Complex internal dynamics underlying visual perception of motion

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Abstract
When ambiguous visual stimuli are presented continuously or repeatedly, they often lead to oscillations between (usually) two perceptions. Because of these oscillations, it has been thought that the underlying neural dynamics also arises from a binary or two-state system. Contradicting the binary assumption, it has recently been shown that the perception of families of ambiguous visual stimuli is governed by continuously varying, idiosyncratic biases. These biases differ considerably from one observer to the next, are quite stable even over long intervals, but have fine-scale temporal dynamics at least partly described by random walks (Wexler et al., 2015). Here I study bias patterns in the motion quartet, an ambiguous apparent motion stimulus. Presenting the motion quartet at different orientations results in bias patterns that are robust and idiosyncratic. However, the patterns are even more complex than those that have been described previously (Wexler et al., 2015). There are two qualitatively different extremes: preference for a translation axis, and preference for a rotation direction. The general case is a multidimensional combination of these extreme patterns. When measured repeatedly over 9 hours, the bias patterns usually remain stable, but also sometimes evolve both within dimensions (e.g., change of preferred axis) and across dimensions (change from axial to rotational bias).

1 Introduction
Reversible or bistable stimuli have long attracted attention because, in the absence of external cues that favor a particular interpretation, the dynamics of perceptual choice provides a uniquely sensitive probe of the neural mechanisms of perception (Necker, 1832; Wheatstone, 1838; Rubin, 1921; Wallach, 1935; Attneave, 1971; Leopold & Logothetis, 1999; Blake & Logothetis, 2002; Long & Toppino, 2004; Sterzer, Kleinschmidt & Rees, 2009). Such ambiguous stimuli have been used to study the mechanisms of adaptation, priming, context, history, memory, cue integration, cortical dynamics, to cite some examples. It is often assumed that neural dynamics is isomorphic to overt perceptual dynamics. For example, if the perception of stimulus switches between two interpretations, then the underlying neural representations must also be binary. Here I show that this assumption underestimates the complexity of the underlying brain circuits. By measuring
the population distribution and temporal evolution of the individual observers’ biases in the perception of a well-known twofold-ambiguous stimulus—the motion quartet—I show that the biases reflect complex and multidimensional internal states.

The motion quartet (also called the “bistable quartet” or “stroboscopic alternative motion”) is a two-frame ambiguous motion stimulus, illustrated in Figure 1a (Schiller, 1933; Gengerelli, 1948; Ramachandran & Anstis, 1983b). In the first frame of the usual version of the quartet, two identical objects appear at opposite corners of an imaginary square; in the second frame, the same two objects appear in the other two corners. If the visual system matches each of the objects in the second frame to a single and unique object in the first frame, two apparent motions can be perceived, illustrated in Figures 1b and c. Because the distances in the two solutions are the same, neither the slow-motion prior nor any other perceptual cue can disambiguate the two solutions. The motion quartet has been used to probe contextual and priming effects in motion perception (Ramachandran & Anstis, 1983b; Ramachandran & Anstis, 1983a; Anstis & Ramachandran, 1987), hysteresis and sequence effects (Hock et al., 1993; Maloney et al., 2005), and analogies between visual and tactile motion perception (Carter, Konkle, et al., 2008; Liaci et al., 2016; Haladjian et al., n.d.), as well as to study the neural correlates of visual consciousness (Sterzer & Kleinschmidt, 2007; Zhang et al., 2012) and the effects of neuroanatomy on motion perception (Genç et al., 2011; Shimono et al., 2012).

The subject of interindividual differences in vision has always elicited a certain amount of interest, going back to philosophers’ questions about the subjective appearance of colors (Locke, 1690) and the “personal equation” in astronomy (Bessel, 1823), as well as more recently (Coren & Porac, 1987; Wilmer, 2008; Grzeczkowski et al., 2017), including in the context of multistable stimuli (Kleinschmidt et al., 2012). Nevertheless, most visual psychophysics is carried out with the tacit assumption that the appearance of suprathreshold stimuli is invariant across observers, or that any variations are small and can be ignored. This assumption is probably the reason why the large individual differences in the appearance of The Dress—a photograph that spread on the internet in 2015—impressed not only naïve observers but psychophysicists as well (Witzel et al., 2017).

