Dynamics of spatial distortions reveal multiple timescales of motion adaptation

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Abstract

Prolonged exposure to consistent visual motion can significantly alter the perceived direction and speed of subsequently viewed objects. These perceptual aftereffects have provided invaluable tools with which to study the mechanisms of motion adaptation and draw inferences about the properties of underlying neural populations. Behavioural studies of the time-course of motion aftereffects typically reveal a gradual process of adaptation spanning a period of multiple seconds. In contrast, neurophysiological studies have documented multiple motion adaptation effects operating over similar, or substantially faster (i.e. sub-second) timescales. Here, we investigated motion adaptation by measuring time-dependent changes in the ability of moving stimuli to distort the perceived position of briefly presented static objects. The temporal dynamics of these motion-induced spatial distortions reveal the operation of two dissociable mechanisms of motion adaptation with differing properties. The first is rapid (sub-second), acts to limit the distortions induced by continuing motion, but is not sufficient to produce an aftereffect once the motion signal disappears. The second gradually accumulates over a period of seconds, does not modulate the size of distortions produced by continuing motion and produces repulsive aftereffects after motion offset. These results provide new psychophysical evidence for the operation of multiple mechanisms of motion adaptation operating over distinct timescales.
INTRODUCTION

The analysis of visual motion information is strongly influenced by recent sensory input. Changes in neural processing following exposure to an unchanging motion signal are manifest in the firing rates of individual motion-selective cells in visual cortex, motion visual evoked potentials and blood-oxygen-level dependent (BOLD) responses to subsequent moving stimuli (for recent reviews see Kohn, 2007; Heinrich, 2007; Krekelberg, Boynton & van Wezel, 2006). This form of short-term experience-dependent plasticity is termed adaptation, and is thought to play a vital role in optimizing efficient coding of motion information over time (e.g. Barlow & Foldiak, 1989; Wainwright, 1999; Clifford, Wenderoth & Spehar, 2000). The perceptual consequences of motion adaptation have been extensively studied via the array of striking aftereffects that result from extended exposure to motion in a given direction. The best known of these is the classic motion aftereffect, whereby subsequently viewed stationary scenes are perceived to drift in the opposite direction to the adapting motion (see Mather, Verstraten & Anstis, 1998). Motion adaptation also results in biases in perceived direction (Levinson & Sekuler, 1976), speed (Wohlgemuth, 1911; Goldstein, 1957) and position (Snowden, 1998), as well as direction-specific elevations in contrast detection thresholds (Sekuler & Ganz, 1963).

A number of previous studies have used perceptual aftereffects to investigate the temporal dynamics of visual motion adaptation (e.g. Sekuler, 1975; Keck & Pentz, 1977; Hershenson, 1989; Clifford & Langley, 1996; Hoffmann, Dorn & Bach, 1999; Bex, Bedingham & Hammett, 1999; Hammett, Thompson & Bedingham, 2000). Invariably, the magnitude of these effects is found to increase as a function of adaptation duration, yielding adaptation
time constants in the order of 3-15 seconds when fitted with an exponential function. Likewise, systematic lengthening of the interval between adapting and test stimuli reveals recovery from adaptation over a broadly similar time scale. The effect of these manipulations is quantitative – altering the strength, but not the nature of the aftereffects induced. Accordingly, formal models of motion-induced aftereffects typically employ a general mechanism (e.g. motion detector gain-control) that is subject to some form of leaky-integrator dynamics (e.g. Clifford & Langley, 1996; van de Grind, Lankheet & Tao, 2003; van de Grind, van der Smagt & Verstraten, 2004).

