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The influence of visual motion on fast reaching movements to a stationary object

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One of the most important functions of vision is to direct actions to objects¹. However, every time that vision is used to guide an action, retinal motion signals are produced by the movement of the eye and head as the person looks at the object or by the motion of other objects in the scene. To reach for the object accurately, the visuomotor system must separate information about the position of the stationary target from background retinal motion signals—a long-standing problem that is poorly understood^{2–7}. Here we show that the visuomotor system does not distinguish between these two information sources: when observers made fast reaching movements to a briefly presented

stationary target, their hand shifted in a direction consistent with the motion of a distant and unrelated stimulus, a result contrary to most other findings^{8,9}. This can be seen early in the hand's trajectory (~120 ms) and occurs continuously from programming of the movement through to its execution. The visuomotor system might make use of the motion signals arising from eye and head movements to update the positions of targets rapidly and redirect the hand to compensate for body movements.

In the first experiment we investigated the role of distant motion signals in the updating of reaching movements to a stationary target. We briefly presented a stationary object while subjects fixated on a bull's-eye at the centre of a screen (see Fig. 1a and Methods). Subjects hit the position of the flashed object as quickly as possible with their index finger. A vertically drifting pattern was presented on the screen throughout the trial. Initially the pattern drifted in one direction, but, at an unpredictable moment, the direction of the drifting pattern was reversed.

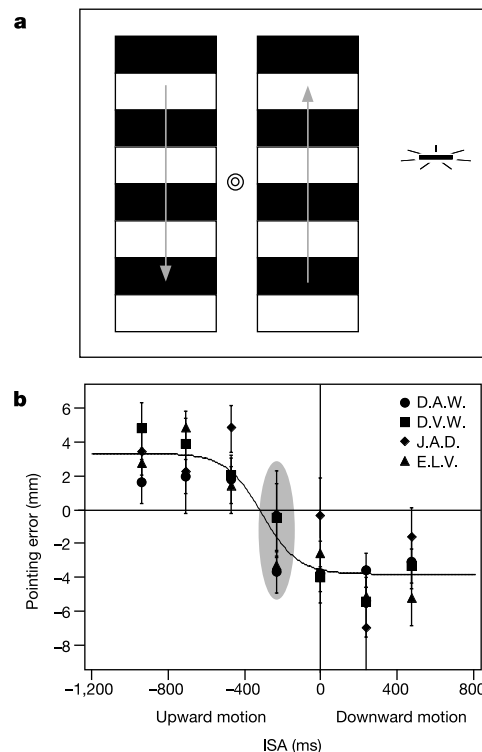


Figure 1 Stimulus and results for the first experiment. **a**, Two patterns were presented that drifted vertically in opposite directions. The two patterns reversed direction after a randomly determined interval. Before or after this reversal, a stationary target was briefly presented near the pattern on the right. The target was stationary, rather than moving, because this allows a measurement of position without the confounding effects of target speed. **b**, Results of the first experiment for four subjects. The abscissa shows the ISA between the flashed target and the motion reversal. (Negative ISA indicates that the target was presented before the motion reversal.) The motion reversal is depicted by the vertical line at 0 ISA. Data have been merged so that the motion nearest the target was upwards, then downwards, as indicated along the abscissa. The ordinate represents the magnitude of the hand's endpoint deviation, which was calculated as the average endpoint of the hand for initially upward motion trials minus initially downward motion trials (see Methods). Each data point shows the time at which the target was physically presented and the hand's endpoint deviation (although the data points show the time at which the targets were presented, reaching movements were completed ~500 ms later). The influence of motion on the endpoint position of the hand varied systematically over time for each subject; the least significant effect was for subject J.A.D. ($F_{(6,77)} = 3.14$, $P = 0.008$). The solid line is a sigmoid fit to the average of the four subjects' data. Results are means \pm s.e.m.

