The Influence of Feature-Specific Attention on Aftereffects Produced by a Multi-Feature Image

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ABSTRACT

This experiment examined whether paying attention to the color, luminance or motion of an adaptation stimulus defined by these three features, would influence the color, brightness and motion aftereffects (CAE, BAE and MAE, respectively). During adaptation, the three-feature image was presented and observers were instructed to pay attention to only one of its features. Following a feature-selective adaptation, each AE was measured in one of three types of attentional conditions. In the same-conditions, an AE was measured for the same feature as the one that was attended to during adaptation (e.g. attention on color followed by a CAE test). In the different-conditions, an AE was measured for a different feature than the one that was attended to during adaptation (e.g. attention on color followed by a MAE test). In the control conditions, each AE was measured after the stimulus was passively viewed. The CAE and BAE did not differ across these three conditions. This suggests that these AEs are not influenced by attention. However, attention seems to influence the MAE. Indeed, the MAE was stronger in the same-condition than in the control condition. Also, the MAE produced in the different-condition was slightly weaker than that produced in the same-condition and slightly stronger than that produced in the control condition; however, these differences were not statistically significant. It is concluded that processes specialized for the analysis of motion as well as those specialized for the analysis of color, luminance and motion together are involved in the production of the MAE and that attention influences them. However, how attention influences these processes remains to be determined. Possible cortical sites which may be involved in the psychophysical results are discussed.

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Since the nineteenth century, psychologists have studied AEs as a means of understanding how our sensory systems process information. A variety of AEs can be experienced. For instance, one can experience a motion AE (or MAE) by viewing a stimulus that is moving in one direction for 30-60 seconds (adaptation stimulus). A MAE is created when one perceives that a subsequently presented stationary object (test stimulus) is moving in the opposite direction from the adaptation stimulus. One experiences a brightness AE (or BAE) when, after staring at a bright object for a minute, a dark image of that object is seen in one's visual field. One experiences a color AE (or CAE) by looking at a colored object for a minute and then looking at an achromatic surface. A CAE is created when one sees an image of the object in its complementary color.

The production of AEs largely depends on the properties of neurons in the visual cortex. Some neurons along the visual pathway respond only to specific features of visual stimuli. There are, for example, cells which respond selectively to color (Hubel & Wiesel, 1968) or movement (Albright, Desimone & Gross, 1984). Physiological observations suggest that a change in the responsiveness of these feature-selective cells is responsible for AEs (e.g. Hammond, Mouat & Smith, 1986; Vautin & Berkley, 1977). The following section discusses how AEs can occur due to changes in the activity of these cells.

The production of aftereffects

Whereas the physiological mechanisms which underlie the perception of AEs are still unclear, electrophysiological recordings in non-primates suggest that cellular adaptation underlies the perception of AEs (e.g. Brindley, 1970; Hammond et al., 1986; Vautin & Berkley, 1977). When neurons in the visual cortex are at rest, their firing rate is said to be at a spontaneous level. Stimulation of the retina by an image increases the firing rate of selective visual neurons which are specialized for the features of the image. When the stimulation is prolonged, neurons selective for the features of the image become temporarily "fatigued" so that their firing rate drops to below the spontaneous level. For instance, the MAE can be induced after prolonged viewing of a series of vertical lines moving in one direction. Adaptation to the moving lines will stimulate cells selective for that direction. When the adaptation is ended, the firing rate of cells selective for the same direction will be reduced. In contrast, the firing rate of cells selective for the opposite direction is either unaffected or increased. This imbalance in the discharges of cells selective for opposite directions is thought to give rise to the MAE. Similarly, changes in the responses of color and luminance selective cells are thought to underlie the perception of the CAE and BAE, respectively.

A study by Tootel et al. (1995a) suggests that the perception of AEs in humans is a result of changes in electrical activity similar to those observed in non-primates. The authors used functional magnetic resonance imaging (fMRI) to measure electrical activation in area MT, where a majority of cells are motion selective, while human observers experienced a MAE. In addition, fMRI activation was compared to the perceived speed of the MAE. The fMRI activations observed during the perception of the MAE correlated with the perceived speed of the MAE. Moreover, the activations observed before, during, and after adaptation to a moving stimulus were very similar to those observed in electrophysiological studies (e.g. Brindley, 1970; Hammond et al., 1986; Vautin & Berkley, 1977). These results support the view that the perception of AEs is correlated with changes in the activity of cells selective for the adaptation stimulus.

Physiological studies (e.g. Hammond et al., 1986; Vautin & Berkley, 1977) also indicate that the magnitude of an AE is a function of the cellular activity produced during adaptation. Indeed, the extent to which a neuron's activity decreases after adaptation is dependent on the extent to which its activity had been increased during adaptation. In agreement with these physiological findings, psychophysical studies (e.g. Burbeck, 1986; Kelly & Martinez-Uriegas, 1993) indicate that stronger AEs will be produced after adaptation to high contrast stimuli than to low contrast stimuli. For example, Kelly and Martinez-Uriegas (1993) presented different achromatic gratings with increasing contrasts during adaptation. After the presentation of each grating, the BAE was measured with a contrast-cancellation method. The authors found that increasing the contrast of the adaptation stimulus increases the contrast of the BAE.

AEs not only reflect the responses of feature-selective cells, they also reflect the activation of cells at a specific location on either the retina or a retinotopic map of the visual field. Indeed, it has been shown that a MAE produced by prolonged viewing of a spiral is seen only when the test stimulus falls upon the portion of the retina which had been stimulated by the spiral (e.g. Masland, 1969). Moreover, the fact that AEs appear to move along with eyes movements suggests that they are precisely fixed on the retina (e.g. Gregory, 1987).

Finally, different AEs are thought to be created at different stages of visual processing. To some extent, the site of adaptation of an AE can be inferred by testing whether monocular or binocular cells are responsible for its production. Showing that an adaptation stimulus presented in one eye can induce an AE in the other eye has been taken as evidence that cells involved in the production of the AE are binocular (e.g. Mitchell, Reardon & Muir, 1975; Wade, 1976; for reviews see Brindley, 1970; Favreau & Corballis, 1976). Cells in the visual pathway are primarily monocular from the retina up to, and including, the lateral geniculate nucleus (LGN), in the thalamus. All cells in the primary visual cortex (V1) are binocular except about 20% of them which are monocular. Therefore, because the cortex is the first site where binocular cells can be found, interocular transfer of adaptation may indicate that adaptation took place in the cortex or beyond. It is thought that monocular cells are involved in the production of CAEs and most BAEs because these AEs do not transfer from one eye to the other (e.g. Brindley, 1970; Coltheart, 1973). Accordingly, the CAE and BAE have been attributed to the adaptation of luminance and color selective cells from the retina up to the LGN (for reviews see Brindley, 1970; Favreau & Corballis, 1976). In contrast, it is thought that binocular cells in the visual cortex are involved in the production of MAEs because this AE transfers from one eye to the other (e.g. Mitchell, Reardon & Muir, 1975; Wade, 1976). Accordingly, the MAE has been attributed to the adaptation of directionally selective cells in, for example, cortical areas V1 (e.g. Hammond et al., 1986) and MT (e.g. Tootell et al., 1995a).

To summarize, physiological and psychophysical studies indicate that AEs parallel the properties of neurons in the visual cortex. First, AEs reflect a change in the responsiveness of cells selective for the feature of the adaptation stimulus (e.g. motion). Second, AEs reflect a change in the responsiveness of cells at a specific location. Third, showing that an AE transfers from one eye to the other points to the possibility that cells involved in its production are binocular and that the AE is created in the cortex. Physiological studies using electrophysiological recordings and psychophysical studies which investigate perceptual phenomena such as AEs give us information on how the visual system processes different features. Whereas some processes are specialized for the analysis of specific features, others are specialized for the analysis of combinations of different features. In the following section, the functional organization of the visual cortex is discussed in more detail.

Functional organization of the visual system

Nerve impulses in the visual system are transmitted from the eye to the LGN via the axons of retinal ganglion cells in primates and humans. The LGN is divided into six layers: two magnocellular layers which receive input from large ganglion cells (M type) and four parvocellular layers which receive input from a smaller type of ganglion cells (P type). From the LGN, fibers stream to V1 in the occipital lobe. Some researchers have postulated that two parallel streams of sensory processing originate from V1 (e.g. DeYoe & Van Essen, 1988; Maunsell, 1987; Ungerleider & Mishkin, 1982). A temporal stream is directed ventrally into the temporal lobe and it mainly consists of connections between areas V1, V2, V4 of the visual cortex and the inferotemporal area (IT). A parietal stream is directed dorsally into the parietal lobe and it mainly consists of connections between areas V1, V2, V3 and the medial temporal area (MT). A schematic illustration of these two streams is given in Figure 1. It is important to notice that the two streams are not entirely segregated because there are extensive interactions between them.

Neural processes in the parietal and temporal streams of the visual system analyze features such as color, luminance or motion. Physiological studies indicate that some neural processes are involved in the analysis of one specific feature. For example, area MT is specialized for the analysis of motion (e.g. Tootel et al., 1995b) —most cells in this area respond selectively to specific directions and speeds of motion (e.g. Maunsell & van Essen, 1983). Moreover, cells in area V1, for instance, respond selectively to a specific feature such as color or motion (e.g. Hubel & Wiesel, 1968). Finally, it has been argued that different features are analyzed by separate visual streams (e.g. De Yoe & Van Essen, 1988; Livingstone & Hubel, 1988; Maunsell & Newsome, 1987; Schiller & Colby, 1983; Ungerleider, 1992; van Essen & Maunsell, 1983; Zeki, 1978). For example, DeYoe and Van Essen (1988) maintain that cells in the magnocellular layers of the LGN respond selectively to luminance and motion, whereas cells in the parvocellular layers respond selectively to color.