It has recently become clear that the perception of each observer is shaped by individual biases that can differ greatly from one observer to the next and that can persist over long periods of time (Carter & Cavanagh, 2007; Afraz et al., 2010; Mamassian & Wallace, 2010; Houlsby et al., 2013; Schütz, 2014; Wexler et al., 2015; Schütz & Mamassian, 2016; Goutcher, 2016; Kosovich & Whitney, 2017). For example, with my colleagues I have recently shown that the perception of two families of stimuli are shaped by individual biases that are a preferred 3D surface orientation for one of the families, and a preferred motion direction for the other family (Wexler et al., 2015). In an internet-based, large-sample experiment we showed that the biases differed greatly—in fact, sometimes maximally—from one observer to the next, the two biases were independent from one another within observers, and were quite stable over durations up to one year. However, a longitudinal experiment showed that the biases could undergo small changes (and sometimes large ones, although more rarely) over time, with dynamics that are at least partly described as random walks. We argued that these biases are persistent states of
the brain, whose internal dynamics and interactions with external stimuli must be understood in order to have a complete description of perceptual processes (Wexler et al., 2015).

In the current study I measure individual biases in the perception of the motion quartet. These biases turn out to have novel and interesting properties. In the first of the two experiments described here, I measured the bias patterns for the motion quartet in a relatively large sample (106 subjects). Conventional studies of ambiguous stimuli like the motion quartet tend to concentrate on their bistable aspect and present the exact same stimulus either continuously or repeatedly with intervening blanks. In the current studies, on the other hand, the two-frame sequence was presented only once on each trial, and its overall orientation varied randomly from trial to trial. Not having witnessed spontaneous oscillations from repeated exposure to the same stimulus, many subjects did not realize that the stimuli are ambiguous, judging from their qualitative reports. In the second experiment, I measured the time evolution of the individual bias patterns by repeatedly measuring them (45 times) over a period of 9 hours.

2 Experiment 1: Population sample of bias patterns

This experiment measured bias patterns for the motion quartet in a fairly large sample of subjects ($N = 106$), at one point in time. The quartet was presented once (2 frames) on every trial, with its orientation varying randomly from trial to trial.

2.1 Methods

In order to obtain a large sample, this experiment was performed by subjects inside an internet browser on their own computers outside the laboratory. I used methods developed in an earlier study (Wexler et al., 2015) in order to control stimuli and experimental procedures as much as possible in this unconventional setting (see below for details). Similar results were obtained in a more traditional laboratory setting, including pilot studies for this experiment, as well as in the second experiment presented later in this article.

2.1.1 Stimuli

Stimuli were displayed and responses collected in an internet browser, with the experiment programmed in Javascript and HTML5. Tablets and telephones were not allowed, in order to control monitor orientation. It was possible to measure video frame rate, which was above 30 Hz for all subjects. Subjects were encouraged to make the browser window full-screen or as large as possible, to minimize extraneous stimuli; the browser window filled at least 60% of the monitor’s area in all cases but one (where it filled 47%). Subjects were instructed to sit upright at a comfortable distance from the monitor. For further details, see Wexler et al. (2015).

Stimulus geometry will be given in pixels. It is impossible to translate from pixels to degrees of visual angle, because both pixel size and the distance between subject and
Figure 1: Visual stimuli and representation of responses. (a) The motion quartet stimulus consists of two frames, labeled 1 and 2, each composed of two circles on opposite vertices of an imaginary square. The only parameter that varied from trial to trial was the overall orientation of the figure, angle $\theta$. (b, c) The apparent motion perceived between frames 1 and 2 is ambiguous: it can be seen along one of two axes that differ by 90°. One of the two perceptions happens to be globally clockwise (CW, b) and the other counterclockwise (CCW, c). (d, e) The subject’s task was to indicate perceived motion direction by selecting one of two icons, (b) or (c). The response will be represented as two opposite-facing arrows (because of the 180° symmetry), colored red if the subject reported CW motion, and green for CCW motion. Each of the gray arrows represents a stimulus orientation that was shown (in random order), so each will be colored red or green in accordance with the response given.

