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Perception of coherent motion, biological motion and form-from-motion under dim-light conditions

E.D. Grossman, R. Blake *

Department of Psychology, Vanderbilt Vision Research Center, Vanderbilt University, Nashville, TN 37240, USA

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Abstract

Three experiments investigated several aspects of motion perception at high and low luminance levels. Detection of weak coherent motion in random dot cinematograms was unaffected by light level over a range of dot speeds. The ability to judge form from motion was, however, impaired at low light levels, as was the ability to discriminate normal from phase-scrambled biological motion sequences. The difficulty distinguishing differential motions may be explained by increased spatial pooling at low light levels.

Keywords: Motion perception; Light level; Form from motion; Biological motion; Coherence; Random dot cinematogram

1. Introduction

As everyone knows, it's hard to see when it's dark. Colors fade to shades of gray, stereoscopic depth perception deteriorates, and reading can become impossible because of reduced visual acuity. These changes in visual performance under dim-light conditions are well explained by changes in the visual mode of processing; a shift from cone- to rod-dominated photoreception, and changes in the balance between center/surround mechanisms of retinal ganglion cells effectively enlarge the cells' summation area (Barlow, Fitzhugh & Kuffler, 1957; Derrington & Lennie, 1982). In general, at lower light levels spatial resolution is compromised in the interests of sensitivity.

However, based simply on experience one is not aware of wholesale changes in the ability to see object movement under dim-light conditions, nor does our reliance on optic flow for navigation seem seriously hampered. Yet mechanisms responsible for motion perception receive inputs from the same 'front-end' mechanisms whose response properties adversely affect vision at low light levels. Moreover, it is well established that the temporal response of the visual system becomes more sluggish at low light levels (e.g. Matin, 1968), which can be modeled as a blurring of the temporal impulse response (Kelly, 1971). To the extent that early temporal filters are involved in the analysis of motion information, one would reasonably expect reductions in light level to impact perception of motion. Much recent research has been devoted to describing the human capacity to perceive motion and to understanding the neural mechanisms involved, but the vast majority of that work has been limited to perception at high luminances. Only a handful of studies have assessed motion perception at low light levels (e.g. Dawson & Di Lollo, 1990) and none of those has examined more refined aspects of motion perception such as form from motion.

Accordingly, this paper compares three aspects of motion perception–coherence detection, form from motion (FFM) and biological motion-at high and low light levels. From a computational standpoint, these motion tasks would seem to involve different processing operations. Detection of coherent motion requires integration of motion signals over space and time, while FFM and biological motion require spatial and temporal differentiation of motion signals. Adding to its complexity, biological motion entails dynamic, hierarchically arranged pendular motions which, when viewed

* Corresponding author. Tel.: +1-615-343-7010; fax: +1-615-343-5027.

E-mail address: randolph.blake@vanderbilt.edu (R. Blake)

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under optimal conditions, group to produce the global perception of biological activity.

2. General methods

2.1. Observers

Four observers (two naive) voluntarily participated in these experiments. All received practice on each task before formal data collection. All procedures were approved by the Vanderbilt Institutional Review Board.

2.2. Displays

Animation sequences were generated on a calibrated Sony color monitor (800 h × 600 v pixels, 75 Hz framerate) under the control of a Macintosh PowerPC. The monitor was viewed monocularly from a distance of 94.5 cm with a patch covering the untested eye. All experiments utilized approximately 50 black dots seen against a gray background. Individual 'dots' were actually small square clusters of pixels together subtending 1 arc min. Dot motion was produced by spatially displacing dots from frame-to-frame of the animation sequence, with a constant interframe interval of 53 ms (i.e. four video frames). For the biological motion animations, dot step-size (and, hence, dot speed) was optimized to yield the most natural appearing biological motion sequences. For the motion coherence and the FFM displays, dot speed was set to the average of the dot speeds present in the biological motion sequences, 3.2° s^{-1}.