Figure 1b shows that the endpoints of the reaching movements were shifted either upwards or downwards in the direction of the nearby motion. Target flashes presented well before (for example -940 ms) or well after (for example 470 ms) the motion reversal (at 0 ms) produced systematic shifts in the hand's position. Because the target in these cases was presented sufficiently long before or after the motion reversal, the entire reaching movement—both programming and execution—was performed during unidirectional motion (average movement onset and movement duration were 224 and 262 ms, respectively). For this reason it is unclear whether the motion influenced the programming phase or the on-line phase of the reaching movement, or both.

The target flash presented 235 ms before the moving pattern reversed direction addresses this question: because the average reaction time was 220 ms, motion was in one direction during most of the programming phase and in the opposite direction during the movement. This condition produced a markedly reduced shift in the movement endpoint (grey oval in Fig. 1b). The only way in which the shift in the hand's endpoint could be reduced to this extent would be if the contributions of visual motion to programming and on-line control were approximately equal.

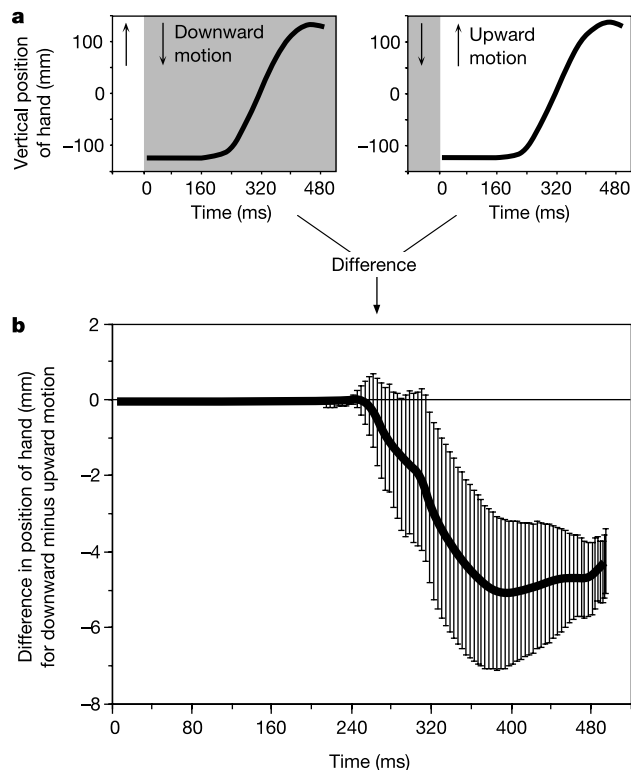


Figure 2 Average hand trajectories from experiment 1 for subject E.L.V., where the target flash occurred coincidentally with the motion reversal. **a**, The two trajectories show both sequences of visual motion (upwards followed by downwards, and vice versa). The grey region in each box represents the presentation of downward visual motion, and the white region indicates upward motion. The abscissa in each graph shows time; the target was presented at 0 ms. The ordinate shows the hand's vertical position (the visual motion on the screen was drifting vertically, so we were interested in the vertical position of the hand). **b**, The hand's trajectory during upward motion in **a** is subtracted from that for downward motion to give the difference in hand position over time. The ordinate shows the shift in the hand's position: negative values indicate that the hand deviated in the direction of visual motion. In this example condition, the target was presented synchronously with the motion reversal (0 ms), so the entire reaching movement was performed during unidirectional visual motion. There is a significant deviation in the trajectory of the hand as a function of time ($F_{(73,584)} = 3.2$, $P < 0.001$). Results are means \pm s.e.m.

Fast reaching movements were subject to on-line control, which is consistent with previous studies in which the target's location is physically altered at the beginning of the reaching movement^{10–14}. Because a continuously moving background was present in this first experiment, the data allow a close examination of how the representation of target location is updated over time and how this representation is used to adjust an ongoing response.

The left-hand side of Fig. 2a shows the average hand trajectory for one subject when there is downward visual motion near the target during the course of the reach (this sample trajectory is taken, in part, from the data point at 0 ms interstimulus asynchrony (ISA) for subject E.L.V. in Fig. 1b; initially the visual motion nearest the target was upwards, but when the target was presented the motion reversed direction, so that the reach was executed during downward motion only). When the trajectory for upward motion (right-hand side of Fig. 2a) is subtracted from this, giving the difference in hand position over time (Fig. 2b), it is clear that the hand continuously shifted in the direction of the nearby motion (increasingly negative values indicate a stronger influence of visual motion on hand position; see Supplementary Information for additional data).

