The motion aftereffect

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The motion aftereffect is a powerful illusion of motion in the visual image caused by prior exposure to motion in the opposite direction. For example, when one looks at the rocks beside a waterfall they may appear to drift upwards after one has viewed the flowing water for a short period – perhaps 60 seconds. The illusion almost certainly originates in the visual cortex, and arises from selective adaptation in cells tuned to respond to movement direction. Cells responding to the movement of the water suffer a reduction in responsiveness, so that during competitive interactions between detector outputs, false motion signals arise. The result is the appearance of motion in the opposite direction when one later gazes at the rocks. The adaptation is not confined to just one population of cells, but probably occurs at several cortical sites, reflecting the multiple levels of processing involved in visual motion analysis. The effect is unlikely to be caused by neural fatigue; more likely, the MAE and similar adaptation effects provide a form of error-correction or coding optimization, or both.

Find a small waterfall and gaze steadily at a rock in the middle of the fall for about 30 s. Now transfer your gaze to the river bank, and you will find that it appears to be streaming upwards. You are experiencing the motion aftereffect (MAE), and you have adapted your neural motion-detectors. If you cannot find a waterfall, read Box 1. It is over 30 years since the only book to date to be devoted to the MAE was first published[1], although study of the motion aftereffect has recently seen an upsurge of interest[2]. First reported by Aristotle[3] (*c.* 330 BC), the MAE was rediscovered by the Czech physiologist Purkinje[4,5]. Wohlgemuth published a landmark article on the MAE in 1911 (Refs 6,7). Holland's book was just too early to include Barlow and Hill's important discovery[8] that the MAE was caused by visual processing in single visual cells.

Barlow and Hill recorded the firing rate of motion-sensitive ganglion cells in the rabbit retina during and following prolonged stimulation with a rotating random-dot pattern. When the retina was exposed to the stimulus, the ganglion cell's firing rate was initially brisk but gradually reduced over the first 15–20 s. When motion stopped, the firing rate fell below its baseline level, recovering gradually over 30 s. This time course is closely related to our perceptual experience of a motion aftereffect. It is not surprising then that aftereffects became known as the 'psychologist's microelectrode'[9] because inferences regarding neural processes could be based on psychophysical experiments. As Mollon put it, 'if it adapts, it's there'[10].

Since Barlow and Hill's revolutionary findings, sophisticated computers have replaced discs on turntables and stopwatches, and brain-imaging techniques can reveal directly the activity in the brain. Here, we give a brief overview of modern developments.

Methods of measurement

The MAE is not easy to measure. After prolonged inspection of a moving 'adapting' stimulus, a static 'test' stimulus appears to move in the opposite direction. Observers can report the duration of the MAE, which seems to be a square-root function of the duration of the adapting motion[11]. Attempts to null the MAE by moving the test stimulus slowly in the opposite direction to the MAE (i.e. in the same direction as the adapting motion) fall foul of the fact that the MAE produces a sensation of motion without displacement, so that any landmarks in a stationary test field remain fixed in position despite the apparent motion.

A new kind of test field[12,13] contains an adjustable mixture of drifting and randomly twinkling dots. If an MAE made the twinkling dots appear to drift to the left, a just large enough percentage of rightward drifting dots is added to null the MAE. Measuring the duration of a subjective aftereffect records only the visible MAE, but titrating the signal-to-noise level can reveal a weak, persisting adaptation even after the visible MAE has terminated.