In contrast to the data emerging from psychophysical studies, physiological evidence from the macaque middle temporal cortical area (MT) suggests that multiple distinct motion adaptation mechanisms may be operating over different time scales. Several studies have demonstrated that a prolonged period of adaptation (i.e. several seconds or more) in the preferred direction of a MT neuron reduces its firing rate to subsequent stimuli (van Wezel & Britten, 2002; Kohn & Movshon, 2003, Krekelberg, van Wezel & Albright, 2006). These gradual changes are specific to the adapted sub-region of the receptive field, suggesting they are inherited from changes implemented earlier in the visual pathway, such as primary visual cortex (Kohn & Movshon, 2003). Adaptation and recovery time constants estimated from adaptation effects in cat primary visual cortex (e.g. Vautin & Berkley, 1977; Giaschi, Douglas, Marline & Cynader, 1993) are similar to those found with behavioral aftereffect measurements, supporting the presumed causal link between these neural changes and the perceptual aftereffect phenomena. In addition to these gradual changes, a more rapid form of adaptation in MT has also been reported. Following a step change in image speed, many MT neurons display an initial transient peak in firing rate that decays to a sustained level within
tens of milliseconds (Lisberger & Movshon, 1999; Priebe, Churchland & Lisberger, 2002; Priebe & Lisberger, 2002; Perge, Borghuis, Bours, Lankheet & van Wezel, 2004). In contrast to the effects of more prolonged adaptation, this reduction in responsiveness is maintained when stimuli are moved to different sub-regions of the receptive field, indicating that it either reflects mechanisms intrinsic to MT, or else is mediated by feedback from higher levels of the cortical hierarchy (Priebe et al., 2002).

At present it is unknown what perceptual consequences, if any, this form of rapid motion adaptation might have. Traditional aftereffect paradigms, that require observers to make judgements about test stimuli presented after a period of adaptation, are not well suited to assessing processing changes occurring over such brief timescales. Here we take a new approach to this issue. Rather than measuring motion perception directly, we investigate the influence that moving objects exert on the appearance of other stimuli. In particular, we exploit the fact that motion signals can markedly distort the perceived position of nearby objects (see Whitney, 2002 for a review). As illustrated in Figure 1a, when two spatially aligned static stimuli are briefly flashed adjacent to oppositely moving gratings, they appear to be offset in the direction of motion (Whitney & Cavanagh, 2000; Durant & Johnston, 2004; Eagleman & Sejnowski, 2007). By carefully manipulating the relative timing of moving and static objects, we show that the magnitude of this positional distortion decays rapidly after the onset of motion, in a manner comparable to the transient-sustained response profile generated by short-term motion adaptation in MT neurons. The same stimulus configuration can also be used to elicit an aftereffect: if the static objects appear some time after the offset of an extended period of motion, they are typically perceived to be misaligned in the direction opposite to the inducing motion (Snowden, 1998; McGraw, Whitaker, Skillen...
& Chung, 2002; Whitney & Cavanagh, 2002; see also Nishida & Johnston, 1999). We further demonstrate that by varying motion duration, the initial rapid decay of motion influence can be dissociated from such aftereffects, providing behavioural evidence for the operation of distinct mechanisms of motion adaptation operating over different timescales.

METHODS

Observers

Three observers participated in each of the experiments: the two authors and one inexperienced psychophysical observer (MK) who was naïve to the specific aims and hypotheses. All observers had normal or corrected-to-normal visual acuity and viewed the display binocularly.

Stimuli and general procedure.

Visual stimuli were computed within MATLAB and displayed by a Cambridge Research Systems ViSaGe on a Mitsubishi DiamondPro 2045U monitor (framerate 100Hz, 1024 x 768 pixel resolution where one pixel subtends 2 arcmin, mean luminance 47 cd/m², calibrated using a Photo Research PR-650 Spectrascan Colorimeter). The basic task configuration is illustrated in Figure 1a. Observers were required to judge the vertical alignment of two 1-D Gaussian target stimuli (width 1 deg., \( \sigma_{\text{vertical}} \) 1.33 deg, horizontal edge-to-edge separation 5 deg., duration 20 ms), presented adjacent to two inducing gratings that drifted in opposing directions (up/down, width 1 deg., horizontal edge-to-edge separation 1 deg., full screen height 25.6 deg, spatial frequency 1 cyc.deg\(^{-1}\), temporal frequency 5 Hz, starting phase
randomized on each trial). To avoid the gradual accumulation of motion adaptation within an experimental session, the direction of motion was alternated on each successive trial and an inter-trial interval was imposed that was longer than the preceding period of motion (inter trial interval = motion duration + response latency + 500ms). A small cross was positioned in the centre of the screen, serving as an aid to fixation (width/height 10arcmin). To avoid the potential use of the fixation cross (or its afterimage) as a reference for making the alignment judgement, it was subject to square wave contrast reversal at 10Hz and was removed during the target presentation interval.