The main stimulus consisted of two frames, each containing two disks lying on the opposite corners of an imaginary square (labeled 1 and 2 in Figure 1a). The disks had radii of 20 pixels, and were drawn in black on a medium gray background. They were drawn so that their centers were at a distance of 150 pixels from the center of the imaginary square to its corners) is about 3.3° of visual angle.

The entire figure (the imaginary square) was oriented at one of 24 angles: 3.75°, 11.25°, 18.75°, ..., 176.25°. (The orientations were between 0 and 180° because adding 180° to the stimulus orientation leaves the stimulus unchanged.) In addition to the disks, a white
cross (30 pixels wide) was displayed in the center of the window, which the subject was
instructed to fixate. The fixation cross was displayed alone for 750 ms, followed by the first
frame with the fixation cross for 500 ms, immediately followed by the second frame and
cross for 500 ms. Two icons showing the CW and CCW percepts (similar to Figures 1b,c)
were then displayed on the right and left sides of the window (chosen randomly), each
at a distance of 200 pixels from the window’s horizontal center. The subject selected and
clicked on icon corresponding to his or her perceived motion, using the computer mouse.

2.1.2 Procedure

The main experimental block consisted of 48 trials, composed of two sub-blocks of 24 trials,
in which the stimuli were presented in each of the 24 angles, in random order (different
random order for every subject). The order of the stimuli was identical in the two sub-
blocks, in order to measure subjects’ consistency. Prior to the main experimental block,
subjects were given written instructions, and performed 20 practice trials, similar to the
trials in the main block but excluded from data analysis. Trials followed one another
without pause, with breaks every 16 trials. The main experimental block had a median
duration of 2.6 min.

2.1.3 Subjects

106 subjects took part in the experiment (40 men and 66 women, ages 18-66, median
27). Prior to taking part in the current experiment, these subjects had participated in
a separate internet-based longitudinal study on the evolution of individual biases in the
perception of ambiguous visual stimuli (Exp. 3 in Wexler et al., 2015). The stimuli used
in the prior longitudinal study were different from those used here. The subjects had
been originally recruited through an announcement to a mailing list of several thousand
people willing to participate in cognitive science experiments (organized by the Relais
d’information sur les sciences de la cognition (RISC), Paris, France). The current exper-
iment was carried out as the final session of the prior longitudinal study. Subjects were
paid 1€ for their participation in this session. Informed consent was obtained prior to
the experiment in accordance with the Declaration of Helsinki. In France, the legal ethics
committees do not examine non-invasive behavioral studies.

2.2 Results

The results of 12 representative subjects are shown in Figure 2, using the graphical repre-
sentation explained in Figures 1d and e. For clarity, only the data from the first sub-block
are shown. The full data, of all 106 subjects and both sub-blocks, are shown in Figure A1
in the Appendix.

A simple hypothesis is that the perceptual decision on each trial is a stochastic choice,
with 50% chance of responding CW and 50% CCW, independent of all other trials. If
so, the response patterns should resemble random, isotropic mixtures of red and green
arrows (because stimulus orientations were presented in random order). This is visibly
Figure 2: The results of 12 representative subjects in Experiment 1. The data is represented using the graphical representation explained in Figures 1d and e. Each trial is shown as two opposite-facing arrows, corresponding to the orientation of the quartet stimulus. The arrows are colored red if clockwise motion was reported, green if counterclockwise. For clarity, only the data from the first sub-block are shown. Subjects are ordered so that those with axial biases appear in the beginning, and those with rotational biases at the end. For subjects who have a significant axial bias, the preferred axis is shown in black. The full data, of all 106 subjects and both sub-blocks, are shown in Figure A1 in the Appendix.

not the case for a majority of subjects (as can be seen in Figures 2 and A1), whose data show large-scale spatial patterns.

