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THE IMPORTANCE OF THE TYPE AND AMOUNT OF DEPTH IN
THE DISAMBIGUATION OF MOTION SIGNALS

Michelle Charlene Kwas

A Thesis
in
the Department
of
Psychology

Presented in Partial Fulfillment of the Requirements
for the Degree of Master of Arts
Concordia University
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ABSTRACT

The Importance of the Type and Amount of Depth
in the Disambiguation of Motion Signals

Michelle C. Kwas

Two moving gratings can be perceived as separate surfaces sliding over one another in their respective directions, or as a coherent plaid pattern occupying one plane, moving in a third direction. Traditionally, these plaid stimuli have been employed to study the motion integration process as a 2-dimensional phenomenon, however, the investigation has expanded to explore the 3D influences on this process. It is believed that depth information aids surface segmentation, which in turn determines which motion percept is predominant. The present study examined, more extensively, the underlying mechanisms by which depth information is employed in the grouping of local 1-D motion signals. The two gratings of the plaid were separated by three amounts of depth, defined by binocular disparity, relative contrast or transparency, and a ratio of perceived coherent to component motion was measured. As expected, perceived coherent motion decreased as depth information was increased. Following, observers adapted to the aforementioned depth plaids and were tested with two plaids, one which contained an intermediate amount of depth (corresponding to the same type of depth as in the adapting stimulus) and a zero depth plaid. As with many aftereffects, adaptation may be stimulus-specific with a maximum effect for matching adapt and test stimuli. In contrast, the adaptation effect increased with the degree of adapting depth (transparency was the exception, whereby no effect of adaptation was observed). Curiously, no effect was found for the zero depth test stimuli,

indicating some degree of stimulus-dependency. A conceptual model is proposed, which suggests the presence of a general mechanism responsible for computing an estimation of depth between 1-D components of an image. This computational process uses the converged input from depth sensitive neurons, preferentially selective for the type and amount (in some cases) of surface segmentation, and the resulting combined depth information is used in the motion integration process.

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STATEMENT OF THE RESEARCH PROBLEM

Visual images provide an immensely rich source of information about the external world, more so than any of the other senses. The preeminence of vision is mirrored in the proportion of cortex predominantly devoted to visual function: approximately 60% of the monkey cortex (see Felleman & Van Essen, 1991 for a schematic representation of these connections). This reason and others have been ample motivation for many researchers to investigate the ability of such an extensive system. As a result, of all the sensory organs, most is known about vision. Multiple physical dimensions help shape our visual experience, such as color, pattern, intensity, location, size, depth, and motion. This visual information is utilized by people, as well as animals in such an effortless and efficient manner, that it is easy to underestimate the computational complexity of ordinary visual routines. The most classic example is driving a car on a busy street, an activity that requires the integration of many ongoing visual tasks: reading traffic signs and lights, searching for familiar landmarks, judging motion and distance and of course anticipating the actions of unpredictable pedestrians.

Of particular interest has been motion, one of the best-studied functions of visual perception, which has been examined from psychophysical, neurophysiological, neuropsychological and computational perspectives. Visual motion processing is crucially important, as is evident from its involvement in a wide range of perceptual functions, some of

which include the segregation of figure and ground, estimation of the 3-D structure of objects (structure-from-motion) and the environment (depth-from-motion), self-locomotion, estimation of object motion, orienting attention, controlling eye movements, and object recognition (see Nakayama, 1985 for a more detailed review). Hence, motion cues are utilized in a diverse range of computational tasks, whereby, only few are directly related to the perception of object motions *per se* (DeYoe & van Essen, 1988).

As Sereno (1993) emphasizes, the very fact that some animals may lack certain visual abilities, such as color and stereo vision, but that all animals with vision have motion-processing capabilities, underlines the crucial importance of this domain of visual functioning. Motion perception proves to be an instrument necessary for survival for many animals, such as the lynx, for example, who's main food source is the beaver. The lynx must rely predominantly on its ability to detect the beaver's movements, without which, the lynx could mistakenly identify the beaver as a log. Of course, animals are not alone in their dependence on an acute system of motion processing; they share this characteristic with humans. Any damage to the motion system therefore has the potential to have devastating consequences for perhaps all of the aforementioned functions of motion. A clinical report by Zihl, von Cramon & Mai (1983) demonstrated just this. Their patient had bilateral damage to the occipital-temporal region (areas important for motion analysis) and consequently was impaired on several

tests of movement perception. Here are some observations from her daily life:

She had difficulty, for example, in pouring tea or coffee into a cup because the fluid appeared to be frozen, like a glacier. In addition, she could not stop pouring at the right time since she was unable to perceive the movement in the cup (or a pot) when the fluid rose....In a room where more than two other people were walking she felt very insecure and unwell, and usually left the room immediately, because "people were suddenly here or there but I have not seen them moving." ...She could not judge the speed of a car, but she could identify the car itself without difficulty. "When I'm looking at the car first, it seems far away. But then, when I want to cross the road, suddenly the car is very near." (Zihl, von Cramon & Mai, 1983, p. 315).

Indeed, the major problem for vision scientists specializing in motion is not to question the importance of their vocation, but rather to investigate just how the visual system is able to compute rapidly the motion and three-dimensional shape of objects in the environment from the time varying light intensities that project onto the eye. A great challenge for the understanding of motion analysis is the manner in which local motion signals arising from low-level motion analyzers with ambiguous and limited receptive fields integrate to compute an unambiguous and accurate global motion percept (Mather & West, 1993; Cavanagh & Mather, 1989;

Derrington & Badcock, 1992; and Derrington, Badcock & Holroyd 1992). This is the well known aperture problem.

The Aperture Problem

To extract useful information from the environment, the visual system must first analyze and then integrate the local 1-D components which form the 2-D retinal image. Only then can higher levels of analysis construct a more global estimation of the 3-D world. The eye's windows to the outside world consist of the restricted and very small "view" that each individual cell has of the visual field. These localized "views" are referred to as receptive fields, and they vary in their preferred stimulus size, color, orientation, disparity, direction, speed and type of motion, among others. In the motion domain, the early stages of analysis are accomplished by detectors whose task is the initial measurement and encoding of the motion of the 1-D components (i.e. contours or edges). The motion cell's receptive field is analogous to an aperture. It "sees" the world only as it is at a particular location and therefore only responds to edge motion which is within its finite aperture, while it is completely unaware of the surrounding global object motion. Neurons at this level are strongly direction-selective with the limit of detecting only movement which is perpendicular to the orientation of the edge (Movshon et al., 1985). Motion which is parallel to the contour does not produce change in the optical stimulation and hence is invisible to these local-movement analyzers.

A line segment, having a particular orientation, moving through the receptive field of this type of motion sensor will always create a percept of pattern motion orthogonal to the edge, regardless of its true pattern direction and velocity. It thus gives rise to a family of possible physical motions along a constraint line which are consistent with the resulting apparent motion. For a schematic representation of the aperture problem, see Figure 1. Figure 1A demonstrates how the receptive field "sees" only part of the image and consequently giving rise to many possible physical vectors along a constraint line which can lead to the same percept. Figure 1B illustrates how this occurs perceptually. The ambiguity which the neurons in the earliest stage of motion analysis are subject to is commonly referred to as the aperture problem. The component-motion detectors demonstrate the aperture problem physiologically, but this phenomenon can also be illustrated psychophysically. If one views a straight moving contour behind a circular aperture, the grating appears to move in a direction orthogonal to its orientation. In this case, the direction of motion is inherently ambiguous and can only be estimated to within 180 degrees (Wohlgemuth, 1911).

As shown by Wallach (1935), the shape of the aperture is important for determining the perceived direction of motion: A grating viewed through a rectangular aperture appears to move in a direction parallel to the long axis of the aperture (the *barber-pole illusion*). Recent studies (Nakayama & Silverman, 1988; Shimojo, Silverman & Nakayama, 1989) suggest that this effect is due to motion detection of line terminators at the

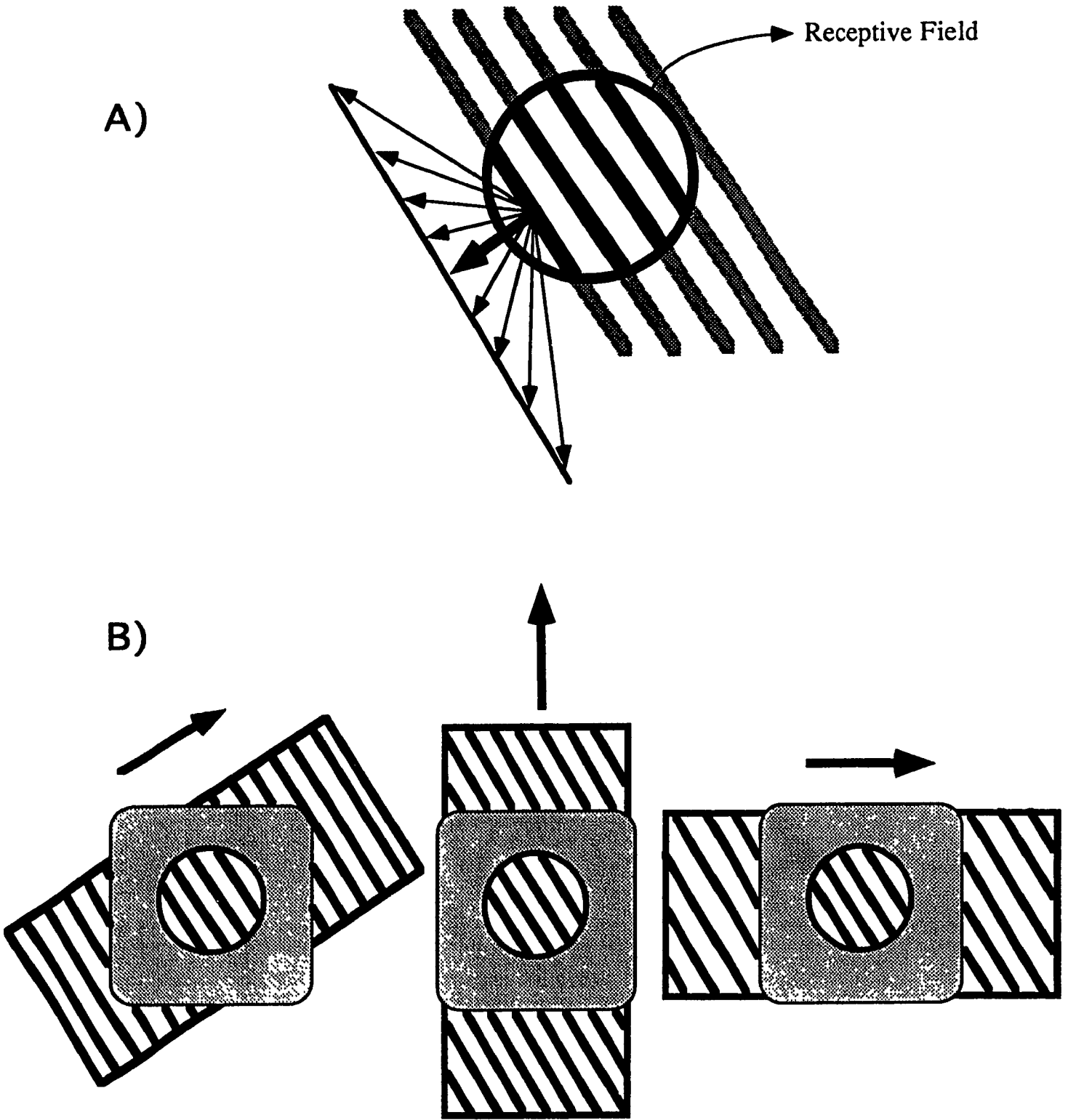


Figure 1. A) The aperture problem. All the possible motion vectors along a constraint line.

B) An example of how three different physical motions lead to the same percept.

edges of the aperture (the longer orientation will have the most terminators reporting motion unambiguously). To avoid the biasing effect of the barber-pole illusion, it is perhaps preferable to study the basic mechanisms involved in motion analysis with circular apertures.

The ambiguity of motion direction within a circular aperture can be resolved by the addition of a second superimposed grating of a different orientation. This creates a plaid pattern that now is perceived to cohere and move in a new direction that is different from the two original component directions, perhaps by the velocity space combination rule proposed by Adelson & Movshon (1982). Refer to Figure 2 for a schematic illustration of this stimulus. Adelson & Movshon (1982) were the first to employ the plaid stimulus to study the aperture problem. This innovation represents a conceptually straightforward means to research the integration process of motion physiologically, computationally, and psychophysically.

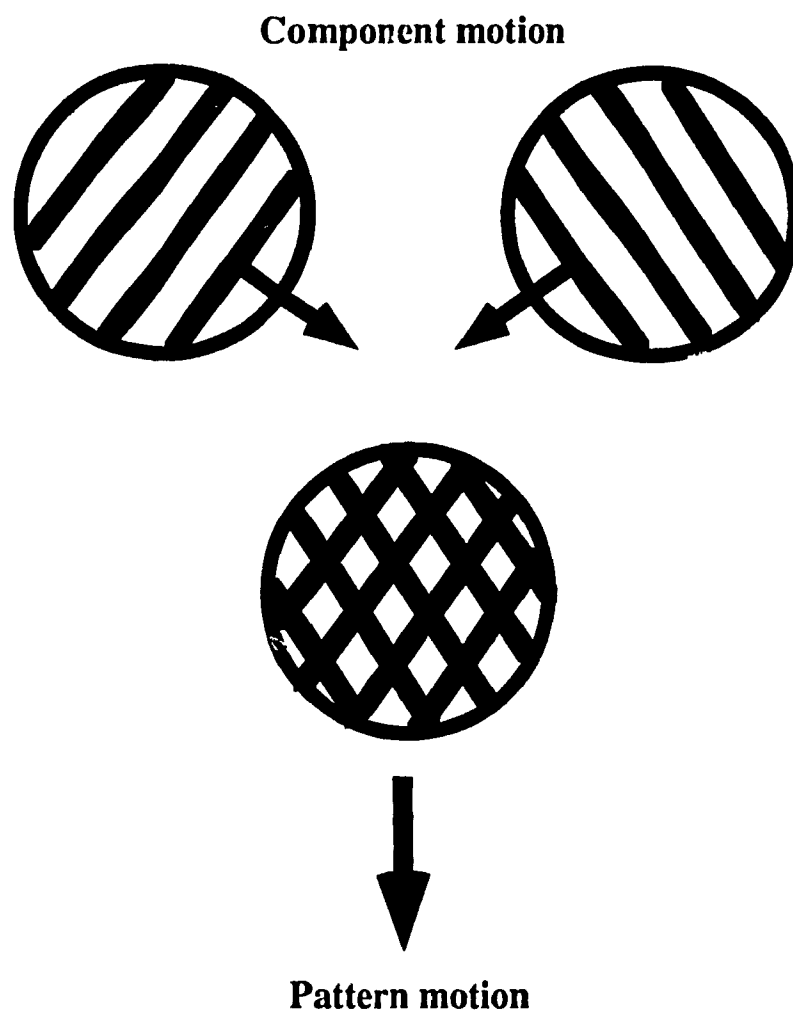


Figure 2. Solution to the aperture problem: The plaid.
When the two gratings are superimposed the direction
of motion becomes unambiguous.

A Brief Anatomical and Physiological Review

The thalamo-cortical (geniculo-cortical) pathway is composed of two major subdivisions, the parvocellular and magnocellular (important for motion analysis) pathways. Parvocellular-cells (P) in the lateral geniculate nucleus in the thalamus (LGN) originate from the B type ganglion cells and project principally to layer $4C\beta$ of V1 (primary visual cortex) and to a lesser extent to layer 4A (Hubel & Wiesel, 1972). Within V1 the P pathway leads mainly to the superficial layers 2 and 3, but subsequent stages of analysis are less clearly identified. Livingstone and Hubel (1987; 1988) argued that some connections would exist between the blobs and both layers $4C\beta$ and $4C\alpha$. On the other hand, magnocellular cells (M) in the LGN originate from the A type ganglion cells and project to layer $4C\alpha$ of V1. Outputs from this layer lead mainly to layer 4B. This layer projects either directly to, or passes through the thick stripes (V2) in the second visual cortical area before reaching the midtemporal cortical area (MT). Layer $4C\alpha$ also sends axons to the superficial layers in V1 (see Livingstone & Hubel, 1988 for a schematic representation of these connections). Area MT then projects to areas MST (medial superior temporal area) and intraparietal sulcus in the parietal lobe, which includes areas VIP and LIP, the ventral intraparietal area and lateral intraparietal area, respectively (Maunsell & Van Essen, 1983). Further, MST and LIP send their projections to area 7a (Andersen et al., 1990, as cited by Sereno, 1993).

The distinctiveness of the M and P pathways is also revealed by their physiological properties. When recorded in the LGN, most M cells are not sensitive to color and possess less acuity because of their larger receptive field centers as compared with P cells. P cell responses, on the other hand, are slower and more sustained than those of M cells. P cells [most] are also sensitive to color and need higher contrast stimuli to respond. This functional segregation continues in higher cortical areas. In the M pathway, cells in V1 are somewhat selective for disparity (Poggio et al., 1985), but are better characterized by their directional-selectivity to moving oriented stimuli. These neurons, however, are without selectivity for colour. Contrary to V1, cells in V2 show high disparity and orientation selectivity, and somewhat less direction selectivity (De Yoe & Van Essen, 1985; Hubel & Livingstone, 1987). In MT, an area "upstream" from V1 and V2 in the M pathway, neurons are primarily selective for aspects of motion, including direction and speed of the stimulus (Albright, 1984; Maunsell & Van Essen, 1983; Rodman & Albright, 1987). These cells have larger receptive fields than V1 cells (~10 times larger in diameter) and in addition, Maunsell and Van Essen (1983) found that nearly two thirds of MT units tested were selective for horizontal disparity. The authors interpret this as indicative of MT playing a role in analyzing the motion of visual stimuli in 3-D space. The same four categories of disparity-selective neurons were found as previously demarcated in cortical area V1 and V2: tuned excitatory, tuned inhibitory, near, and far (Poggio & Fischer, 1977).