To quantify motion-induced shifts in perceived position, the vertical offset of the target stimuli was manipulated in a method of constant stimuli (7 levels x 30 trials). To produce an offset, the two target stimuli were displaced by equal and opposite amounts (up/down). Since the direction of motion alternated on each trial, these offsets were expressed relative to the inducing motion (i.e. positive offsets indicate a misalignment in the same direction as the inducing motion). This approach further served to null the effect of any alignment bias intrinsic to the observer. Data were accumulated over several experimental sessions to obtain a full psychometric function (see Figure 1b), which was then fitted by a logistic function of the form:

\[ P(\text{offset in direction of motion}) = \frac{1}{1 + e^{-\frac{PSA-x}{TH}}} \]
where $X$ is the vertical offset of the target stimuli; PSA is the point of subjective alignment, the physical offset required to null any motion-induced positional shift; and $TH$ is the observer’s alignment threshold.

**Time-course of motion-induced positional shifts**

The stimulus onset asynchrony (SOA) between the target stimuli and the moving inducers was manipulated for three different motion durations – 2000ms, 3600ms and 5000ms. A SOA of zero corresponds to when the 20ms presentation of the target stimuli coincided with the first two 10ms frames of the motion sequence. Two steps were taken to minimise temporal uncertainty associated with the appearance of the targets. First, SOA conditions were completed in separate blocks, ensuring that no variation in stimulus timing occurred within an experimental session. Second, the fixation cross always appeared a fixed time interval (1000ms) prior to the onset of the motion stimuli. This provided a temporal cue for conditions in which the targets appeared prior to motion onset. The order in which observers completed the conditions was pseudo-randomised (conditions first sampled without replacement until one session had been completed of each, process then repeated).

**Dissociating stimulus and motion onset**

In the time-course experiment described above, the inducing stimuli begun to drift as soon as they appeared on the screen. In this instance, the onset of motion is synchronous with the onset of the stimulus itself. To dissociate these two factors, a control condition was run in which the first static frame of the inducing stimuli was presented for 1000ms (see Figure 4a). Target presentation was synched to the onset of motion: the 20ms target presentation
coincided with the last video refresh of the first motion frame plus the second motion frame.
The total duration of the motion sequence was fixed at 2000ms.

Pre-adaptation to motion

A pre-adaptation technique was used in which observers were presented with two 2000ms
periods of motion in the same direction separated by a variable inter-stimulus interval (ISI).
Presentation of the target stimuli was either at the onset of the second period of motion, or
800ms later (completed in separate sessions). To avoid the introduction of spurious apparent
motion signals, the final frame of the first motion sequence and the initial frame of the second
motion sequence had identical phase. The length of the inter-trial interval was increased to
avoid cumulative adaptation across trials (inter trial interval = 4000ms + ISI + response
latency + 500ms). Two additional manipulations of the initial (i.e. pre-adaptation) motion
sequence were subsequently employed to investigate the selectivity of the observed effects:
(i) the direction of motion was reversed relative to the second motion sequence, or (ii) the
horizontal edge-to-edge separation was increased from 1 deg. to 9 deg. All other methods
were identical to those in the time-course experiment described previously.

RESULTS

Figure 2 shows the profile of motion-induced positional biases revealed by manipulating the
relative timing of the moving inducer patterns and the static target stimuli. In this and
subsequent figures, shifts of perceived target position in the direction of motion are indicated
by negative PSA values (a physical offset in the opposite direction being required to achieve
perceptual alignment). Negative SOA values denote conditions in which the target stimuli appeared prior to the onset of motion. Despite differences in the absolute magnitude of induced positional misperceptions across observers, all showed very similar profiles as a function of SOA.

