



Sensitivity to biological motion drops by $\sim 1/2$ log-unit with inversion, and is unaffected by amblyopia

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Abstract

The low-level deficits associated with amblyopia have been studied extensively, but very little is known about potential impairments to higher-level visual processing such as object recognition or structure-from-motion. Studies on biological motion, a complex form of structure-from-motion depicting human actions, have demonstrated that normal observers can analyze these patterns more effectively when they are shown in their original upright configuration as opposed to inverted upside-down (feet-up head-down). We measured this inversion effect quantitatively for both the dominant and amblyopic eyes of amblyopic observers. We found a modest ($\sim 30\%$) loss in sensitivity in the amblyopic eye for both upright and inverted actors, which we attribute to low-level deficits. However, we found no difference in the inversion effect between the two eyes, both showing an average $1/2$ log-unit drop in sensitivity between upright and inverted displays. Our data provide a quantitative estimate of the inversion effect for biological motion, and demonstrate that higher-level processing in the motion hierarchy is not affected by amblyopia.

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1. Introduction

It is well known that abnormal early visual experience can result in impaired vision, amblyopia, in the deprived eye. The deficits cannot be corrected by optics because their origin is neural (see [Kiorpes, 2006](#); [Levi, 2006](#) for recent reviews). Reduced acuity is the clinical standard for preliminary diagnosis ([Ciuffreda, Levi, & Selenow, 1991](#)), but decades of psychophysical investigations have exposed other impairments in pattern analysis, ranging from undercounting of visual objects ([Sharma, Levi, & Klein, 2000](#)) to impaired conjunction of multiple attributes ([Neri & Levi, 2006](#)). Some studies have suggested that amblyopia affects computation not only at low, but also at higher-level stages in the visual processing hierarchy ([Giaschi, Regan, Kraft, & Hong, 1992](#); [Ho et al., 2006](#)). Consistent with these proposals, it has been claimed that cortical abnormalities associated with amblyopia

extend well into extrastriate cortex, reaching areas that are believed to support complex visual processes such as object recognition ([Lerner et al., 2006](#); [Lerner et al., 2003](#); [Muckli, Kiess, Tonhausen, Singer, & Goebel, 2006](#)).

We wished to test this proposal, namely that amblyopia may affect visual analysis at the higher cognitive level, by measuring how efficiently motion information delivered to the amblyopic eye is organized into complex patterns for the perception of human actions. More specifically, our displays only contained dots that moved along the trajectories generated by the main joints of two fighters ([Neri, Luu, & Levi, 2006](#)). These point-light displays are often referred to in the literature as ‘biological motion’ stimuli ([Johansson, 1973](#)), and several lines of evidence indicate that the ability to process these stimuli relies on higher-level structures in the cortical hierarchy (e.g., [Battelli, Cavanagh, & Thornton, 2003](#); [Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001](#); see [Blake & Shiffrar \(2007\)](#) for a more detailed survey of the literature on this topic). It is well known that, like for faces ([Valentine, 1988](#)), these stimuli are easier to recognize if

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they are presented in upright as opposed to upside-down configuration (Pavlova & Sokolov, 2000; Sumi, 1984). This ‘inversion’ effect is generally regarded as a demonstration of the involvement of top-down influences from higher-level stages in the processing hierarchy (Blake & Shiffrar, 2007). We therefore speculated that, if amblyopia negatively affects the computations performed at these higher levels and/or their subsequent top-down modulations, the benefit obtained from presenting biological motion in an upright configuration should be largely reduced for the amblyopic eye, resulting in little or no difference in amblyopic sensitivity to upright and inverted displays.