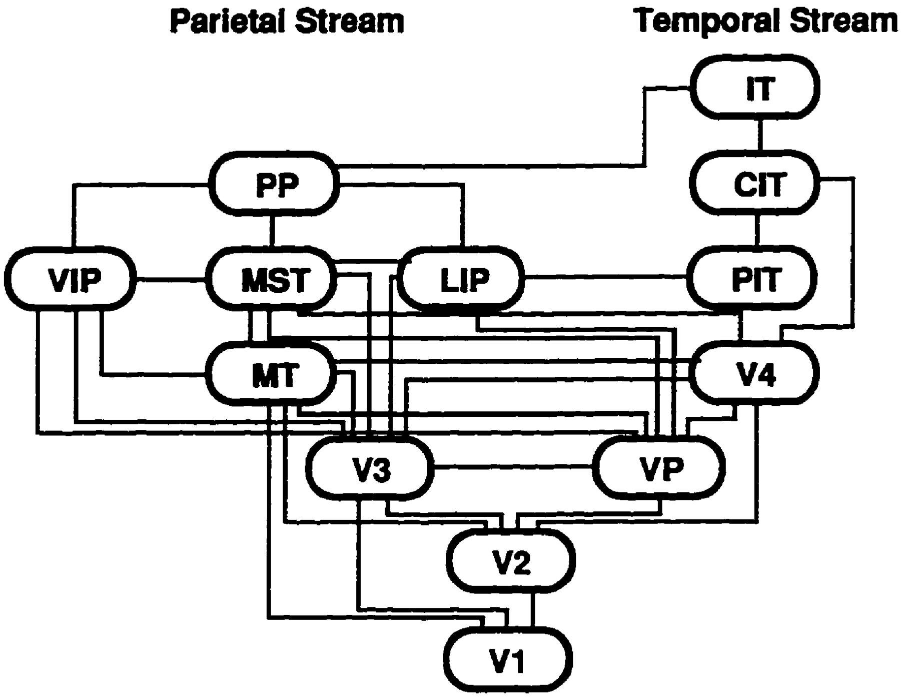


Figure 1. A schematic illustration of the parietal and temporal streams of the visual system. Lines linking the areas represent major axonal projections that have been identified. Abbreviations: PP, Posterior parietal; AIT, anterior inferotemporal area; CIT, central inferotemporal area; LIP, lateral intraparietal area; MST, medial superior temporal area; MT, middle temporal area; PIT, posterior inferotemporal area; V1, visual area 1; V2, visual area 2; V3, visual area 3; V4, visual area 4; VIP ventral intraparietal area ; VP, ventral posterior area. (Adapted from Maunsell, 1995.)

Psychophysical studies support the idea that some visual processes are specialized for the analysis of one specific feature (e.g. Favreau & Cavanagh, 1981; Flanagan, Cavanagh & Favreau, 1987). For example, Favreau and Cavanagh (1981) have suggested that separate channels, some specialized for the analysis of color and others for the analysis of luminance, are involved in the coding of spatial frequency. The authors examined whether adaptation to square-wave gratings defined by color or luminance could produce shifts in the perception of the spatial frequency of test gratings defined by color or luminance. The results showed that spatial frequency shifts were observed when the adaptation and test gratings were defined by the same feature. However, color-defined test gratings did not shift after adaptation to luminance-defined gratings and vice-versa. These results suggest that processes specialized for color analysis and those speciaized for luminance analysis are separately involved in spatial frequency shifts.

Physiological studies indicate that other neural processes are specialized for the analysis of combinations of different features. Indeed, there are cells in the visual cortex which respond to combinations of features. For instance, cells in areas V3 and V4 can be selective for orientation, luminance, color and motion (e.g. Kiper, Levin & Gegenfurtner, 1995 for area V3; Logothetis, 1994, for area V4). Moreover, area IT, for example, is specialized for the analysis of combinations of different features —most cells in this area respond to many different features (Desimone, Albright, Gross & Bruce, 1984; Sáry, Vogels & Orban, 1993). Finally, physiological findings (e.g. Ferrera, Nealey & Maunsell, 1994; Nealey & Maunsell, 1994) indicate that the functional segregation observed in the LGN is not preserved in the visual cortex. For instance, Nealey and Maunsell (1994) recorded the activity of cells in area V1 while selectively blocking inputs from either the magnocellular or parvocellular pathway of the LGN and found that the neuronal responses in V1 were reduced to a similar extent by the inactivation of either pathway. This suggests that individual neurons in V1 receive inputs from both the parvocellular and magnocellular pathways.

Psychophysical studies support the idea that some visual processes are specialized for the analysis of combinations of different features (e.g. Cavanagh, 1989; Flanagan, Cavanagh & Favreau, 1990; Landy, 1993; Rivest, Boutet & Intriligator, 1997). For example, a study by Flanagan et al. (1990) indicates that processes specialized for the analysis of orientation, luminance and color together are involved in the production of tilt-aftereffects (TAEs). A TAE is perceived when, after adaptation to bars tilted in one direction, vertical bars appear tilted in the opposite direction. TAEs were initially associated with the fatigue of cells selective for the luminance and the orientation of the adaptation stimulus (e.g. Coltheart, 1971). This may be due to the fact that the first studies on TAEs (e.g. Gibson & Radner, 1937) used adaptation and test bars defined by luminance only. However, more recently, Flanagan et al. (1990) demonstrated that it is possible to create TAEs when the adaptation bars are defined by luminance and the test bars are defined by color, and vice-versa. This effect was attributed to cells which respond to a combination of orientation, luminance and color. Similarly, the MAE was originally created by adaptation to moving stimuli defined by luminance only. For example, in 1911, Wolgemuth reported using a black and white rotating spiral to induce a MAE. Accordingly, the MAE was initially associated with cells which respond selectively to motion and luminance (e.g. Barlow & Hill, 1963). However, more recent investigations indicate that it is possible to create a MAE when the moving adaptation stimulus is defined by color and the static test stimulus is defined by luminance, and vice-versa (e.g. Mullen & Baker, 1985). This suggest that processes which analyze motion, luminance and color together, such as cells selective for these three features, can be involved in the production of the MAE.

Thus, it appears that some visual processes are specialized for the analysis of one specific feature and others are specialized for the analysis of many different features. Moreover, the aforementioned psychophysical studies suggest that these two types of processes can be involved in the production of AEs. In this thesis, processes specialized for the analysis of a specific feature are called feature-specific processes and processes specialized for the analysis of many features together are called multi-feature processes.

The present experiment investigated whether feature-specific attention can influence the processes involved in the production of the CAE, BAE and MAE. Feature-specific attention is dependent on the selection of one feature of a visual stimulus over another. For example, one may pay attention to the color of a stimulus rather than to its movement. A typical AE paradigm —a series of adaptation periods followed by AE tests— was used here. During adaptation, an image defined by color, luminance and motion was presented and observers were instructed to attend to one feature of the image. Prolonged viewing of the stimulus produced a CAE, a BAE and a MAE. Theoretically, feature-specific and multi-feature processes could be involved in the production of these AEs. For example, populations of cells which respond selectively to color and those which respond to combinations of color, luminance and motion could be involved in the production of the CAE. The experiment examined whether paying attention to one feature influences the AE related to that feature only and/or the AEs related to the other features of the image.

The questions addressed in this study were examined by comparing each AE across three types of attentional conditions. In the same-conditions, an AE was measured for the same feature as the one that was attended to during adaptation (e.g. attention on color during adaptation followed by a CAE test). In these conditions, an AE can be enhanced if the analysis of that feature and/or the analysis of many features are changed by attention. In the different-conditions, an AE was measured for a different feature than the one that was attended to during adaptation (e.g. attention on color followed by a MAE test). In these conditions, an AE can only be enhanced if the analysis of many features is changed by attention. In the control conditions, each AE was measured after passive viewing of the stimulus during adaptation. In these conditions, the AEs should not be influenced by attention.

An influence of feature-specific attention on the AEs was expected because this type of attention was shown to modulate other types of visual tasks as well as cellular activities. The next section reviews studies which investigated the role of feature-specific attention on visual processes other than AEs.

The role of feature-specific attention on visual processes other than AEs

Several psychophysical experiments indicate that a given feature of a stimulus defined by many features can be processed more effectively when attention is focused on that feature (e.g. Gogel & Sharkley, 1989; Rossi & Paradiso, 1995). For example, Rossi and Paradiso (1995) conducted an experiment in which observers discriminated either the spatial frequency or the orientation of cosinusoidal gratings (Gabor patches) presented successively at the fovea. On a third of the trials, observers also performed another task where they were requested to detect the presence of a grating in the periphery. The spatial frequency or orientation of the grating varied across trials. The authors found that the features of the Gabor patches affected the detectability of the peripheral grating: detection of the grating improved when its frequency or orientation was similar to that of the Gabor patches. They concluded that feature-specific attention was responsible for this effect: when observers attended to the orientation of the Gabor patches, detection of the peripheral grating was better when its orientation was similar to that of the Gabor patches; when observers attended to the spatial frequency of the Gabor patches, detection of the peripheral grating was better when its frequency was similar to that of the Gabor patches.

Physiological studies indicate that some neurons respond more vigorously when attention is devoted to an image having a particular feature than when the image is passively viewed (e.g. Haenny & Schiller, 1988; Moran & Desimone, 1985; Motter, 1994; Spitzer & Richmond, 1991; see review by Maunsell, 1995). For example, a study by Motter (1994) indicates that color and luminance selective cells in area V4 of the rhesus monkey will discharge more nerve impulses when the animal is selecting a stimulus having a particular feature (i.e. either color or luminance) than when the stimulus is presented without any behavioral requirement. Bars were presented within each neuron's receptive field and their activity was recorded under three conditions.