Previous studies suggest that the perceived position of briefly presented static stimuli is distorted by motion signals occurring after their appearance (Whitney & Cavanagh, 2000; Durant & Johnston, 2004; Eagleman & Sejnowski, 2007). For example, Eagleman and Sejnowski suggest that the magnitude of motion-induced positional shifts reflects the accumulation of motion signals within a temporal window spanning ~80ms after stimulus presentation. Consistent with this suggestion, we find that positional shifts begin to occur when target stimuli are presented immediately prior to the moving inducers, and reach maximum when target presentation is coincident with motion onset (SOA = 0ms). Simple temporal integration of a uniform motion signal predicts that the magnitude of induced biases should be maintained for any further delays of targets presentation up until ~80ms before motion offset. However, this prediction is clearly not borne out in the results. Instead in all conditions, induced positional biases undergo a rapid decelerating decay after motion-onset, reaching an asymptotic level slightly less than half of the peak effect beyond SOAs of ~800ms. The resulting initial time-course is remarkably similar in form to the transient-sustained response profiles produced by short-term motion adaptation in MT neurons (e.g. Lisberger & Movshon, 1999; Priebe, et al., 2002). To quantify this temporal profile, we first normalised PSAs relative to the peak shift in each condition and averaged across observers (see bottom row in Figure 2). We then simultaneously fitted the segments of the composite
time-course functions ranging from motion onset to 800ms prior to motion offset with an exponential decay function:

\[ PSA = a + (1 - a)e^{-\frac{SOA}{\tau}} \]

where \( a \) is the normalised effect at asymptote and \( \tau \) is the time constant of the exponential. The best fitting function was obtained with \( a = 0.41 \) and \( \tau = 446\text{ms} \), and successfully explained 91% of the variance.

Another distinctive feature of the time-course data is that the initial rapid attenuation of induced positional shifts can be dissociated from the gradual development of a repulsive positional aftereffect. Consistent with the results of earlier studies (Snowden, 1998; McGraw et al., 2002; Whitney & Cavanagh, 2003), we find that the perceived positions of target stimuli presented after motion offset were shifted in the opposite direction to the moving inducers (indicated by positive PSA values). Whereas rapid attenuation of positional misperceptions after motion onset is evident in all conditions, the size of the repulsive aftereffect is clearly dependent on the duration of motion – little or no aftereffect followed 2000ms of motion, but progressively larger effects follow periods of motion lasting 3600ms and 5000ms.

In principle, two types of explanation of the rapid attenuation of induced positional distortions after motion onset are possible: (i) reduction/suppression of the motion signal over time (i.e. adaptation), or (ii) changes in the susceptibility of positional judgments to induced biases. The appeal of the former is strengthened by the fact that there is a known neural
correlate – indeed, the transient-sustained temporal profile of the motion-induced shift shows a striking resemblance to the time-course of short-term motion adaptation in MT. However, it is possible that the motion signal itself could remain uniform over time, but that positional judgements are particularly vulnerable to distortion at motion onset. One potential reason for this might be that the moving inducers act to mask the target stimuli when their respective onsets are close in time, making them more difficult to localise. Several lines of evidence suggest that the susceptibility of positional judgements to distortion by motion is heightened under conditions where positional sensitivity is low. For example, motion-induced positional shifts tend to be larger when stimuli are spatially blurred (e.g. De Valois & De Valois, 1991; Fu, Shen & Dan, 2001; Whitaker et al, 1998), when they are presented at peripheral locations of the visual field (e.g. De Valois & De Valois, 1991; Whitney & Cavanagh, 2003; Kanai, Sheth & Shimojo, 2004), or when they are subjected to spatial crowding (Kanai et al., 2004). If excessive masking were responsible for the marked peak in the magnitude of positional biases at motion onset, we would expect to see a concomitant deterioration in positional sensitivity at this time. Contrary to this prediction however, no systematic differences were found between observers’ alignment thresholds for target stimuli presented at, or shortly after the appearance of the moving inducer stimuli (see Figure 3). An additional possibility is that the susceptibility of positional judgments to distortion at motion onset has a high-level cognitive basis. It has been argued that positional distortions reflect the tendency for observers to treat moving and static stimuli as being parts of a single object (see Eagleman & Sejnowski, 2007). Synchronous presentation of inducing and target stimuli might increase the probability of ‘binding’ the stimuli in this way, resulting in larger misperceptions of perceived position. To investigate this possibility, we ran an additional condition in which we dissociated the onset of motion from the appearance of inducing stimuli (see Figure 4a).
Although this manipulation reduces the likelihood of attributing the stimuli to a common source, a consistent shift in perceived position was obtained for target stimuli presented at the onset of motion, regardless of whether this coincided with the appearance of the inducing stimuli (see Figure 4b).