We measured sensitivity quantitatively by using a well-established noise masking technique, where sensitivity is determined by counting the number of noise dots that bring recognition to threshold levels (Morrone, Burr, & Vaina, 1995; Neri et al., 2006; Neri, Morrone, & Burr, 1998). We observed a difference of about 1/2 log-unit between the number of tolerated noise dots for upright versus inverted displays (ratio upright/inverted between 2 and 4). The magnitude of this effect was virtually identical for the amblyopic and non-amblyopic eyes. We found a slight reduction in overall sensitivity for the amblyopic eye compared to the non-amblyopic eye, but this reduction affected upright and inverted displays equally, so it cannot be attributed to higher-level processing. We conclude that amblyopia does not affect the higher-level stages involved in the analysis of biological motion, and provide evidence that abnormal visual development may not affect higher-level vision processes once the lower-level deficits are taken into account.

2. Methods

2.1. Motion capture

We obtained a natural sample of human fighting by filming two athletes (recruited from the UC Berkeley Martial Arts team) who performed a mixture of kicking, boxing and close-body contact (Fig. 1a) while wearing sports clothes which we had fitted with battery-driven body lights (ClubThings, Los Angeles, CA). There were 13 such light markers on each actor: 1 on the head, 2 shoulders, 2 elbows, 2 wrists, 2 hips, 2 knees, and 2 feet. We filmed them in a dimly lit room using a camera device (Logitech QuickCam) which generated digital AVI movies at 10 Hz and 640×480 pixel² resolution. The movies were processed by customized Matlab software which we wrote for the specific purpose of computer-assisted motion capture. The program performed basic cluster analysis to identify extensive regions of high luminance corresponding to the body lights, and attempted to place markers that would track the motion of individual clusters throughout all frames in the movie. A graphical user interface allowed us to view the outcome of this automated tracking frame-by-frame, and correct the numerous errors made by the program. This human/computer mixed procedure allowed us to track each joint in $x-y-t$ (we interpolated the sequence to obtain 30 Hz sampling), and tag all disappearances caused by occlusion. We tracked 22.7 s of fighting.

2.2. Observers

Five amblyopic observers participated in our study, see Table 1 for details. The acuities listed in Table 1 were determined using a Bailey-Lovie chart, and we specify both the full line letter acuity and the isolated letter acuity.

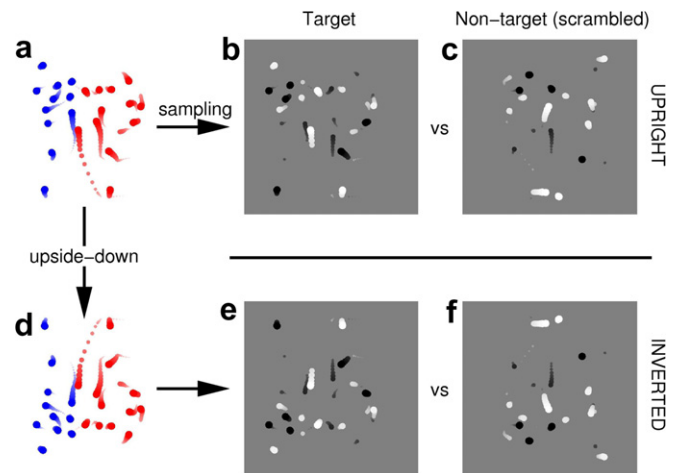


Fig. 1. The database consisted of a 22-s sequence of motion-captured fighting between two athletes, shown in different colours for clarity (a). For the purpose of providing a static depiction of the moving stimulus, throughout the whole figure the size and contrast of each dot are reduced as the dot position refers to more remote frames (no such manipulations were applied to the real stimulus). We presented two intervals on each trial. One interval (‘target’) displayed a 1.5-s excerpt from the database, sampled so that each moving dot had a limited lifetime of 120 ms and could be either bright or dark (b). The other interval (‘non-target’) contained another excerpt, but scrambled so that the structure of the fighters was destroyed while preserving the local motion of individual dots (c; see Section 2). Each trial could be of either ‘upright’ or ‘inverted’ type (mixed within the same block). On ‘upright’ trials, stimuli were extracted from the original database (a). On ‘inverted’ trials, stimuli were extracted from an upside-down version of the database (d), thus generating upright and inverted excerpts for ‘target’ and ‘non-target’ intervals (e and f, respectively).