First, cell activity was recorded while a bar defined by color or luminance was presented; the animal did not have to perform a task on these stimuli. Then, cell activity was recorded while the animal was performing a task in which a stimulus with a particular feature had to be selected. A fixation point defined by either color or luminance was first presented in order to indicate to the animal which feature would have to be selected. Following the presentation of the fixation point, six bars were presented, one of them being within the neuron's receptive field. In the match conditions, the bar presented within the neuron's receptive field was defined by the same feature as the fixation point. In the non-match conditions, the bar presented within the neuron's receptive field was defined by a different feature than the fixation point. The monkey had to indicate the orientation of the bar defined by the same feature as the fixation point. The author found that a majority of neurons showed the strongest responses when the animal was performing the task in the match conditions. However, some neurons showed no change in their responses, and others showed weaker responses, when the animal was performing the task in the non-match conditions than when no task was performed. These results suggest that neurons' responses are enhanced when a stimulus presented within their receptive field is the target of attention. Motter (1994) concluded that the neuronal modulation observed "have little to do with either the task difficulty or the particular sensitivity to the stimulus dimension per se, but rather appears to be associated with the act of selection of stimuli having a particular stimulus feature" (p. 2187).

Physiological studies also indicate that paying attention to one feature of an image defined by two features increases the responses of neurons selective for either one or both features of the image. In these experiments, an image defined by two features is presented, and the activity of cells selective for both features is recorded while attention is devoted to one feature of the image. For example, Braitman (1984) presented colored checkerboard patterns and recorded the activity of color and pattern selective cells in the posterior inferotemporal cortex while monkeys were shifting attention from one stimulus feature (its color) to another (its pattern). The author found that shifting attention from one stimulus feature to the other increased the activity of 60% of the recorded cells. Maunsell and Hochstein (1991) recorded the responses of color and/or orientation selective neurons in area V4 while monkeys were matching colored-oriented patches according to their color or orientation. Among the neurons recorded while the animal performed the color match and the orientation match, 28% responded differently depending on whether the animal was matching orientation or color. For example, the responses of some cells were about twice as strong when the patches were presented in orientation matching trials than when they appeared in color matching trials. There was almost an even split between neurons which showed significant differences in responses between orientation and color matching: 56% of the neurons showed an enhanced response during color matching and 44% showed an enhanced response during orientation matching. Thus, the enhancement in responses did not depend on most neurons being more active during one of the two tasks, nor did they depend on the stimulus being attended to or not. Rather, the enhancements depended on "the fact that the animal was attending to one or another stimulus dimension" (p. 467), thus suggesting that the act of paying attention to one feature of the stimulus produced the enhancement in cellular activity.

In contrast, a perceptual learning study conducted by Boutet, Rivest and Intriligator (1995) suggests that paying attention to one feature of an image defined by two features mainly improves the processing of cells selective for the attended feature exclusively. In this experiment, observers were trained to repeatedly detect either the color or motion of an image defined by these two features. During training, the image was always presented at the same retinal location. First, whether training improved the detection of the feature that was judged during training was examined. Then, whether training with one feature (e.g. color) improved the detection of another feature (e.g. motion) was explored. Finally, whether the improvement was restricted to the retinal location used during training was examined. It was observed that an improvement in performance on the motion detection task occurred only if observers performed this task during training; when observers performed the color detection task during training, no improvement on the motion task was found. It was also observed that the improvement on the motion task was restricted to the retinal location used during training. The results suggest that feature-specific attention mainly influences the activity of cells selective for the attended feature: cells selective for motion may have been activated more when observers were trained to judge motion than when they were trained to judge color.

The next section discusses the possible influence of feature-specific attention on AEs. As far as I know, whether the BAE and CAE can be modulated by feature-specific attention has not been investigated by past research. Nevertheless, there is one study which examined the influence of feature-specific attention on the MAE. A review of this study is given below.

The influence of feature-specific attention on the MAE

Chaudhuri (1990) conducted an experiment to examine whether paying attention to the color of a moving colored stimulus could influence the duration of the MAE. He presented observers with a moving textured background which changed in color and measured the duration of the MAE by asking observers to indicate when their perception of the MAE stopped. The MAE was measured after two adaptation conditions: in one condition, observers indicated when the stimulus became red; in the other condition, they observed the color changes without performing any task. The duration of the MAE did not differ between these two conditions, suggesting that paying attention to color during adaptation does not influence the MAE. These results indicate that paying attention to a feature other than motion —color— does not influence the MAE.

However, it is possible that Chaudhuri (1990) did not observe an influence of feature-specific attention because he measured the duration of the MAE. Indeed, Anstis (1986) suggested that using duration to measure an AE may be problematic since it is difficult for an observer to determine when an AE has finally disappeared. Anstis (1986) also mentioned that duration can be easily influenced if, for example, the observer changes his/her criterion for evaluating when the AE has stopped. Chaudhuri's (1990) study must be replicated with a more reliable measure than duration before concluding that feature-specific attention does not play a role in the modulation of the MAE.

While there is not much information regarding the influence of feature-specific attention on AEs, many studies investigated the role of other types of attention on the MAE and on a CAE contingent upon orientation. A review of these studies is given in the following section.

The influence of spatial-attention on AEs

The possible influence of attention on AEs was first examined by Wolgemuth (1911). In his experiments, observers adapted to a moving spiral while either passively looking at alpha-numeric characters presented at the fixation point or discriminating them. The type of attention required to perform the discrimination task is spatial: observers must bring their attention to one region of the visual field —the fixation point— at the expense of the inducing stimulus —the spiral. Wolgemuth (1911) found that the duration of the MAE did not differ between these two conditions. He concluded that attention does not influence the production of the MAE since its duration did not differ whether or not attention was distracted from the adaptation stimulus. In agreement with Wolgemuth (1911), Takeuchi and Kita (1994) showed that the duration of the MAE, produced by adaptation to a moving spiral or to a looming wheel, did not differ whether or not observers perform an alphanumeric discrimination task during adaptation.

Houck and Hoffman (1986) examined the influence of spatial attention on an AE other than the MAE. They showed that a CAE contingent upon orientation —the McCollough AE— is unaffected by attention. The McCollough AE is established by presenting observers with, for example, an alternation of a green-vertical grating and a red-horizontal grating. After viewing these alternating gratings for several minutes, observers are presented with black and white gratings having the same orientation and spatial frequency as the vertical and horizontal adaptation gratings. The AE is such that the vertical test grating appears red and the horizontal one appears green. In their experiments, Houck and Hoffman (1986) presented many adaptation gratings, for example, green-vertical and red-horizontal patterns. Different gratings were simultaneously presented at central and peripheral locations. Observers paid attention to either the central or peripheral locations during adaptation. After this adaptation, the strength of the McCollough AE was measured at both the central and peripheral locations. The authors found that the AEs were not different for the unattended and attended locations, showing that the McCollough AE can be created even when observers are not paying attention to the adaptation stimulus.

Despite these findings, other studies challenge the idea that AEs are not influenced by attention. Chaudhuri (1990) was the first to demonstrate that the MAE can be influenced by spatial attention. In his study, observers adapted to a leftward or rightward moving textured background while being exposed to a sequence of rapidly changing numbers and letters. During adaptation, observers could either perform a discrimination task on the characters or passively view them. Chaudhuri (1990) found that the duration of the MAE produced by this adaptation was reduced by almost 70% when the observers performed the discrimination task. Chaudhuri (1990) explains his results as follows: "If the MAE is a consequence of depressed activity in a population of directionally selective neurons during the post-adaptation period, then the results reported here would imply that the adapting pattern has a reduced effect on the same neurons if the visual system actively attends to an alternative stimulus" (p. 62). Thus, performing the alphanumeric task during adaptation may have had the effect of diminishing the responses of cells responsible for the production of the MAE and as a result, its duration was decreased. In the present experiment, an increase in cellular activity was expected. While in Chaudhuri's (1990) experiment, the alphanumeric task may have reduced the responses of directionally selective cells during adaptation, in this experiment, a task was used to bring attention to one feature of the stimulus during adaptation in an attempt to enhance the processes involved in the production of the AEs.

In agreement with Chaudhuri (1990), Shulman (1993) found that the duration of the MAE is reduced when observers perform an alphanumeric discrimination task while adapting to rotating disks. In another experiment by Shulman (1993), observers adapted to two sets of disks: an inner set rotating clockwise and an outer set rotating counterclockwise or vice-versa. Observers paid attention to either set during adaptation. The author found that when observers were subsequently exposed to an intermediate set of stationary disks, they perceived this middle set as moving in the opposite direction from the attended set. In other words, the direction of the MAE was determined by the direction of the attended set. Finally, other researchers have shown that the duration (Giorgiades & Harris, 1996; Takeuchi & Kita, 1994) and velocity (Giorgiades & Harris, 1996) of the translational MAE is reduced when, during adaptation, observers perform an alphanumeric discrimination task at fixation. Taken together, these results suggest that the MAE can be influenced by spatial attention.

In summary, the above studies indicate that different types of AEs are affected differently by spatial attention: it appears that while the MAE produced by translation and rotation can be modulated by spatial attention, the MAE produced by spirals and looming motion as well as the McCollough AE cannot. These different results may be due to the fact that different studies used different types of stimuli in order to induce an AE. It may be that some AEs are created in cortical areas that can be influenced by attention while others are not. Past research indicates that spatial attention can influence the activity of neurons in areas V1, V4, MT and IT of the cortex (see review by Maunsell, 1995).