It stands to reason that if rapid adaptation of the motion signal underlies the attenuation of positional distortions after motion onset, it ought to be possible to pre-adapt observers and selectively eliminate the early transient peak effect for subsequent motion onsets. To examine this possibility, we presented observers with two 2000ms periods of motion separated by a variable ISI. The presentation of the target stimuli was synched to the onset of the second period of motion (see methods for details). Results are shown in Figure 5 (circular symbols). When the ISI was brief (e.g. 20ms), observers showed moderate shifts of perceived position in the direction of motion. In all cases, these shifts were consistent with asymptotic levels previously reported for target stimuli presented >800ms after motion onset (compare with Figure 2). Lengthening the ISI produced a systematic increase in the magnitude of the effect, consistent with progressive recovery from short-term motion adaptation. Exponential functions fitted to the data yielded recovery time constants in the order of 200ms (NWR = 221 ms, PVM = 162ms, MK = 200ms, Pooled data = 186ms). For comparison, positional shifts obtained with target stimuli presented 800ms after the onset of the second period of motion are represented by the square symbols in Figure 5. Manipulation of the ISI between the two motion intervals had no effect in this instance, indicating that pre-adaptation specifically reduces the initial transient peak effect observed at motion onset. To further investigate the selectivity of the rapid adaptation mechanism, we next repeated the experiment whilst manipulating either the spatial location or direction of the motion sequence
in the pre-adaptation phase. As shown in Figure 6, comparable attenuation of the peak effect at motion onset occurred regardless of whether the pre-adaptation motion sequence was positioned at the same, or a more peripheral retinal location. In contrast, no change in the magnitude of the peak positional shift was found when the two motion sequences moved in opposing directions.

DISCUSSION

Correspondence with short-term motion adaptation in MT

To what extent can the rapid attenuation of positional distortions after motion onset be considered a behavioral analogue of short-term motion adaptation in MT? The decay and asymptote of the positional shifts we have measured is certainly qualitatively similar to the transient-sustained neuronal response profiles reported previously (e.g. Lisberger & Movshon, 1999; Priebe, et al., 2002), as is the pattern of recovery from adaptation. Furthermore, the direction specificity and broad spatial tuning observed is entirely consistent with the selectivity of short-term motion adaptation reported in MT (Priebe & Lisberger, 2002; Priebe, et al., 2002). Interpreting more quantitative comparisons between these neural and behavioural phenomena is difficult, not least because the precise role played by area MT in the generation of motion-induced positional shifts has yet to be established. Similarities do exist in terms of the relative magnitude of transient and sustained components (see Priebe, et al., 2002, figure 2). In the sample of MT neurons reported by Priebe and colleagues (2002) the mean ratio of transient to sustained response levels was 2.43, corresponding to a 59% reduction. Remarkably, the best fitting exponential decay function to the motion-position results also yielded an asymptotic level that was 59% of the peak effect (a peak-normalised
effect size of 0.41), although the precision of this correspondence is likely to be coincidental.