Tuning of the MAE

Any low-level neural filtering mechanism is likely to lose sensitivity with prolonged firing, possibly by a gain reduction[14,15]. This adaptation will distort the pattern of firing in an array of filters in response to any stimulus, compared with its unadapted response. The distorted response pattern will alter the appearance, including the detectability, of a subsequently viewed stimulus. This change in appearance is a manifestation of the aftereffect. The existence of an aftereffect is taken as evidence for the existence of an adaptable filter specifically tuned to the stimulus property in question and, by manipulating the degree of similarity between the adapting and test stimuli, the degree

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Box 1. Experiencing the motion aftereffect

A

B
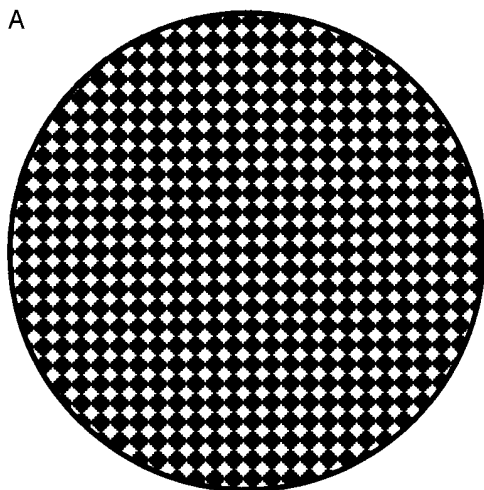
You can enlarge the Figure (A or B) on a photocopying machine and rotate it on a turntable at 33 or 45 rpm for 30 s, while gazing steadily at the center of the turning disc. Stop the turntable suddenly, while still gazing at the center. The dots will appear to turn back in the opposite direction, and the previously contracting logarithmic spiral will appear to expand. This striking illusion is the motion aftereffect (MAE). There is a complete Web Page dedicated to the motion aftereffect, written by Frans Verstraten and Hiroshi Ashida. It can be accessed through the

Vision Science homepage (http://www.visionscience.com/VisionScience.html).

You can find several demonstrations of motion aftereffects on the Web. One example can be found on George Mather's Web Page (http://epunix.biols.susx.ac.uk/Home/George_Mather/Linked%20Pages/Motion/MAE.HTML). Only good typists with access to QuickTime should attempt this.

Another good example can be found on the pages of Illusionworks® (http://www.illusionworks.com/spiral.htm).

of stimulus specificity of the adaptation, and therefore the filter's response selectivity, can be inferred. From such manipulation, it is clear that the MAE is tuned, since it is maximal when the adapting and test fields share spatial and temporal properties and presumably stimulate the same neural channels. The tuning may not be strong – adaptation to motion can generate an aftereffect even on a uniform bright field; this MAE has been likened to 'a rice pudding getting nearer you in a fog'[16]. But MAEs are generally strongest when the spatial frequencies of a drifting adapting grating and of a counterphase-flickering test grating are identical[7–19]. The MAE falls to about half strength if the adapting and test field frequencies differ by one octave. Favreau[20] suggested that there are, not one, but two MAEs. One component of the MAE is short-lived and very broadly tuned for spatial parameters. This component shows interocular transfer and so must involve binocularly driven cells. It is probably not color-selective. The second component is longer in duration and shows spatial-frequency specificity. This component is probably monocular and color-selective.

We should mention two related aftereffects, 'direction repulsion' and 'direction-selective adaptation'. In direction repulsion[21], inspection of motion in a particular direction causes the apparent direction of test motions to be shifted away from the axis of the adapting motion. Thus, after inspection of a field of random dots drifting towards 2 o'clock, a test field of dots that actually drifts towards 3 o'clock appears to be drifting towards 4 o'clock. The repulsion is maximum when the angle between adapting and test motion is 30°, and diminishes to zero by 90°.

In direction-selective adaptation, inspection of a pattern moving to the right elevates the contrast threshold (that is, reduces the sensitivity) for subsequent patterns moving to the right far more than for patterns moving to the left[22–24].

Aftereffects from relative motion also occur (see Box 2).

Higher-order aftereffects

MAEs are thought to originate not only at early stages but also at later (higher) levels of visual motion processing (see Box 3). For example, the MAE is reduced in duration when the observer's attention is distracted by a difficult letter-reading task[25]. Culham and Cavanagh[26] adapted their observers to a radial counterphase-flickering grating, rather like a flickering rotating wheel. This is a directionally ambiguous stimulus that either just flickers or sometimes moves in random directions. However, if the observers fixated the center of the wheel while attentively tracking a dark bar of the grating, they perceived clear motion. If this so-called attention-based motion perception was maintained for a while it resulted in an MAE – but only if the test pattern was dynamic (for example, a counterphasing grating). When a static test pattern was used, no MAE was perceived.