For the high luminance condition, background light level was 3.6 cd m^{-2}. For the low luminance condition the monitor remained unchanged but the observer viewed the display through a pair of tightly fitting welder's goggles outfitted with a filter that reduced the effective light level by 2 log-units (0.036 cd m^{-2}); again, a patch was worn over one eye. Throughout this paper we refer to these two light levels as 'high' and 'low' because, with one exception, we have not used artificial pupils and, therefore, cannot specify the exact retinal illumination associated with these light conditions. Based on published figures, however, there is no doubt that our 'high' level stimulates the photopic system and the 'low' level stimulates the scotopic system exclusively. Each testing session spanned approximately 45 min, and testing at the low light level was always preceded by a period of dark adaptation lasting at least 10 min. In none of the experiments did performance improve during the course of a testing session, confirming that with this adaptation period the scotopic system reached a stable level of motion sensitivity. Prior to formal data collection, we confirmed that: (a) color perception was impossible at this low light level (using a custom-designed color chart displayed on the monitor); and (b) visual acuity was reduced approximately 20-fold (as assessed using a conventional letter chart generated on the computer monitor).

2.3. Experiment 1: coherence detection

This first experiment used random dot cinematograms (Williams & Sekuler, 1984) to measure the minimum motion signal needed to discriminate weakly coherent motion from random motion. These stochastic animation sequences are particularly useful since much progress has been made in understanding the neural concomitants of perception of coherence in these dot displays (e.g. Britten, Newsome, Shadlen, Celebrini & Movshon, 1996).

2.3.1. Methods

Random dot cinematograms (RDC) composed of 50 dots/frame were viewed within a circular aperture 5.5° in diameter. Following a 2IFC procedure, observers viewed two successive RDC presentations each approximately 0.5 s in duration. During one interval, all 50 dots selected their directions of motion randomly from frame-to-frame (incoherent motion, or 'noise'), and in the other interval a fraction of dots ('signal dots') moved upward while the remainder of dots were free to move in any direction. Signal dots were randomly reselected from frame-to-frame, which prevented observers from tracking a single dot. For both signal and noise dots, dot speed was 3.2° s^{-1}, and the apparent motion of the dots was very smooth. The percentage of signal dots varied randomly from trial-to-trial within limits, according to a method of constant stimuli. Observers completed two hundred fifty trials in each condition, with fifty trials devoted to each of five signal levels.

2.3.2. Results and discussion

Probit analysis was used to fit psychometric curves to the percent-correct scores, and from those curves we determined the signal level associated with 75%-correct performance. Those threshold values and associated standard errors are shown in Fig. 1A. A t-test confirmed that the differences between coherence thresholds in the high and low luminance conditions were not statistically significant ($P > 0.05$). For all observers coherence detection was just as easy in the low luminance condition as it was in the high condition.

Because observers viewed the display through natural pupils, the drop in retinal illuminance at the low light level was not exactly 2 log units—pupil dilation at the lower light admits more light. So we repeated this entire task on one observer who monocularly viewed the display through a 3 mm artificial pupil for both high and low luminance conditions. By maintaining a con-

stant effective pupil size, the artificial pupil precisely controls the amount of light entering the eye. It was necessary, incidentally, to use a bite-board to steady head position and, therefore, maintain accurate alignment of the observer's eye and the artificial pupil. Thus we had to replace the goggles with neutral density filters fitted to optical bench components to control light level. The resulting light reaching the eye was 25.5 trolands in the high luminance condition and 0.25 trolands in the low condition. Otherwise, procedures were the same as before. Results for this replication are shown by the pair of histograms in the far right-hand part of Fig. 1A. Even with artificial pupils, coherence thresholds were equivalent for the two light conditions, replicating the result with natural pupils.