The randomness of the response patterns was tested using a procedure based on the number of boundaries between CW and CCW responses. If one considers \( n = 48 \) independent binary variables on a circle (with equal probability of CW and CCW values), the number of boundaries \( b \) between CW and CCW regions follows a binomial distribution

\[
P(b, n) = \frac{n!}{[2^{n-1}b!(n-b)!]},
\]

which was taken as the null hypothesis. The large-scale spatial structure of many of the response patterns, with large homogeneous regions, results in an improbably small number of boundaries, as in the Wald-Wolfowitz runs test (1940). The Benjamini-Hochberg correction (1995) was applied to take into account multiple tests, with false-discovery ratio set to 0.05. Using this procedure, I found that 71% of the subjects had response patterns that differed significantly from random and independent choices of CW or CCW at each orientation.

In fact, as can be seen in Figures 2 and A1, most subjects’ response patterns seem to cluster around two distinct types. In one pattern, many subjects’ responses show four alternating CW/CCW regions of about equal size (i.e., 90°). Subjects presenting this pattern are shown at the beginning of Figures 2 and A1. This pattern is indicative of an axial bias, or a preference for translation, in either direction, closest to a particular axis. This is illustrated in Figure 3. The overall orientation of the four-region pattern determines the preferred axis, as shown in Figures 3a and b.

A second, qualitatively different pattern can be seen in subjects at the end of Figures 2 and A1: all or nearly all responses being either CW or CCW. This kind of pattern will
be called a rotational bias, a preference for motion compatible with either clockwise or counterclockwise rotation.

When individual data was tested for the two bias patterns, sizable fractions of the subject pool showed statistically significant biases of one or the other type: 41% of the subjects had a significant axial bias, while 45% had a significant rotational bias (with corrections for multiple tests using a Benjamini-Hochberg procedure with a false-discovery rate of 0.05). The axial bias was tested as follows: for each trial, I took one of the two reported translation directions, and multiplied the angle by 2 (the standard way of handling axial data), and applied the Rayleigh test Mardia & Jupp, 1999. The orientation of the preferred axis (the black arrows in Figures 2 and A1 was calculated by multiplying the angle of the perceived axis vector by 2, taking a circular mean, and diving the resulting angle by 2. Rotational bias was tested using a sign test on the raw response data.

Individual biases are represented in Figure 4 as points in a 3D space. The first two dimensions are the cartesian components of the preferred axis vector, whose direction is the orientation of the preferred translation axis, and whose length is the strength of the axial bias. (Since axial bias is bi-directional, each subject is represented by two opposite points in the first two dimensions.) The third dimension is the rotational bias, calculated by taking the mean of each subject’s raw responses, with +1 corresponding to CW and −1 to CCW. The subjects with a significant axial bias are colored blue in Figure 4a, and those having a significant rotational bias colored yellow.

Interestingly, there were 3 subjects who had statistically significant biases of both the axial and the rotational types (colored red in Figure 4). This result is important because
Figure 4: Individual biases in Experiment 1. (a) A 3D representation of the biases. Each point represents one subject. The first two dimensions are the $x$ and $y$ components of the axial bias, and the third dimension the rotational bias. The color of the points reflects the results of statistical tests of the two bias types. (b) The distribution of axis directions for subjects with a statistically significant axial bias. Each subject’s axis is represented by two marks on opposite sides of the yellow circle. The curve is the probability density function of axis directions, obtained by smoothing the directions using a semicircular kernel with width $15^\circ$. (c) The distribution of rotational biases for subjects with significant rotational bias. This quantity runs from $-1$ (corresponding to all responses CCW) to $+1$ (all CW).
it shows that the two bias types are not mutually exclusive. Rather, individual biases are properly seen as a multidimensional combinations of the two underlying bias types. Although only a small fraction of subjects had significant axial and rotational biases, many more appear to have combinations of the two bias types (Figure A1), and would have likely been significant in an experiment with a larger volume of data (more than 48 trials).