2.3. Stimulus design and psychophysical tasks

Each trial could be of either ‘upright’ or ‘inverted’ type, depending on whether stimuli were drawn from the original fighting sequence (obtained as described in the previous section and depicted in Fig. 1a) or from a sequence that was identical to it, with the only exception that it was inverted upside-down (Fig. 1d). Upright and inverted trials were randomly mixed within the same block, and observers were not informed of the presence of inverted stimuli. Each trial consisted of two intervals, one containing a ‘target’ stimulus (Fig. 1b) and the other one containing a ‘non-target’ stimulus (Fig. 1c). The order of the two was randomly chosen, and the task was to indicate the ‘target’ interval by pressing one of two buttons (temporal 2-alternative forced choice) where the target was described to the observers as the interval most closely portraying a fighting interaction between two humans. Before testing, they were shown a noise-free, fully sampled version of the entire sequence so that they knew what we meant by this. All subjects immediately recognized the fighting action in the noise-free stimulus, and had no trouble converting our instructions into a behavioural strategy for alternative forced choice.

For each interval, we randomly selected a short segment from the fighting sequence (depending on trial type, we used the upright or the inverted version). The duration of the segment was 1.5 s for S1–4, and 2.4 s for S5 (this subject, the oldest in our sample, felt more comfortable with a slightly longer duration). The selected segment was displayed using a limited lifetime sampling technique in which the 26 trajectories were randomly sampled by 12 dots (9.2 arcmin diameter) which only lived for 120 ms (matching the temporal integration window of local motion detectors (Burr, 1980)), after which they sampled a different trajectory (Fig. 1b and c and Fig. 1e and f). Dot appearance and disappearance was asynchronous across dots to avoid motion transients from simultaneous tran-

Table 1
Visual characteristics of amblyopic observers

Observer	Age (yrs)	Gender	Strabismus (at 6 m)	Eye	Refractive error (diopter)	Line letter acuity (isolated letter acuity)
<i>Strabismic</i>						
S1 (■)	19	F	L EsoT 4 ^Δ & L hyper 2 ^Δ	R	−1.50/−0.50 × 180	20/12.5 ^{−2}
S3 (◆)	22	F	L EsoT 6–8 ^Δ & hyperT 4–6 ^Δ	R	−0.75/−0.25 × 5	20/50 (20/32 ⁺¹)
				L	+1.25 +1.00	20/16 20/40 (20/32 ⁺¹)
<i>Strabismic and anisometric</i>						
S2 (●)	22	F	R EsoT 4–6 ^Δ & hypoT 4 ^Δ	R	+2.75/−1.0 × 160	20/80 ^{−1} (20/50 ^{−1})
				L	−1.00/−0.50 × 180	20/16 ^{−1}
S4 (▲)	22	F	L EsoT 4–5 ^Δ & hyperT 3–5 ^Δ	R	Plano	20/10 ^{−1}
				L	+5.50/−3.00 × 55	20/127 (20/100 ^{−2})
S5 (▼)	55	F	Alt. ExoT 18 ^Δ	R	+2.75/−1.25 × 135	20/40 (20/25 ⁺¹)
				L	−2.00	20/16 ^{−2}

sitions of all sampling dots (see Neri et al., 1998). Dots could be randomly bright (74 cd/m²) or dark (0 cd/m²) on a gray (37 cd/m²) background (ensuring that no change in mean luminance ever took place in our experiments) and did not change colour during their lifetime. The trajectories were sized so that their overall centre of mass (across the entire sample) was centred on a Iiyama monitor driven by a VSG graphics card (Cambridge Research Systems), and they did not extend outside a 6.4° × 6.4° region. Subjects fixated on a central marker at 114 cm distance from the monitor (fixation was only loosely enforced) using only one eye (the other one being patched), alternating between their amblyopic and non-amblyopic eye between blocks.