Less similar are the time constant estimates derived from psychophysical and physiological measures. Adaptation (~450ms) and recovery (~200ms) in the current study was an order of magnitude slower than that found physiologically – Priebe et al. report adaptation time constants ranging from 8-85ms (mean 25.9ms) and a mean recovery time constant of 86ms. A number of factors could potentially contribute to this discrepancy. First, it is clear that motion-induced positional shifts do not provide an instantaneous measure of motion-related neural activity. Rather, the magnitude of these effects reflects the accumulation of motion signals over a period of at least 80ms after the positional judgment is triggered (e.g. Whitney & Cavanagh, 2000; Eagleman & Sejnowski, 2007). The impact of this temporal summation is to smear the impact of changes to the motion signal in time. Clear evidence of this can be seen in the time-course data around the time of onset and offset of the inducing motion. Although these changes in the motion signal are abrupt, they produce gradual changes in the behavioral effect (see Figure 2). As described previously, motion-induced positional shifts begin to occur even when the presentation of target stimuli precedes the onset of motion. Likewise, the gradual decline in the magnitude of induced shifts starts at a time point discernibly earlier than motion offset. It is likely therefore, that the decay in the magnitude of the effect after motion onset is temporally extended compared to the underlying neural processes that drive it. An additional consideration is the fact that the inducing motion signal is unlikely to be coded by the response of a single motion-sensitive neuron, but rather by the pattern of responses across a larger population of such neurons. The precise time-course of motion-induced positional shifts is more likely related to the temporal characteristics of this combined population activity. Indeed, even simple population coding schemes (e.g. the ratio
between responses in two channels) can produce aggregate responses with markedly different
dynamics than their constituent components (for example see Hammett et al., 2000).

Relationship with traditional aftereffect measures

A further consideration is how the different effects revealed by the dynamics of motion-
induced positional distortions relate to mechanisms of motion adaptation studied with more
traditional motion aftereffect paradigms. Previous psychophysical studies have found that the
properties of motion aftereffects differ depending on whether the test stimulus used is static
or dynamic. Motion aftereffects in static patterns can be induced by adaptation to motion
sequences defined by luminance (first-order motion), but not by contrast (second-order
motion, Nishida & Sato, 1995). They also tend to be tightly coupled to the retinal location,
spatial frequency and chromatic composition of the adapting stimulus (e.g. Masland, 1969;
Cameron, Baker & Boulton, 1992; McKeefy, Lavers & McGraw, 2006) and only transfer
partially between the two eyes (Moulden, 1980). In contrast, motion aftereffects measured
with dynamic test stimuli result from adaptation to both first- and second-order motion
(Ledgeway, 1994), are relatively insensitive to changes in basic visual properties (e.g. Ashida
& Osaka, 1994; Snowden & Milne, 1997) and exhibit complete inter-ocular transfer (Nishida,
Ashida & Sato, 1994). These differing properties are thought to reflect the fact that static and
dynamic motion aftereffects tap into adaptation occurring at different stages of motion
processing (e.g. Mather et al., 2008). Recently, Kanai and Verstraten (2005) have reported
that dynamic motion aftereffects can be produced from relatively brief (sub-second) exposure
to motion, an effect that they interpret as a perceptual manifestation of fast neuronal
adaptation. Whilst it is tempting to suggest that these aftereffects might share a common
neural substrate to the rapid adaptation effects we observe, some caution is necessary.
Whereas our rapid adaptation effects can be dissociated from repulsive positional aftereffects, available evidence suggests that the tuning characteristics of dynamic motion aftereffects and repulsive positional aftereffects are indistinguishable (McGraw et al., 2002; McKeefry, et al., 2006; McGraw & Roach, 2008). In addition, the recovery time constant of 2s reported by Kanai and Verstraten is approximately ten times larger than that found in the present study.