In the subjects with significantly axial patterns, the distribution of axial directions was highly non-uniform (see Figure 4b), with peaks in the cardinal directions (88% of the subjects had axis directions closer to the cardinals than to the main diagonals, significantly above 50% by bootstrap), and with a higher peak in the vertical than in the horizontal direction (63% of the axes closer to vertical than horizontal, significantly above 50% by bootstrap). Of the subjects with a significant rotational pattern of responses, a majority (73%, significantly above 50% by bootstrap) had a bias in the CW direction (Figure 4c).

2.3 Discussion

The results of this experiment have shown that when the motion quartet is presented at different orientations on successive trials, perceptual decisions about the direction of motion depend on large-scale bias patterns. The bias patterns seem to be multi-dimensional combinations of two extreme types. The first type is axial bias, favoring translation, in either direction, along a given axis (which can vary between 0° and 180°). The second type of bias pattern is rotational, favoring motion that is globally clockwise or counterclockwise. Quite a few subjects have bias patterns that are pure or almost pure axial, or rotational. Other subjects have patterns that seem like combinations of axial and rotational, with several subjects having statistically significant biases of both types.

If a subject has an axial bias with a vertical axis, or an axial bias with a horizontal axis, or a clockwise rotational bias, or a counterclockwise one, or some combination of axial and rotational biases—is this a permanent condition? In our previous work on individual perceptual biases, it has been shown that such biases are on the whole stable, but also sometimes change, either continuously or discontinuously (Wexler et al., 2015). In our previous study, we probed the temporal evolution of the individual biases with daily measurements over a period of several months. In the second experiment in the current study, I measured changes over time in the bias pattern for the motion quartet, testing each subject 45 times over a period of 9 hours.

3 Experiment 2: Temporal evolution of individual biases

In this experiment I directly tested the stability of the individual bias patterns, by measuring them every 12 minutes over a period of 9 hours, for a total of 45 measurements in every subject. One possibility is that the bias patterns are stable, at least over this duration. A second possibility is that the bias type—axial or rotational—remains stable, but with the axis or direction of rotation changing over time. Finally, it is possible that bi-
ases vary over their parameter space (such as Figure 4a), which would additionally allow changes from axial to rotational biases, or vice versa.

There is a possible criticism of the conclusion from Experiment 1 that the individual differences in the bias patterns are somehow intrinsic to the subject: the variety of individual response patterns (e.g., Figure 2) could have been due to the different order of trials for every subject. For example, perhaps the first few orientations seen by each subjects somehow fixed the subject’s subsequent response pattern. If so, one should find much less interindividual variation if the trials were in the same order for all subjects. This was tested in Experiment 2, in which trials were always in one and the same (but ‘random’) order for all subjects, and for all blocks for every subject.

3.1 Methods

In contrast to Experiment 1, this experiment was performed in the laboratory.

The stimulus was very similar to that in Experiment 1. On every block a single repetition of the same 24 orientations as in Experiment 1 was tested. The orientations were presented in random order, but in the same random order on every block, for every subject. (This was done in order to test whether the variety of individual response patterns found in Experiment 1 could have been due to the different order of trials for every subject.)

Stimulus disks were presented with their centers at 2 degrees of visual angle (dva) from the center of the monitor. Each disk had radius of 0.25 dva. Subjects were instructed to fixate a red disk drawn at the center of the monitor (radius 0.1 dva). On each trial the fixation disk was presented alone for 500 ms, followed each of the two frames (with the fixation disk) presented for 400 ms, followed by the response icons, as in Experiment 1. Stimuli were presented on a Sony GDM F520 monitor at an approximate distance of 57.3 from the subject, whose head was restrained with a chinrest during the experimental blocks. The experiment was performed in an experimental room with normal indoor lighting.