Consequently, these segregated pathways are believed to subserve different visual capacities that grow in complexity in subsequent cortical areas. These observations and the strong neural connectivity that exists on the one hand between the M pathway and MT region, and on the other hand between the P pathway and the inferotemporal region (IT) have led some researchers (e.g. Livingstone and Hubel, 1987) to suggest that the M and P pathways may feed two different systems. This suggestion has been intimately related to the observations collected by Ungerleider and Mishkin (1982). They elegantly demonstrated, following monkey cortical ablations, that the inferotemporal region was primarily responsible for the processing of color and form (What, ventral stream), while the MT region was more associated with the processing of motion and spatial relations (Where, dorsal stream). Perhaps this is better interpreted as a functional bias, with each stream associated with one or two perceptual properties, but should not be considered as exclusive segregation (Maunsell, Nealey & DePriest, 1990). An overemphasis on segregation of function can be misleading (DeYoe & Van Essen, 1988). Often, multiple cues help to determine a property of the external world, creating a more robust percept. It is useful to view neural information processing as taking place in a system which is at once functionally specialized and massively interconnected, and in which more complex response properties related to information about the physical properties of the 3-D world are elaborated (Sereno, 1993).

Two-Stage Analysis of Motion

In brief, the major cortical pathway in motion analysis begins in layer 4B (and layer 6) of V1 and either goes directly to or passes through the thick stripes of V2 and then proceeds to MT. MT then sends projections to MST, which in turn projects to areas VIP and LIP. Subsequently, MST and LIP project "upstream" to area 7a. For a schematic illustration of the two motion pathways see Figure 3. It is widely assumed that pattern motion (when local 1-D components are integrated to form a global motion percept) and component motion (when the components are not integrated, but are perceived as slipping over each other in their respective directions) are processed at different levels of the motion pathway (Movshon, Adelson, Gizzi & Newsome, 1985; Rodman & Albright, 1989; Snowden, Treue, Erickson & Anderson, 1991; Derrington & Suero, 1991; Wilson, Ferrera, & Yo, 1992). Movshon et al. (1985) employed both a single sinusoidal grating (component) and a plaid (pattern) stimulus to investigate the motion selectivity of MT neurons. Their results revealed that virtually all neurons tested in cat and monkey striate cortex (V1) and in cat superior colliculus and lateral suprasylvian area are component-motion selective. In addition, they found that approximately 25 percent of the neurons in monkey MT are pattern-motion selective, about 40 percent were component-selective (like V1 cells), and the remainder were unclassified. Their study provides evidence that the aperture problem exists for motion sensors in V1, but not for the subpopulation of pattern-selective neurons in MT.

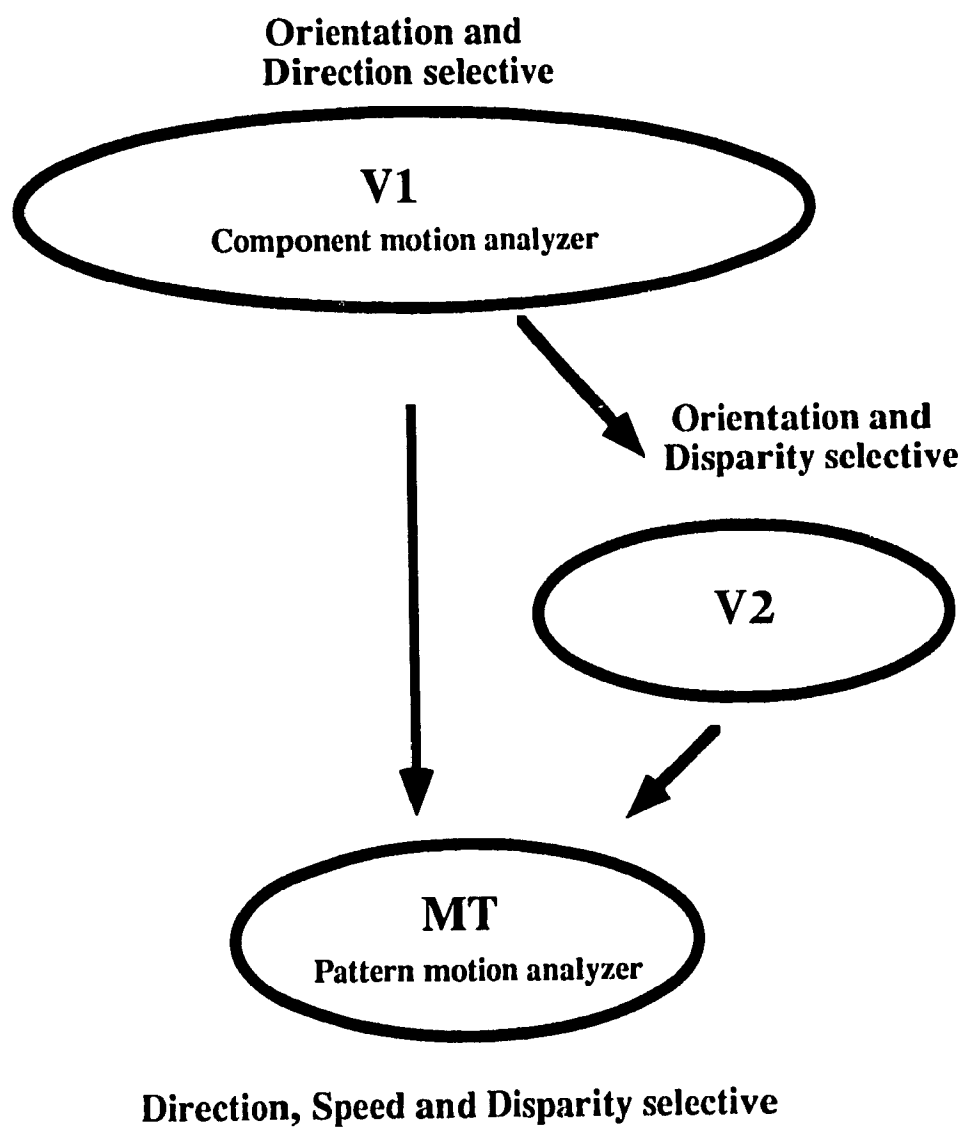


Figure 3. Schematic representation of the two motion pathways.

Further physiological studies by Rodman & Albright (1989) and Snowden et al. (1991) replicated this observation. Albright (1984) also distinguished two classes of neurons in area MT. Those he termed "Type I" preferred orientations which were perpendicular to their preferred direction of motion, while those called "Type II" responded optimally when the stimulus orientation was parallel to their preferred direction. The study by Albright, Rodman and Gross (1986) complements these results by demonstrating the existence of MT component-motion and pattern-motion neurons which correspond directly to the Type I & II cells reported by Albright (1984).

On the basis of these results, researchers suggested that there are at least two stages of motion processing in the motion stream. The first involves local measurements of image motion where individual components are analyzed. Motion detecting neurons at this stage are characterized by marked orientation selectivity and a limited spatial receptive field. Orientation selectivity restricts the contribution of individual detectors to one-dimensional motion signals; motion is detected only along the axis perpendicular to the preferred orientation. All motion sensitive neurons in the primary visual cortex and a substantial fraction of cells in MT have properties characteristic of this first stage of processing. At the second stage, these local motion signals are integrated to construct a representation of the global two-dimensional velocity field, a representation consistent with human perceptual experience of motion. This stage is embodied by a small subset of neurons, also in MT.

Wilson, Ferrera and Yo (1993) propose a computational model of 2-dimensional motion which incorporates a simple, linear motion energy pathway and a nonlinear motion pathway. They suggest that these pathways probably correspond to the Fourier and non-Fourier motion processing streams possibly reflected in the V1-to-MT and V1-to-V2-to-MT motion pathways, respectively. The Fourier motion process extracts luminance-based motion energy of the component gratings, and the non-Fourier motion process is responsible for e.g. texture boundary motion. The authors suggest that the latter of the two is often overlooked, and they emphasize that both motion pathways are important for two-dimensional motion perception.

The Plaid: An Appropriate Stimulus to Study Motion Analysis

Research is either limited or empowered by the tools that are available to study the phenomenon of interest. With sufficiently complex and rich stimuli vision scientists can extract information about the neuronal mechanisms in the motion system. In this case, it is evident that the plaid stimulus has become a valuable tool to those studying the analysis of motion. Adelson and Movshon (1982) initiated the use of plaids to study motion, and since that time many researchers have continued to employ them in their investigations. To reiterate, the plaid is composed of two overlapping moving rectangular-wave gratings of different orientations.

How does the visual system analyze the plaid stimulus? Individually, the gratings may stimulate the detectors at the first stage of processing. Neurons located here would only be stimulated by one-dimensional motion cues and hence each would "receive" only one type of information (one-dimensional motion from each grating). The message from these component responsive neurons would be a percept of two separate gratings (two objects) sliding over one another. These early signals would then be integrated by the second-stage pattern responsive neurons, who are capable of "seeing" two-dimensional motion, and hence can "receive" one type of motion signal (one object). This would yield the percept of a coherently moving plaid pattern.

The work of von Grünau & Dubé (1991; von Grünau & Dubé, in press) has illustrated that under prolonged inspection many plaids are ambiguous, in the sense that two alternative perceptual experiences seem to be possible, and the visual system switches between the two in a way similar to the situation found with other ambiguous stimuli, such as the Necker cube (von Grünau, Wiggin & Reed, 1984; Hochberg, 1981; Attneave, 1971; Carlson, 1953). An observer experiences both coherence and transparency, switching continuously between the two percepts: transparency, where the two gratings are seen as separate and transparent objects sliding over one another in their original respective directions, and coherence, in which the two component gratings integrate to form the plaid pattern, which moves in a novel direction. Thus, an observer's bistable

perception switches between pattern/coherent motion and component/transparent motion.

Consequently, the authors investigated whether these two organizations are based on motion processes that can be adapted independently. They asked whether in the absence of change of the ambiguous motion plaid stimulus, would adaptation to either component (one drifting rectangular-wave grating) or pattern motion (a rectangular-wave plaid manipulated to always induce coherent motion) reliably predict a change in the relative predominance of the two percepts. Observers viewed the adapting stimulus for 20 seconds, followed by the test stimulus, with a duration of 15 seconds. During the test period, observers indicated by constant key press, the length of time passed in each percept as it switched. This produced an accurate and more extensive measure of the integration process. Their results demonstrated that the two percepts could be manipulated through adaptation. The proportion of the coherent motion percept could be altered in such a way that adaptation to an unambiguously coherent stimulus resulted in a reduction of time for that particular percept; whereas adaptation to an unambiguously transparent stimulus, resulted in a corresponding increase in coherence. From their results, they concluded that the underlying motion processes are quite independent, but not completely, as there is still some mutual inhibition as seems evident from the bistable switching.

What may be the neural basis for the switching of perception between coherent and transparent motion? Like many visual experiences, such as the classic example of the waterfall illusion, this motion switching may be attributed to the effects of adaptation. The neurons at the first stage perhaps fatigue after prolonged inspection, and hence the dominant percept switches to that governed by the neurons responsible for the second stage of motion integration, which will also eventually fatigue. The psychophysical evidence described above supports this interpretation. Consistent with this view, a number of recent studies have contributed to the overwhelming consensus that a neuronal two-stage process of motion analysis is responsible for motion signal integration in the visual system (e.g. Derrington, Badcock & Holroyd, 1992; Derrington & Badcock, 1992).

Parameters Which Affect the Motion Integration Process

Not all signals of the first stage originating from a single spatial locus can be integrated. This makes sense ecologically, because not all local movements in the external world belong to the same object and hence should not be integrated and interpreted as global motion (stemming from one object). This is the challenge which the visual system must overcome in order to reconstruct a valid impression of the 3-D world; the motion system must define an object by deciding which local motions are consistent and which are inconsistent with that particular object. The process by which the visual system accomplishes this task is commonly referred to as

motion signal integration. As stressed previously, the plaid stimulus represents an efficient tool to study the conditions or parameters which allow signals from two or more component motions to be integrated (thus resolving the ambiguity of one-dimensional motion). As a result, several of these key variables have indeed been isolated with psychophysical techniques, in order to compliment or even modify those theories put forth by the aforementioned neurophysiological studies.

Adelson & Movshon (1982) began the study of stimulus conditions under which perceived coherence occurs in the plaid. Following a presentation period of 1.5 seconds, their subjects' task was to indicate, in a two alternative forced-choice procedure, whether they perceived coherent or transparent motion in a plaid constructed from overlapping sinewave gratings. Their results demonstrated that coherence was optimal when the spatial frequency, contrast and velocity were the same in both gratings, and if the angle between the component directions was sufficiently large. Any large deviations in these dimensions caused a reduction in the coherent motion percept and a compensatory increase in the transparent motion percept. From these results, the authors suggested that some spatial frequency selective and contrast sensitive processes must precede the analysis of coherent motion. In addition, from their masking experiment findings, they theorized that coherence depended also on the output of oriented analyzers. Thus so far, the motion system seems to extract component qualities such as orientation, contrast, velocity, direction of component motion and spatial frequency early in visual processing, and

requires the two gratings to be sufficiently similar in these parameters before integrating them at later stages of motion analysis.

Yet another variable in the motion signal integration process has been explored. Considerable neuroanatomical, neurophysiological and psychophysical evidence has led to the belief that there are limited avenues for interaction between color and motion processing pathways in the primate cerebral cortex (Livingstone & Hubel, 1988; Van Essen, 1985; Cavanagh & Anstis, 1991; Ramachandran & Gregory, 1978). Contrary to this traditional view, Krauskopf & Farell (1990) presented evidence to indicate that the chromatic properties of visual stimuli have important effects on the detection of motion. With the use of the plaid stimulus in which the sinusoidal components were defined by color, each grating was constructed to stimulate one of the three possible chromatic channels. Using a similar method as the previous authors, stimulus presentation lasted 1 second and observers indicated if their perception was coherence or transparency. As expected, plaids composed of two identical isoluminant gratings designed to stimulate only one color channel produced the most perceived coherent motion. Those plaids constructed of two gratings, each of which stimulated different chromatic channels, resulted in an increase in transparent motion. Again, this supports the rule of similarity between the component gratings, meaning, that they must be sufficiently similar to induce coherent motion.

Some researchers have suggested that an additional key parameter affecting motion integration is the tracking of unambiguously moving

features within the pattern. In terms of the plaid, these features are the "blobs", formed by the intersection of the two gratings. This view postulates that the eyes track the moving blobs thus defining the motion of the plaid (Gorea & Lorenceau, 1989). However, several other studies provide evidence contrary to this notion. Welch (1989) demonstrated that pattern speed discrimination was determined by the speed of its components. In addition, the speed discrimination for the blobs was different than the discrimination for the plaid. Likewise, Sinha (1993) found that coherence was maintained even for plaids comprised of illusory gratings, therefore having no true blobs to track. In support of this argument, Cavanagh and Mather (1989) stated that with the use of multiattribute plaids (plaids composed of two gratings, each defined by a different form cue) which produce highly complex blobs which should be difficult for the visual system to detect, are still able to yield pattern motion (Stoner & Albright, 1992a; Albright, 1992; Krauskopf et al., 1989). These studies add to the mounting evidence against the idea that "blob behavior" is solely responsible for motion integration. It seems more likely that the 2-stage motion analysis is still the most accurate theory, but that does not dismiss the idea that feature-tracking may play some role in this analyzing process.

The importance of both spatial frequency and contrast as physical attributes necessary for motion integration is supported by other psychophysical evidence provided by Stoner & Albright (1992a). In their investigation of the motion signal integration process, they studied whether motion coherency rules are form-cue invariant. The traditional plaid stimulus consists of a homogeneous-cue pattern, in which both gratings are defined by the same figural cue (i.e. luminance). Stoner & Albright used a heterogeneous-cue plaid pattern (previously referred to as multiattribute plaids) to determine whether the motion stream would integrate motion signals from different figural cues to yield a coherent pattern motion percept. Their plaids were constructed from luminance and flicker-defined components. The results illustrated not only that motion signal integration was possible in this situation, but that there was a striking similarity to the behavior of the homogeneous-cue plaid. The perception of coherent motion was dependent upon component similarity in the dimensions of spatial frequency and contrast even when these components were defined by cues that were physically very different. Hence, these data reveal that the contrast and spatial frequency mechanisms, that gate the coherence processes, are form-cue invariant, at least for luminance and flicker contrast cues.

Depth Related Parameters Affecting Motion Integration

As previously mentioned, one of the percepts in the bistable plaid is transparency. This percept necessarily implies that there is some sort of depth between the gratings, because in order to have two surfaces sliding across one another, one must be in front of the other. However, this depth relation is somewhat ambiguous, as the grating "in front" is not always the same, they switch over time. This would seem to imply that depth cues are also a parameter which gates motion integration. Indeed, there is plenty psychophysical evidence in support of this.