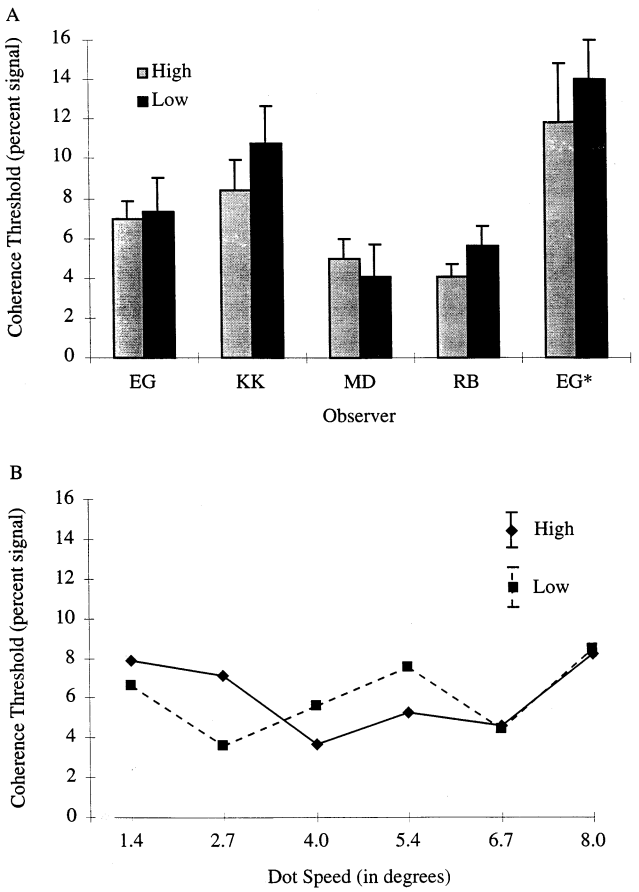

Fig. 1. (A) Coherence detection thresholds (75% correct) for each observer estimated from probit analysis. Error bars indicating ± 1 standard error were determined using the bootstrap procedure described by Maloney (1990). Light gray bars indicate high luminance conditions and dark bars indicate low luminance conditions. Observer EG repeated the task using an artificial pupil. (B) Thresholds estimated using a staircase procedure that tracks the signal level producing the 71%-correct level of performance on a 2AFC task. The observer viewed two circular patches of dots, one displaying incoherent random motion and the other weak coherent motion in noise. Following each 1-s presentation the observer selected which patch — left or right — contained signal dots. Dot speed was varied randomly over blocks of trials. All other aspects of the displays were identical to those used in Experiment 1. Each data point is based on three staircase repetitions, and the error bars show average standard errors for the low and high light level conditions.

To what extent does this equivalence of motion sensitivity generalize to other dot speeds? To find out, we retested two observers at a faster dot speed (1.6° s^{-1}) and a slower dot speed (4.8° s^{-1}). Speed was manipulated by changing the pixel step-size while keeping the interframe interval constant at 53 ms. For these remeasurements, thresholds were estimated using a 2AFC staircase procedure (two correct reduces signal level; one incorrect raises signal level) that converges onto the signal level yielding 71% correct detection. Each staircase started at a coherence level where detection was easy, and migrated to levels varying in 3% steps. A staircase was terminated after 12 reversals, and threshold was defined as the average signal level associated with the last eight turnaround values; five staircase repetitions were devoted to each of the two light levels at each speed. For neither observer did performance differ significantly between the high and low luminance conditions ($P > 0.05$). Finally, a third observer was retested over an even larger range of speeds (1.4–8.1° s^{-1}), and again there were no consistent differences between the two luminance conditions (Fig. 1B). The equivalence of motion thresholds at low and high light levels dovetails with results reported by Mayser, Eckle, Braun, Gegenfurtner and Sharpe (1998) on speed discrimination at different light levels. Testing with dot displays somewhat like ours, they found that speed discrimination was unimpaired at low light levels within the range of speeds where we find no differences in coherence thresholds.

There is no doubt one can create conditions under which motion coherence thresholds would be seriously impaired at low luminance levels. In our experiment, we had to use relatively large dots in order for observers to see them under scotopic conditions; small dots visible under photopic conditions were simply invisible at our very low light level. Likewise, high dot densities viewed at low light levels can adversely affect motion perception, with the individual dots tending to blur together and form a flickering mass with no sense of motion. Under these conditions, however, it would be misleading to fault motion mechanisms per se, for the limiting factors (dot size and density) are spatial in origin. Our results imply that motion mechanisms operate with normal efficiency when their inputs are scaled to compensate for scotopic vision's reduced spatial resolution.

2.4. Experiment 2: biological motion

Our second experiment tested a unique form of shape from motion involving the perception of animate activity based on the kinematics of just a handful of dots. Termed biological motion, this unique form of motion perception was first described by Johansson (1973). In

his work, he placed 12 lights on the major joints and head of an actor wearing dark clothing and then filmed the individual as that person walked. A single, static frame of this movie sequence looks like an irregular cluster of dots, but upon viewing successive frames as an animation one immediately perceives a person walking. Johansson's seminal work, along with subsequent experiments on biological motion (e.g. Ahlström, Blake & Ahlström, 1997), confirm that human observers are remarkably sensitive to the spatio-temporal structure in these novel displays.