Blocks began every 12 minutes. The median duration of one block was about 54 s, so subjects had a break of about 11 minutes between blocks. During these breaks they were free to do what they wished, for example to read, study, listen to music, eat, and so on; they could also leave the experimental room, for example to use the restroom or smoke. 30 s before the start of each block, the computer emitted a series of beeps and flashes to warn the subject to put his or her head into the chinrest, and that the block was about to begin. Before the start of the series of 45 blocks, subjects performed a practice block, identical to the experimental blocks. Six subjects took part in the experiment (ages 23 to 37, median 28, 4 women and 2 men), and were paid 10€/hour.

3.2 Results

The complete time series of the bias patterns of all six subjects are shown in Figure A2, in the Appendix. The first thing to note about these data is that, clearly, the samples are not independent of one another; in most cases, the shape of the bias pattern is retained from one measurement to the next. Two statistical tests demonstrate this retention or
The behavior of the time series was analyzed in a different way, by calculating mean response ($+1 = \text{CW}$, $-1 = \text{CCW}$) for each session, and analyzing the time series of the means using the autoregressive integrated moving-average (ARIMA) framework (Box & Jenkins, 2008). The analysis, using the forecast package in R (Hyndman & Khandakar, 2008), automatically identified the best model by searching through ARIMA($p,d,q$) mod-
els with $p, d, q \in (0, 1)$. The search was performed by applying the KPSS unit-root test (Kwiatkowski et al., 1992) to determine the differencing order ($d$), and then searching the $p, q$ subspace for the model that best fits the series, subject to penalties from the Akaike information criterion (Hyndman & Khandakar, 2008). The same analysis was carried out on the 3-month time series by Wexler et al. (2015).

The most common time series model found was ARIMA(0, 1, 1), identified by the automatic method for three subjects as the best model. This model is equivalent to an underlying random-walk or Brownian-noise variable, observed through independent measurement noise (Box & Jenkins, 2008; Wexler et al., 2015). The time series of two other subjects were fitted by ARIMA(1, 1, 0) and ARIMA(1, 0, 0) models, while the final subject—the same one who had no significant autocorrelations—was fitted with a white-noise ARIMA(0, 0, 0) model.

### 3.3 Discussion

By repeatedly measuring bias patterns to obtain time series of significant length, the results of this experiment showed that the bias patterns at successive samples (separated by 12 minutes) were not independent, but generally remain stable over time. However, there were significant changes, both within bias types (changes in preferred axis for axial biases, and in preferred rotation direction for rotational biases), and between bias types (an axial bias that became a nearly complete rotational bias).

A time-series analysis of mean responses, averaged over stimulus orientation, revealed that the time series of a plurality of our subjects were best described by one particular model, a random walk measured through noise. The same result was obtained by Wexler et al. (2015) on different measures coming from biases pertaining to different stimuli (biases for surface orientation in structure-from-motion stimuli, and biases for motion direction in transparency-from-motion stimuli). This model, as well as the other time-series results, fit in with a picture that the individual biases are reflections (through noisy measurements) of persistent brain states. These brain states evolve, either through exposure to external stimuli or through internal neural dynamics, and their evolution can at least partly be described as a random walk.

It should be noted that, although in this experiment trials were always in the same order for all subjects and all blocks (in contrast to Experiment 1), there was wide variability, both between and within subjects (Figure A2). Thus, variation in response patterns is due to variable and evolving states of the visual system, rather than different order of stimuli in Experiment 1. Nor could the between-subject variability in Experiment 1 been (all) due to differences in experimental conditions in that internet-based experiment, as the data in Experiment 2—performed in controlled laboratory conditions—also shows a great deal of between-subject variability.
4 General discussion

The results of this study show that complex structures underlie the perception of the motion quartet. When a two-frame quartet is shown at orientations that vary from trial to trial, responses as a function of orientation are organized around two distinctive types of pattern in most subjects. One of the patterns consists of four clockwise/counterclockwise lobes of about 90°, which corresponds to a bias for translation (in either direction) along a preferred axis, whose orientation depends on the orientation of the pattern. In subjects who have this pattern the distribution of preferred axes has peaks in the cardinal directions, with the vertical direction more common than the horizontal. The other pattern is a prevalence of uniformly clockwise or counterclockwise responses, a bias for rotation in one of these directions. In subjects with rotational bias, clockwise preference is more common than counterclockwise.