The grouping of motion signals arises from mechanisms sensitive to the physical properties related to occlusion. The luminance of the intersections where the two superimposed rectangular-wave gratings overlap determines the dominant motion percept. Stoner, Albright & Ramachandran (1990) demonstrated that a range of intersection luminances corresponding to those occurring under natural conditions of transparency yielded most reports of transparency in moving plaids, and that intersection luminances outside of this range resulted in an increasing amount of coherence. The coherence was measured again by the two alternative forced-choice task following a stimulus presentation of 1.5 seconds. From these findings, one can conclude that when the luminance relations are representative of those derived from physically transparent gratings, motion signals are not integrated, resulting in component motion. If on the other hand, the intersection luminance is not consistent with transparency,

indicative of a single surface, motion signals are grouped together, and the result is pattern motion.

More recently, Vallortigara & Bressan (1992) provided additional evidence supporting the view that segmentation cues arising from occlusion and depth influence motion grouping. Relative contrast of the two gratings, as a cue to depth, interacts with occlusion cues to determine component motion in plaids. If a high contrast (black) grating is placed in front of a lower contrast (grey) grating, via an opaque occlusion cue, subjects report a higher ratio of component motion as opposed to when the layering order is reversed. The grating that contrasts more with the background tends to be seen as the closer grating and hence implies apparent depth. When occlusion and relative contrast support the same depth relation, then the result is component motion.

Consistent with Vallortigara & Bressan (1992), Trueswell & Hayhoe (1993) also demonstrated the combined effects of depth cues on the motion signal integration process in plaids. They introduced binocular disparity and explored its interaction with a perceived transparent layering order cue. In their plaids, via a transparency cue, the lower contrast grating (grey) appeared in front of the high contrast grating (black), and the uncrossed disparity of one of the gratings (alternately) was manipulated so as to either be consistent or not to the transparency depth cue. Both the perceived transparent layering order and the binocular disparity between the gratings determined the probability of component motion. A greater amount of disparity was required to induce component motion if the two

cues were inconsistent. The authors interpreted this as indicative of a second level of motion processing that determines motion directions by attempting to satisfy multiple constraints relating to surface segmentation and layering cues.

Further evidence for the interaction of relative contrast and intersection luminance was found, using a different sort of plaid. Work by von Grünau, Kwas and Dubé (submitted) illustrates that a "polar plaid" comprised of a combination of a concentric circle grating and a radial grating will behave in a similar manner compared to the traditional plaid, manipulated along the same dimensions. Specifically, increasing the relative contrast between the two components and/or using unnatural intersection luminances will prevent integration from occurring.

Adelson (1984) offered additional support for depth as a key parameter as he demonstrated that the presence of disparity between the gratings seemed to destroy the percept of coherence. Dubé, von Grünau & Kwas (1992; von Grünau, Dubé & Kwas, in press) examined the influence of binocular disparity in rectangular-wave plaids more extensively by investigating its interaction with intersection luminance. In addition, adaptation to stationary random dot stereograms was employed to test how the switching between component and pattern processes is influenced by binocular disparity mechanisms. Perceived component motion was systematically related to the amount of disparity. The larger the disparity, the greater the amount of perceived transparency, and hence the more intersection luminance that was required to overcome the disparity in order

for motion integration to be successful in producing a coherent motion percept. Further, it was concluded that stationary disparity can determine the dominance of different motion processes. Adaptation to stationary disparity increased perceived coherence in the test plaids (with and without disparity) as compared to adaptation to zero disparity. These results illustrate that a depth sensitive mechanism is implicated in the choice between seeing two transparent surfaces or only one surface in motion integration. The signal from this mechanism contributes under normal circumstances (plaid with disparity) to the choice in favor of component motion. Adaptation weakened this signal such that thereafter pattern motion became relatively stronger.

Kwas, von Grünau and Dubé (1993; submitted) extended these findings with disparity and an adaptation paradigm. Rectangular-wave plaids with and without disparity were tested for their level of coherence following adaptation to either component (one grating) or pattern (cohering plaid) motion. They found that unambiguous adaptation to a component or pattern stimulus resulted in a reduction of time for only that particular associated percept in plaids with or without disparity. Therefore adaptation to a motion type (component versus pattern) can either silence or empower the disparity effect in motion integration.

"Talking" Between Streams

The above study adds to the mounting evidence that visual stimulus attributes traditionally unrelated to motion *per se* can profoundly affect the way in which motion is perceived and this is indicative of cooperation between separate streams in the visual system (Cavanagh & Anstis, 1991). Many of the computational, physiological and psychophysical approaches have supported the early segregation of visual information into non-interactive parallel pathways (Livingstone & Hubel, 1988) responsible for attributes such as motion, color and form (Trueswell & Hayhoe, 1993). An alternative approach is that there is an exchange of information between the different pathways in determining a better perceptual solution (Trueswell & Hayhoe, 1993; Cavanagh & Anstis, 1991; Shimojo, Silverman & Nakayama, 1989). The visual system's processing of motion signals appears to rely on more complex surface segmentation mechanisms which are sensitive to and extract information from both monocular depth cues present in transparent surface occlusion and opaque occlusion and stereoscopic cues, such as binocular disparity.

Overview of the Experiments

The experiments described below further explore the parameters gating the process of motion integration. What has been shown in past research, is that there is strong evidence for the influence of depth information on the motion integration process. However, the extent and the mechanism of the interaction are still largely undetermined. Just how

detailed the cross-talk between the motion and depth modules is, is not yet obvious. It is not known, for example, if depth information that is used by the motion integration process is stimulus-specific or resembles more a general impression of depth. To understand this, a design which incorporates an accurate means of measuring coherent motion is needed, along with the manipulation of the amount and kind of depth information. Likewise, for better comprehension, the use of many depth cues may prove to be valuable in order to test for differences or similarities with which the visual system processes depth information stemming from different kinds of depth relations and to study the degree of specificity or generality of the underlying mechanisms. The present studies attempt to do just this.

Precisely, the experiments examine the effect of depth information on coherent motion in moving rectangular-wave plaid stimuli. Furthermore, three types of depth plaids were employed for this investigation: disparity-, relative contrast- and transparency-defined plaids. The two experiments progress through an increasingly more detailed analysis of how multiple constraints relating to surface segmentation and layering order have to be satisfied for the integration of local 1-D motions. They provide a rich source of new psychophysical data regarding the intimacy of motion and depth modules.

With the exception of work by von Grünau & Dubé (in press), past research has not concentrated on obtaining accurate measures of the total time spent in both percepts of the bistable plaid (coherence and transparency), as it is manipulated along some dimension. Instead, studies

have put emphasis on whether or not integration is possible in certain conditions, and when it is most likely to occur or not. This is evident by the most commonly used method of measuring coherent motion by researchers in this area: the two alternative forced choice task (2-AFC) whereby the subject has to report only one percept (i.e. coherence *or* transparency). Likewise, most researchers measure this following only brief durations of stimulus presentation (~1 second). As previously discussed, the percept seems very time-dependent (switching) and thus much detail may be lost with such a procedure. A longer presentation period is thus required to obtain a more accurate and complete understanding of motion integration processing. For example, a plaid which may seem coherent in the first second of presentation may actually progress to produce a higher proportion of transparent motion, given a longer measuring time. A better method of allowing subjects to accurately report their switching percepts is by extending stimulus presentations to approximately 15 seconds, during which subjects continuously report their changing percepts by key press. This provides a method of analyzing the proportions of coherence and transparent percepts as well as their time course (von Grünau & Dubé, in press). This method was used for the present experiments.

Experiment 1 was designed to explore the effect of increasing the amount of depth information in the plaid on integration processing. This provided a baseline measure of coherence with plaids which contained varying degrees of disparity, relative contrast and transparency cues to

depth. By "amount of depth" I refer not only to the quantitative measure of depth separating two [or more] surfaces, but also I mean a qualitatively more robust or veridical percept of multi-surfaces. One part of this experiment was similar to parts of the study by von Grünau & Dubé (1992; in press) who investigated the influence of disparity on the perception of moving plaids. Likewise, the study by Stoner et al. (1990), which manipulated the amount of transparency and tested its effect on perceived coherence, but employed a much different method of coherence measuring (the 2-AFC and short presentation periods, as previously described), served as a model for another part of this experiment. The present study was a modified replication of part of theirs. However, relative contrast as it affects motion coherence, has not previously been studied in this extensive manner. Therefore, the investigated hypothesis for the first experiment was as follows: As the depth information (regardless of the type) between the components of a plaid is increased, the chance of successful motion integration is decreased. As expected, as the depth in the plaid was increased, there were subsequent decreases in coherent motion, indicating that integration occurred less often. Obviously then, depth information is affecting motion analysis, but this alone does not determine the underlying mechanisms for this interaction, nor does it specify how these mechanisms relay their depth information to the process of motion integration. This is the goal for the next study. Experiment 1 sets the stage for Experiment 2 by attaining these baseline levels to then test for adaptation effects which should help determine the answers to the above questions.

Experiment 2 tested the hypothesis that the depth information used in the process of motion integration is *not* stimulus-specific. If the integration process uses depth information which is conveyed directly to it by populations of neurons which are preferentially responsive to a particular amount of depth, then it operates in a stimulus-specific manner. The contrary view is that the depth information is grouped somewhere to form a more general impression of depth, prior to being projected to higher cortical areas involved in motion grouping. To accurately test this question, an adaptation paradigm was employed, which used the plaids from Experiment 1 as the adapting stimuli, and tested their effect on coherent motion in test plaids with a constant level of depth (or none at all: control). As past research has not investigated the differential effect on coherent motion by adapting to varying degrees of disparity, relative contrast or transparency, this study will bring new insights into this phenomenon. With some aftereffects, adaptation may be stimulus-specific, in the above sense, with a maximum effect for matching adapt and test stimuli. Contrary to this, support for the above hypothesis was obtained, as the adaptation effect increased with the degree of adapting disparity and relative contrast. Transparency plaids, however, did not follow this pattern.

In concert, this set of experiments contributes to the body of data being collected in the field of motion integration, more specifically, data on the parameters governing motion signal integration. They demonstrate that cues unrelated to motion *per se* interact quite intimately to determine

integration and hence indicate the existence of cross-talk between different functional visual streams. This adds to our understanding of the functioning visual system, its limits and complexity.

EXPERIMENT 1

On the basis of the work by Stoner et al. (1990) and von Grünau & Dubé (1992; in press) it was hypothesized that increasing the depth information in a stimulus should help the motion system to perceive two surfaces, and hence should decrease the probability that the motion integration of local 1-D components will be successful. To investigate this hypothesis, rectangular-wave plaids which incorporated disparity, relative contrast or transparency surface-segmenting cues, were used. Each plaid type was manipulated so as to display different amounts of depth information. In this way, it was possible to obtain baseline ratios of coherent and transparent motion as determined by different kinds and amounts of depth. There was no adaptation, and subjects simply reported the percept of coherent and transparent motion while viewing the different sorts of stimuli. This study was especially important, as it served to establish the baseline data which were used to test for possible adaptation effects explored in Experiment 2.

Method

Subjects

Seven subjects, six of which were naive, participated in all conditions. The observers were recruited from diverse educational backgrounds, with normal or corrected-to-normal vision. The two males and five females, ranged in age from 23 to 34 years old. All were right handed and were tested for stereoscopic vision prior to their participation in the experiment.

Apparatus

A Macintosh IIfx equipped with a NuVista⁺ graphics board, and a high resolution Apple Color Monitor were employed to generate and present the stimuli. Subjects' right hand rested beside a standard-sized Macintosh keyboard, on which the subjects' responses were made by depressing one of two adjacent keys. Responses were measured in seconds, with 68 milliseconds precision, and accumulated by the computer. To insure proper fusion, observers viewed the stimuli through a prism stereo viewer, adapted from a Bernell-O-Scope. Stimulus luminance was calibrated by a photometer, which expressed the units as candela per meter squared (cd/m^2).

Stimuli

The physical dimensions which differentiated the three classes of stimuli are defined by the type of depth cue that each incorporated: binocular disparity, relative contrast (via occlusion) or transparency. Each display consisted of two superimposed gratings, oriented at 60 and 120 degrees with respect to the horizontal.

Both gratings were rectangular-wave with a spatial frequency of 0.3 cycle per degree (cpd) and a duty cycle of 0.75. The gratings drifted perpendicular to their orientation in symmetrical downward-oblique directions, and their drift rate was fixed at 1.0 Hz.

The gratings appeared within a circular aperture subtending 12.3 degrees of visual angle, which was bounded by a thin (0.4°) black circle to emphasize its borders. A small fixation point of 0.25° diameter was placed in the center of the display. This was centered within a square area with 16.3° sides, filled with black/white random-dot noise. The noise granularity was of 3 pixels, with a density of 0.5. The averaged luminance of the random-dot display was 28.1 cd/m². The background was defined by an equal-luminance gray of 44 cd/m², which filled the rest of the screen (96° x 69°).

To induce binocular disparity, two versions of the stimulus were needed. They were separated by a center-to-center distance of 24.5°, and were displayed simultaneously and observed through the prism stereo viewer. To provide equal viewing conditions, two [identical] versions of the relative contrast and transparency plaid types were also constructed

such that the stereoscope was necessary throughout all experimental sessions. The three regions of the plaid which were manipulated to elicit the different cues to depth consisted of: (A) the diamond-shaped areas where the two gratings overlapped (which will be referred to as the intersections); (B) the narrow bars of both gratings (which will be termed gratings); and (C) the wide bars (which will be called background). Figure 4 A, B and C depict a complete illustration of these plaid areas.

1) *Binocular Disparity Plaids*

This depth cue was created in the same way as the disparity plaids used in the study by Dubé, von Grünau & Kwas (1992). The two horizontally displaced versions of the particular stimulus were identical except that one grating was phase-shifted in one of the versions, in such a way as to create uncrossed horizontal disparity. Each version was seen only by one eye, and the two were fused to produce a single image of the stimulus, including a particular disparity between the two gratings. As a result, one grating in the stimulus had a fixed amount of uncrossed disparity with respect to the other grating. Disparities included 15.7, 31.4 and 47.1 min. of arc, in addition to a control plaid which contained zero disparity. The stimulus which was used as the zero disparity plaid also contained no relative contrast or transparency and thus was used as the zero depth plaid for all three plaid types (see Figure 5 for an example of this stimulus). To view an example of the disparity plaids refer to Figure 6.

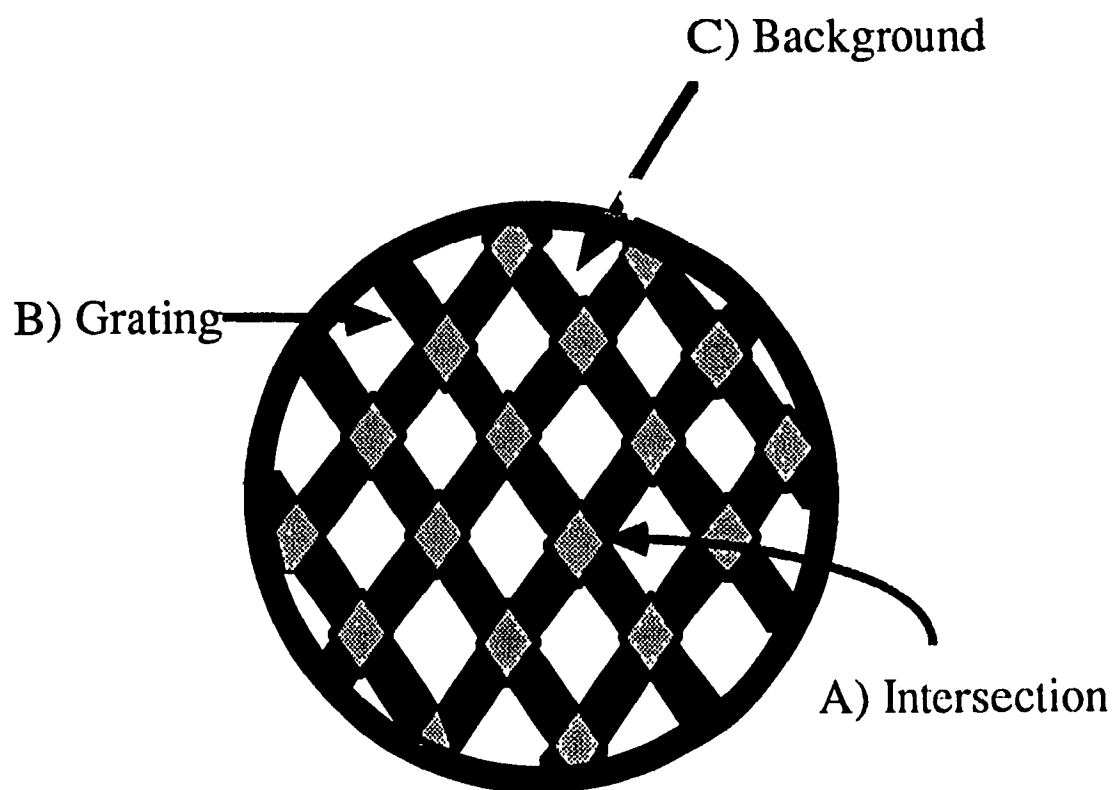


Figure 4. Schematic representation of the three plaid regions.