Other studies investigated whether paying attention to one component of an adaptation stimulus, which has two distinct motion components, can influence the subsequent production of a MAE. In these experiments, observers devoted their attention to selecting only one component of an image defined by two components of the same feature —motion. The next section reviews these studies.

The influence of component-specific attention on MAEs

Lankheet and Verstraten (1995) used a stimulus, composed of two superimposed random dot patterns moving in opposite directions, to examine if the MAE could be influenced when attention is devoted to one component of an image defined by two motion components. When observers passively viewed the stimulus, the perceived direction of motion was ambiguous. However, when they paid attention to only one of the two moving patterns, they perceived movement in the direction of the attended pattern. Most importantly, the MAE produced by adaptation to this stimulus was always perceived in the opposite direction from that of the attended one. This was true even though, during adaptation, observers were exposed to both directions. The authors concluded that attention can "differentiate between different motion components in the same part of the visual field" (p. 1409). Similarly, Iordanova, Riscaldino, Gurnsey and von Grünau (1996) used an adaptation stimulus composed of first- and second-order motion, each giving a different motion direction signal. Each type of motion produced a different MAE. The strength of both kinds of MAEs was measured after an adaptation period where observers were instructed to pay attention to first-order motion, to second-order motion, or to passively view the stimulus. When the stimulus was passively viewed, both MAEs were about equally strong. When attention was devoted to one type of motion signal during adaptation, the direction of the MAE was opposite to that of the attended signal. Furthermore, the strength of the MAE related to one type of motion was increased when observers paid attention to only that type of motion during adaptation as compared to when they passively viewed the stimulus. Hence, these studies show that the MAE can also be influenced when attention is devoted to a specific signal in a stimulus that is composed of two signals of the same feature.

The present experiment investigated whether paying attention to one feature of a multi-feature image could enhance the CAE, BAE and MAE produced by adaptation to the image. The CAE and BAE have not been examined in this context by previous research. While the influence of feature-specific attention on the MAE has already been investigated by Chaudhuri (1990), this experiment used a different adaptation stimulus, namely an image defined by color, luminance and inward motion. In addition, the present study used a more reliable measure: the strength of AEs—not their duration—was measured. The experiment also examined if paying attention to one feature during adaptation would only enhance the AE related to that feature, or if it would also enhance the AEs related to the other features. This was done by comparing the AEs across two conditions: in the same-conditions, where an AE was measured for the same feature as the one that was attended to during adaptation; in the different-conditions, where an AE was measured for a different feature than the one that was attended to during adaptation. A brief description of the experiment is given below.

Description of the experiment

A typical AE paradigm —a series of adaptation periods followed by AE tests— was used. During adaptation, observers were exposed to a stimulus defined by color, luminance and motion. Each feature in the stimulus simultaneously produced a CAE, BAE and MAE, respectively. During the AE tests, the CAE, BAE and MAE was measured separately. The average color saturation required to null the CAE, the average intensity required to null the BAE, or the average speed required to null the MAE were measured.

During adaptation, feature-specific attention was modulated by asking observers to perform an attentional task —the method of single stimulus (MSS) task (Westheimer & McKee, 1977)— on only one feature of the image. On each trial, observers judged whether the "contrast" of one feature of the image —either its saturation, its luminance or its speed— was more or less than the average "contrast" seen in previous trials. The "contrasts" for each feature were chosen so that observers performed at a success rate of about 70% on the MSS task. This rather low criterion level of performance was chosen for the three features for two reasons. First, a study by Spitzer, Desimone and Moran (1988) indicates that a higher level of attention, and higher cellular modifications, are modulated when the effort required to perform the task is increased. In their experiment, rhesus monkeys performed a discrimination task at an accuracy of about 70% or about 90% and the responsiveness of neurons processing the task was recorded. The authors observed that neuronal responses were larger and more selective in the 70% accuracy condition than in the 90% accuracy condition. They concluded that more attention is required to perform the more difficult task (i.e. a task performed with an accuracy of about 70%) and that increasing the amount of attention directed towards a stimulus enhances the responsiveness and selectivity of the neurons that process it. In view of these results, accuracy on the attentional task (MSS task) was maintained at about 70%

correct responses in the present experiment. Thus, one can assume that, when observers performed the MSS task on one feature of the image during adaptation, the level of effort required to perform the task was sufficient to modulate feature-specific attention. Second, using an accuracy level of 70% for each of the three features ensured that approximately the same level of attention was required to perform the MSS task. In other words, a consistent level of accuracy across all features was taken to indicate that a similar level of attention was devoted to each feature whether color, luminance or motion was judged.

After adaptation, one of three types of attentional conditions was tested. In the same-conditions, an AE was measured for the same feature as the one that was attended to during adaptation (e.g. attention on color during adaptation followed by a CAE test). In the different-conditions, an AE was measured for a different feature than the one that was attended to during adaptation (e.g. attention on color followed by a MAE test). In the control conditions, each AE was measured after passive viewing of the image during adaptation. According to the literature presented earlier on feature-specific attention, two possible outcomes were predicted with regards to these three conditions. These outcomes and a rationale for their prediction are presented below.

Predicted outcomes and rationale

This section first discusses the expected results if paying attention to a specific feature during adaptation exclusively influences processes specialized for the analysis of that feature. Second, it discusses the expected results if paying attention to any feature during adaptation exclusively influences processes specialized for the analysis of more than one feature of the adaptation stimulus. Taking the MAE as an example, an illustration of the processes involved in the production of the MAE and of the possible influence of attention is given in Figure 2.

First, lets consider the possibility that paying attention to a specific feature during adaptation will influence processes specialized for the analysis of that feature only. This hypothesis stems from studies which suggest that paying attention to one feature of a multi-feature image mainly influences the responses of cells selective for the attended feature only (e.g. Boutet et al., 1995). For the MAE, for example, it is possible that paying attention to motion will exclusively influence motion processes; it may be that cells which respond exclusively to motion will send more nerve impulses when attention is devoted to motion than when attention is devoted to another feature as well as when attention is not devoted to a specific feature. An enhancement in cellular activity during adaptation should be reflected in the AEs. Indeed, it has been shown that the magnitude of an AE is a function of the extent to which the adaptation stimulus is effective at increasing the responses of cells responsible for the production of the AE (e.g. Kelly & Martinez-Uriegas, 1993; Vautin & Berkley, 1977). Therefore, this possibility would be supported if, in this experiment, AEs were the strongest when, during adaptation, attention is devoted to the same feature as the one producing the AE (same-conditions). For the MAE, if the same-condition produced the strongest MAE, it would be concluded that paying attention to motion during adaptation enhances processes specialized for the analyis of motion only.

Second, let's consider the possibility that paying attention to any feature during adaptation will exclusively influences processes specialized for the analysis of more than one feature of the adaptation stimulus. For example, the MAE may be produced by cells which respond to combinations of color, luminance and motion (e.g. Kiper et al., 1995; Logothetis, 1994) and these cells could be influenced whether, during adaptation, attention is devoted to motion, color or luminance. Indeed, studies like the ones by Braitman (1984), Maunsell and Hochstein (1991) and Motter (1994) suggest that paying attention to one feature of a multi-feature stimulus can enhance the responses of cells selective for all features of the stimulus. If this is the case, processes specialized for the analysis of many features would be enhanced no matter what feature of the image was attended. As a result, AEs would be the strongest whenever attention is devoted to any feature of the image during adaptation (same- and different-conditions) and the AEs would be as strong no matter what feature is attended. For the MAE, if results showed that paying attention to motion (same-condition) and paying attention to color or luminance (different-condition) produces similar MAEs, and that these MAEs are stronger than not paying attention at all (control condition), it would be concluded that paying attention to any feature enhances processes which analyze many features together.

A complete description of the methodology that was used for the experiment is given in the following section.

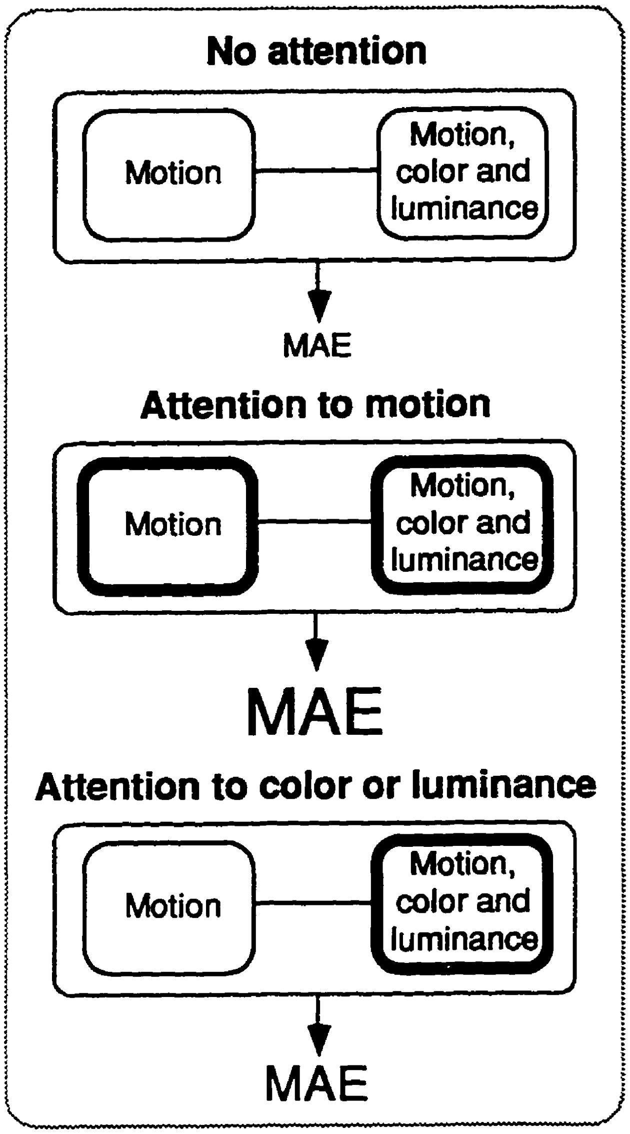


Figure 2. A schematic illustration of the processes involved in the production of the MAE and of the possible influence of attention. Each third of the figure illustrates whether, during adaptation, there is no attention, attention to motion, or attention to color or luminance. The small boxes represent processes which could be involved in the production of the MAE: processes involved in motion analysis and those involved in the analysis of many different features. Although processes which analyze the three features together —color, luminance and motion— are the only ones illustrated here, it is assumed that processes which analyze motion and either color or luminance can also be involved. These two types of processes are not influenced when attention is not devoted to any feature during adaptation (control condition). The rectangles with a thick contour illustrate the processes which could be influenced when attention is devoted to motion (same-conditions) and when attention is devoted to color or luminance (different-conditions).