More evidence for a higher-order MAE comes from studies of interocular transfer (see Box 3). The MAE transfers completely in experiments where the test pattern is dynamic[27], while the interocular transfer for static test patterns is much less[28]. This indicates that higher, binocularly driven motion-selective neurons are involved. Higher-order MAEs are extensively addressed in Ref. 29.

Box 2. Aftereffects from relative motion, not retinal motion

The large textured disc (see Fig.) rotates clockwise. The inner stationary ring is textured and appears to turn counterclockwise, while the outer ring is blacked out and looks (and is) stationary. After 2.5 seconds the large textured disc rotates counterclockwise. The outer stationary ring is textured and appears to turn clockwise, while the inner ring is blacked out and looks (and is) stationary. This sequence is repeated for 3 minutes. The rings never move! Yet when all motion is stopped, the rings show aftereffects, clockwise for the inner ring and counterclockwise for the outer ring. (Any motion aftereffects from the large back-and-forth textured surround would cancel out.) The aftereffects in the motionless rings arise from *relative* motion induced in them by the surround[a,b].

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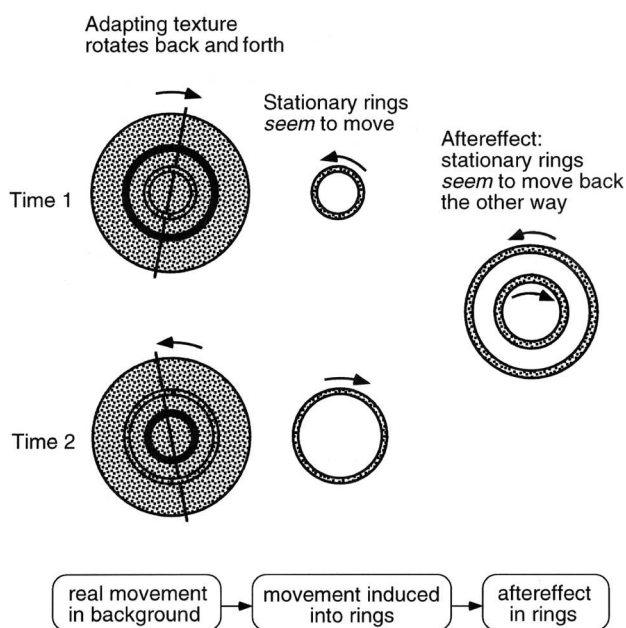
Physiological substrate

Barlow and Hill[8] explained the MAE in terms of the discharge characteristics of single neurons in the visual system. In their experiment, as described earlier, the firing rate of the ganglion cells dropped below its baseline level when the motion stopped, recovering gradually over 30 s. No rebound effect was found; following a continuous adapting motion in the null direction, spontaneous activity did not change. The transient reduction in spontaneous activity was regarded as corresponding to an MAE. Barlow and Hill note that '…it seems unlikely that similar effects occur at a retinal level in man.' However, there is much disagreement on whether the human MAE takes place in cortical areas V1, MT (middle temporal visual area or V5), or MST (medial superior temporal area).

Motion and direction selectivity can be reliably found in neurons of the primary visual cortex (V1), particularly in layers 4B and 4C. Both layers are part of the pathway projecting from the magnocellular layers of the LGN (reviewed in Ref. 30). The magnocellular pathway is insensitive to color and to stationary contours, but makes brisk, transient responses to moving stimuli.

The motion-direction-sensitive neurons of layer 4B project either directly or via visual area V2 to area MT (Ref. 31), where 80–90% of the neurons are sensitive to motion[32]. (The retina also projects via the superior colliculi to the pulvinar and from there to MT, but the role of this pathway in the MAE is not clear[33].) Lesions in MT can seriously impair visual pursuit movements[34] and motion-direction discrimination[35] and even cause selective motion blindness[36,37]. The functional properties of area MT neurons are reviewed in Ref. 38. Area MT projects to area MST, where the neurons have very large receptive fields and typically respond to complex motion patterns such as radial and circular motion[39].