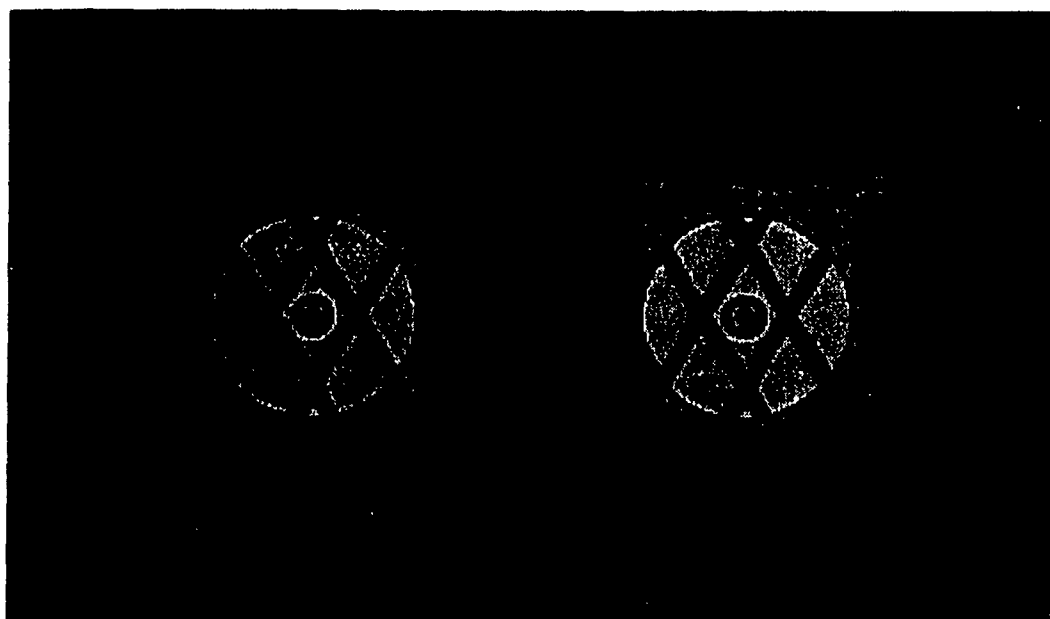


Figure 5. The zero disparity, relative contrast and transparency plaid.

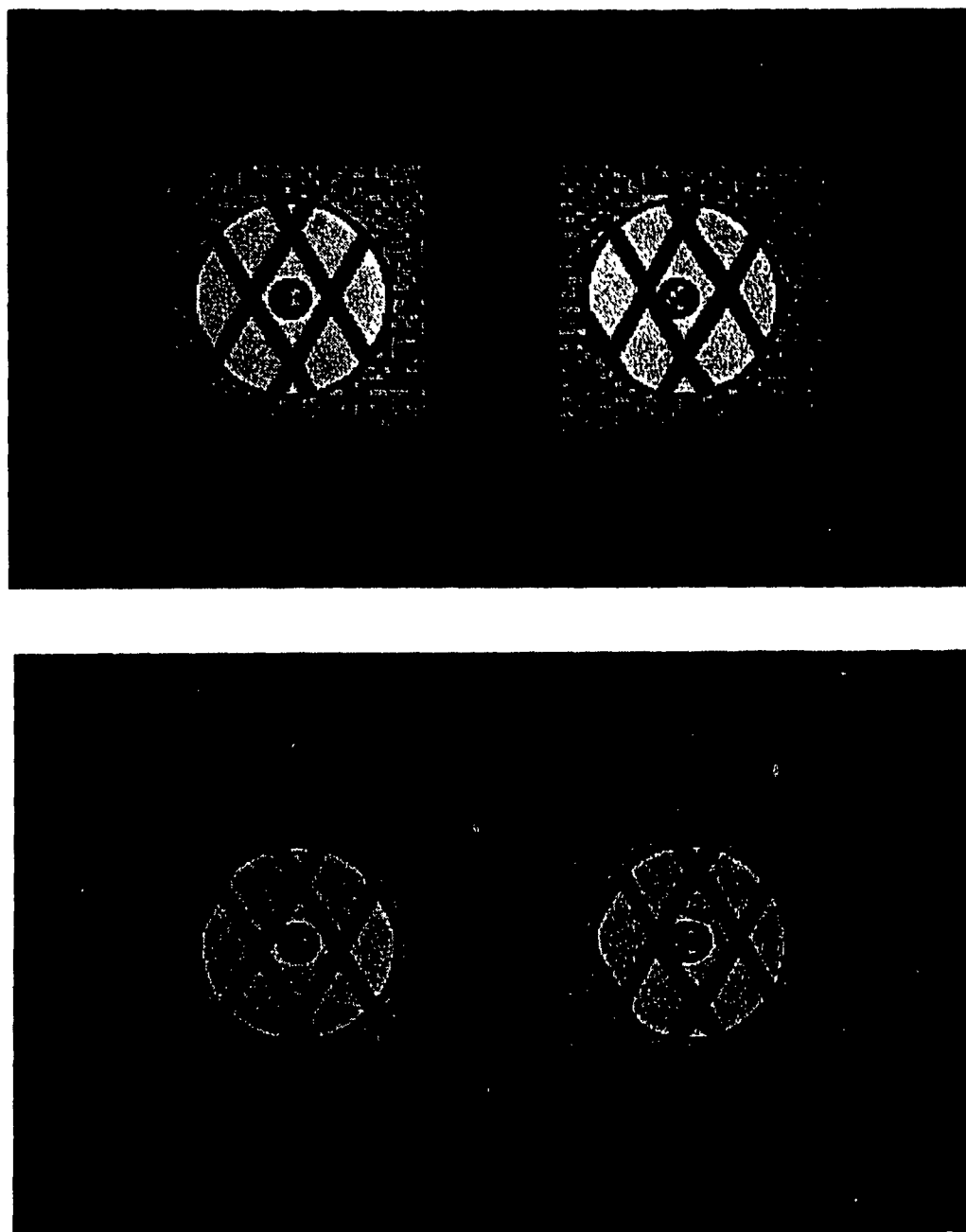


Figure 6. Two examples of the disparity plaid type:
The top stimulus is the medium disparity
and the bottom plaid contains high disparity.

2) *Relative Contrast Plaids*

These plaids were developed similar to those which were employed by Vallortigara & Bressan (1992). A high contrast grating (with respect to the background) was placed in front of a low contrast grating, via an opaque occlusion cue. The intersection was of the same luminance as the high contrast grating, and thus this region partially occluded the low contrast grating. Grating pairs were selected according to differing degrees of contrast relative to each other and their background. The three resulting plaids, with increasing differences in contrast, consisted of the following grating pair luminances: 7.04/54.60 cd/m²; 2.80/73.50 cd/m²; and 0.83/96.20 cd/m². As with the disparity plaids, a "zero" relative contrast stimulus was constructed, whereby the two gratings and the intersection all were of equal luminances (24.80 cd/m²). An example of the relative contrast stimuli is illustrated in Figure 7.

3) *Transparency Plaids*

Stimuli of this type consisted of modified versions of those used by Stoner, Albright & Ramachandran (1990). The two gratings were identical and their luminance was held constant at 24.8 cd/m², while the background was at a constant 63.6 cd/m². Perceptual transparency was manipulated by varying only the luminance of the intersections. The three levels were chosen such that all were compatible with the physics of transparency (see Stoner et al., 1990) and consisted of 18.9, 14.0, and 10.0 cd/m² in ascending order of optimal conditions for pure transparency (equivalent to

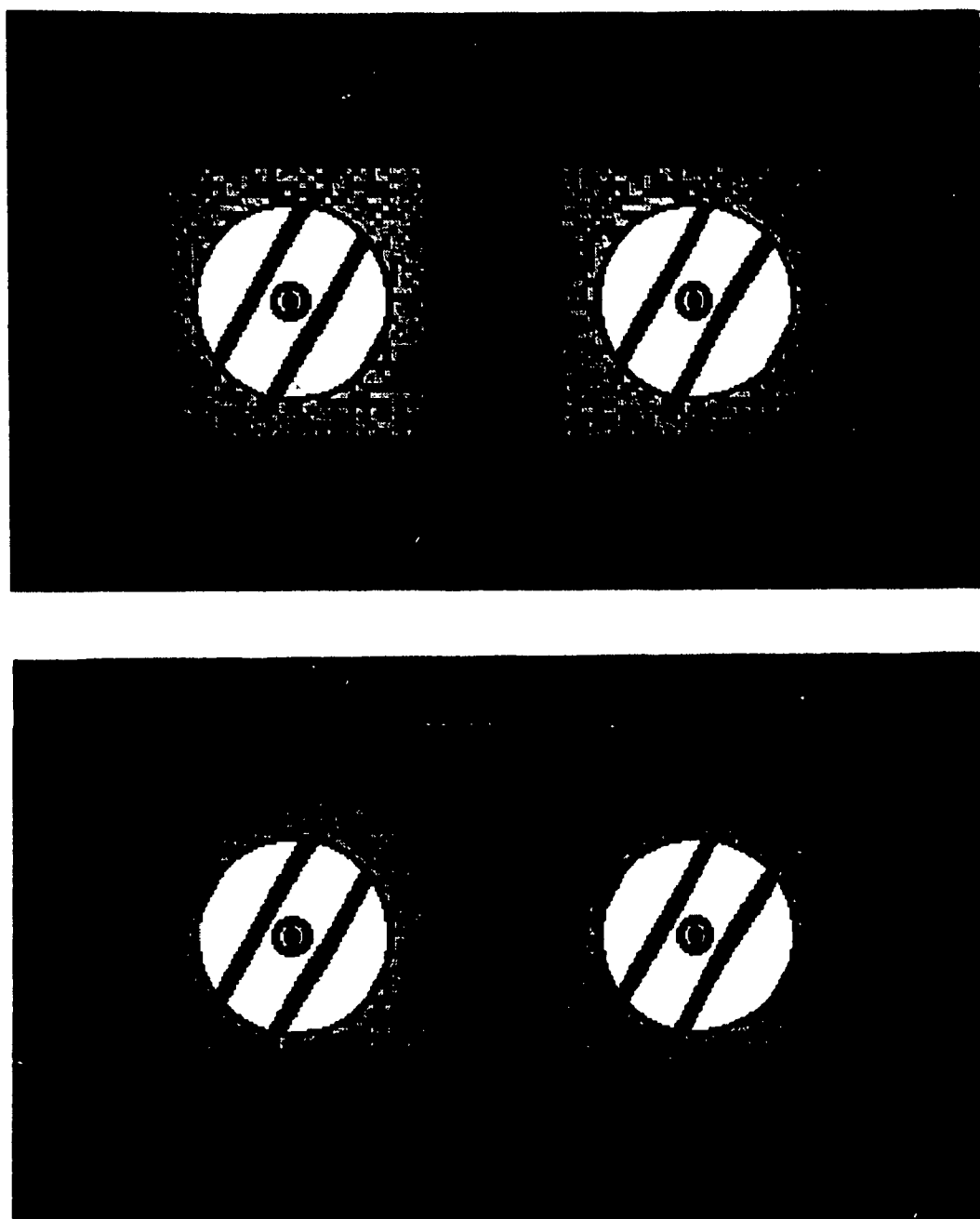


Figure 7. Two examples of the relative contrast plaid type:
The top stimulus is the medium relative contrast and
the bottom plaid contains high relative contrast.

the neutral density filter case). As a control, a plaid with an intersection luminance of 24.8 (isoluminant to the gratings) served as a "zero" transparency stimulus (at the edge of the physical transparency region). Refer to Figure 8 for an example of the transparency stimuli.

Procedure

Subjects were tested individually in a quiet and darkened visual perception laboratory. Procedural information was delivered vocally by the experimenter prior to each session. Subjects were seated in front of the screen and viewed the display through the stereo viewer, which was fixed at a distance of 17 cm from the screen. The observers were made aware of the fixation point and instructed to fixate it and to maintain their fixation continuously while viewing the test stimulus.

The three types of depth plaids, each containing four levels of depth (three depth values and a control) were separated into three experimental sessions. Each session was divided into 3 blocks, each of which presented only one level of depth and the control stimulus, both with 10 repetitions, for a total of 20 trials per block. [The zero depth stimulus was, therefore, always paired with a particular level of depth. This procedure was implemented to test for possible context effects that the depth level may have on the controls. Its importance will be more relevant for Experiment 2.] Stimuli within each block were presented in a randomly permuted order. Each stimulus presentation lasted 15 seconds, in which time subjects

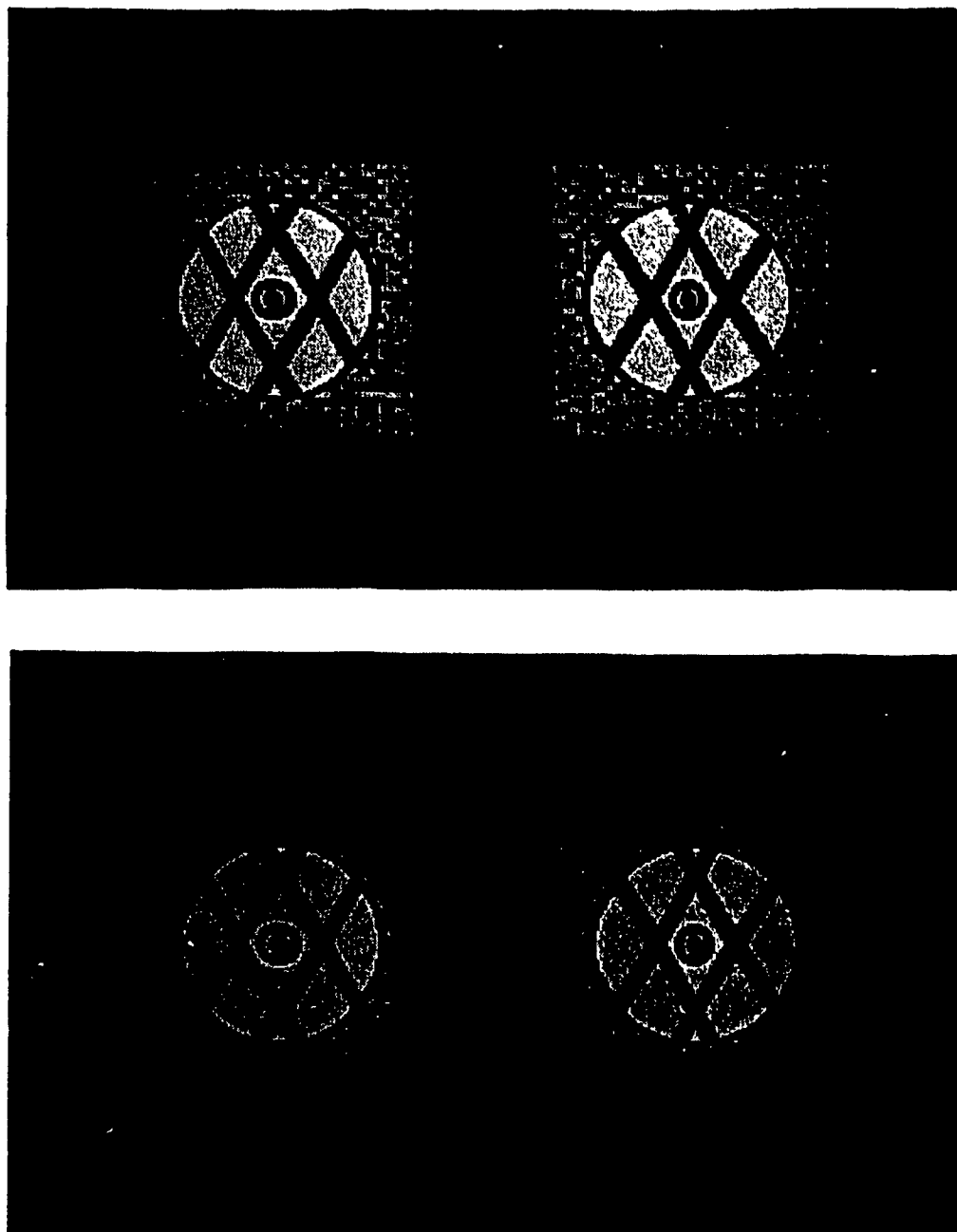


Figure 8. Two examples of the transparency plaid type:
The top stimulus is the medium transparency and
the bottom plaid contains high transparency.

responded by depressing the appropriate keys to indicate the presence and duration of the two percepts (coherent or transparent motion).

Each trial was initiated by the subject with a key press, according to readiness (e.g., good fixation) and comfort. Subjects completed all blocks in all of the sessions, and the sequence in which they proceeded was randomized between subjects. One block lasted approximately 10 minutes, for a total of 30 minutes per experimental session. The overall participation time necessary to complete the experiment was therefore roughly one hour and 30 minutes. Debriefing of subjects occurred following the completion of all experimental sessions. Responses were recorded and accumulated by the computer. The relative amounts of the two percepts were calculated as the ratio $C/(C+T)$, where C and T stand for the total time of coherent and transparent motion, respectively.

Results

From the 10 repetitions of each stimulus, the computer calculated the mean time (in seconds) each key was depressed for each stimulus type in all experimental blocks and sessions. A ratio of coherence for each stimulus for each subject was calculated by dividing the mean time obtained for coherence by the mean time of coherence and transparency added together $[C/(C+T)]$.

The zero depth stimulus (control) was presented in each block and thus always paired with a particular level of depth (i.e., for the three types of depth plaids). Accordingly, to test for possible context effects that the depth level may have had on the controls, an analysis of variance (ANOVA) was performed on the control coherence ratios with the amount of depth it was paired with (3 levels) as the factor. This was repeated three times, once for the control data from each of the disparity, relative contrast and transparency depth plaids (see Appendices A, B & C). Subjects' coherence ratios for the zero disparity plaids slightly increased as the disparity in the paired plaid increased, $F(2,12)= 5.348$, $p<0.05$. However, no differences in coherence ratios were produced between the zero relative contrast plaids or the zero transparency plaids. Thus these values were pooled and an average measure of coherence was calculated for the zero relative contrast and the zero transparency plaids, respectively. Regardless of their small differences, an average of the three zero disparity plaids (for

each subject) was also calculated to yield an adequate estimate of coherence, appropriate for later analyses.