METHOD

A typical AE paradigm was used: there were alternating series of adaptation periods followed by AE testing periods (see Figure 3 for an illustration of the paradigm). During adaptation, each trial consisted of the presentation of a wheel having three features (color, luminance and motion) and an attentional task (MSS) was performed on only one feature of the wheel. During the AE testing periods, observers were asked to report one AE —either the CAE, BAE or MAE. The strength required to null each AE was measured using multiple interleaved staircases.

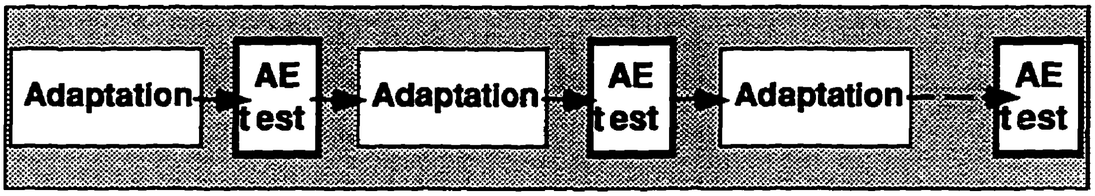


Figure 3. A schematic illustration of the paradigm that was used in the experiment.

Observers

Seven observers participated in the experiment —four were naive concerning the goal of the experiment. Six of the seven observers were tested in all conditions of the experiment. However, the BAE results of one of these observers differed by more than two standard deviations below the results of the other observers, therefore, they were discarded. To replace these data, a seventh observer was tested for the BAE only. Observers were recruited from Glendon College, York University. All observers had normal or corrected visual acuity and none were colorblind.

Apparatus

The experimental display was presented on a 14" Macintosh color monitor and was generated with a Macintosh Quadra 650. The monitor was calibrated for luminance, hue and saturation using a Minolta Chromater CS100 following the manufacturer's guidelines. Observers sat 57 cm away from the monitor with their heads and chins supported by a rest. The display consisted of a wheel with varying color, luminance and motion. This wheel was presented during the adaptation period and was slightly modified during the testing period depending on which aftereffect was tested (CAE, BAE or MAE). A description of the basic wheel used during the adaptation period and how it was modified in order to test each AE follows.

Display

Wheel used during the adaptation period—adaptation stimulus

A schematic illustration of the wheel is presented in Figure 4. The wheel had a diameter of 14.5° and it was divided into 12 pie-shaped sectors. It was presented on a uniform grey background of 25 cd/m^2. A circular fixation point appeared in the middle of the wheel. Six sectors were defined by color and six by luminance and motion. The different sectors were adjacent to each other. The color sectors were of a uniform green of the same mean luminance as the background. The luminance and motion sectors consisted of a dark and light sinewave grating of about 1.5 cycle/deg with a contrast of 59%. The sinewave grating moved towards the fixation point, making the wheel appear to loom inward. This inward movement was used such that nystagmus eye movements could be avoided and fixation could be easily maintained.

For technical reasons, the feature color was presented separately from luminance and motion. Indeed, motion and spatial resolution are low in the color system and judging saturation while the luminance varies is subjectively difficult. Thus, the color sectors were drawn separately from the motion and luminance sectors.

During adaptation, each feature of the wheel —its color, its luminance and its motion— was presented at three different "contrasts" such that an attentional task —the

MSS task— could be performed during adaptation. For example, on the first trial, the color sectors may have had a green saturation of 85% and the luminance and motion sectors a luminance of 25 cd/m^2 and a speed of 1.15 deg/sec. On the next trial, the color sectors may have had a green saturation of 90% and the luminance and motion sectors a luminance of 20 cd/m^2 and a speed of 1.00 deg/sec. The three "contrasts" were chosen individually so that each observer performed the MSS task with an accuracy of about 70% correct responses. A description of the procedure that was used to establish these values is given in the *pre-testing* section below.

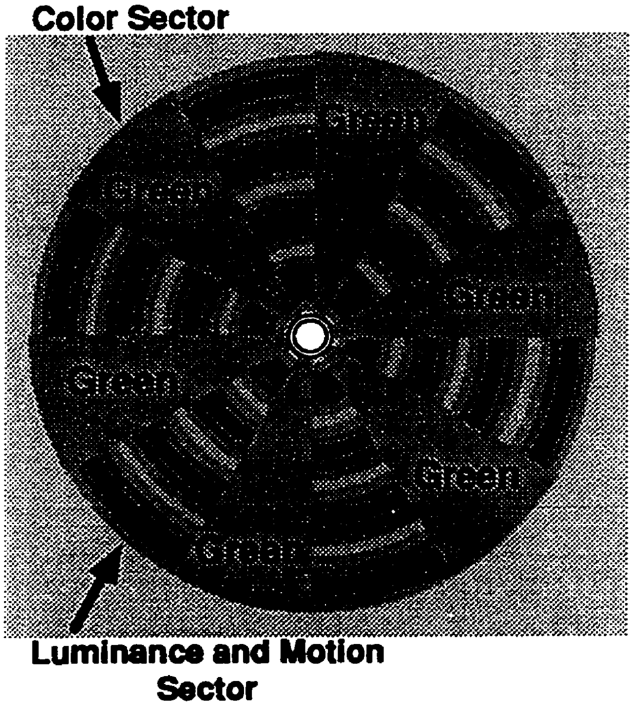


Figure 4. A schematic illustration of the wheel that was used during adaptation. Note that the relative size of the figure elements — i.e. spatial frequency, fixation point and diameter of the wheel— are not proportional to the elements presented in the actual display. Moreover, the sinewave grating in the luminance and motion sectors was moving towards the fixation point.

The color "contrasts" were a change in the green saturation of the background expressed in percent saturation —0% saturation being white and a 100% being arbitrarily defined as the chromaticity of the green phosphor alone. The luminance "contrasts" were a percent increase in the mean luminance (cd/m^2) of the sinewave grating. The motion "contrasts" were a change in the speed (deg/sec) at which the sinewave grating moves toward the fixation point.

Wheels used during the AE testing period—test stimuli

One AE testing period consisted of one trial. The strength of each type of AE was measured across 47 AE testing trials with multiple interleaved staircases. The green saturation (%) necessary to null the CAE (the "reddish" appearance of the color sectors), the intensity (cd/m^2) necessary to null the BAE (the bright appearance of the luminance and motion sectors) and the speed (deg/sec) of the inward motion of the sectors necessary to null the motion AE (the appearance of outward motion of the luminance and motion sectors) were recorded. To do so, the wheel was the same as in the adaptation period except that it was modified for each AE test. A description of these modifications follows.

For testing the CAE, the color sectors were presented with more or less green saturation than the grey background (CAE testing wheel). For testing the BAE, the luminance and motion sectors were of a uniform grey with more or less luminance than the grey background (BAE testing wheel). For testing the MAE, the luminance and motion sectors were moving either inward or outward at various speeds and their average luminance was the same as the background (MAE testing wheel).

Procedure

Except in the control conditions, observers performed an attentional task during adaptation. The strength required to null either the CAE, BAE or MAE was measured over the course of the 47 AE testing trials. One experimental session consisted of alternating series of adaptation periods, each followed by one AE testing period. A description of the attentional task and of the AE testing periods is given in the following section. The procedure that was used during each experimental session and the attentional conditions are also described.

Attentional task: the method of single stimuli (MSS)

Feature-specific attention was modulated during adaptation by asking observers to perform the following attentional task on only one feature of the wheel. Many trials were used during the adaptation periods. At each trial, each feature of the wheel was presented at one of three different "contrasts". While looking directly at the fixation point, observers discriminated one feature of the adaptation wheel —either its color, its luminance, or its motion— using the MSS (Westheimer & Mckee, 1977). Observers judged whether the "contrast" of one feature of the wheel was more or less than the average "contrast". When discriminating motion, for example, observers were first shown the wheel moving inward at an intermediate speed. They were told that this is a standard speed, that many wheels would be presented at different speeds and that they would have to judge whether each wheel moves faster or slower than this intermediate speed. Observers were then presented with a number of trials where the speed of the wheel varied randomly. At each trial, the wheel was presented with either a high, intermediate or low speed and observers judged whether the speed of the wheel was faster or slower than the intermediate speed by pressing a key. Similarly, when judging color, observers judged whether the green in the wheel was more or less saturated than the green with an intermediate saturation; when judging luminance, observers judged whether the luminance of the motion and luminance sectors was brighter or darker than an intermediate luminance. There was a total of 214 discrimination trials over which all possible combinations of the color, luminance and motion “contrasts” were presented in random order.