Petersen, Baker and Allman[40] recorded from MT neurons in the owl monkey during motion adaptation. The neurons were adapted for 20 s with random dots which were either stationary, or moved in either the preferred or the null direction. Following adaptation – and after a 5 s delay – a bar swept through the receptive field of the cell in the preferred or null direction. Neural responses to the bar in the preferred direction of movement were suppressed by adaptation in the preferred direction, but actually enhanced by adaptation in the null direction. The authors attributed this latter enhancement to the habituation of an inhibitory input tuned to the null direction. These findings are compatible with psychophysical models which postulate direction-specific channels tuned to opposing motion directions (e.g. Refs 41,42).

Giaschi *et al.*[43] also examined the time course of responsiveness of simple and complex motion-sensitive cells in the cat. During and following 2 min adaptation to a high-contrast drifting grating, a large number of neurons showed reduced responsiveness to motion in both the adapted as well as the non-adapted opposite direction. Adaptation to the non-preferred direction had less pronounced effects, reducing responsiveness in some neurons while facilitating it in others. The time course of adaptation in simple cells could be described by an initial, fast exponential decay with a time constant of about 8 s, followed by a slow exponential decay with a time constant of about 88 s.

A functional MRI study[44] revealed enhanced MRI signals during and after exposure to expanding or contracting patterns, especially in areas identified as MT, and to a smaller extent in areas V2 and V3a – but not in V1. The prolonged MRI activation was highly associated with the illusory motion perception: simultaneous recording of MAE strength and fMRI-signal strength during the stationary test phase resulted in an excellent fit between the time courses of the psychophysical data and MRI activation (best fit exponents were 8.3 s and 9.2 s, respectively).

Box 3. Interocular transfer of the MAE

Some visual cells in the cortex are monocular, responding to inputs from the left eye only (L) or from the right eye only (R). Other cells are binocular, some responding to inputs from either the left OR the right eye (L v R) and others responding only when the left AND right eyes are both stimulated at once (L & R).

Viewing motion with both eyes (Fig. A) adapts all classes of cells to motion (left-oblique hatching), and then viewing a static test exposes them all to the test field, so 100% of the tested cells are also adapted (cross hatching).

Viewing the motion with the left eye (Fig. B) adapts only the L and L v R cells to motion (left-oblique hatching), and viewing a static test with the right eye tests only the R and L v R cells (right-oblique hatching), so the MAE generated by the L v R cells (cross-hatched) is diluted by the unadapted R and (perhaps) L & R cells. The result is that the MAE 'transfers' across eyes, but only at about 60% strength[a,b].

People with a childhood squint (Fig. C) never develop binocular visual cells, are blind to stereo depth, and show no interocular transfer of the MAE[c–e].