The means were then calculated for each of the four levels of depth, within each of the three plaid types. After contrasting the means within each plaid type, the effect of different levels of depth on perceived coherence was explored further by grouping data from all of the experimental blocks and sessions by plaid type, which led to three analyses of variance. For example, an ANOVA was performed on coherence ratios with Amount of disparity (4 levels: 0, 15.7, 31.4 and 47.1 min. of arc) as the factor. This design was repeated for the relative contrast and transparency plaid types (shown in Appendices D, E & F).

Disparity plaid data yielded a monotonic trend, as shown in Figure 9, whereby subjects' coherence ratios decreased as the amount of disparity increased. The zero disparity plaid (zero) led to an average ratio of 0.5092, which was higher than the mean ratio for the 15.7 min. of arc plaid (low): 0.2748. The low disparity plaid was surpassed by an even lower coherence ratio attained by the 31.4 min. of arc plaid (medium) which yielded 0.1493. Finally, the largest disparity plaid (high), 47.1 min. of arc, led to the lowest mean among the disparity plaids, with 0.0831 perceived coherence. The one-way ANOVA demonstrated that these differences in coherence ratios, as a function of amount of disparity were significant, $F(3,18)=28.591$, $p<0.001$. Posthoc analysis (Tukey hsd) revealed that zero disparity plaids differed from all other disparity plaids and that the low disparity plaid differed from the high disparity plaid at the

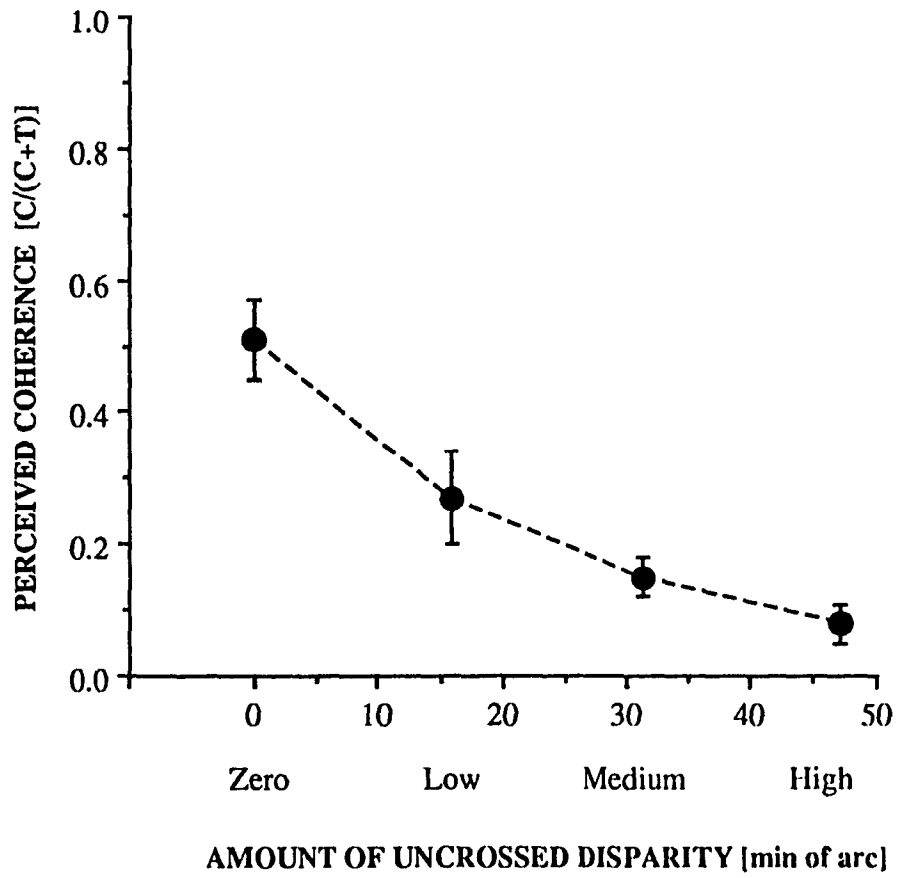


Figure 9. Perceived Coherence in Plaids Containing Different Amounts of Uncrossed Disparity.

0.01 alpha level. Although there was a trend, the differences between the low and medium, as well as the medium and high disparity plaids did not reach significance ($p > 0.05$). See Appendix D, Table 2.

A similar monotonic trend was also observed for the relative contrast data (see Figure 10); mean coherence ratios decreased as the amount of relative contrast increased in the plaids. The mean for the zero relative contrast plaid (24.80/24.80 cd/m^2), 0.5916, produced a higher ratio than the low contrast plaid (7.04/54.60 cd/m^2), with 0.0915. The medium contrast plaid (2.80/73.50 cd/m^2) with 0.0416, had a lower ratio than the low, but a higher one than the 0.0292 displayed by the high contrast plaid (0.83/96.20 cd/m^2). The one-way ANOVA performed on this data also revealed that these differences in coherence ratios, as a function of varied relative contrast, were significant [$F(3,18)=42.280$, $p < 0.001$]. In addition, further analysis (posthoc Tukey, hsd) demonstrated that the zero relative contrast plaids differed from all other relative contrast plaids ($p < 0.01$). Again, in spite of their obvious trend, the low, medium and high contrast plaids did not differ significantly ($p > 0.05$). This is shown in Appendix E, Table 2.

In contrast to the behavior of the preceding depth plaids, where monotonic trends were observed, the transparency data led to a U-shaped function, which is shown in Figure 11. The zero transparency plaid (24.8 cd/m^2) and the high transparency plaid (10.0 cd/m^2) attained the highest coherence ratios with 0.4690 and 0.4027, respectively. While the low (18.9 cd/m^2) and medium (14.0 cd/m^2) transparency plaids produced about

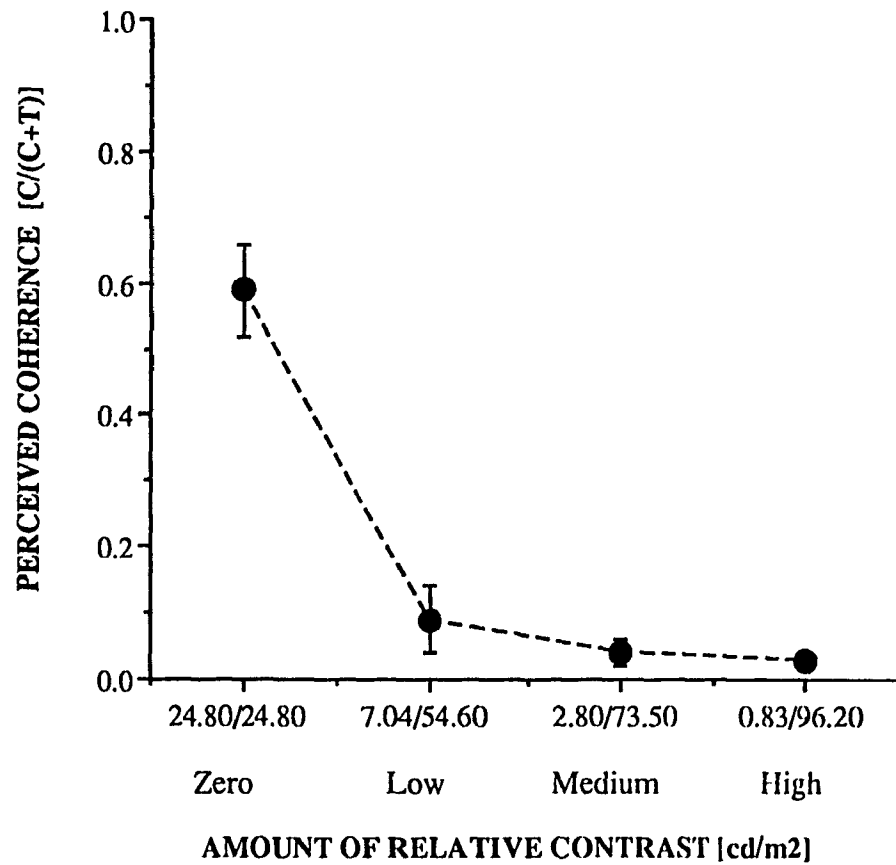


Figure 10. Perceived Coherence in Plaids Containing Different Amounts of Relative Contrast.

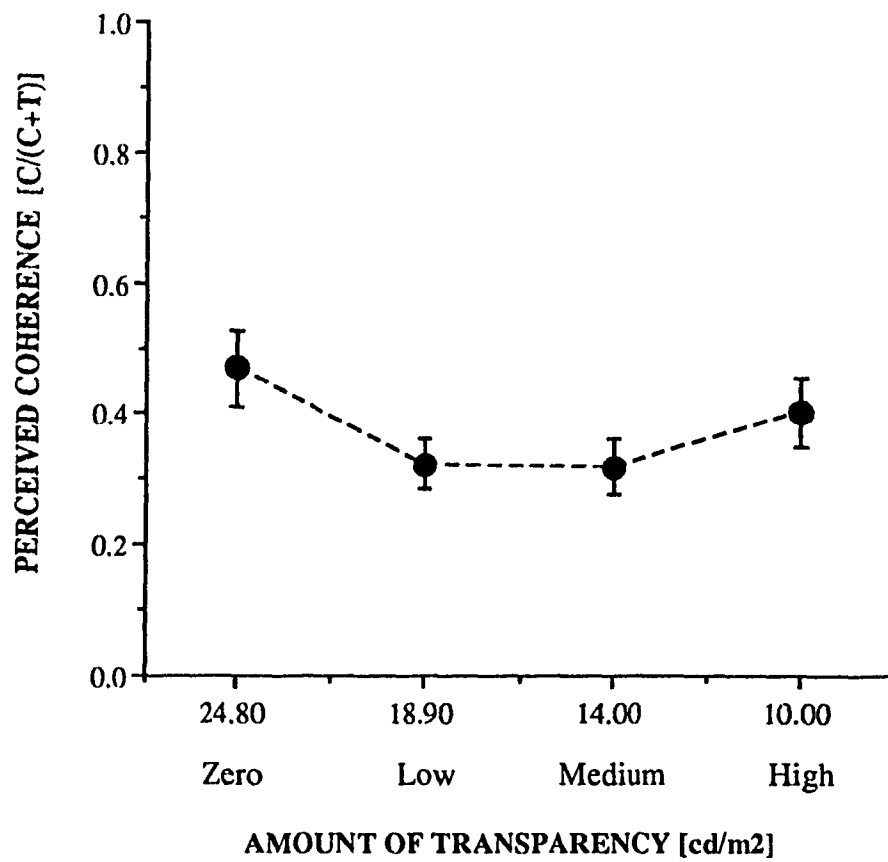


Figure 11. Perceived Coherence in Plaids Containing Different Amounts of Transparency.

equally lower ratios of 0.3231 and 0.3184, respectively. The one-way ANOVA showed that coherence ratios indeed varied significantly as a function of transparency, $F(3,18)=11.984$, $p<0.001$. The posthoc analysis (Tukey hsd) in this case revealed that the zero transparency plaid differed from the low and medium transparency plaids ($p<0.01$), but not the high transparency plaid ($p>0.05$). In addition, the medium was different from the high transparency plaid ($p<0.05$), but not from the low one ($p>0.05$). Refer to Appendix F, Table 2.

Discussion

The results of this experiment yielded baseline measurements of coherent motion for different amounts of disparity, relative contrast and transparency. There was no context effect on the control plaids for the relative contrast and transparency conditions. The controls for the disparity plaids, on the other hand, demonstrated a slight dependence on the plaid which it was presented with. As the disparity in its paired plaid increased, the perceived coherence for the control stimulus, increased. This context effect may be due to simultaneous comparison or contrast. The larger the disparity in the plaid, the smaller the perceived coherence. The control may therefore be perceived as more coherent when compared to the less easily cohering high disparity plaid. Likewise, the same stimulus may be seen to be less strongly cohering when compared to a less compelling disparity such as that from the low disparity plaid. This possible effect is weak, as it occurs only with the disparity plaids and is, therefore, of less interest for the moment, but will be of greater importance for Experiment 2. It is important to know if there are any context effects involved with this type of procedure, as Experiment 2 will mirror it, but in addition with the use of an adaptation paradigm. It is, therefore, necessary to know how much of an effect (on control stimuli) may be due simply to context effects and how much to the adaptation effect. According to the present results, it seems context effects are

minimal, if existent at all. This point will be discussed further in Experiment 2 when analyzing the behavior of the controls.

The data demonstrate a positive correlation between the degree of depth information and the corresponding change in coherence. Increasing the depth between the gratings in the plaid stimulus induces a subsequent decrease in perceived coherent motion. For example, the high depth plaids yielded the least amount of coherent motion, followed by the medium and then the low, and finally, by the zero disparity plaids which produced the greatest coherent motion. This is mainly true for the disparity and relative contrast plaids' results. Transparency data reflect roughly the same pattern but are a special case as illustrated by their U-shaped function. As the transparency increases (intersection luminance more natural for the physics of transparency), the perceived coherence decreases, as with the other plaid types. After a certain value of intersection luminance, there appears to be a cut off point, and coherent motion again rises. This exact value is uncertain at this point, as only three different levels of intersection luminance were employed, too few to ascertain details in the pattern of behavior. The high transparency, which was intended to be the optimal level and hence to induce the least coherent motion, seemed instead to be on the border of the transparency zone as indicated by its unexpectedly high coherence ratio, similar to the zero plaid. Instead, the low and medium transparency plaids attained equally optimal conditions for transparency as demonstrated by their lower perceived coherence. As with those results found by Stoner et al. (1990) there is a transparency zone, but the values

for that window of acceptance differ slightly in this experiment. Had it been possible to incorporate additional steps of intersection luminance (on the computer) such that all would be within the zone as opposed to on the border, then the high would have been the optimal level of transparency, and the same pattern as with the disparity and relative contrast plaids would likely have been demonstrated with the transparency data.

EXPERIMENT 2

The same rectangular-wave plaids that were used in Experiment 1 were employed as adaptation stimuli for this study. Following adaptation to one type of depth plaid, coherence levels were obtained with test stimuli incorporating the same type of depth cue (and either contained a fixed intermediate level of depth or none at all). After an adaptation period subjects simply reported the percept of coherent and transparent motion while viewing the different sorts of test stimuli. On the basis of the literature on plaid motion and depth, it was hypothesized that depth information is grouped somewhere to create a general impression of depth prior to being projected to higher cortical areas involved in motion grouping. The largest adaptation effects might therefore be obtained for the highest depth plaids. This would indicate that quantitative depth information is relayed to the motion integration processes by some general depth analyzer, hence implying a sophisticated cross-talk between different functional visual streams.

Method

Subjects

The same seven subjects as those in Experiment 1 participated in this study. All were exposed to the entire set of experimental conditions. The observers had normal or corrected-to-normal vision. All were right handed and were tested for stereoscopic vision prior to their participation in the experiment.

Apparatus

The apparatus was identical to that used for Experiment 1.

Stimuli

This study employed the same three classes of stimuli as in Experiment 1, whereby each class was defined by the type of depth cue it incorporated: binocular disparity, relative contrast (via occlusion) or transparency (via intersection luminance). Each display consisted of two superimposed gratings, oriented at 60 and 120 degrees with respect to the horizontal. Both gratings were rectangular-wave with a spatial frequency of 0.3 cycle per degree (cpd), as seen through the stereoscope, and a duty cycle of 0.75. The gratings drifted perpendicular to their orientation in symmetrical downward-oblique directions, and their drift rate was fixed at 1.0 Hz.

The gratings appeared within a circular aperture subtending 12.3 degrees of visual angle, which was bounded by a thin (0.4°) black circle to emphasize its borders. A small fixation point of 0.25° diameter was placed in the center of the display. This was centered within a square area with 16.3° sides, filled with black/white random-dot noise. With a noise granularity of 3 pixels, and a density of 0.5, the averaged luminance of the random-dot display was 28.1 cd/m^2 . The background was uniform gray with a luminance of 44 cd/m^2 , which filled the rest of the screen ($96^\circ \times 69^\circ$).

To induce binocular disparity, two versions of the stimulus, separated by a center-to-center distance of 24.5° , were displayed simultaneously and seen through a prism stereo viewer. To provide equal viewing conditions, two [identical] versions of the relative contrast and transparency plaid types were also constructed such that the stereoscope was necessary throughout all experimental sessions. The three regions of the plaid (intersections, gratings and background) were manipulated to produce the different depth cues.

All stimuli employed for this experiment were those used in the previous study and thus for illustrations of them refer back to Experiment 1, Figures 5 through 8.

1) *Binocular Disparity Adaptation Plaids*

This depth cue was established in reference to the disparity plaids used in the study by Dubé, von Grünau & Kwas (1992). The two versions

of the particular stimulus were identical except that one grating was phase-shifted in one of the versions, in such a way as to create an uncrossed horizontal disparity.

Each version was seen only by one eye through the stereoscope, and the two were fused to produce a single image of the stimulus, including a particular disparity between the gratings. One grating in the stimulus had a fixed amount of uncrossed disparity with respect to the other grating. Adapting disparities were 15.7, 31.4 and 47.1 min. of arc.

2) *Binocular Disparity Test Plaids*

Two plaids were tested following adaptation. One test plaid contained the "medium" uncrossed disparity level from the three adaptation disparity plaids (31.4 min. of arc), while the other was the zero stimulus as used in Experiment 1 (no disparity between the two gratings).

3) *Relative Contrast Adaptation Plaids*

These plaids were developed similar to those which were employed by Vallortigara & Bressan (1992). A high contrast grating (with respect to the background) was placed in front of a low contrast grating, via an opaque occlusion cue. The intersections were of the same luminance as the high contrast grating, and thus these regions partially occluded the low contrast grating. Grating pairs were selected according to differing degrees of contrast relative to each other and their background. The three resulting adaptation plaids, with increasing values of contrast difference,

consisted of the following grating pair luminances, : 7.04/54.60 cd/m²; 2.80/73.50 cd/m²; and 0.83/96.20 cd/m².