One of the purposes of using a drifting pattern that reversed direction was to reveal the time course of the influence of motion on hand position. Figure 3a shows the average hand trajectories during upward and downward motion in response to the target presented 235 ms before the motion reversed direction (results are for the

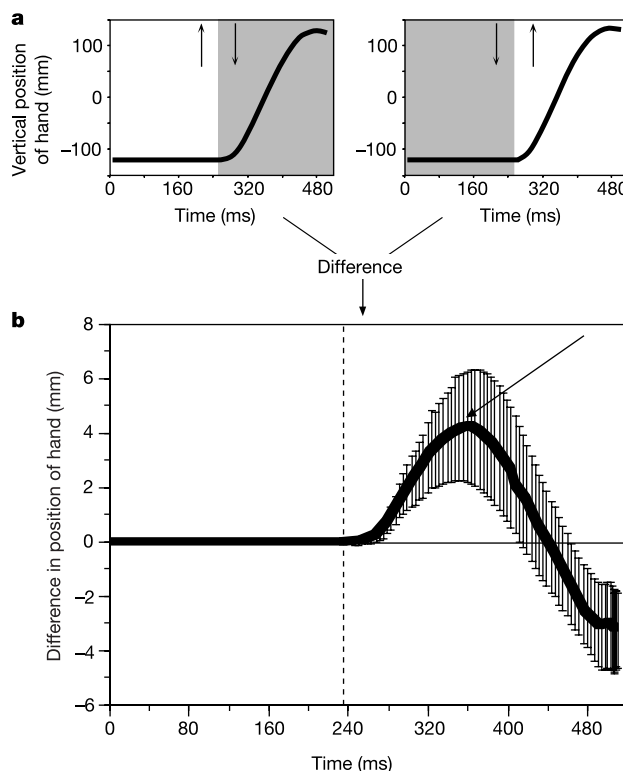


Figure 3 Average hand trajectories from experiment 1 for subject ELV, where the target was presented 235 ms before the motion reversal. **a**, As in Fig. 2, the grey region in each box represents the presentation of downward motion, and the white region represents upward motion. The target was presented at 0 ms. **b**, The trajectories of the hand for the two sequences of motion in **a** are subtracted (upward–downward minus downward–upward). The vertical dashed line represents the motion reversal. The ordinate shows the shift in the hand's position over time. The hand's position began to deviate in the initial direction of motion (increasingly positive values), but eventually the hand shifted in the opposite direction (arrow), which is consistent with the subsequent (reversed) direction of motion. There is a significant deviation in the trajectory of the hand as a function of time ($F_{(80,320)} = 12.96$, $P < 0.001$). Results are means \pm s.e.m.

same subject as in Fig. 2). Figure 3b shows the difference between these curves, which reveals the influence of the motion reversal on the hand's trajectory. In this case, visual motion is in one direction during most of the programming phase and in the opposite direction during the execution of the reaching movement. Interestingly, the trajectory of the hand follows the same pattern: the hand deviates in the direction of the initial motion and subsequently shifts in the opposite direction, mimicking the motion reversal.

Because there is a significant visuomotor delay, some time must pass before visual information can influence the trajectory of the hand. This delay can be estimated from the data in Fig. 3b. Immediately after movement onset (236 ms), the hand begins to deviate in the direction of the initial visual motion. The hand eventually starts to shift in the opposite direction (arrow in Fig. 3b), reflecting the influence of the motion reversal on the hand. The delay between the actual motion reversal (dashed vertical line at 235 ms) and the moment that the data curve reaches a plateau (350 ms) gives a minimum visuomotor delay of ~114 ms (see Supplementary Information for an alternative method of calculating the delay). The upper limit on the visuomotor delay is ~201 ms, based on the moment (437 ms) at which the average deviation of the hand's position differs significantly from that estimated from the minimum visuomotor delay ($t_{(73)} = 2.05$, $P < 0.05$); this is consistent with the fact that the hand's relative position becomes negative at 437 ms. (Estimates of visuomotor delay for additional

subjects are provided in Supplementary Information). The range of this estimated visuomotor delay (~114–201 ms) is similar to that for actual changes in target location^{1,10,12,14,15}, indicating that the influence of visual motion on the updating of fast reaching movements occurs on the same time scale as actual changes in target position; that is, motion-generated position reassignment might be equivalent to a shift in the real position of the target¹⁵. This is surprising, because it indicates that information unrelated to the target (extraneous visual motion) might be processed as fast as information specific to the target, such as actual target location.