In the ‘non-target’ interval, we scrambled the trajectories of both agents by selecting a different segment from the original sample for each trajectory, similarly to Blake, Turner, Smoski, Pozdol, and Stone (2003) (see also Neri et al., 2006). This procedure ensures that the raw motion content averaged across trials is identical for ‘target’ and ‘non-target’ (scrambled) intervals because each individual joint is sampled uniformly in both. Moreover, target and non-target stimuli cannot be discriminated by analyzing individual motion trajectories. It is necessary to integrate local motion information to perform the task. Although we cannot be entirely sure as to which cues were used by our observers in discriminating between target and non-target interval after they had integrated local motion signals, we can safely rule out a differential role of any low-to-mid-level cues in the comparison between upright and inverted thresholds. The inverted stimulus is simply an upside-down version of the upright one, so it preserves all low and mid-level statistics (Bertenthal & Pinto, 1994; Tadin, Lappin, Blake, & Grossman, 2002). Because it is only this comparison that is relevant to our analysis, we can safely conclude that our interpretation of the data is not confounded by potential low-to-mid-level cues.

2.4. Threshold estimation

We disrupted performance by masking the stimuli with noise dots. Each noise dot trajectory was generated as if it came from one of the dots sampling the tracked stimulus, except it was then rotated by 0°, 90°, 180° or 270° randomly for each lifetime and its starting positions could be anywhere within a 7.7° × 7.7° region. This ensured that the local motion of the noise dots was identical to those sampling the stimulus (except for rotation). We measured the percentage of correct target identifications as a function of number of noise dots (on a 2-up 1-down staircase, two separate staircases were run in parallel for upright and inverted trials), and fitted a Weibull function to this psychometric curve to obtain the threshold estimate (α parameter).

3. Results

When asked to discriminate point-light fighters (Fig. 1b and e) from their scrambled version (Fig. 1c and f), observ-

ers could tolerate between 5 and 120 noise dots per second. Individual thresholds are plotted in Fig. 2, where each point refers to the eye (solid for amblyopic, open for non-amblyopic) of an individual observer. Thresholds for trials on which the fighters were in their upright configuration (depicted in Fig. 1a–c) are plotted on the x axis in Fig. 2, while thresholds for trials on which the stimuli had been inverted (depicted in Fig. 1d–f) are plotted on the y axis. All points fall below the unity line (paired t -test for upright > inverted (one-tailed) returns $p < 0.03$ (solid) and $p < 0.01$ (open)), confirming and extending previous demonstrations that upright biological motion is easier to