4) *Relative Contrast Test Plaids*

Two plaids were tested following adaptation. One test plaid consisted of the "medium" relative contrast level from the three adaptation relative contrast plaids (2.80/73.50 cd/m²), while the other was the zero stimulus as used in Experiment 1 (no relative contrast between the two gratings: 24.80 cd/m² for both).

5) *Transparency Adaptation Plaids*

Stimuli of this type consisted of modified versions of those used by Stoner et al. (1990). The two gratings were identical and their luminance was held constant at 24.8 cd/m², while the background was at a constant 63.6 cd/m². Perceptual transparency was manipulated by varying only the luminance of the intersections. The three levels used for adaptation were identical to those transparency plaids used in Experiment 1 and hence were compatible with the physics of transparency. They had intersection luminances of 18.9, 14.0, and 10.0 cd/m² in ascending order of optimal conditions for pure transparency (equivalent to the neutral density filter case).

6) *Transparency Test Plaids*

Two plaids were tested following adaptation. One test plaid consisted of the "medium" transparency level from the three adaptation transparency plaids (14.0 cd/m^2), while the other was the zero transparency stimulus as used in Experiment 1 (intersection luminance of 24.8 cd/m^2 , isoluminant to its gratings).

Procedure

All subjects were tested individually in a quiet visual perception laboratory with dim background lighting. Procedural information was delivered vocally by the experimenter prior to each session. Subjects were seated in front of the screen and viewed the display through the stereo viewer, which was fixed at a distance of 17 cm from the screen. The observers were made aware of the fixation point and instructed to fixate it and to maintain their fixation and fusion continuously while viewing the adaptation and test stimuli.

The three types of depth plaids, each containing three levels of adaptation, were separated into three experimental sessions. Each session was divided into 3 blocks, in each of which the subject adapted to only one level of depth and tested with the two test stimuli (a depth and the zero stimulus), both with 10 repetitions for a total of 20 trials per block. For a schematic presentation of the adaptation paradigm refer to Figure 12.

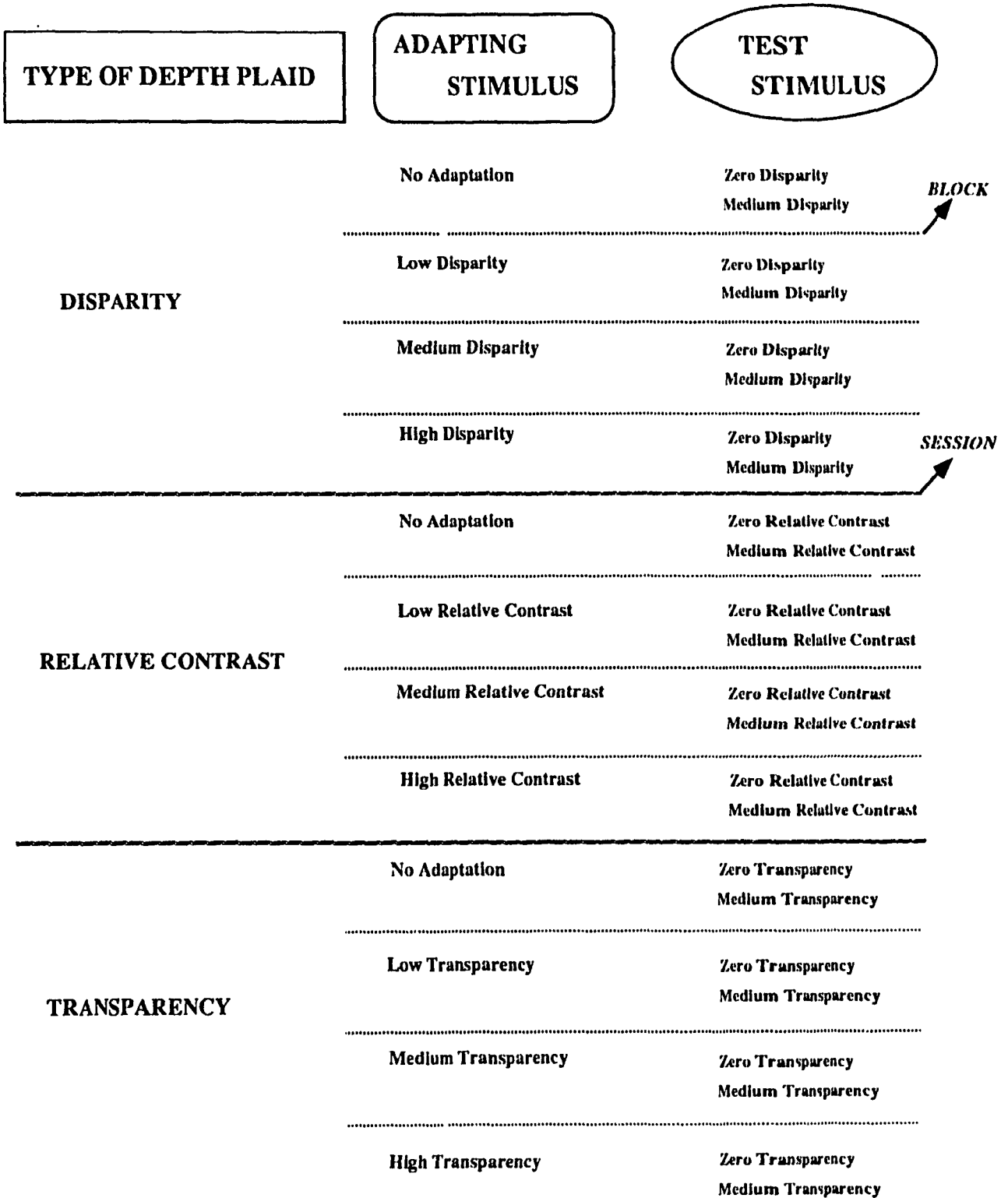


Figure 12. Design of the adaptation paradigm used in Experiment 2.

Stimuli within each block were presented in a randomly permuted order and there was time between blocks to neutralize adaptation effects. Each adaptation period lasted 20 seconds, which was immediately followed by a test with a duration of 15 seconds. Following adaptation, subjects responded in the testing period by depressing the appropriate keys to indicate the presence and duration of the two percepts (coherent or transparent motion).

Each trial was initiated by the subject with a key press, according to readiness (e.g., good fixation) and comfort. Subjects completed all blocks in all of the sessions, and the sequence in which they proceeded was randomized between subjects. One block lasted approximately 20 minutes, for a total of 60 minutes per experimental session. The overall participation time necessary to complete the experiment was therefore roughly three hours. Debriefing of subjects occurred following the completion of all experimental sessions. Responses were recorded and accumulated by the computer. The relative amounts of the two percepts were calculated as the ratio $C/(C+T)$, where C and T stand for the total time of coherent and transparent motion, respectively.

Results

A ratio of coherence for each test stimulus (i.e., for each adaptation level, within each plaid type) was calculated for each subject in the same manner as in Experiment 1 [$C/(C+T)$]. The means were then computed for each test stimulus in each adaptation condition. Three analyses of variance (ANOVA) were done to explore the effect that adaptation to different amounts of depth had on perceived motion coherence in test plaids either containing a "medium" amount of depth information or none at all ("zero"). To illustrate, an ANOVA was performed on disparity coherence ratios with Adaptation stimuli (4 levels: NO adapt, 15.7, 31.4 and 47.1 min. of arc) and Test stimuli (2 levels: 31.4 and 0 depth) as factors. Note, that the data for "NO adapt" was taken from the disparity data in Experiment 1. This was justified by the facts that the same observers participated in all of the conditions, and that each condition (in both experiments) was run as a separate session. They are simply the subjects' means for both the medium and zero disparity plaids and will serve as baseline information to test for adaptation effects. This was repeated for relative contrast and transparency coherence data (see Appendices G, H & I).

Disparity data, as shown in Figure 13, yielded a monotonic trend, in which the coherence ratios increased as the level of disparity in the adapting stimulus increased. This, however, occurred only for the means of the medium disparity stimulus, not the zero one. To illustrate,

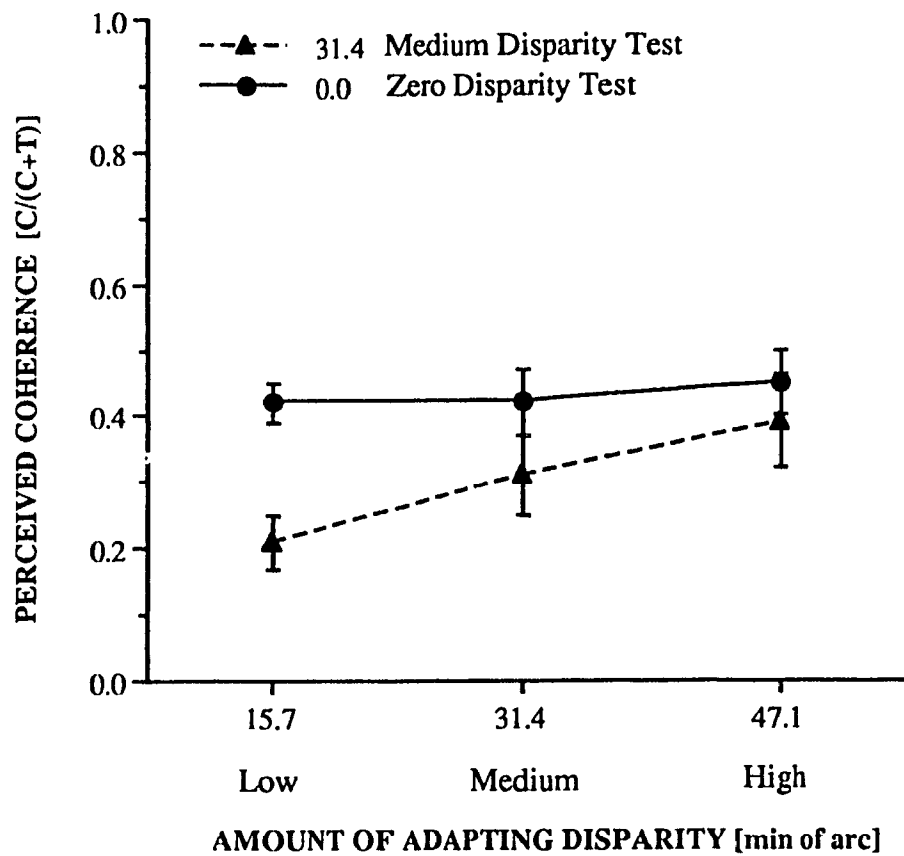


Figure 13. Adaptation to Different Amounts of Uncrossed Disparity and the Subsequent Amount of Perceived Coherent Motion in Plaids Containing Either "medium" or "Zero" Uncrossed Disparity.

following NO adaptation, the medium test plaid produced a mean ratio of 0.1493, and after low adaptation (15.7 min. of arc) the ratio elevated to 0.2063. This increased further to 0.3095 by adapting to medium disparity (31.4 min. of arc) and even more so following adaptation to the high (47.1 min. of arc) disparity plaid, to a ratio of 0.3867. In contrast, the zero test plaid produced the following ratios in the same adaptation conditions as aforementioned: NO=0.5092; low=0.4167; medium=0.4234; and high=0.4471. The two-way ANOVA supported this pattern of results with a significant Adaptation by Test stimulus interaction, $F(3,18)=12.919$, $p<0.0001$. The main effects of Adaptation and Test stimulus were also significant [$F(3,18)=4.754$, $p<0.05$; and $F(1,6)=35.202$, $p<0.001$, respectively], but are of little interest due to the interaction. Posthoc comparisons (Tukey hsd) were performed to isolate the interaction effect (Appendix G, Tables 1 & 2). In regards to the medium disparity test plaid, the analysis demonstrated that the difference between the NO and the low adaptation did not reach significance ($p>0.05$), but the differences between the NO and medium as well as between the NO and high were significant ($p<0.01$). Similarly, the difference found between the low and medium adaptation was not significant ($p>0.05$), however, the difference between the low and high showed significance ($p<0.01$). Following the same pattern, the difference was not significant between the medium and high adaptation conditions ($p>0.05$). In contrast to the medium disparity test, the posthoc analysis exploring the effect of adaptation on the zero test plaid

yielded no significant differences between any of the conditions ($p>0.05$), hence producing the interaction.

The relative contrast plaid data exhibited the same pattern of results as the one observed for disparity data (refer to Figure 14). As the difference in relative contrast increased in the adapting stimulus, the coherence ratios increased in a monotonic fashion. Once again, this was only illustrated with the medium relative contrast test plaid (2.80/73.50 cd/m^2), and not the zero test (24.80/24.80 cd/m^2). With the lowest ratio of coherence, 0.0416, the NO adapt condition was exceeded by the low adapt's (7.04/54.60 cd/m^2) mean ratio of 0.1152. Likewise, the medium adaptation (2.80/73.50 cd/m^2) led to an even higher ratio, 0.1696, but was lower than that produced by adaptation to high relative contrast (0.83/96.20 cd/m^2), 0.2377. On the other hand, the zero test plaid produced the following ratios in the same adaptation conditions as aforementioned: NO=0.5916; low=0.5649; medium=0.6143; and high=0.6214. The two-way ANOVA supported this pattern of results with a significant Adaptation by Test stimulus interaction, $F(3,18)=3.806$; $p<0.05$. The main effects of Adaptation and Test stimulus were also significant [$F(3,18)=8.260$, $p<0.01$; and $F(1,6)=83.003$, $p<0.001$, respectively], but are of little interest due to the significant interaction. Posthoc comparisons (Tukey hsd) were performed to isolate the interaction effect (Appendix H, Tables 1 & 2). In reference to the medium disparity test plaid, the analysis demonstrated that the difference between the NO and the low adaptation did not reach significance ($p>0.05$), but the differences

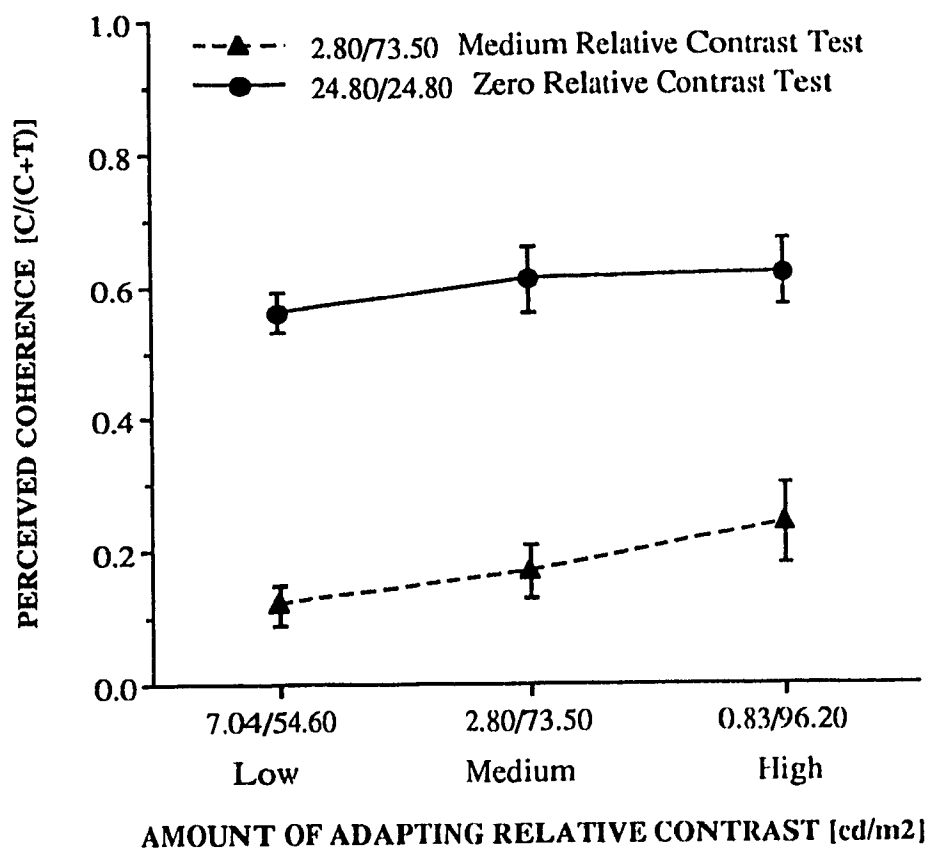


Figure 14. Adaptation to Different Amounts of Relative Contrast and the Subsequent Amount of Perceived Coherent Motion in Plaids Containing Either "Medium" or "Zero" Relative Contrast.

between the NO and medium as well as between the NO and high were significant ($p < 0.05$). Similarly, the difference found between the low and medium adaptation was not significant ($p > 0.05$), however, the difference between the low and high reached statistical significance ($p < 0.05$). Following the same pattern, the difference was not significant between the medium and high adaptation conditions ($p > 0.05$). In contrast to the medium disparity test, the posthoc analysis exploring the effect of adaptation on the zero test plaid yielded no significant differences between any of the conditions ($p > 0.05$), hence producing the interaction.

The pattern of the transparency plaid data was again different from that of the other two plaid types. Figure 15 illustrates that the data reflected a flat function, in which the amount of transparency in the adapting stimulus did not predict a corresponding change in the coherence ratio. This was true for both the medium transparency test plaid (14.0 cd/m²) and the zero one (24.8 cd/m²). NO, low (18.9 cd/m²), medium (14.0 cd/m²) and high (10.0 cd/m²) adaptation mean ratios did not differ much (0.3184, 0.3165, 0.3038 and 0.2753, respectively) for the medium transparency test plaid. The zero test plaid also demonstrated fairly consistent ratios following the same adaptation conditions: NO=0.4690; low=0.4337; medium=0.4606; and high=0.4469. The two-way ANOVA supported this pattern with only a significant main effect for Test stimulus, $F(1,6)=37.808$, $p < 0.001$.