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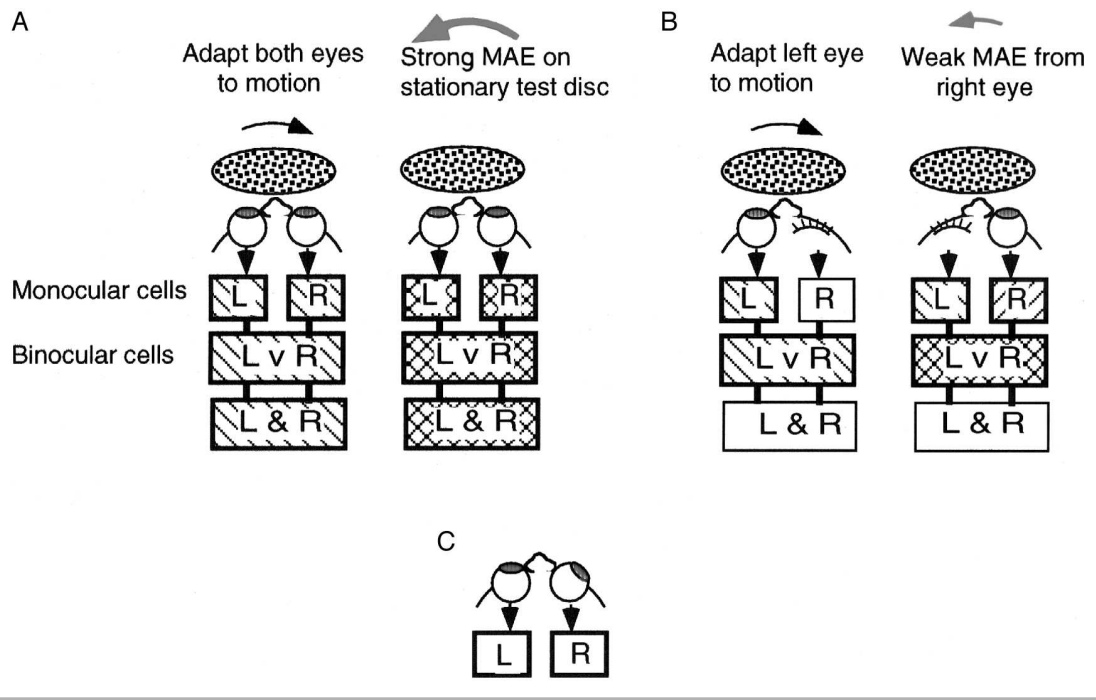
Most MAE theories (e.g. Ref. 41) require direction-specific adaptation of channels tuned for opposing directions. Such direction-specific adaptation has been reported both in the extrastriate cortex[40] and in area V1 (Ref. 43). Neural responses were reduced more by adaptation to the preferred than to the non-preferred direction.

MAEs seem to be related to the reduction in responsiveness of the adapted population of neurons in V1, with almost no change in the response of non-adapted neurons. This is consistent with the original imbalance theory of Barlow and Hill[8], who found no evidence for repulsion effects (as described above) in rabbit ganglion cells. Repulsion effects (inhibitory interactions) between neurons can be found in extrastriatal neurons of areas such as MT. This is consistent with the enhancement found in the activity of non-adapted neurons[40]. The strength of repulsion effects would appear to vary with the neural level of processing, with weak effects at the V1 level and strong ones at the MT level.

Theoretical models

Models are designed to link the MAE with neural adaptation to a particular direction of motion, which consequently reduces the sensitivity of cells tuned to that direction relative to cells tuned to other directions. The responses of the adapted and unadapted cells are then compared to generate a motion percept.

Sutherland[45] proposed that the direction of seen motion depends upon the firing ratios of cells sensitive to movement in opposite directions. After exposure to prolonged movement in one direction a stationary image would produce less firing than normal in the cells that had just been stimulated, hence apparent movement in the opposite direction would be perceived. Sutherland's prediction of adaptation effects in single visual neurons was first confirmed by Barlow and Hill[8], who measured responses in rabbit retinal ganglion cells, and was later confirmed by a number of workers recording from cat and monkey cortical cells.

An adequate explanation for the MAE must involve two parts: (1) adaptation in first-stage motion sensors/detectors; and (2) some form of competitive comparison between different detectors at a second stage of analysis (opponent-processing is minimally sufficient, but cannot accommodate two-dimensional interactions; see below). MAEs arise when unadapted detectors win the competition against adapted detectors. Mather and Harris[46] suggest that, say, leftward- and rightward-sensitive motion detectors receive inputs from the same retinal region, and in turn feed into an opponent comparator which fires faster when exposed to leftward motion and more slowly when exposed to rightward motion. The motion sensors might be considered analogous to red-sensitive (R) and green-sensitive (G) retinal cones in the color domain, and the comparator to a R+G− opponent ganglion cell. Exposure to leftward motion might adapt a leftward sensor (stage 1), reducing sensitivity to leftward motion (directionally selective adaptation) and yielding a rightward MAE on a stationary test field. However, it might also adapt the left–right opponent comparator (stage 2), reducing sensitivity to both leftward and rightward motion, but without giving rise to an MAE. Which of these actually occurs? Raymond and Braddick[47] found that adaptation to rightward motion reduced sensitivity to rightward motion, as measured by a reliable signal-to-noise-ratio technique, but did not alter sensitivity to leftward motion. The 'null' point (at which observers were equally disposed towards reporting leftward or rightward motion) did not shift leftwards, indicating that no MAEs were generated. This would suggest that global movement-direction analysers sensitive to opposite directions are independent rather than opponent. However, the issue of opponency is still unresolved.