The “contrasts” at which each feature were presented were chosen individually so that each observer performed the attentional task with an accuracy of about 70% correct. The procedure used to establish the “contrast” values is explained in the following section.

Pre-testing

The pre-testing stage was used to determine which color, luminance and motion “contrasts” were needed so that each observer performed each respective MSS task with an accuracy of about 70% correct responses. In this stage, one session consisted of 25 adaptation trials. For each session, observers judged the “contrast” of only one feature of the wheel. When judging color, for example, the three “contrasts” were initially set at 85, 90 and 95% green saturation. Observers were tested on the MSS task with these “contrasts” and the correct responses were recorded. Observers were then tested successively on a number of sessions where the amount of saturation of the two extreme “contrasts” was either increased or decreased by 1 or 2% until the “contrasts” that resulted in about 70% correct responses were found. A similar procedure was used to determine the luminance and motion “contrasts”. For luminance, the three “contrasts” were initially set at 15, 20 and 25 cd/m^2 and the amount of luminance of the two extreme “contrasts” was either increased or decreased by 1 or 2 cd/m^2. For motion, the three “contrasts” were initially set at 1.00, 1.15 and 1.29 deg/sec and the speed of the two extreme “contrasts” were either increased or decreased by 0.07 or 0.08 deg/sec. The "contrasts" needed for each observer and the accuracy with which they performed on the respective MSS task with these "contrasts" are presented in Table 1. For each observer, these "contrasts" were used in all experimental sessions.

Table 1. "Contrasts" —green saturation, luminance and speed—needed for each observer to perform each MSS task at about 70% accuracy in the *pre-testing* stage. The percent correct responses obtained for each MSS task is also indicated.

	Color "contrasts"		**Luminance "contrasts"**		**Motion "contrasts"**	
Observer	**Saturation (%)**	**Accuracy (%)**	**Luminance (cd/m^2)**	**Accuracy (%)**	**Speed (deg/sec)**	**Accuracy (%)**
CN	88 - 90 - 92	75	18 - 20 - 22	75	1.71 - 1.79 - 1.86	69
EB	86 - 90 - 95	69	13 - 20 - 27	75	1.07 - 1.15 - 1.21	75
IB	89 - 90 - 91	62	19 - 20 - 21	63	1.15 - 1.21 - 1.29	62
IP	88 - 90 - 92	69	19 - 20 - 21	69	1.07 - 1.15 - 1.21	69
JO	84 - 85 - 86	65	19 - 20 - 21	70	1.15 - 1.21 - 1.29	65
JW	89 - 90 - 91	75	19 - 20 - 21	75	1.07 - 1.15 - 1.21	69
TM	49 - 50 - 51	69	9 - 10 - 11	63	1.07 - 1.15 -1.21	62

AE testing periods

To measure the strength of an AE over the course of the 47 testing trials, multiple interleaved staircases were used. For example, when measuring the strength of the CAE, the 47 testing trials were distributed among four staircases: two starting at high saturation and two starting at low saturation. On the first testing trial of a given staircase, the CAE test wheel was shown and the color sectors were presented with a specific amount of green saturation. While fixating at the center, observers had to judge whether the color sectors appeared "reddish" or "greenish" by pressing a key. The saturation in the following AE test wheels was adjusted in small steps opposite to the observer's answer on the previous AE test wheel. If the observer reported that the color sectors of the previous CAE test wheel appeared greenish, in the following AE test wheel, the color sectors were presented with a determined increase in saturation; if the observer reported that the sectors appeared reddish, in the next CAE test wheel, the color sectors were presented with a determined decrease in saturation. Increases and decreases in saturation were determined using specific step sizes and range of saturation values. For the CAE, the staircases were established with minimum/maximum step sizes of -40.00/40.00 and with an operating range from 0.00 to 100.00 % saturation.

At each AE test trial, the amount of saturation presented was chosen randomly from one of the four staircases until one of them terminated—a staircase was terminated when two reversals were answered. In this example, a reversal was answered when a small increment and decrement in the green saturation of the testing wheel had been correctly perceived as an increase and decrease in saturation. In other words, a reversal was answered if observers perceived the testing wheel as being greenish when the saturation was increased, or if observers perceived the testing wheel as being reddish when the saturation was decreased. Once a staircase was terminated, the saturation presented was randomly chosen among the trials necessary to terminate the remaining staircases. For each observer, the saturation necessary to null the CAE was determined by calculating the average and standard deviation across the last value of each of the four terminated staircases.

The procedure was identical for measuring the strength of the BAE and MAE. However, when measuring the strength of the BAE, at each testing trial, observers had to judge whether the uniform grey sectors were darker or brighter than the background. For the BAE, the staircases were established with minimum/maximum step sizes of -20.00/20.00 and with an operating range from -85.36 to 85.36 cd/m^2. For each observer, the average intensity (cd/m^2) and standard deviation across the staircases was recorded. When measuring the strength of the MAE, at each testing trial, observers judged whether the luminance and motion sectors were moving inward or outward. For the MAE, the staircases were established with minimum/maximum step sizes of -0.07/0.07 and an operating range from -0.30 to 0.30 deg/sec. For each observer, the average speed of inward motion (deg/sec) and standard deviation across the staircases was recorded.

While conducting the experiment, it was noticed that for two observers, having 47 testing trials across four staircases did not lead to a sufficient number of trials per staircase to allow all staircases to finish. To avoid this situation, these observers were tested with three staircases: two starting at low values and one starting at a high value.

Experimental sessions

During one experimental session, the 47 AE testing trials were distributed as follows: the first AE testing trial was preceded by an adaptation period of 30 trials and the 46 following ones were preceded by an adaptation period of 4 trials (see Figure 5).

On each adaptation trial, the three features of the wheel were randomly presented at one “contrast” and feature-specific attention was modulated by asking observers to judge the “contrasts” of only one feature. During one adaptation trial, the adaptation wheel was presented for 1.00 sec. If observers did not press a key after 1.00 sec, the wheel disappeared and the computer produced a noise to prompt the observer to make a judgment.

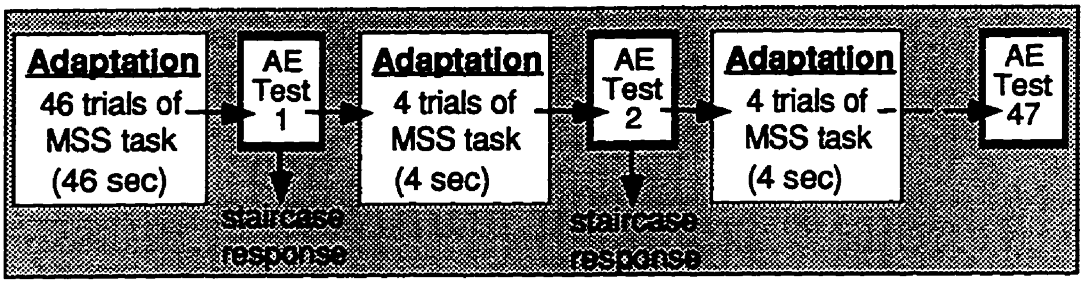


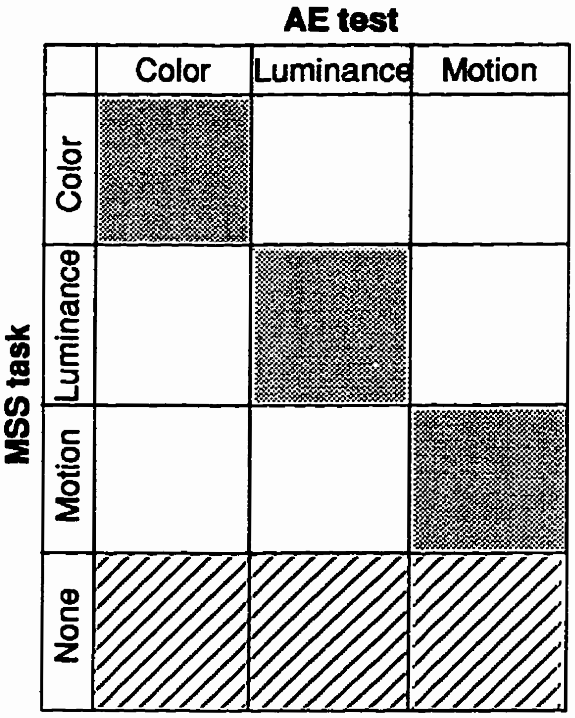
Figure 5. A schematic illustration of the procedure that was used for one experimental session.

Between each adaptation period and its following AE test, the computer gave verbal prompts so that observers knew when they were switching from the adaptation to the AE testing task. For example, before a MAE test, the computer said "motion"; the MAE testing wheel was then presented and observers pressed a key to indicate whether the luminance and motion sectors appeared as moving inward or outward. The motion testing wheel remained on the screen for 1.17 sec. If observers did not press a key after 1.17 sec, the wheel disappeared and the computer produced a noise to prompt the observer to make a judgment. The procedure was identical for the CAE test and the BAE test.

After each session, either the green saturation (%) necessary to null the CAE, the intensity (cd/m^2) necessary to null the BAE or the speed (deg/sec) of the inward motion of the sectors necessary to null the motion AE was recorded. The observer's accuracy (% correct responses) on the adaptation task was also calculated.