The two bias patterns are actually extremes in a continuum. Although many subjects have the extreme patterns, others have combinations of axial and rotational biases. Thus, individual biases patterns are actually points in a multidimensional space, with several subjects having biases that have significant contributions of both bias types.

A second experiment, using repeated measurements over nine hours, showed that biases are usually stable over time, but also sometimes undergo significant change. I have found cases where an axial bias changes preferred axis, and a rotational bias changes preferred direction. In at least one case, an axial bias became almost completely rotational.

Certain findings presented here agree with earlier observations on the motion quartet, but place these earlier observations in a broader context. It has long been known that, when the quartet is in its usual upright orientation, perception of vertical motion is more common than that of horizontal motion (Gengerelli, 1948), with this difference attributed to the difference between intra- and inter-hemispheric connections (Genç et al., 2011; Shimono et al., 2012). This discrete fact can now be seen as part of a larger picture: observers who have an axial bias have a preferred axis with a population distribution estimated by Figure 4b. This distribution has a larger peak centered on vertical than horizontal orientations, but, interestingly, oblique preferred axes also occur. The changes in bias patterns over time cast doubt on a purely anatomical explanation of vertical preference, but brain anatomy may play a role in the vertical-horizontal asymmetry in the population distribution of preferred axes.

Another observation that enlarges previously known facts is that, when the quartet is shown over several cycles, some observers perceive a rotation in a consistent direction (clockwise or counterclockwise), rather that back-and-forth translation along a particular axis (Ramachandran & Anstis, 1983b). Once again, this can be seen in the context of the current findings, as likely to arise in subjects having rotational (rather than axial) bias. Interestingly, the consistent rotation percept is reported as disappearing above a certain temporal frequency (Ramachandran & Anstis, 1983b), which may indicate that individual bias patterns depend on temporal frequency—a possibility not tested here.

Adding to our previous results on individual biases (Wexler et al., 2015), the current study demonstrates an additional family of stimuli governed by robust-but-evolving bi-
ases with large individual differences. However, the biases governing the motion quartet are more complex than the SFM and TFM biases reported by Wexler et al. (2015), which were shown to exist in a two-dimensional parameter space (i.e., a large part of between-and within-subject variability can be described by two parameters). Here I have shown that the motion quartet biases exist in a three-dimensional space, but their actual dimensionality may be even higher. For example, if it is found the bias patterns depend idiosyncratically on temporal frequency (as is likely—see previous paragraph), position in the visual field, stimulus size, or other stimulus parameters, the dimensionality of the biases will be shown to be higher than three. Other studies of idiosyncratic biases may have also demonstrated high-dimensional idiosyncratic biases (Carter & Cavanagh, 2007; Afraz et al., 2010; Houlsby et al., 2013; Kosovicheva & Whitney, 2017), but precise estimation of dimension is difficult. The question is important because the biases are actually brain states that can be measured psychophysically, that govern perception of families of stimuli, and that evolve in response to stimuli or autonomously. Understanding the spaces in which they evolve and the laws governing this evolution is crucial to complete description of perception.

5 Acknowledgments

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Figure A1: Data of all 106 subjects in Experiment 1, with each rectangle corresponding to one subject. Data from each of the two identical sub-sessions are shown separately. The border color of the rectangle reflects the results of statistical tests of the two bias types (blue: significant axial bias, orange: significant rotational bias, red: significant axial and rotational biases, black: neither significant). Subjects are ordered so that those with axial biases appear in the beginning, and those with rotational biases at the end.
Figure A2: Full times series of all six subjects in Experiment 2. The 45 measurements for each subject (in the temporal order shown by numerals for the first subject) were over a period of 9 hours, and were taken at 12-minute intervals.
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