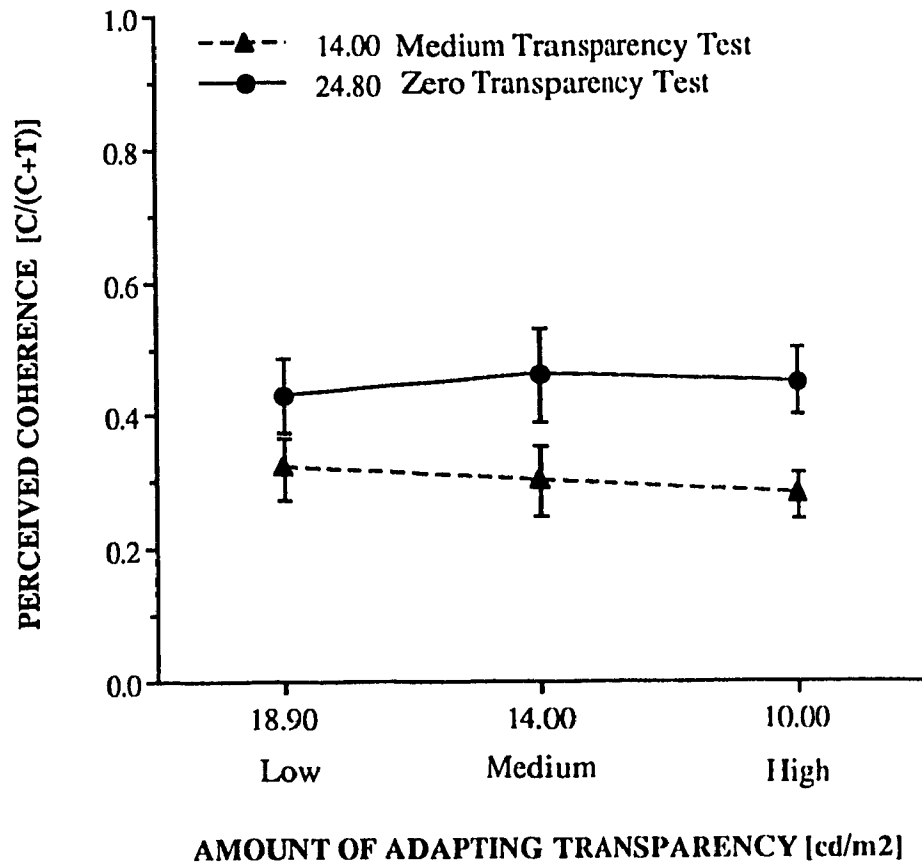


Figure 15. Adaptation to Different Amounts of Transparency and the Subsequent Amount of Perceived Coherent Motion in Plaids Containing Either "Medium" or "Zero" Transparency.

This suggests, that the only real pattern in this set of results is the difference between the mean coherence ratios exhibited by the medium and zero transparency test plaids, with 0.3035 and 0.4525, respectively (Appendix E, Table 3).

Discussion

Interestingly, the results from the transparency plaid data did not demonstrate an effect of adaptation. Regardless of the amount of transparency, the perceived coherence did not stray from baseline levels. This observation suggests that the effect of transparency cannot be fatigued. There could be many reasons for this, one of which is related to the type of depth cue it is. Transparency lends information in reference to overlapping surfaces, but requires other cues (i.e. color, contrast, texture, disparity etc.) to determine which of those surfaces is in front of the other (and by how much). The optimal level of transparency (within the transparency zone) would only mean that conditions are optimal for there to be two surfaces overlapping, not for an increase in distance between those surfaces. Its baseline data from Experiment 1 support this notion, as demonstrated by the U-Shaped function. If transparency, as a cue to depth, would have the potential to provide information in reference to the amount of depth present, then baseline results should have produced a monotonic pattern similar to the other depth cues. Even at its optimal level, perceived coherence exceeded that produced by plaids containing either disparity or relative contrast, thus again supporting the weakness that this type of cue has in regards to precise depth estimation. Locally, this cue has importance for surface segmentation, but its signal alone does not provide unambiguous depth positioning and hence cannot produce a continuum of depth. The very fact that its baseline level of perceived coherence is just

slightly under ambiguous perception (where ambiguous is 50% coherence) is evidence for transparency's inability to produce precise information in regards to which surface is in front, and by how much. If it contained a mechanism specific for measuring the amount of distance between surfaces it would then follow that (more) unambiguous motion should be perceived. For example, the greater the distance is between two or more surfaces, the more difficult it should be to make judgmental errors as to which surface is in front. Therefore, the more certain the observation of multiple surfaces, the greater the difficulty for the visual system to infer one surface, and hence coherent motion. This does not seem to be the case with the transparency cue. Due to its ambiguous perception, it is almost impossible to adapt to depth which perhaps explains why there was no adaptation effect observed for this cue type.

Unlike transparency, an adaptation effect was observed for the other two plaid types. More precisely, as the amount of disparity (or relative contrast) was increased in the adapting stimulus, the larger the adaptation effect observed (this was true only for the test plaid containing depth). This conclusion is suggested by the gradual increase in perceived coherent motion following progressively larger adapting disparity values (or relative contrast values). One explanation for this effect may be in terms of actual adaptation time. It seems that the greater the distance is between the two surfaces, the more often dual surfaces are perceived and this therefore increases the time spent in that perception, which directly corresponds to time spent fatiguing depth. The longer the time spent

fatiguing a mechanism, the more the visual system is impaired for its corresponding perception, as illustrated by larger adaptation effects. Another explanation for these data may stem from a consideration of strength. When two surfaces are separated by increasingly larger distances, the largest distance yields the strongest impression of depth, and therefore the visual system is more certain of the existence of depth. The stronger the certainty, the more neurons would be active and hence can be fatigued. Of course the optimal theory would be an interaction of these two points. A more detailed and thorough discussion of these and other points will follow in the General Discussion.

The zero test stimuli for disparity and relative contrast did not show an effect of adaptation. Regardless of the level of depth in the adapting stimulus, there was no deviation from baseline level of perceived coherence. This suggests that in some ways, adaptation to depth is coarsely channel-specific. By this I mean that fatiguing a particular depth cue has the greatest effect on test stimuli containing depth, but does not alter the perception produced from a depth-free environment. Unchanging perceived coherence also supports a lack of possible contextual effects which were discussed previously in Experiment 1. A concern here was that if there was an effect of adaptation, would it be due solely to adaptation or also be affected by the stimulus with which it was presented closely in time (the medium test plaid). This is why it was important to test for context effects in Experiment 1. As seen by those results, context

effects were minimal, and could therefore be assumed to be nonexistent in this experiment.

One possible confound which may have affected the results can be ruled out by the fact that the controls were not affected by adaptation. It might have been possible that instead of adapting solely to a depth property, the depth cue was only indirectly responsible for the adaptation effect. To illustrate, when two surfaces are separated by depth, then the visual system perceives multiple surfaces, and hence perceives that motion which corresponds to more than one moving object: transparency. When this occurs, then perhaps the depth information is simply helping the system to adapt to a motion type, and not to depth *per se*. Had this been the case, then we should have observed an effect on the controls, which by their nature yielded about equal amounts of both motion types. In fact other studies have shown that stimuli identical to the controls used in these experiments are indeed affected by adaptation to motion type (von Grünau & Dubé, in press). For this reason, this possible confound can securely be ruled out as explanation for data attained here. It seems more plausible that the visual system was adapting to depth and not to the type of motion produced by the depth information.

GENERAL DISCUSSION

In the natural environment, multiple sources of information are made readily available for the perceiver to use both consciously and unconsciously in determining a more robust perceptual solution. It is, therefore, not inconceivable that the motion system uses information other than motion itself, such as cues associated to surface segmentation and real-world constraints like depth layering, in the resolution of complex motion problems. Past related research in this domain has demonstrated that there is indeed an interaction between the depth and motion modules, whereby depth cues in the stimulus determine whether motion signal integration is possible or not. The aim of the present studies was to provide more evidence in support of this argument. They thus investigated more extensively not only the qualitative effect of different kinds of depth cues relating to surface segmentation on the integration of local 1-D motions, but also the quantitative effect on coherent motion of different levels of depth information in a stimulus. This research succeeds in providing more compelling evidence supporting a model of motion grouping which necessarily relies intimately on not only the presence of depth in the stimulus, but also the kind and amount of that depth-related information.

The first experiment, which was designed to test the influence of varying the degree of depth present in the stimulus, demonstrated that increasing the amount of depth via disparity, relative contrast or transparency (which was a special case) seemingly separates the component

gratings to a greater extent, making integration increasingly difficult and hence less frequently successful. This implies that the motion pathway is highly sensitive to depth cues which provide information in reference to the presence of multiple surfaces. The very fact that additional increases in depth between the gratings is more powerful in preventing integration indicates an underlying mechanism which has accurate depth estimation and uses this information in motion grouping. As well, the motion system is able to distinguish the difference between differently defined depth in the stimulus, as illustrated by the varying degrees of coherent motion produced by the three depth plaids. Consequently, by some means the motion system is able to detect distinct differences in the way local components are segregated into different planes, again evident of a sophisticated use of depth information.

Experiment 2 further examined this phenomenon by investigating more extensively, the manner by which the depth processes influence motion integration. By use of an adaptation paradigm, it was possible to estimate the kind of interaction between the two modules. In general, results from this study demonstrated that after adaptation to depth (with the exception of the transparency cue) there is a subsequent increase in coherent motion perceived in the test stimulus. This indicates, that adaptation to depth weakened the normally strong influence the depth modules have in "telling" the integration process that multiple surfaces are present. Under conditions which would normally allow depth modules to prevent integration (reflected in low levels of perceived coherence) after

adaptation, these same depth modules are somewhat silenced as evidenced by the elevation in successful integration (increased coherence). The degree of strength adaptation has in this silencing of the depth influence is determined by the size of depth in the adapting stimulus. This is supported by the present findings, whereby adaptation to the high depth plaids induced the greatest increase in coherent motion. Again, this suggests the complexity of the influence of depth on motion analysis, as indicated by the importance of both the type and level of depth present in the image. How might this interaction between depth information and motion integration be occurring in the visual system?

Implications Towards a Conceptual Model

Following adaptation to different levels of depth and testing with a constant depth level several outcomes were possible. For example, had the results produced a flat function this would have been evidence for a very simple motion detector which responds in the same way regardless of the amount of depth present in the stimulus. The results from both this experiment and the previous one do not support this interpretation. Secondly, had the results reflected channel-specific behavior, with the greatest adaptation effect occurring when the adapting and test stimuli matched in depth, this would have been indicative of a more sophisticated relay of information from depth sensitive cells than the previously discussed alternative. This would have suggested distinct depth channels in the motion stream, each having depth sensitive cells with differential

selectivity for depth level. This implies further that these subpopulations of neurons showing preferential responsivity to a particular depth level (within a particular cue to depth) have a direct and non-interactive effect on motion grouping processes. By non-interactive I mean, *without* the pooling of depth information from all types of depth detectors both within and outside a specific cue to depth, prior to the motion integration decision. Evidence for this alternative, however, was also not found.

What in fact was demonstrated by the obtained results indicated that the largest adaptation effect occurred following adaptation to the stimulus which contained the largest depth information. This suggests the presence of a more generalized depth analyzer which responds more vigorously the greater the depth. This is consistent with the results: when depth information was the largest (irrespective of how it was created--with the exception of transparency), this general analyzer fatigued to a greater extent and thus could not assist motion grouping processes as strongly as it "normally" would have (without adaptation).

This does not, however, completely dismiss the existence of channel-specific behavior within those functional streams which specialize in a particular kind of depth. Studies have shown, for example, that disparity sensitive cells are preferentially selective to not only the type of disparity, but also to the amount of disparity (Stevenson, Cormack & Schor, 1992; Sekuler & Blake, 1990). It is not inconceivable, for example, that the neurons which are qualitatively sensitive to the specific properties of depth (regardless of the kind of depth cue) determine how much depth is in the

stimulus, and then relay their quantitative measure of depth to some generalized depth analyzer, a "mediator" type of neuron somewhere within the motion stream, which responds more vigorously the greater the depth. This cell, receiving pooled depth information from the various depth-detecting neurons would calculate the total depth present in the stimulus and the converged depth estimation would be used by the motion integration process (facilitating or preventing motion grouping). To illustrate, if we adapt to a large amount of, for example, disparity, then disparity-selective cells tuned to large disparities would fatigue, but all the while they would be sending messages to the mediators saying that there is large depth and hence strongly fatiguing these depth-analyzing neurons. Consequently, the adapting stimulus, while directly adapting only those disparity cells selective for large disparities also indirectly fatigues the general depth analyzers (i.e. "telling" them continuously that a large amount depth is present) and hence this gives the obtained results: the larger the adapting depth, the larger the effect on motion integration. The result would be a strong adaptation effect.

The anatomical locus of such mediators or even the existence of such a general depth analysis itself is still debatable. Whether this information is derived relatively early on in motion analysis and sent directly to higher cortical areas involved in motion analysis, or analyzed at higher cortical areas and simply fed back to early motion grouping mechanisms via neural back projections is not yet determined. Most researchers tend to support the former alternative (Trueswell & Hayhoe, 1993; Vallortigara &

Bressan, 1991; Shimojo, Silverman & Nakayama, 1989). Something important to note is that the test stimuli, in the present study, containing no depth information, were unaffected by adaptation of any depth level. For the validity of this conceptual model, the constraint would be that if there is no depth in the test stimulus, the depth analyzing processes (wherever or however they occur) would be unaffected and hence silent. This makes physiological sense, since a depth detector cannot respond if there is no depth present in the environment. In any case, motion integration is not dependent exclusively upon depth cues, it simply takes advantage of their presence or absence as a means of confirming a particular percept. Following adaptation to even the largest disparity and relative contrast, perceived coherence was always much lower than that produced by the controls. This suggests, that not all depth-sensitive or analyzing neurons were "silenced" by adaptation and thus were still able to influence integration, but to a weaker extent. This clearly illustrates the close relationship between depth cues and motion grouping.

Studies by Trueswell and Hayhoe (1993) and Vallortigara and Bressan (1991) offer additional support for the combined effects of depth cues on motion grouping. If they converge to reflect consistent depth layering, then integration is less likely to occur as opposed to when the cues provide conflicting information (in reference to the stimulus or to real world constraints). This conflict between depth cues acts as perceptual glue between the components and yields stronger percepts of coherence. Trueswell and Hayhoe (1993) suggest that this is inconsistent with a

simplistic view of integration whereby there are distinct non-interactive channels in the motion pathway each determining surface segmentation. Rather, it is more likely that there is plenty of collaboration and cross-talk to collectively produce an accurate and robust solution. The specialized analysis that is characteristic of each particular pathway, each possesses some degree of capability of representing two-dimensional contours. It is this common ability in processing that would allow for comparisons and contrast of image analysis between different functional channels or pathways. The integration process must have access to the *combined* information of the separate pathways. For the process of motion analysis to receive the combined information, implies a mechanism that completes perceptual computation to determine an estimation of depth (between different components of an image). Such a notion is consistent with the conceptual model put forth presently. The mediator (however it is defined) would be doing just that: it computes the addition and subtraction of depth information which is converging from the different depth-sensitive neurons. If, however, there is no real depth present, then this mechanism would not be stimulated, and consequently could not provide a perceptual estimate of the depth relationship between the two 1-D patterns. Thus, without aid of depth-related information (i.e. the zero depth plaids used in the present studies), there is more ambiguity in determining multiple surfaces and hence, higher proportions of coherent motion are observed (integration is more successful). For a schematic illustration of this model, refer to Figure 16. As illustrated, all the depth cues would feed