Attentional conditions

Each observer was tested in three types of attentional conditions —same-, different- and control conditions. Three experimental sessions (illustrated in Figure 5) were used for the same-conditions, six for the different-conditions and three for the control conditions, for a total of 12 experimental sessions. During each experimental session the features judged during the adaptation and AE testing periods varied. Figure 6 illustrates which features were judged during the adaptation and AE testing periods for each experimental session. The testing order of the 12 experimental sessions was randomly chosen for each observer.



MSS task \ AE test	Color	Luminance	Motion
Color	▒		
Luminance		▒	
Motion			▒
None	▨	▨	▨

Figure 6. A schematic illustration of the 12 experimental sessions. The shaded boxes represent the same-conditions, the striped boxes at the bottom represent the control conditions and the white boxes represent the different-conditions.

RESULTS AND DISCUSSION

The results were analyzed as follows. First, accuracy obtained for each MSS task —luminance, color and motion— during the pre-testing stage was compared. Second, each AE was compared across the three attentional conditions (same-, different- and control).

Evaluation of the performance on the MSS task during the pre-testing stage

In the pre-testing stage, the color, luminance and motion "contrasts" were chosen so that each observer performed each respective MSS task with an accuracy of about 70% correct responses. A statistical analysis was performed in order to verify whether the percent correct responses on the MSS tasks —luminance, color and motion— differed in the pre-testing stage. A one-way repeated measures ANOVA with three levels was performed on the percent correct responses obtained in the three types of MSS task. The average percent correct responses and standard deviations are presented in Table 2.

Table 2. Average percent correct responses and standard deviations obtained for each MSS task in the pre-testing stage (7 observers).

Feature Judged	Average	Standard deviation
Color	69.14	± 4.78
Luminance	70.00	± 5.38
Motion	67.29	± 4.65

The results were not significantly different [F (2, 12) = 1.776, p = .21]. This analysis shows that, in the pre-testing stage, the "contrasts" were effectively chosen such that observers did not perform differently on the MSS task whether they judged color, luminance or motion. In light of these results, it is assumed that a similar level of attention was devoted to each feature of the wheel when observers performed the MSS task during the adaptation period.

Comparison of each AE across the three attentional conditions

The results were analyzed separately for the CAE, the BAE and the MAE. The AE obtained for each one of the four adaptation conditions —when, during the MSS task, observers judged the color, the luminance and the motion of the wheel, and when they passively viewed it— was averaged across six observers.

The following analyses were performed for each AE separately. A one-way repeated-measures ANOVA with four levels was performed on the average results obtained in the four adaptation conditions. In order to evaluate the specific predictions, focused comparisons using the Multiple-Plan Contrast Analysis were performed (Rosenthal & Rosnow, 1985). In particular, the AEs obtained in the same-conditions and in the different-conditions were each compared to those obtained in the control conditions. The AEs obtained in the same-conditions were compared to those obtained in the different-conditions. The analyses performed and the results obtained for each AE are presented below.

CAE

For each adaptation condition, the average green saturation (%) required to null the CAE (i.e. "reddish" appearance of the color sectors) across all observers was calculated. These averages and their corresponding standard errors are illustrated in Figure 7. Individual data are illustrated in Appendix A.

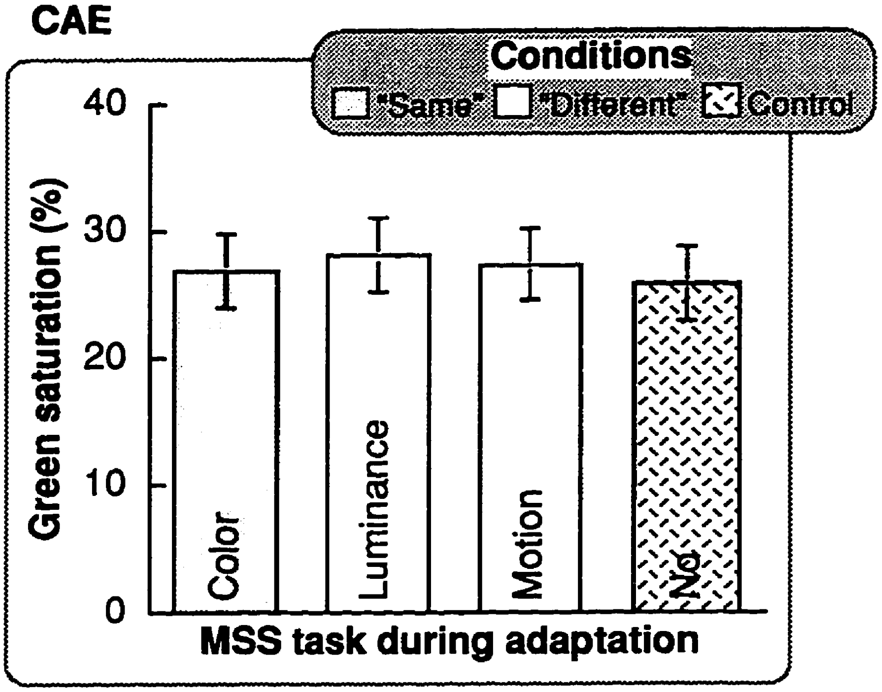


Figure 7. Average green saturations (6 observers) obtained in the four adaptation conditions —MSS color, MSS luminance, MSS motion, and no MSS— for the CAE. The three attentional conditions —same-, different- and control— are represented by different shadings. One error bar represents one standard error.

A one-way repeated-measures ANOVA was performed on the average saturation obtained in each adaptation condition. The results were not significantly different [F (3, 15) = 1.638, p = .22]. Despite this non-significant finding, the comparisons planned in light of the predictions were evaluated using Multiple-Plan Contrast Analyses. For these comparisons, the MS error term of the ANOVA was used. First, the average saturation obtained in the same-condition (MSS color; weight: 1.00) was compared to that obtained in the control condition (no MSS; weight: -1.00). There was no difference [F (1, 15) = 0.922, p = .35]. Second, the average saturation obtained in the same-condition (MSS color; weight: 1.00) was compared to that obtained in the different-condition (MSS luminance; weight: -0.50 and MSS motion; weight: -0.50). There was no difference [F (1, 15) = 0.873, p = .37]. Third, the average saturation obtained in the control condition (no MSS: weight: 1.00) was compared to that obtained in the different-condition (MSS luminance; weight: -0.50 and MSS motion; weight: -0.50). Again, there was no difference [F (1, 15) = 4.174, p = .06].

These results indicate that the saturation of the CAE does not differ whether, during adaptation, observers pay attention to color, luminance or motion, or passively view the stimulus. This suggests that paying attention to any feature of the adaptation stimulus does not influence the production of the CAE.

BAE

For each adaptation condition, the average intensity (cd/m^2) required to null the BAE (i.e. bright appearance of the luminance and motion sectors) across all observers was calculated. These averages and their corresponding standard errors are illustrated in Figure 8. Individual data are illustrated in Appendix B.

A one-way repeated-measures ANOVA was performed on the average intensity obtained in each adaptation condition. The results were not significantly different [F (3, 15) = 1.493, p = .26]. Despite this non-significant finding, the planned comparisons were evaluated using Multiple-Plan Contrast Analyses. For these comparisons, the MS error term of the ANOVA was used. First, the average intensity obtained in the same-condition (MSS luminance; weight: 1.00) was compared to that obtained in the control condition (no MSS: weight: -1.00). There was no difference [F (1, 15) = 1.210, p = .29]. Second, the average intensity obtained in the same-condition (MSS luminance; weight: 1.00) was compared to that obtained in the different-condition (MSS color; weight: -0.50 and MSS motion; weight: -0.50). There was no difference

[F (1, 15) = 0.135, p = .72]. Third, the average intensity obtained in the control condition (no MSS; weight: 1.00) was compared to that obtained in the different-condition (MSS color; weight: -0.50 and MSS motion; weight: -0.50). There was no difference [F (1, 15) = 0.815, p = .38]. Upon inspection of individual results (see Appendix B), one can see that for a given attentional condition, the intensity of the BAE greatly varied across observers; this confirms that attention does not have a systematic effect on the BAE and further shows a large variability in all conditions, especially in the control condition.

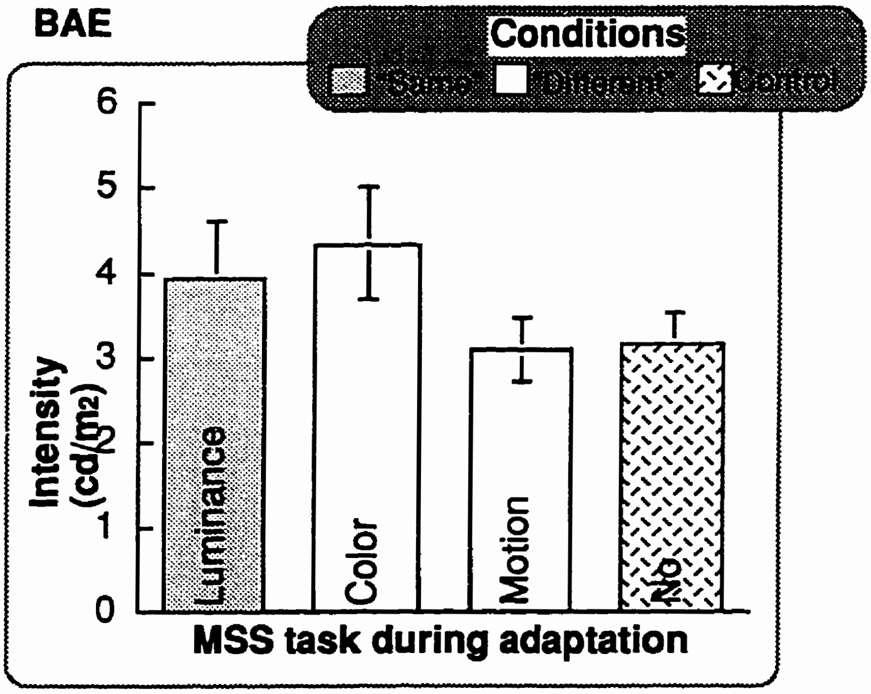


Figure 8. Average intensities (6 observers) obtained in the four adaptation conditions —MSS luminance, MSS color, MSS motion, and no MSS— for the BAE. The three attentional conditions —same-, different- and control— are represented by different shadings. One error bar represents one standard error.