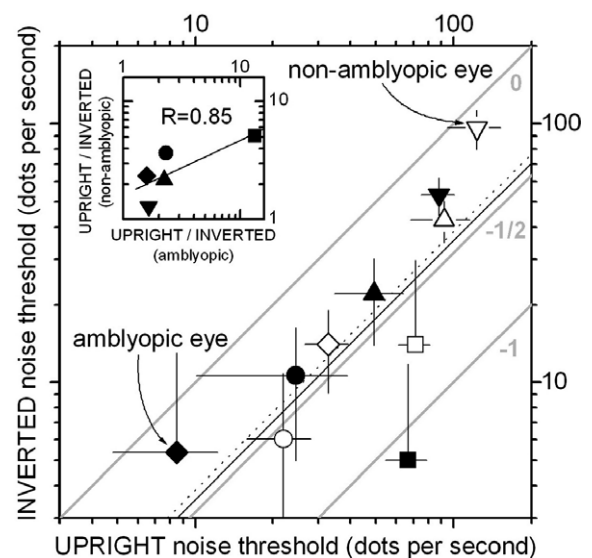


Fig. 2. Noise thresholds (in units of noise dots per second) are plotted for upright (x axis) and inverted (y axis) stimuli, for both amblyopic (solid) and non-amblyopic (open) eyes. Different symbols refer to different subjects (■ S1, ● S2, ◆ S3, ▲ S4, ▼ S5). Grey lines indicate sensitivity drops between upright and inverted of 0, $-1/2$ and -1 log-units (as labeled). Thin black lines show best-fit sensitivity drops across observers for amblyopic (solid) and non-amblyopic (dotted) eyes. Inversion causes a drop in sensitivity of roughly $1/2$ log-unit for both eyes. Inset plots upright/inverted ratios in individual observers (same symbols as in main panel) for amblyopic (x axis) versus non-amblyopic (y axis) eye, showing a correlation across observers of 0.85 between eyes.

discriminate than upside-down biological motion. The notable difference between Fig. 2 and previous results is that we measured sensitivity thresholds, whereas previous studies reported percentage correct values (Pavlova & Sokolov, 2000; Sumi, 1984). Our procedure involved measuring the whole psychometric curve and using it to estimate a threshold (see Section 2), while previous studies only looked at one point on the curve.

Measuring thresholds requires more data collection and the use of additional tools for manipulating signal-to-noise ratios, but it also comes with more detailed information. Specifically, we are able to provide a quantitative measure of the sensitivity drop caused by inversion. This measure can then be related to well-known concepts in signal detection theory. The three grey lines in Fig. 2 indicate sensitivity drops between upright and inverted conditions corresponding to 0 (no drop), $-1/2$ and -1 log-units. The two thin black lines show the average drops (across subjects) for amblyopic (solid) and non-amblyopic (dashed) eyes. For both eyes, we observe an average drop in sensitivity between upright and inverted close to $-1/2$ log-unit (-0.45 for amblyopic eye, -0.42 for non-amblyopic eye). There is some individual variability: one subject (inverted triangle) shows almost no effect, another subject (square) shows an effect close to -1 log-unit.

A comparison of the absolute threshold values for amblyopic and non-amblyopic eyes shows that the former are overall less efficient than the latter by an average factor of 0.71. This can be seen by comparing the performance of each eye of the same observer in Fig. 2 and noting that, for a given observer (with the exception of S2), the amblyopic eye (solid symbol) is shifted down and to the left (along the diagonal). This factor is identical for upright and inverted conditions, meaning that although the amblyopic eye generally performed more poorly than the non-amblyopic eye, this loss in efficiency was independent of inversion.

4. Discussion

4.1. Internal controls for low-level deficits

We designed our experiments to test a specific hypothesis: that amblyopia may impair higher-level stages in the processing of biological motion. In order for any test of this sort to be valid, we had to ensure that low- and mid-level processing of motion information was not a limiting factor for the amblyopic visual system in our experiments, or at least that any amblyopic impairment of low-level processing could be factored out and not confound our conclusions about the implications of our results for higher-level processing. We achieved this goal in two ways.

First, we selected stimulus parameters that rendered the motion of individual dots easily visible to our sample of amblyopic observers. We used large dots of very high contrast, and piloted our stimuli on each observer to ensure that the details of the display could be optimally discerned by their amblyopic eye. This strategy worked very well, as

demonstrated by the fact that the amblyopic eye (solid symbols in Fig. 2) could tolerate an average amount of noise equal to 70% of that tolerated by the non-amblyopic eye (open symbols). Moreover, there was no correlation between the acuity loss in individual observers and the performance loss in our task for the amblyopic eye as opposed to the non-amblyopic eye. To the contrary, we found a strong correlation ($R = 0.85$; without the outlier (square symbol) $R = 0.66$) between amblyopic and non-amblyopic eye for the inversion effect (threshold ratio upright/inverted), meaning that if a given observer showed a strong (or weak) inversion effect in one eye he/she also showed an equally strong (or weak) effect in the other eye (inset in Fig. 2). This result indicates that the source of the inversion effect was common to both eyes, and (together with the above-mentioned lack of correlation for acuity) independent of the amblyopic deficit.