The present results show that visual motion information can cause shifts in fast reaching movements to the location of a briefly presented, unrelated stationary object. Previous studies have found that goal-directed reaching can, in some circumstances, be influenced by perceptual illusions, indicating that the awareness of a stimulus might determine the behavior^{15–22}. Figure 3b shows that this did not occur in the present experiment. The trajectory of the hand was modified continuously as the direction of visual motion changed. In this particular case, the hand first moved in the direction of the initial motion (for example upwards, after upward visual motion; the first significant deviation of the hand upwards occurred ~35 ms after movement onset). However, the target flash is never perceived to be shifted upwards in this situation; the flash always appears either shifted downwards or not shifted at all⁷. The hand initially moved upwards, which is in a direction opposite to that of the perception. If reaching movements depended on awareness of the target's location, the hand should never have been shifted upwards; clearly visual motion influences the representation of target position for fast reaching movements without requiring explicit awareness of the target's position.

One possibility is that the visual motion influenced the perceived speed or position of the hand. To confirm that visibility of the hand is not necessary, we repeated the experiment while visibility of the hand was occluded. The results (see Supplementary Information) were similar to those of the first experiment (Fig. 1b), indicating that the influence of motion on reaching is not due to the visual representation of hand speed or location.

The influence of visual motion on fast reaching movements is greatly reduced when there are significant cues to the target object's position. For example, when the duration of the target is increased sufficiently, the endpoints of the movements are accurate (Fig. 4a). This is an interesting situation, because when the visual information about the location of the target is first used to guide the reaching movement, the visuomotor system has no knowledge of the duration of the target; in other words, at the beginning of the programming phase a brief target flash is identical to a long one, as far as the motor system is concerned. Therefore, for long-duration targets we might expect the trajectory of the hand to deviate in the direction of the visual motion early in the movement, but then to correct itself as the duration of the target increases. This is precisely what we observed (Fig. 4b). During the initial phase of the reach, the surrounding motion signals influenced the position of the hand. However, when there was continued retinal information about target location, the representation of position was recalibrated and the hand's trajectory was updated on-line. The implication is that for any abruptly appearing object, even one that remains visible, there is an influence of visual motion on the hand's early trajectory. The influence of motion on fast reaching movements (revealed in the first experiment) is therefore not restricted to flashed targets that disappear long before the onset of the hand's movement.

Fast reaching movements ultimately depend on a comparison of target and hand position in a common coordinate system^{10,23,24}, a comparison that is likely to be computed only on demand²⁵. However, information about target location must initially be represented in retinotopic coordinates. If this early representation of space were influenced by motion, we would naturally expect

