, & Harris, 1991; Magnussen & Greenlee, 1985; Magnussen & Johnsen, 1986) and neural responses (Dragoi, Sharma, & Sur, 2000) with longer exposures generally leading to stronger, longer-lasting effects. However, recent findings suggest the existence of multiple timescales of adaptation spanning several orders of magnitude (Baccus & Meister, 2002; Ulanovsky, Las, Farkas, & Nelken, 2004; Wark, Fairhall, & Rieke, 2009) and leading to qualitatively different effects depending on the exposure time of the adapting stimulus (Patterson et al., 2013). This suggests that the two adaptation protocols in question may affect the response properties of neurons in different ways. It is not clear, however, that these differences in neuronal adaptation translate to the perceptual adaptation effects typically reported in psychophysical studies, and a systematic comparison of the DAE conducted with a range of adaptor durations would be required to elucidate this issue.

Bridging the gap between psychophysics and physiology

The current study was, in part, motivated by electrophysiological work, suggesting that neurons in the retina can adapt to the mean (Meister & Berry, 1999), variance (Smirnakis et al., 1997), or other higher-order statistics (Wark et al., 2009) of their visual input. These adjustments to neural responses operate on a short timescale and have been suggested to improve sensory coding by altering the neural dynamic range according to the current environment (e.g., Brenner, Bialek, & de Ruyter van Steveninck, 2000; Dean et al., 2005). An alternative interpretation of these effects is that they arise from more prosaic aspects of neuronal encoding, such as a fixed neuronal threshold or nonlinear gain control, which can produce statistic-dependent neuronal effects (e.g., Bair & Movshon, 2004; Borst et al., 2005; Yu & Lee, 2003).

To better understand the link between the perceptual and neural consequences of adaptation to stimulus

statistics, we examined the perceptual aftereffects following adaptation to stimulus ensembles and whether they could be accommodated within a static population code. For instance, we investigated whether perceptual adaptation effects are driven by a single pooled representation or summary statistic of the adapting stimulus or by the full range of local values comprising the adaptor. Our data from Experiment 1 appear to support the latter interpretation as altering the variance of the adaptor directions while keeping the mean direction constant led to systematic changes in the magnitude of the DAE. This pattern of results would not be expected if a single perceived direction was the sole cause of the repulsive shifts in perception and suggests that the population code preserves the ability to detect changes of variance in stimulus ensembles. On the other hand, adaptation to stimuli with asymmetric compositions led to shifts in DAE tuning profiles consistent with the perceived global direction of the adaptor stimulus, indicating that the global percept of the stimulus also influences adaptation-induced changes in perception. Our model simulations show that both effects naturally emerge from a framework in which adaptation selectively reduces the gain of the direction-selective neurons by an amount that is proportional to their response to the adapting stimulus (see Goddard, Clifford, & Solomon, 2008; Schwartz, Sejnowski, & Dayan, 2009, for similar population coding models of the tilt illusion).

In one of the few studies to investigate adaptation to stimulus statistics using both electrophysiological and psychophysical techniques, Dahmen et al. (2010) examined how auditory spatial processing is influenced by the recent history of sensory input in human observers and anesthetized ferrets. Using interaural level differences, which rapidly changed according to one of six Gaussian distributions, they showed that the perceived laterality of a test stimulus was biased by the mean of the distribution, and increasing the variance of the distribution reduced observers' spatial sensitivity. Importantly, corresponding changes in the neural responses of neurons were observed in the inferior colliculus of ferrets, which could account for these changes in bias and sensitivity. These shifts in perceptual bias following adaptation to distributions with different means are directly analogous to those reported here; in both cases, altering the mean of the adaptor caused repulsive shifts in perception away from the mean of the distribution.

Modeling through reductions in neuronal gain

The most commonly reported effect of adaptation is a reduction in the responsiveness of neurons tuned for the adapting stimulus, and models that depict adapta-

tion as a selective reduction of gain across a population of neurons have had a degree of success in simulating the perceptual consequences of adaptation (e.g., Clifford et al., 2000; Price & Prescott, 2012; Series et al., 2009). However, recent physiological recordings suggest that adaptation can also alter the selectivity of single cells with growing evidence to suggest that adaptation can cause attractive (Ghisovan, Nemri, Shumikhina, & Molotchnikoff, 2009; Kohn & Movshon, 2004; Krekelberg et al., 2006; Wissig & Kohn, 2012) and repulsive (Dragoi, Rivadulla, & Sur, 2001; Dragoi et al., 2000) shifts in neuronal tuning preferences. Indeed, some authors suggest that changes in neuronal tuning are required to accurately simulate the repulsive biases induced by adaptation (Jin et al., 2005) and argue that this additional factor is necessary to predict the magnitude of adaptation-induced biases from the levels of response suppression reported in neurophysiological data. In the current study, however, we were able to simulate the magnitude and tuning of the DAE using empirically reported levels of gain reduction (Yang & Lisberger, 2009). The reason for the discrepancy between the studies is unclear; however, the explanation is likely to reside in two key differences between the adaptation paradigms. First, although the current study focused on the DAE, the study by Jin et al. (2005) attempted to simulate the tuning properties of the tilt aftereffect (Clifford, Pearson, Forte, & Spehar, 2003; Clifford et al., 2000). Although both aftereffects display similar characteristics, differences exist in the size and angular dependence of the effects (see Clifford, 2002, for a review). It is also likely that the adaptation protocols employed in the two studies targeted distinct populations of neurons located in different cortical sites (e.g., Albright, 1984) and that these visual areas exhibit different types of adaptation effect (Kohn & Movshon, 2004), potentially explaining the discrepancy between the results of the two studies. A second key difference between the studies was the adapting stimuli employed in each study. Whereas the data modeled by Jin et al. were collected using a sinusoidal grating adaptor, the current study used random dot stimuli. Physiological studies have reported attractive shifts in the tuning preferences of MT neurons following adaptation to grating stimuli (Kohn & Movshon, 2004), but no systematic tuning changes were reported for random dot pattern adaptors (Yang & Lisberger, 2009). These differences may be due to the fact that, whereas sinusoidal gratings lead to orientation-selective responses in early visual cortex, random dot patterns contain broadband orientation information and are therefore ineffective at driving early motion mechanisms in V1. This information from early stages of processing is likely inherited by MT neurons (Kohn & Movshon, 2003) and could be used to determine the tuning properties of these cells. Irre-

spective of the mechanism, these physiological findings suggest that the DAE generated by random dot stimuli can be explained solely in terms of gain reduction, and this may underpin the differences between our simulations and those of Jin et al.

In summary, we have demonstrated that adaptation to broad and asymmetric distributions of directions and bidirectional motion broadens the tuning, shifts the peak, and reduces the magnitude of the DAE, respectively. A simple population-coding model in which adaptation is simulated as a reduction in response gain can accommodate the range of perceptual biases induced by adaptation to multidirectional motion signals. The challenge for future work will be to establish whether the relationship between changes to perceptual sensitivity and bias induced by sensory adaptation can be accommodated within a population-coding framework. Ongoing work in our laboratory is working on a solution to this challenging computational problem (Roach, McGovern, & Webb, 2013).

Keywords: adaptation, aftereffects, direction of aftereffect, population coding, modeling

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