Nevertheless we did observe a 30% loss for the amblyopic eye (as mentioned in the preceding paragraph). We can attribute this loss entirely to low-level processing by relying on the second feature of our experimental design (see Mather, Radford, and West (1992) for evidence that low-level manipulations of motion information affect biological motion processing, but see also Ahlström, Blake, & Ahlström, 1997 for some discrepancies on results obtained by manipulating contrast polarity of the dots). In our experiments, performance in the inverted condition is always assessed by comparing it against performance in the upright condition, separately for each eye. The 30% loss in performance mentioned above was observed for both upright and inverted trials, so it does not affect the ratio between the two conditions. It is only this ratio that pertains to the inversion effect and to its implications for the involvement of higher-level processing in our experiments. By focusing on this ratio, we are effectively using the upright condition as an internal control for factoring out any performance loss that was not related to the upright-versus-inverted comparison, leaving us with an uncontaminated estimate of potential higher-level deficits. We can safely conclude that, once this internal control is used to interpret our data, no difference was present between amblyopic and non-amblyopic eyes. In both cases, inversion of the biological motion display led to a sensitivity loss of $\sim 1/2$ log-unit (ratio upright/inverted between 2 and 4).

4.2. Relation to other studies on the inversion effect

The sensitivity loss that we measured here is highly consistent with previous estimates of the inversion effect in other perceptual domains, such as face processing. An extensive literature review of the face inversion effect showed that the upright/inverted threshold ratio is up to a factor of ~ 2 (Martelli, Majaj, & Pelli, 2005). A similar figure was found for upright versus inverted words (Martelli et al., 2005), and we also found similar ratios for our amblyopic subjects (inset to Fig. 2) with the exception of one (square symbol), who showed an overall stronger

effect. Finally, we measured an average upright/inverted ratio of ~ 2 (2.2 to be precise) in 5 normal subjects for biological motion. This value is obtained by analyzing previously published data from Figure 2a in Neri et al. (2006), more specifically by taking the abscissa values for the red symbols and contrasting solid (upright) with open (inverted). In that paper we measured noise thresholds in very similar conditions to those used for the present study, with the following two exceptions: (1) the non-target interval only contained one scrambled agent, so the task consisted of selecting the interval that contained 2 agents as opposed to 1 agent, and (2) on inverted trials only one agent was inverted (for the non-target interval it was always the non-scrambled agent). We find that, despite these differences, there is remarkable consistency between our measurements in normal and amblyopic subjects.

4.3. No impairment in higher-level motion processing

There is some controversy as to whether amblyopia causes impairments in motion processing that are not simply attributable to the unquestioned losses in contrast and pattern sensitivity that are associated with this condition. A recent study of monkeys with experimental amblyopia (Kiorpes, Tang, & Movshon, 2006) showed that, consistent with human amblyopes (Steinman, Levi, & McKee, 1988), motion sensitivity functions are shifted toward lower spatial scales, but they also report a specific deficit for long temporal offsets, suggesting an abnormality in temporal integration, possibly at a stage downstream from the initial spatial filtering stage. Some studies have claimed that performance in certain tasks requiring mid-to-low level motion analysis is affected by amblyopia (Ho et al., 2006; Simmers, Ledgeway, Hess, & McGraw, 2003), while others have found no loss in other tasks that would seem to target similar stages in the motion processing hierarchy (Hess, Mansouri, Dakin, & Allen, 2006; Levi & Tripathy, 2006; Tripathy & Levi, 2006). The question of whether amblyopia affects low- and/or mid-level motion perception remains therefore open, and our experiments do not provide any useful information in this respect.