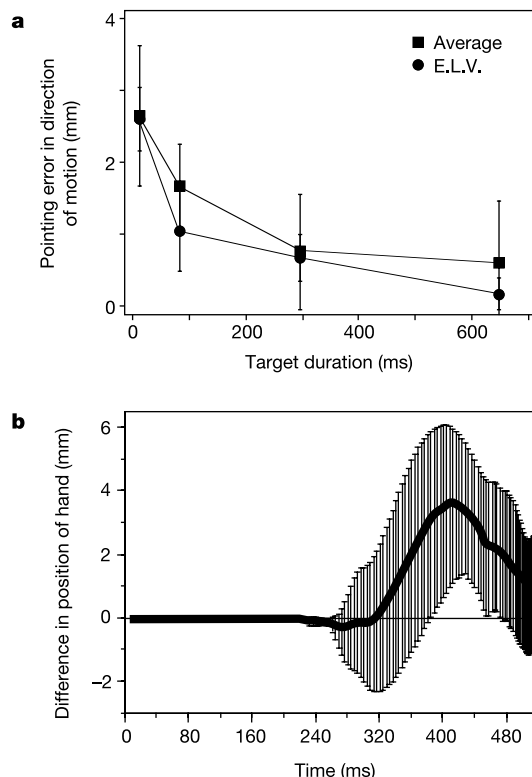


Figure 4 Deviations in reaching movements as a function of target duration. **a**, The endpoints of reaching movements to briefly presented targets were shifted in the direction of visual motion. When the duration of the target exceeded ~600 ms, reaching movement endpoints did not exhibit the bias. Data for E.L.V. and the average for nine subjects are shown. **b**, The error in the hand's trajectory is plotted for the 640 ms target duration condition in **a**. See Supplementary Information for additional results. As in Figs 2b and 3b, the difference in the hand's position for the two directions of motion is plotted. Positive values on the ordinate indicate that the hand deviated in the direction of visual motion. There is a significant overall effect of motion on the position of the hand ($t_{(299)} = 4.97$, $P < 0.001$). Results are means \pm s.e.m.

subsequent processing that hinges on this information to manifest a similar distortion. Indeed, motion information is known to influence position coding early in visual processing, even at the level of the retina²⁶ (and probably the cortex^{2,4,5,7,27–29}). It is therefore conceivable that retinal motion signals, even those unrelated to the target, such as the vertically drifting grating in our experiments or the motion across the retina during eye and head movements, might cause continuous updating of target positions for reaching movements. Because the most common source of retinal motion is eye and head movements, an intriguing possibility is that the influence of visual motion on the representation of target position is an adaptive mechanism that allows the hand's trajectory to compensate rapidly for movements of the eye and head with respect to the world.

If visual motion is used to help compensate for ego-motion when executing actions, then we might expect the removal of motion cues to cause increased errors in goal-directed reaching movements. In an experiment, subjects reached to targets while they were passively rotated in a chair (that is, subjects did not have control over their rotation). This form of ego-motion was employed because visual motion might be especially useful for the compensation of passive (unintended) movements of the body. There were three conditions in this experiment. In the first, subjects reached to the remembered locations of targets (light-emitting diodes (LEDs)) while in complete darkness (no visual cues were available). Because this removes not only retinal motion information but also static position cues, a second condition presented intermittent background illumination at ~4 Hz (the background consisted of 25 LEDs that were strobed; see Methods). This effectively eliminated motion information but left static position cues intact. In the third condition—the only condition in which motion information was available—the 25 background LEDs were continuously visible. When no background was visible, endpoints of the reaching movements were biased in the direction of the subject's rotation (subjects overshot the target, underestimating the magnitude of their rotation, which is consistent with previous studies³⁰). There was a significant improvement (decrease) in this bias when retinal motion was available, compared with both the intermittent illumination condition ($t_{(136)} = 4.4$, $P < 0.001$) and the condition in which no lights were visible ($t_{(132)} = 6.4$, $P < 0.001$; see Supplementary Information). In other words, the background visual motion caused a deviation in the reaching movement, and this helped to counteract a bias towards underestimating the magnitude of ego-motion.

Although retinal motion information might be useful for controlling action in cases of whole-body rotation, could it be useful in cases where just the eye moves? Because the relative positions of the hand and target do not change during an eye movement, it seems that any influence of motion on reaching movements would be counterproductive. To test this, we conducted an experiment similar to the previous one, except that subjects moved their eyes (smooth pursuit) rather than rotating their entire bodies (see Supplementary Information). Results showed that pointing movements were more accurate when there was a stationary background (providing retinal motion as the subject moved his or her eyes) than when the background was intermittently visible or not visible. Retinal motion, produced by either eye or body movements, therefore reduces a systematic bias in reaching movements.