Not a great deal is known about the perception of biological motion from point-light displays, except that it is remarkably robust. Biological motion is easily perceived when the signal dots are placed in a field of randomly moving noise dots, when the action dots are placed between the joints rather than on them (Bertenthal & Pinto, 1994), and even when some of the dots are missing (Ahlström et al., 1997). Observers show no difference in sensitivity to biological motion defined by luminance, texture or random contrast polarity (Ahlström et al., 1997). One of the few manipulations that disrupts the perception of biological motion is inversion: upside down walkers are more difficult to recognize (Sumi, 1984). Similarly, phase-scrambling the starting positions of the individual dots — which destroys the hierarchical structure of the point light display — seriously perturbs perception of biological motion (Ahlström et al., 1997).

There is circumstantial evidence suggesting that distinct neural mechanisms may be involved in processing of biological motion. Specifically, there are several case studies of brain-damaged people with selective deficits in motion perception. Schenk and Zihl (1997a,b) described several patients with lesions encompassing anterior parts of the superior temporal sulcus. These patients performed normally on coherence detection and shape from motion tasks, but they exhibited difficulty perceiving biological motion. The complementary pattern of results was reported in a patient studied by Vaina, Lemay, Bienfang, Choi and Nakayama (1990). This individual suffered bilateral damage in extrastriate visual areas, including portions of posterior parietal and temporal lobes. This patient experienced difficulty perceiving coherent motion in random-dot cinematograms, and he performed poorly on a speed discrimination task. Yet the patient experienced no difficulty seeing biological motion from point-light sequences—he was able immediately and accurately to describe the actions being portrayed. This kind of dissociation strongly implies that perception of biological motion and of coherent translational motion may rely on different neural mechanisms.[1] In view of this possibility, we felt it worthwhile to investigate perception of biological motion under the same light level conditions employed in our coherence detection experiment.

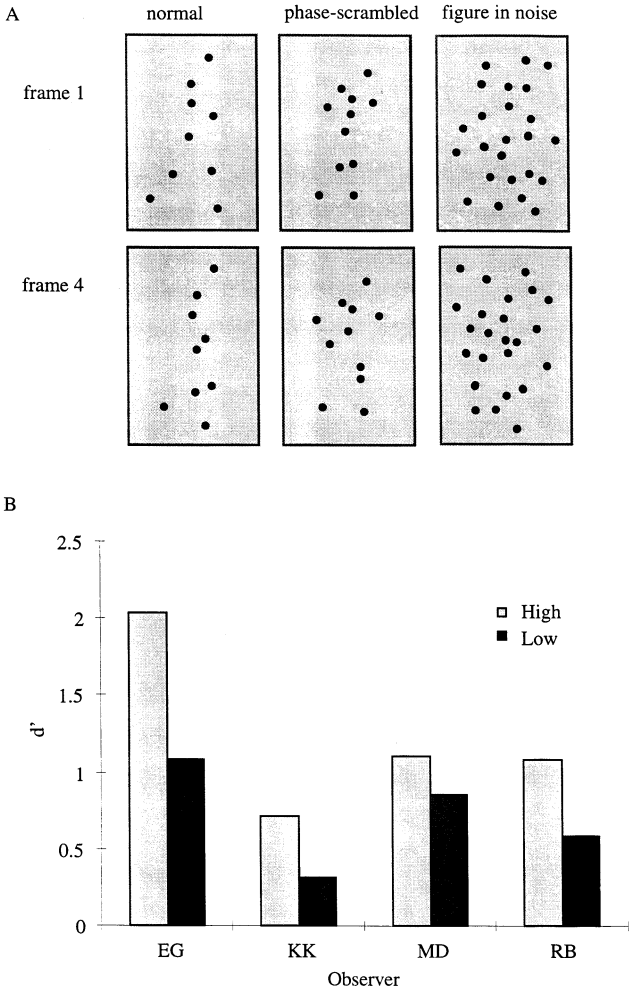

Fig. 2. (A) Two (nonconsecutive) frames from animation sequences depicting normal biological motion (left-hand panels) and phase-scrambled biological motion (middle panels). In the actual experiment, sequences were shown within a field of dynamic noise dots, two examples of which are shown in the right-hand panels. (B) Values of d' for each observer in the biological motion task calculated from hit and false alarm rates.