Generality of rapid adaptation effects

Short-term adaptation is by no means a unique property of neural responses in MT: rapid decay of firing rates after the appearance of an optimal stimulus is characteristic of neurons in a variety of visual cortical areas (e.g. Kulikowski, Bishop & Kato, 1979; Müller, Metha, Krauskopf & Lennie, 1999; Hegdè & Van Essen, 2004; Motter, 2006; Mayo & Sommer, 2008). An interesting question therefore is whether different forms of perceptual biases induced between stimuli present in the visual field could be exploited to reveal behavioral indices of rapid adaptation in other domains. One advantage of the paradigm employed here is that motion only affects perceived spatial position when presented within a relatively restricted temporal window (i.e. ~80ms after the target stimuli, Eagleman & Sejnowski, 2007). Other effects, characterised by temporal integration over much wider intervals, may be less well suited for this purpose. For example, biases in the perceived orientations of spatially adjacent stimuli (the ‘tilt illusion’) occur when stimuli are separated in time by as much as 200-400ms (Durant & Clifford, 2006; Corbett, Handy & Enns, 2009). Identification of induced perceptual biases requiring near synchronous stimulus presentation will afford the best temporal resolution for future investigations of this kind.
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Figure 1. (a) Stimulus configuration employed to measure motion-induced shifts in perceived position. The motion of two gratings drifting in opposing directions (indicated by the arrows) induces a perceived vertical offset between briefly flashed target stimuli that are physically aligned. (b) Typical psychometric function showing quantification of the induced shift. In this, and subsequent figures, positive offset values indicate a shift in the direction of the inducing motion.

Figure 2. The time-course of motion-induced shifts in perceived position. Points of subjective alignment are plotted as a function of stimulus onset asynchrony (SOA) for motion durations of (a) 2000ms, (b) 3600ms and (c) 5000ms. Negative SOA values indicate conditions in which target stimuli appeared prior to the onset of motion. To aid comparison across conditions, the range of SOAs in which the inducing and test stimuli overlapped in time is indicated by the grey rectangle. Data for individual observers are shown in the upper three rows, in which error bars indicate ± 1 standard error. The bottom row shows mean (filled symbols) and individual (unfilled symbols) shifts once normalised relative to the observer’s peak effect.

Figure 3. Positional sensitivity at, and shortly after the onset of motion. Mean (filled symbols) and individual (unfilled symbols) alignment thresholds are shown as a function of SOA. Data has been collapsed across motion durations.

Figure 4. Dissociating the effect of motion and stimulus onset. (a) Space time schematic showing the presentation of target stimuli synched to both the appearance and onset of motion of the inducing patterns (upper plot, motion & stimulus onset condition), or to the onset of motion alone (lower plot, motion onset only condition). (b) Shifts in perceived position for each condition. Unfilled symbols show data for each individual observer, whereas filled symbols show the mean.

Figure 5. The recovery of motion-induced position shifts from short-term adaptation. (a-c) Points of subjective alignment for each individual observer, plotted as a function of the temporal interval between two 2000ms periods of motion. Circular symbols denote conditions in which target presentation was synched to onset of the second period of motion (i.e. SOA = 0ms). Square symbols indicate when target presentation was 800ms later (SOA = +800ms). (d) Mean (filled symbols) and individual (unfilled symbols) positional shifts, rescaled to range between mean peak and asymptotic levels described in Figure 2.

Figure 6. Specificity of short-term adaptation effects on motion-induced positional distortions. Individual points of subjective alignment are shown for target stimuli presented at the onset of a 2000 period of motion following either: no pre-adaptation (white bar, data replotted from Figure 2); pre-adaptation to motion in the same direction and at the same location (black bars, data replotted from Figure 5); pre-adaptation to motion in the opposite direction (light grey bars); or pre-adaptation to motion at a different location (dark grey bars).
**Mean Motion Interstimulus Interval (ms)**

- **Scaled Shift**
- **Variable ISI**
- **Target presented at motion onset**
- **Target presented 800ms after motion onset**

**Graphs**

**Points of Subjective Alignment (arcmin)**

- **NWR**
- **MK**
- **PVM**

**Motion Interstimulus Interval (ms)**