Reaching quickly to targets seems effortless despite the frequency and even the unintentionality of ego-motion. The experiments here suggest that part of the reason for this precision and speed might be the use of visual motion signals as a means of rapidly gauging and compensating for errors that occur when the eye or body moves. □

Methods

Stimuli were presented on a CRT monitor (NEC, Itasca, Illinois, USA) with a refresh rate of 85 Hz, controlled by a Macintosh G4 computer (Apple Computer, Cupertino, California,

USA). The stimulus consisted of a pair of horizontally striped patterns (gratings) that drifted vertically in opposite directions (Fig. 1a). Each grating subtended $5.76^\circ \times 26.76^\circ$, and each was centred at $\pm 5.76^\circ$ eccentricity. The gratings had a sinusoidal luminance modulation of 0.17 cycles per degree at 85% contrast on a dark background (0.03 cd m^{-2}) and translated at 2.7 Hz. Subjects were seated 48 cm from the monitor in a darkened room with a chin rest to stabilize the head. Two of the authors and two naive subjects participated in the first experiment (a total of six additional subjects participated in the subsequent experiments). Subjects were right-handed and had normal or corrected-to-normal visual acuity. Reaching movements were recorded, by using a single infrared emitter on the tip of the index finger, with an Optotrak 3020 (Northern Digital, Inc., Waterloo, Ontario, Canada) at 250 Hz, under the control of the same computer that generated the stimuli.

A fixation bull's-eye was provided at the centre of the screen. In each trial there was a random vertical offset in the position of the bull's-eye within a range of 1.16° . Subjects were asked to fixate on the bull's-eye at all times. In each experimental trial, the two gratings (Fig. 1a) were initially stationary for ~500 ms and then began to translate in opposite directions. The initial direction of the gratings' motion was random in each trial. After a randomly determined interval between 1,050 and 1,750 ms the gratings both abruptly reversed direction and translated for an equivalent period. At varying periods of time before or after the gratings reversed direction (ISA, from 940 ms before to 470 ms after the reversal), a target bar (84.2 cd m^{-2}) was presented (as in Fig. 1a) for ~24 ms. The target subtended $2.89^\circ \times 0.29^\circ$ and could be located in one of three randomly determined positions, either vertically centred or 1.16° above or below centre. The Optotrak began recording the position of the hand immediately after the target was presented. Subjects pointed, with their right index finger, as quickly as possible to the position of the target, hitting the CRT with their finger. The distance between the hand's resting position and the target on the monitor was ~31–42 cm. The onset of the reaching movement was calculated by using a threshold hand velocity (50 mm s^{-1} for 20 ms). The end of the reaching movement was calculated as the moment that the hand's deceleration peaked (the subject hit the immobile CRT at a high velocity, and the resulting instantaneous deceleration of the hand marked the moment that the finger hit the screen). In the first experiment there were 90 trials for each of the seven possible ISAs. To measure average hand trajectories (in Figs 2–4) a minimum of 300 additional trials were collected in separate experimental sessions for each of the conditions of interest (the additional trials explain why the endpoints shown in Fig. 1b are not identical to the average endpoints shown in Figs 2–4). The average trajectory was calculated as the normalized position of the hand, every 4 ms for each of the (three) target positions, as a function of motion direction.

In the last experiment, subjects were seated in a vestibular chair that rotated sinusoidally (through $\sim 90^\circ$) at a peak frequency of $\sim 0.2 \text{ Hz}$. A chin rest was provided to immobilize the head. The head was located 20 cm from the axis of rotation. Subjects fixated on a red LED (16 cm distance) that was attached to the head (so the eye was fixed with respect to the body). Vision was monocular and the room was completely dark; subjects could not see their hand under any of the conditions. While subjects were stationary, a ~100-ms target LED (~40 cm distance) was presented in one of five randomly determined locations. Subjects began to rotate ~1 s later, clockwise and anti-clockwise on alternate trials. At a randomly determined time (1.4–2.8 s after the start of rotation), subjects were instructed to point as quickly as possible to the remembered location of the target. Endpoints of the reaching movements were determined as described above. In one condition there were 25 additional LEDs in the background that were continuously visible throughout the experiment (see Supplementary Information). In a second condition, the background LEDs were strobed at ~4 Hz (visible for ~30 ms, off for ~200 ms). In a third condition, there was no visible background. There were 100 trials in each of the three conditions. The mean endpoint position of the hand was calculated for each of the five target positions and two directions of rotation (reach error = mean endpoint minus the actual location of the target).