2.4.1. Methods

Observers viewed 0.5 s animation sequences and judged whether the sequences were normal, biological sequences or sequences disrupted by phase-scrambling. The biological motion sequences were originally created by videotaping an actor performing several dozen activities (e.g. walking, kicking, throwing an object) with reflective tape on his major joints (Fig. 2A). The succes-

[1] In this regard, it is interesting to note that individual neurons in the upper bank of the anterior superior temporal sulcus (STS) of macaque monkeys are selectively responsive to motion from biological sources (Milner & Jeeves, 1985; Oram & Perrett, 1994). Some of these cells even respond preferentially to a point light figure walking in a specific direction.

sive frames of those animations, in turn, were imported into the computer where the reflective tape markings were replaced with circular black dots which were scaled in size to match those used in the previous experiment. Dot positions from frame to frame were coded into successive matrices animated using MatLab©. Phase-scrambled versions of each biological sequence were created by independently randomizing the starting frame for each dot, thus breaking the hierarchical, pendular relations among dots while preserving the individual motions of the dots. All movie sequences—normal and phase-scrambled—were embedded in a field of dynamic noise dots whose paths of motion were drawn from a distribution representing the range of displacements in the biological sequences. The introduction of the noise dots was necessary to render the task more difficult; without noise, observers could readily discriminate normal from phase-scrambled sequences. Each display had approximately 12 signal dots (variable depending on the motion represented by the biological figure) and 40 noise dots within a 5.8° square aperture.

Observers initiated each sequence and indicated by keypress whether the sequence was normal or phase-scrambled. Each observer completed 200 trials in the high and in the low luminance condition. The black dots comprising the animation sequences appeared against a gray background 3.6 cd m^{-2} in luminance. Once again, goggles with filters were worn to reduce the light level by 2 log-units.

2.4.2. Results and discussion

Hits (responding 'biological' when a sequence was biological) and false alarms (responding 'biological' when a sequence was phase-scrambled) were used to calculate d' values for each observer at both of the two light levels; the resulting d' values are shown in Fig. 2B. For all four observers, performance on this discrimination task was better at the higher light level ($P < 0.05$). Performance under dim-light conditions cannot be attributed to an inability to see the individual dots. Indeed, dot density on this task was comparable to that used in Experiment 1. Instead, observers reported difficulty grouping dots into a meaningful figure.

In biological motion sequences, individual dots move at different speeds depending on their limb positions and on the activity being portrayed. Is the difficulty in recovering the structured motion in the biological motion attributable to a loss in perceiving the different relative speeds of the dots? This seems very unlikely because, as pointed out earlier, speed discrimination is quite good at scotopic light levels (Mayser et al., 1998). It is noteworthy, by the way, that performance between the two conditions differed even for observer EG (the first author), who has amassed extensive practice with these sequences.

2.5. Experiment 3: form from motion

Biological motion can be construed as a special case of form-from-motion (FFM). In traditional demonstrations of FFM, a rigid shape is specified by the common motion of a subset of tokens seen within a larger background of tokens undergoing different motions. Thus, for example, a cluster of upward moving dots stands out as a 'figure' against a background of randomly moving dots. Presumably the mechanisms underlying FFM involve some form of spatial differentiation among motion vectors, for luminance boundaries defining the global shape simply do not exist in these kinds of displays. This last experiment tested FFM at low and high luminance conditions.