Motion adaptation can cause two-dimensional shifts in direction. It not only makes a stationary test pattern appear to move in the opposite direction, but can also repel the perceived direction of test motions by up to 20° (Ref. 21). This suggests the existence of motion sensors with 'petal-shaped' tuning curves that respond to motion directions over a range of 45° or more[41]. Mather[42] proposed a 'distribution of activity' model, according to which perceived direction is given by the weighted average of activity across a collection of cells tuned to all motion directions. (For recent views of MAE models see Refs 46,48.)

A function for aftereffects?

Does the MAE have a functional value or is it simply a design fault in the visual system? The naive view that neurons can 'fatigue' rather like over-exercised muscles, perhaps owing to depletion of neurotransmitters, is almost certainly incorrect, since some neurons appear to resist adaptation altogether. Although cortical neurons in the cat certainly do adapt to motion[49], retinal and geniculate cells do not[50]. If some visual neurons do not fatigue, why should any? Furthermore, the time course of recovery from adaptation does not seem to match that expected from neural fatigue. While simple MAEs generally last for less than a minute, contingent MAEs (those that depend on the presence of another feature, such as color) can last for days or weeks. Here we discuss two theoretical notions – 'error correction' and 'coding optimization'.

Error correction

Random variations in the sensitivity of motion detectors would cause a skew in the distribution of their firing rates, so that perceived motion would be altered. How could this potential problem be overcome ? First, one must assume that, over a long enough time interval, all directions of motion are equally likely. Secondly, a monitoring device must check whether the activity of individual motion-sensitive neurons are showing equal time-averaged activity. Thirdly, some mechanism must alter the activity of individual neurons in order to restore the equality of neuronal activity to the desired state, by altering their response characteristics (increasing or decreasing their firing rate to a particular input pattern).

In principle, this mechanism would be like a 'graphic equaliser' on a sound system, in which different frequency bands in the input signal are processed by different channels whose gain (volume) can be adjusted manually by the listener, to suit their own taste and the acoustics of the room. In the visual system, the gains of individual channels (neurons) would be set automatically by a comparison of actual and ideal time-averaged activity[51,52]. In normal circumstances, such a mechanism would act to keep the perceiver's internal representation of motion veridical despite unwanted changes (or drift) in individual components of the visual system. However, prolonged viewing of upward motion would lead to an excess of activity in upward-sensitive neurons, which would be mistaken for a change in their gain, and lead to a reduction in their output. This reduction would manifest itself as a downward MAE.