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Abundant gene conversion between arms of palindromes in human and ape Y chromosomes

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Eight palindromes comprise one-quarter of the euchromatic DNA of the male-specific region of the human Y chromosome, the MSY¹. They contain many testis-specific genes and typically exhibit 99.97% intra-palindromic (arm-to-arm) sequence identity¹. This high degree of identity could be interpreted as evidence that the palindromes arose through duplication events that occurred about 100,000 years ago. Using comparative sequencing in great apes, we demonstrate here that at least six of these MSY

palindromes predate the divergence of the human and chimpanzee lineages, which occurred about 5 million years ago. The arms of these palindromes must have subsequently engaged in gene conversion, driving the paired arms to evolve in concert. Indeed, analysis of MSY palindrome sequence variation in existing human populations provides evidence of recurrent arm-to-arm gene conversion in our species. We conclude that during recent evolution, an average of approximately 600 nucleotides per newborn male have undergone Y–Y gene conversion, which has had an important role in the evolution of multi-copy testis gene families in the MSY.

The human MSY palindromes, designated P1–P8, are surprisingly large, with arm lengths that range from 9 kilobases (kb; P7) to 1.45 megabases (Mb; P1) (see Table 2 and Figs 2, 3 and 5 of the accompanying manuscript¹). The paired arms of each palindrome are separated by a non-duplicated spacer that measures 2–170 kb in length. Fifteen gene and transcript families have been identified in the palindrome arms (none in the spacers), and all seem to be expressed predominantly or exclusively in testes¹. Similar to the palindrome arms in which they reside, these gene families are characterized by extremely low sequence divergence between the copies found in a single Y chromosome.

The DAZ gene family of the MSY resides exclusively in the arms of palindromes P1 and P2 (ref. 2). Near identity between DAZ copies in a single Y chromosome led some investigators to conclude, based on molecular clock reasoning, that DAZ gene amplification had occurred only within the last 200,000 years³. However, multiple Y-linked copies of DAZ also exist in apes and Old World monkeys^{3–6}. This suggests that palindromes P1 and P2, which contain the DAZ genes, might predate the divergence of humans from other primate lineages. This may be true for the other MSY palindromes as well. In that case, the near identity observed between palindrome arms could be the consequence of gene conversion—“the non-reciprocal transfer of information from one DNA duplex to another”. Gene conversion sometimes involves transfer between repeated sequences on the same chromosome⁸.

To test the ancient origins/gene-conversion hypothesis, we looked for evidence that MSY palindromes were present in the common ancestor of humans and chimpanzees. Specifically, we searched for orthologues of the eight human palindromes in chimpanzees (*Pan troglodytes*), bonobos (pygmy chimpanzee, *Pan paniscus*) and gorillas (*Gorilla gorilla*). In each species, and for each palindrome, we attempted to amplify, by polymerase chain reaction (PCR), and sequence the two inner boundaries (between spacer and arms) and the two outer boundaries (between arms and surrounding sequences). We successfully amplified both inner boundaries in multiple palindromes (Table 1). In all of these cases, the PCR products were observed only when male genomic DNAs were used as templates, and never when using female genomic DNAs (data not shown). This implies that the PCR products were amplified from the male-specific regions of the great ape Y chromosomes. In all cases, the boundary sequences were essentially identical in humans and great apes (Fig. 1a; see also Supplementary Information). Only for P7 did we successfully amplify both outer boundaries (in chimpanzee and bonobo). These findings suggested that: (1) most palindromes found in the modern human MSY were

Table 1 Ape MSY palindromes confirmed by sequencing of inner boundaries

Species	Palindrome					
	P1	P2	P4	P6	P7	P8
Chimpanzee	Y	Y	–	Y	Y	Y
Bonobo	Y	Y	–	Y	Y	–
Gorilla	–	–	Y	Y	–	–

Sequence alignments provided in Supplementary Information. Y indicates confirmation of MSY palindromes.