2.5.1. Methods

For the FFM task, observers had to judge the shape—horizontal versus vertical—of a rectangle defined solely by motion. The stimulus consisted of a 5.8° square aperture in which 50 dots moved downward at a 45° angle (see Fig. 3A). When the dots entered a virtually defined rectangular area their directions of motion were allowed to deviate within the range $\pm 30°$. This display was designed to eliminate luminance flicker or density cues along the borders of the shape within the aperture, as well as to maintain a constant dot speed throughout the display. Dot luminance, density and speed matched those used in the coherence detection experiment. Observers saw nine successive animation frames of the stimulus during the 477 ms exposure duration (interframe interval of 53 ms); following each presentation the observer indicated the orientation of the rectangle by a key press. The total area of the rectangle remained constant (approximately 30% of total display area), but its aspect ratio (height to width) varied randomly over trials according to a method of constant stimuli (1.16–1.80 in five equal steps). The angle of deviation for the 'signal' dots defining the rectangular region and the specific aspect ratio values of the rectangle were chosen to span a range yielding near-chance to near-perfect performance on this 2AFC task. The rectangle, regardless of orientation, could appear anywhere within the display area, thus making it impossible for observers to base their judgment on direction of dot motion at any specific region within the display. Correct responses required global integration of dot motions within the 'shape' region.

Because of the difficulty of the task, observers received practice before formal testing began. Initially during practice, the dots defining the shape were brighter than the others, causing the rectangle to 'pop-out' from the background. Next, observers received training with rectangles defined solely by motion, with the aspect ratio of this figure set to a value sufficiently large to support near-perfect performance. Once ob-

servers were comfortable with the task, they participated in blocks of trials generating a total of three hundred test trials for each luminance condition.

2.5.2. Results and discussion

Probit analysis was used to fit psychometric functions to the percent-correct scores of each observer in the high and low luminance conditions. From these curves we determined the aspect ratio associated with 75% correct performance, and those threshold aspect ratio values are shown in Fig. 3B. All observers showed a significantly lower thresholds in the high versus low luminance conditions.

At the high light level, observers had no problem visualizing the cluster of dots defining the rectangular region—perceptual grouping was automatic and effortless, and task difficulty depended entirely on judging the aspect ratio of this shape. At the low light level, however, grouping and boundary formation were quite difficult. This difficulty was not attributable to the inability to perceive the differences in dot directions, as confirmed in a control task in which observers were required to select in which of two intervals deviant directions were present (the other interval containing coherent motion only). On this control task, observers performed without error, indicating that the differences in dot directions were conspicuous. The difficulty of the FFM task stemmed from the difficulty of judging the shape of the region defined by motion direction.