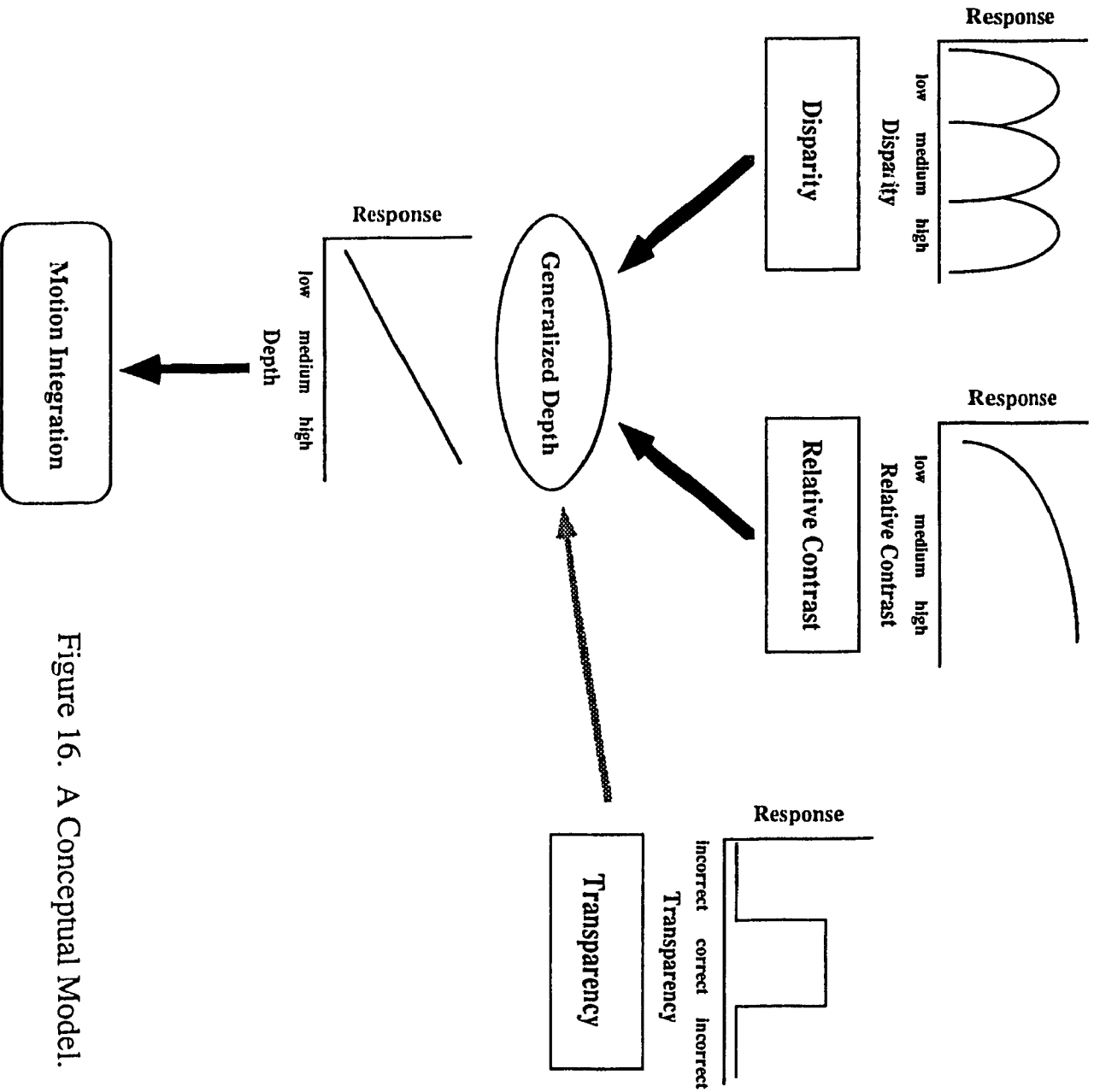


Figure 16. A Conceptual Model.

their information to the Generalized Depth analyzer before this computed amount of depth is used in motion integration. Disparity and relative contrast are both on the same "level" of diagram, indicating that they have about equally strong influence on the integration process. Transparency, on the other hand, is placed at a different location, as it conformed itself as a weaker depth cue, affecting motion integration to a lesser degree. More detail on depth cue differences will follow. Each cue's responses are outlined: disparity responding in a channel-specific manner; relative contrast as perhaps exponentially responsive; and transparency basically responding in terms of a step-function (i.e. all-or-nothing). Notice that the generalized depth detector (or mediator) receives their combined information, and its response is ~linear (e.g. decides how much depth is present). After computation, the generalized depth detector sends input to the motion integration process.

Testing the Model

An elegant and direct test of this conceptual model could be accomplished with use of a cross-adaptation paradigm, whereby following adaptation to one type of depth-defined plaid, coherence is measured in a plaid containing a different cue to depth, but of the same amount of depth as in the adapting plaid. If there are distinct channels along the motion pathway with specialization for detection of certain stimulus properties relating to surface segmentation, and if the responses for these differently selective subsets of neurons are not first integrated by some general depth

analyzer, then no cross-adaptation should occur. This is presently being explored by Kwas, von Grünau and Dubé and preliminary data yield compelling support for a general depth analyzer which computes the proportion of depth information in the image prior to sending the combined depth information to higher cortical areas of motion analysis. A level of disparity and one of relative contrast which were found to produce about equal amounts of coherent motion in the plaid were chosen for the study. Adaptation to the disparity-defined plaid and testing with both the disparity and relative contrast plaids, demonstrated that cross-adaptation was indeed possible in the determination of grouping motion signals: adaptation to disparity increased coherence in both depth plaid types. The reverse was also true. Interestingly, while all effects were strong, the greatest adaptation effect was observed when adapting and test stimuli were defined by the same cue type, compared to the cross-adapt conditions. Despite the speculative nature of these results, they still support the proposed model, which favors depth-pooling prior to integration of motion. In addition, these findings place emphasis on the fact that before the combining of depth information, depth sensitive neurons are without doubt specialized in their preference for the kind and amount of depth stimulation, thus perhaps explaining the biases found in cross-adaptation.

Different Types of Depth Plaids and their Role in Motion Integration

For the present study, three types of different depth cues were tested: disparity, relative contrast, and transparency. While the first two resulted

in very similar outcomes, transparency was a special case, as illustrated by the specific results in both of the experiments. It was found that once transparency was within the range corresponding to values consistent with the physics of two filter-like overlapping surfaces, then this cue to depth reached its maximum influence on motion integration. Whatever the level of coherence that is induced by this level of transparency, it cannot decrease further, unless information from other surface cues converges to indicate the existence of two separate planes. Only then could there be additional segregation of the components and consequently further reduction in coherence (or integration). Recent physiological evidence indicates that this cue appears to influence the response of pattern motion cells in area MT (Stoner & Albright, 1992a; b), but present results are in favor of the view that depth defined by transparency alone is limited in its power to prevent the grouping of motion signals and requires much assistance from other surface segmenting cues to disambiguate motion signals. Consistent with this is evidence provided by a recent computational study by Kim & Wilson (in press), who suggest that effects of transparency are limited and dependent upon the angle between component motion directions, which can either allow or inhibit its influence on coherent motion.

Experiment 2 confirms this notion. Due to its ambiguity as a depth layering cue, transparency could not induce any adaptation effects. Even at its optimal level, transparency never equaled the power displayed by the other two depth cues in preventing motion grouping: coherence was at

much higher levels than those allowed by disparity and relative contrast plaids. In fact, coherence levels were only slightly lower than for the zero depth plaids. This again supports the weakness that this type of cue has in regards to precise depth estimation. Locally, this cue has importance for surface segmentation, but its signal alone does not provide unambiguous positioning and hence cannot produce a continuum of depth. Due to its ambiguous perception, it is almost impossible to adapt to a particular depth, which perhaps explains why there was no adaptation effect observed for this cue type.

In contrast, plaids which conveyed depth information by disparity or relative contrast behaved similar to each other but much differently from transparency plaids. The strength and variability of the output from these particular surface segregating mechanisms in reference to inhibiting unitary motion (coherence) far outweighs that of transparency mechanisms. A direct relation was observed between progressive increases in the degree of depth information within the stimulus and the corresponding decrease in coherence, with the high depth plaids being strongest in preventing local motions from being integrated. These two cues offer the same type of output, whereby they provide accurate estimation of depth separating the components of an image. It seems, they are capable of relaying precise estimation of the distance separating two (or more) surfaces, as demonstrated by their monotonic functions in both experiments. Unlike transparency, these cues are able to provide unambiguous depth layering and *in addition* the degree of separation between those layers. It is

important to discuss possible differences in strength between disparity and relative contrast as depth cues. Even though the present set of studies supports the idea that these two cues behave the same, it may be that disparity is more powerful than relative contrast in producing veridical solutions. When viewing a stimulus containing disparity, it is relatively easy as an observer, to detect and give an approximate measure of depth. Relative contrast, while it is certainly capable of providing depth information, may be less efficient in allowing for very precise depth estimation in an image. As already mentioned, there is evidence to suggest that different populations of cells are selective to the amount of disparity, but what is less known, is if relative contrast has underlying neural mechanisms such as this. The strength exerted by relative contrast should not be refuted, as it proved itself just as powerful as the disparity plaids in affecting motion integration. Even so, it is of interest to discuss the role these different depth cues have in surface segmentation, which may possibly rank order their strength in motion integration. While transparency is capable of detecting multiple surfaces, it fails to determine which surface occludes the other(s). Relative contrast is able to establish multiple surfaces and provide information in reference to which surface is closer. Finally, there is ample evidence to suggest that disparity is most powerful, as it can successfully accomplish multiple surface detection, proper layering order and in addition, provide by how much depth separates those layers.

Recent work by Wilson, Ferrera and Yo (1993) proposes a physiological model of 2-dimensional motion which incorporates a simple, linear motion energy pathway and a nonlinear motion pathway. It is suggested that these pathways probably correspond to the Fourier and non-Fourier motion processing streams possibly reflected in the V1-to-MT and V1-to-V2-to-MT motion pathways, respectively. Trueswell and Hayhoe (1993) suggest that it is this non-Fourier pathway which may be performing a more complex function of early and rapid surface segmentation, and that the resulting information is being fed to higher cortical sites known for motion grouping (MT). Disparity and relative contrast cues prove themselves worthy of the surface segmentation task and they exert much power on motion integration. Taken together, this could imply the presence of the underlying mechanisms (for perhaps both the specialized depth sensitive cells, and the aforementioned mediator of depth) responsible for detection of these cues somewhere along this non-Fourier motion pathway.

Implication of Present Research and Future Directions

Present results are consistent with a two-stage view of motion processing. The first of these extracts all component defined information related to the presence or absence of multiple surfaces in the image. This gathered information is then pooled and employed by motion grouping mechanisms in deciding if the resultant motion is consistent with one surface (or object), or if multiple component motions would be a more

veridical perceptual solution. It is rather clear that depth information conveyed by disparity, relative contrast and transparency play an important role in disambiguating local 1-D motion signals. Likewise, it is obvious that the information they extract is relayed and then utilized by higher cortical areas in deciding which local motions should be grouped. There can therefore be no argument posed against the existence and importance of such an intimate relationship between motion and depth processing.

Many future directions instigated by present data are worthy of attention. If there is depth between the components of a plaid, and coherent motion is perceived by an observer, what happens to this depth information? Do we perceive a 3-D plaid moving coherently, or is one grating "pulled" to the depth plane of the other grating and if so, what determines the plane of convergence? Related to this is the question of what happens when progressively larger increments in depth information are introduced, does the observer see the gratings as further apart? To answer these questions, it would be valuable to develop a method of measuring the perceiver's estimation of the depth between the component gratings of the plaid, both prior to and following adaptation. For example, does the observer still see depth in the plaid after adaptation? This would provide information to help isolate the role of depth in motion grouping. Secondly, the investigation of cross-adaptation between different cues to depth should be explored further to isolate the limits of depth influences both on integration and each other. Finally, in light of the proposed model, of much interest is a neurophysiological study which would

incorporate similar experimental manipulations as the present set of experiments did to examine the neuronal basis for the obtained findings, and thus lend support either for or against the proposed conceptual modeling (i.e. the generalized depth mechanism). This would also prove useful by providing insight about the underlying neuronal mechanisms responsible for relative contrast detection (i.e. does they truly behave like disparity?). Together, this would be a critical test of the hypothesized relationship between the proposed model and cortical physiology, and provide valuable information about cortical motion processing.

To conclude then, the present set of studies "suggest that the brief reign of pure visual modules is coming to an end" (Vallortigara & Bressan, 1991) and thus, the aperture problem should not be considered exclusively as a motion problem.

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Appendix A

ANOVA Summary Table and post hoc analysis of the amount of perceived coherence in the zero disparity plaid as a function of stimulus pairing

Table 1

ANOVA Table for the comparison of perceived coherence in the zero disparity plaid as a function of the stimulus pairing level of disparity

Source	df	SS	MS	F
Level	2	.006	.003	5.348 *
Error	12	.007	.001	

* $p < .05$

** $p < .01$

Table 2

Tukey multiple comparisons of the perceived coherence in the zero disparity plaid as a function of the stimulus pairing level of disparity

Comparisons	Mean Absolute Difference	Probability Level
Low vs Medium	.0168	p > .05
Low vs High	.0421	p < .05
Medium vs High	.0253	p > .05

Appendix B

ANOVA Summary Table of the amount of perceived coherence in the zero relative contrast plaid as a function of the stimulus pairing level of relative contrast

Source	df	SS	MS	<u>F</u>
Level	2	.005	.003	1.463
Error	12	.021	.002	

* $p < .05$
** $p < .01$

Appendix C

ANOVA Summary Table for the comparison of perceived coherence in the zero transparency plaid as a function of the stimulus pairing level of transparency

Source	df	SS	MS	F
Level	2	.004	.002	1.795
Error	12	.014	.001	

* $p < .05$
** $p < .01$

Appendix D

ANOVA Summary Table and post hoc analysis of the amount of
perceived coherence across the different levels of disparity

Table 1

ANOVA Summary Table for the comparison of perceived coherence across the different levels of disparity

Source	df	SS	MS	F
Level	3	.740	.247	28.591**
Error	18	.155	.009	

* $p < .05$ ** $p < .01$

Table 2

Tukey multiple comparisons of the perceived coherence across the different levels of disparity

Comparisons	Mean Absolute Difference	Probability Level
Zero vs Low	.2324	p < .05
Zero vs Medium	.3599	p < .05
Zero vs High	.4261	p < .05
Low vs Medium	.1255	p > .05
Low vs High	.1917	p < .05
Medium vs High	.0662	p > .05

Appendix E

ANOVA Summary Table and post hoc analysis of the amount of perceived coherence across the different levels of relative contrast

Table 1

ANOVA Summary Table for the comparison of perceived coherence across the different levels of relative contrast

Source	df	SS	MS	F
Level	3	1.53	.511	42.28**
Error	18	.217	.012	

* $p < .05$
** $p < .01$

Table 2

Tukey multiple comparisons of the perceived coherence across the different levels of relative contrast

Comparisons	Mean Absolute Difference	Probability Level
Zero vs Low	.5001	p < .05
Zero vs Medium	.5500	p < .05
Zero vs High	.5624	p < .05
Low vs Medium	.0499	p > .05
Low vs High	.0623	p > .05
Medium vs High	.0662	p > .05

Appendix F

ANOVA Summary Table and post hoc analysis of the amount of perceived coherence across the different levels of transparency

Table 1

ANOVA Summary Table for the comparison of perceived coherence across the different levels of transparency

Source	df	SS	MS	F
Level	3	.108	.036	11.984**
Error	18	.054	.003	

* $p < .05$

** $p < .01$

Table 2

Tukey multiple comparisons of the perceived coherence across the different levels of transparency

Comparisons	Mean Absolute Difference	Probability Level
Zero vs Low	.1459	p < .05
Zero vs Medium	.1506	p < .05
Zero vs High	.0663	p > .05
Low vs Medium	.0047	p > .05
Low vs High	.0776	p > .05
Medium vs High	.0843	p < .05

Appendix G

ANOVA Summary Table and post hoc analysis of the amount of perceived coherence in both types of test across the different levels of adapting disparity

Table 1

ANOVA Summary Table for the comparison of perceived coherence in both types of test across levels of adapting disparity

Source	df	SS	MS	F
Adaptation	3	.091	.030	4.754*
Error	18	.054	.003	
Test	1	.485	.485	35.202**
Error	6	.083	.014	
A x T	3	.181	.060	12.919**
Error	18	.084	.005	

* $p < .05$

** $p < .01$

Table 2

Tukey multiple comparisons of the perceived coherence on the medium disparity test across the different levels of adapting disparity

Comparisons	Mean Absolute Difference	Probability Level
No Adapt. vs Low	.0570	p > .05
No Adapt. vs Medium	.1602	p < .05
No Adapt. vs High	.2374	p < .05
Low vs Medium	.1032	p > .05
Low vs High	.1804	p < .05
Medium vs High	.0772	p > .05

Table 3

Tukey multiple comparisons of the perceived coherence on the zero disparity test across the different levels of adapting disparity

Comparisons	Mean Absolute Difference	Probability Level
No Adapt. vs Low	.0925	p > .05
No Adapt. vs Medium	.0858	p > .05
No Adapt. vs High	.0621	p > .05
Low vs Medium	.0067	p > .05
Low vs High	.0304	p > .05
Medium vs High	.0237	p > .05

Appendix H

ANOVA Summary Table and Post hoc Analysis for the two Types of Test
after Adaptation to Different Levels of Relative Contrast

Table 1

ANOVA Summary Table for the comparison of perceived coherence in both types of test across levels of adapting relative contrast

Source	df	SS	MS	F
Adaptation	3	.109	.036	8.260**
Error	18	.079	.004	
Test	1	2.92	2.92	83.003**
Error	6	.211	.035	
A x T	3	.050	.017	3.806*
Error	18	.078	.004	

* $p < .05$
 ** $p < .01$

Table 2

Tukey multiple comparisons of the perceived coherence on the medium relative contrast test across the different levels of adapting relative contrast

Comparisons	Mean Absolute Difference	Probability Level
No Adapt. vs Low	.0736	p > .05
No Adapt. vs Medium	.1280	p < .05
No Adapt. vs High	.1961	p < .05
Low vs Medium	.0544	p > .05
Low vs High	.1225	p < .05
Medium vs High	.0681	p > .05

Table 3

Tukey multiple comparisons of the perceived coherence on the zero relative contrast test across the different levels of adapting relative contrast

Comparisons	Mean Absolute Difference	Probability Level
No Adapt. vs Low	.0267	p > .05
No Adapt. vs Medium	.0227	p > .05
No Adapt. vs High	.0208	p > .05
Low vs Medium	.0494	p > .05
Low vs High	.0565	p > .05
Medium vs High	.0071	p > .05

Appendix I

ANOVA summary table for the comparison of perceived coherence in both types of test across levels of adapting transparency

Source	df	SS	MS	F
Adaptation	3	.008	.003	.557
Error	18	.084	.005	
Test	1	.311	.311	37.808**
Error	6	.049	.008	
A x T	3	.006	.002	2.764
Error	18	.012	.001	

* $p < .05$
 ** $p < .01$