Our results relate to later stages in the motion processing hierarchy, which we broadly term ‘higher-level’. Our definition of higher-level in this context refers to stages that are subsequent to optic flow extraction. More specifically, we assume that the motion vector-map has been successfully computed, and that the nature of local flow patterns (such as translation or rotation) has been established. Subsequent to these early stages (which we refer to as low- and mid-level), the visual system needs to retrieve structure from motion, i.e. identify potential semi-rigid shapes that are consistent with the motion patterns contained in the vector-map (Hoffman & Flinchbaugh, 1982; Ullman, 1979; Webb & Aggarwal, 1982). The bottom-up component of this analysis is presumably independent of whether the biological motion stimulus is upright or inverted (both conditions contain structure), but any top-down influence will be affected by

inversion (e.g., Tadin et al., 2002). For example, if the visual system uses stored patterns of human actions to guide structure-from-motion retrieval in our stimuli, this top-down influence may prove useful for upright patterns but not for inverted patterns because the latter do not correspond to those that the visual system has experienced during natural vision and stored in memory. Alternatively, there may be no top-down influence on structure-from-motion retrieval, and structure-from-motion may be carried out equally well for both upright and inverted conditions by strictly bottom-up analysis. In this scenario, knowledge about the natural configuration of human actions would only be used for the purpose of matching the retrieved structures to patterns stored in memory for recognition. Because the stored patterns are presumably upright, inversion of the stimulus would hinder this stage.

We can summarize the above discussion as follows: inversion certainly affects the final recognition stage, and may also affect top-down influences on structure-from-motion retrieval if (as demonstrated by Bülthoff, Bülthoff, and Sinha (1998)) such top-down influences play any role in our experiments. Our interpretation of the data in Fig. 2 relate to these higher-level stages as just defined. In this specific respect, our data show no effect of amblyopia on visual processing of motion information, but of course we cannot exclude that processing at earlier stages in the motion hierarchy is affected by this pathology. Although the lack of amblyopic impairment for biological motion may appear unsurprising, there is evidence that the human visual system undergoes a transition from local to global processing of biological motion (as defined in Bertenthal and Pinto (1994)) at around 5 months of age (Booth, Bertenthal, & Pinto, 2002), so it is not entirely unconceivable that a developmental disorder like amblyopia may have resulted in impaired transition to the global stage. Our results show that this is not the case.

4.4. Motion versus form processing pathways

Previous claims of higher-level impairments in amblyopic vision were restricted to perceptual phenomena (such as object recognition) that are believed to be supported by the form processing pathway (Lerner et al., 2006; Lerner et al., 2003; Muckli et al., 2006). The only claims relating to the motion processing pathway have involved mid-level vision, such as optic flow processing (Simmers et al., 2003). It is therefore possible that, although there may be no higher-level impairments in motion processing as demonstrated by our study, such impairments may be present along the form processing pathway. We cannot exclude this possibility, but we believe it is unlikely for the following reasons.

First, it is widely recognized that biological motion involves computations along both the motion and the form processing pathways (Giese & Poggio, 2003; Lange & Lappe, 2006). If amblyopia affected higher-level stages within the form processing pathway, we would expect at least a partial reduction of the advantage for the upright configu-

ration in biological motion (which we do not observe). It is very unlikely that impairments to the form processing pathway would not be reflected in the processing of complex stimuli like biological motion patterns.

Second, the size of the inversion effect that we measured for biological motion is similar to previous estimates of this effect for tasks involving form processing with no motion processing, such as face and word recognition (Martelli et al., 2005). This result lends strength to the above-mentioned speculation that the cortical pathways involved in the analysis of biological motion stimuli overlap at least partly with those supporting the perception of visual form (Giese & Poggio, 2003). We predict that our experiments on the inversion effect in amblyopia would be replicated with similar results if using other stimuli that do not involve motion, such as faces. We are currently testing this prediction in our laboratory.

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