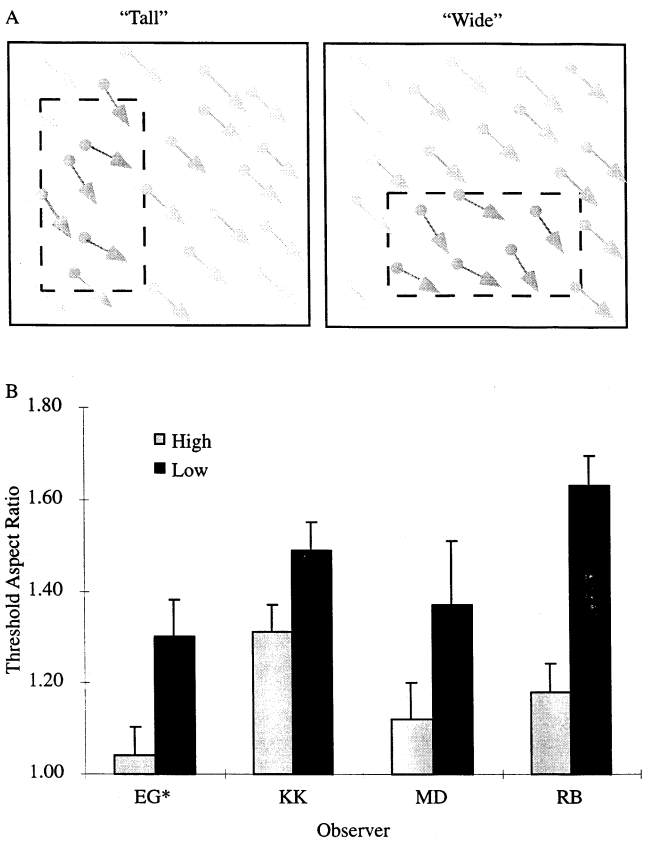

Fig. 3. (A) Schematic of the shape-from-motion display. Each cinematogram contained a rectangular, virtual area (long axis either vertical or horizontal), and dots within this area deviated in motion direction relative to dots in the rest of the display area. Observers judged whether the motion-defined rectangle was 'tall' or 'wide' (guessing if necessary). The actual position of the 'rectangle' varied over trials, making it impossible to monitor dot directions at a given region to perform the task. The ratio of width-to-height (aspect ratio) was varied following a method of constant stimuli. (B) Aspect ratio yielding 75% correct performance, estimated from best-fit probit curves. Error bars denote one standard error, calculated using the bootstrap procedure (Maloney, 1990). Highly experienced observer EG was tested using somewhat smaller FFM rectangles. By reducing the size of the signal area, there were fewer dots defining the rectangle, rendering the task more difficult for her.

3. Conclusion

Generally speaking, good vision depends on good lighting, and this appears to be true for motion perception, too, with one exception. Whereas perception of biological motion and FFM suffer under dim-light conditions[2], detection of coherent motion seems unperturbed so long as dot size and density are sufficient to support spatial resolution of the motion tokens. Now it is possible that motion coherence detection would deteriorate at even lower luminance levels, although work mentioned in a published abstract suggests that coherence thresholds remain low at even dimmer light levels (Mayser et al., 1998). It is also possible that deficits in coherence detection would be found at higher dot speeds, for other work has established that the temporal response of the visual system becomes more sluggish at low light levels (Dawson & Di Lollo, 1990; Takeuchi & De Valois, 1997).

It is conceivable that changes in spatial pooling at low light levels might account for our pattern of results. Physiological evidence indicates that visual receptive fields increase in size at scotopic light levels (Barlow et al., 1957; Derrington & Lennie, 1982). How might this impact motion perception? The maintenance of good sensitivity to coherent motion at low light levels is not surprising, for performance on this task is thought to depend on pooling of local motion signals (e.g. Shadlen, Britten, Newsome & Movshon, 1996). Enlarged motion pooling would not change the ratio of signal-to-noise dots. Tasks that would suffer because of enlarged pooling zones would be those that depend on

[2] We did not use an artificial pupil when testing biological motion and FFM so, therefore, the reduction in light level was not exactly 2 log units. Note, though, that the percentage reduction in retinal illuminance would have been greater for scotopic versus photopic adaptation levels had we used an artificial pupil. If anything, this would further amplify the differences in performance on these tasks at the two light levels.

differential activation among neurons registering motion in nearby regions of visual space. For example, we would expect impairment within processes involved in segregation of one cluster of motion vectors from a background of different vectors, for pooling could blur those motion boundaries. This kind of process, of course, would be required for perception of our FFM stimulus. Motion boundaries may also be highlighted in virtue of the motion opponency described for receptive fields of neurons in the middle temporal visual area in monkey, where opposite directions of motion in adjacent regions of the visual field generate particularly strong responses (Allman, Miezin & McGuinness, 1985). If the balance between these opponent processes shifts with dark adaptation—in a manner comparable to the shifts seen in retinal ganglion cells (Barlow et al., 1957)—motion boundaries would be blurred. To the extent that perception of biological motion depends on spatial relations among relevant motion tokens, spatial pooling also could be responsible for generally poorer performance on this task at low luminance levels.

Finally, it is worth considering our results in light of work by Purpura, Kaplan and Shapley (1988) who measured contrast gain control in parvo- and magnocellular retinal ganglion cells at different levels of light adaptation. At mesopic and scotopic luminance levels, the responses of P cells were severely reduced, rendering them almost 'blind' under these conditions; M neurons, in contrast, maintained high levels of responsiveness. Now to the extent that M cells provide the gateway to motion mechanisms in the brain as commonly believed, we would expect motion perception to survive large reductions in light level. Our results show that this is the case, although observers do experience more difficulty extracting shape from those motion signals and more difficulty assembling local motion signals into globally coherent biological events. In a sense, motion is easy to see at low light levels, but global spatial structure carried by the motion is not. One might therefore construe the impairments in performance on biological motion and FFM as implicating P-pathway involvement in those tasks. It is important to keep in mind, however, that performance on those tasks was possible at the low light level, albeit with decreased efficiency. Any conclusions involving relative activation of M and P channels on FFM and biological motion tasks will require testing under other conditions thought to isolate these two pathways.

Acknowledgements

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