Coding optimization

Barlow[53] suggests that aftereffects such as the MAE help to optimize neural coding. He argues that MAEs occur because adapting stimuli are large enough to cover the receptive fields of many neurons. During continuous motion, many neurons will be active simultaneously, and so will inhibit each other's activity. When a stationary test field is viewed, this inhibition will be sustained and so the appearance of reversed motion will be produced. In this view, aftereffects occur because the adapting stimuli produce correlated activity in a group of neurons, rather than activity in single neurons.
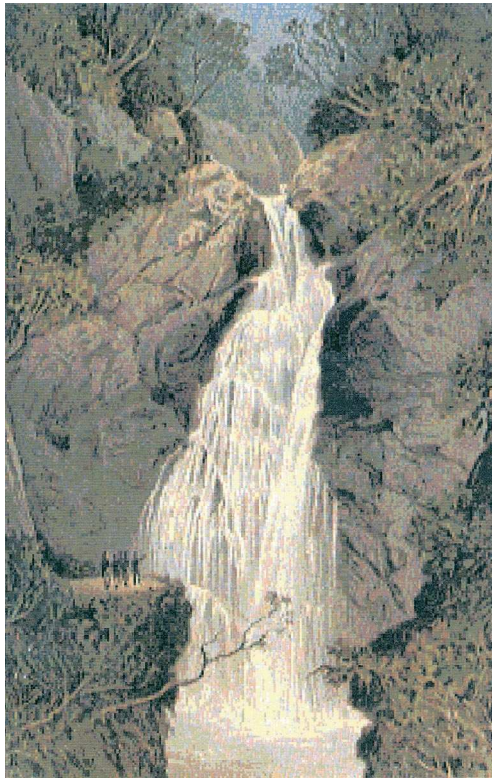
Error-correcting and coding-optimization models of the MAE make similar predictions. They both involve monitoring activity in visual mechanisms over time, suggesting that the build-up and decay of aftereffects should be rather slow processes to allow the visual system time to absorb the change of visual 'diet' between adaptation and testing. They both predict storage of aftereffects if testing does not immediately follow the adaptation (for example, by closing the eyes), because an alteration of visual input and not simply the passage of time is needed to re-adjust the underlying mechanisms.

Shifting the frame of reference

MAEs might play a global role in shifting the subject's entire frame of reference[54] in order to keep the physical and phenomenological worlds in correspondence. Many sensory dimensions have a norm or null point. For example,

Box 4. The waterfall illusion

Robert Addams (in 1834) observed the waterfall illusion at the Falls of Foyers (see Fig.), located on the south-east side of the famous Loch Ness in the Highlands of Scotland. Addams stared at this waterfall for some time and when he turned his eyes to the rocks next to the waterfall they appeared to move upwards for a while. He reported: 'Having steadfastly looked for a few seconds at a particular part of the cascade, admiring the confluence and descussation of the currents forming the liquid drapery of waters, and then suddenly directed my eyes to the left, to observe the vertical face of the sombre age-worn rocks immediately contiguous to the water-fall, I saw the rocky face as if in motion upwards, and with an apparent velocity equal to that of the descending water'.

Different aftereffects might originate in different cortical areas; perhaps local effects in V1 and more global effects in extrastriate cortical areas, such as V4 or MT (Ref. 55). However, it is possible that global and local aftereffects serve a similar purpose. That is, drift or optical errors mean that the range of possible orientations or directions of motion needs to be redistributed across the available mechanisms to suit particular visual environments.

Conclusions

Even more than 2000 years after Aristotle's report of the MAE it is difficult to make firm statements on the actual nature of this illusion. There are good reasons to suggest that the MAE is not caused by neural fatigue alone, because the timing is wrong and because some visual neurons do not even show fatigue. It could be that the MAE provides a form of error correction or coding optimization, or even both. We now also know that adaptation occurs at several cortical sites, reflecting a range of different motion aftereffects. Given the rapid progress of the past few decades[2], there is no doubt that future research will greatly clarify this spectacular and mysterious optical illusion described so vividly by Robert Addams at Loch Ness over 150 years ago (Box 4).

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stationarity (absence of motion) can be thought of as a null- or mid-point on a continuum running from, say, fast motion to the left through to fast motion to the right. Perhaps the brain calculates this null point, or norm, from the stream of sensory information about that particular stimulus dimension, with a tendency for activity in sensory neurons to become normal, standard or neutral[54]. Thus, the value of the null point of a sensory dimension is not wired into the brain, but represents the average activity on that dimension over the recent past. Adaptation biases that activity, and so shifts the null point. Therefore, after adaptation to leftward movement, stimuli that fall on the old null point (stationary) no longer do so, but appear to move to the right. This idea suggests that the brain must continually recalibrate its inputs to optimize the correspondence between the external world and its internal visual representation.

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