These results indicate that the intensity of the BAE does not differ whether, during adaptation, observers pay attention to luminance, color or motion, or passively view the stimulus. This suggests that paying attention to any feature of the adaptation stimulus does not influence the production of the BAE.

MAE

For each adaptation condition, the average speed of inward motion (deg/sec) required to null the MAE (i.e. appearance of outward motion of the luminance and motion sectors) across all observers was calculated. These averages and their corresponding standard errors are illustrated in Figure 9. Individual data are illustrated in Appendix C.

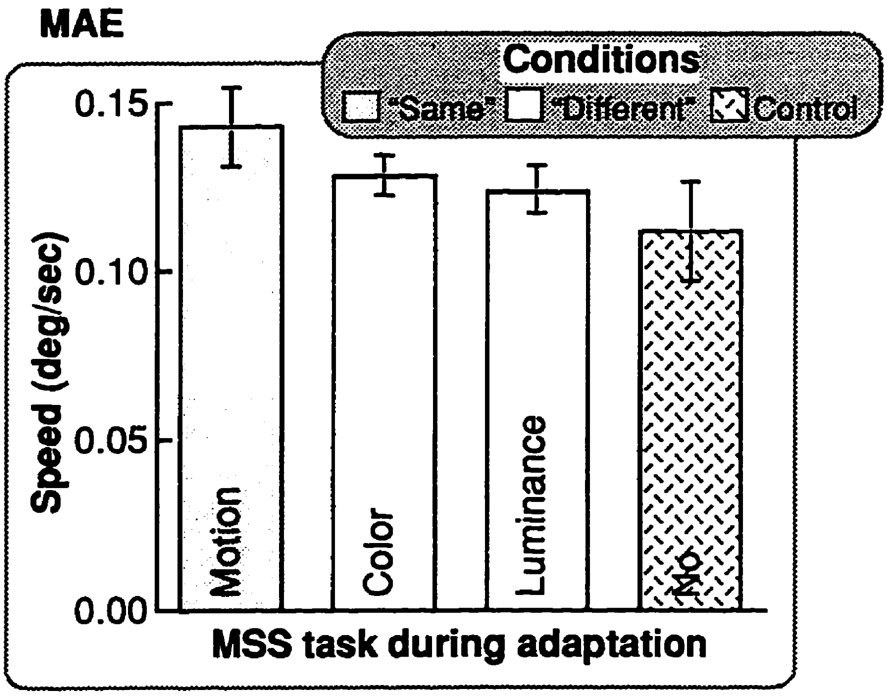


Figure 9. Average speeds (6 observers) obtained in the four adaptation conditions —MSS motion, MSS color, MSS luminance, and no MSS— for the MAE. The three attentional conditions —same-, different- and control— are represented by different shadings. One error bar represents one standard error.

A one-way repeated-measures ANOVA was performed on the average speed obtained for each adaptation condition. The results were not significant [F (3, 15) = 2.468, p = .10]. Despite this non-significant finding, the planned comparisons were evaluated using Multiple-Plan Contrast Analyses. For these comparisons, the MS error term of the ANOVA was used. First, the average speed obtained in the same-condition (MSS motion; weight: 1.00) was compared to that obtained in the control condition (no MSS; weight: -1.00). The average speed was greater in the same-condition than in the control condition [F (1, 15) = 7.211, p = .02]. The speed of the MAE produced when attention was devoted to motion during adaptation was faster than that produced when the stimulus was passively viewed. Second, the average speed obtained in the same-condition (MSS motion; weight: 1.00) was compared to that obtained in the different-condition (MSS color; weight: -0.50 and MSS luminance; weight: -0.50). Although the MAE appears larger in the same-condition than in the different-condition, this difference is not statistically significant [F (1, 15) = 2.794, p = .11]. Thus, the speed of the MAE did not differ whether, during adaptation, attention was devoted to motion, color or luminance. Third, the average speed obtained in the control condition (no MSS; weight: 1.00) was compared to that obtained in the different-condition (MSS color; weight: -0.50 and MSS luminance; weight: -0.50). Although the MAE appears larger in the different-condition than in the control condition, this difference is not statistically significant [F (1, 15) = 2.043, p = .17]. Thus, paying attention to color or luminance did not produce a different MAE than that produced after passive viewing of the stimulus.

In summary, results show that (i) the speed of the MAE produced in the same-condition is faster than that produced in the control condition, and that (ii) the speed of the MAE produced in the different-condition does not differ from that produced in the same-condition, nor does it differ from that produced in the control condition; indeed, the

MAE produced in the different-conditions is in between that produced in the other two conditions. These results are discussed in the following paragraphs.

The results first show that the speed of the MAE in the same-condition is faster than that in the control condition. This indicates that paying attention to motion influences the MAE. Which neural processes are responsible for the enhancement of the MAE? If the MAE only depends on processes which analyze many features together, and if attention influences these processes, then the MAE should not only be increased when attention is devoted to motion, but it should also be increased when attention is devoted to luminance or color. The analyses show that paying attention to color or luminance did not produce a significantly different MAE than passive viewing of the adaptation stimulus. Thus, attention to motion must have mainly influenced processes other than the ones that could have been influenced by attention to color or luminance; paying attention to motion most probably enhances processes mainly involved in motion analysis.

Moreover, the results suggest that processes which analyze many features together are also involved in the production of the MAE and that they are influenced by attention. In addition to not differing from the speed of the MAE in the control condition, the speed of the MAE in the different-condition does not significantly differ from that in the same-condition. Indeed, the MAE produced in the different condition is in between that produced in the control condition and that produced in the same-condition. These findings could only happen if the processes involved in the production of the MAE in the different-condition have something in common with those involved in the production of the MAE in both the same- and control conditions. This common factor must be that processes which analyze motion and either color, luminance, or both features together are involved in the production of the MAE and that they are enhanced by attention. Attention to color or luminance, which should not enhance motion processes, must have enhanced the neural processes which analyze motion and either color, luminance, or both features together. Indeed, if attention to color or luminance had no influence at all, the MAE in the different-condition should be like that in the control condition, and lower than those in the same-condition. Thus, the finding that paying attention to luminance or color did not produce a different MAE than paying attention to motion, and than not paying attention at all, suggests that processes which analyze motion and either color, luminance, or both features together are enhanced by attention.

While the MAE results suggest that processes which analyze motion and either color, luminance, or both features together are involved in the production of the MAE and that they are influenced by attention, this exact influence remains unclear. Indeed, the following possibilities could account for the MAE results. It is possible that the multi-feature processes involved in the production of the MAE are not sufficiently influenced by attention to produce a change in the MAE between the different-condition and the same- and control conditions. It is also possible that attention has an equivalent influence on motion and multi-feature processes, but that the involvement of multi-feature processes in the production of the MAE is minimal compared to that of motion processes. Finally, it could be that spatial attention is responsible for the enhancement in the MAE that was observed in the different-conditions. These possibilities are discussed in more detail in the general conclusions.

GENERAL CONCLUSIONS

This section first discusses the findings related to the CAE and BAE. Second, it discusses the findings related to the MAE. Finally, the role of feature-specific attention on object recognition is examined and questions for future research are outlined.

CAE and BAE

The results show that the CAE and BAE did not differ whether, during adaptation, observers paid attention to color, luminance or motion, or passively viewed the stimulus. This suggests that paying attention to a feature does not influence the CAE and BAE. Which neural processes could be involved in the production of these AEs? Because CAEs and BAEs do not transfer from one eye to the other[1], they are thought to be created by the adaptation of monocular cells in pre-cortical areas (see review by Coltheart, 1973, for the CAE; e.g. Anstis & Harris, 1987, for the BAE). The lack of influence of attention on the CAE and BAE observed in this study may be due to the fact that these AEs are created in pre-cortical areas, where attentional modulation has not been observed (see review by Maunsell, 1995). Moreover, because cells selective for many features together are binocular and are only found in higher order visual areas, for example in V3 (e.g. Kiper et al., 1995) and in V4 (e.g. Logothetis, 1994), it is unlikely that such cells were involved in the production of these AEs. Thus, this study suggests that paying attention to a specific feature does not influence the processes involved in the production of the CAE and BAE, such as cells selective for color and those selective for luminance, respectively. Houck and Hoffman (1986) also found that spatial attention does not

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[1] For BAEs, this is only true if the BAE is induced by adaptation to a low contrast stimulus, but not if it is induced by high contrast gratings (i.e. 100%) (e.g. Mitchell & Ware, 1974). Since, in this experiment, the adaptation was done with a sinewave grating with a low contrast, it is assumed that monocular cells were involved in its production.

influence the CAE contingent upon orientation. This study adds to our current knowledge of luminance processing —the results represent the first empirical evidence suggesting that, like the CAE, the BAE is not influenced by attention.

MAE

First, the results show that paying attention to motion during adaptation produced a significantly greater MAE than passive viewing of the stimulus, but that paying attention to color or luminance did not. This suggests that paying attention to motion mainly enhances neural processes specialized for the analysis of motion only, such as cells which respond selectively to motion. A study by Boutet et al. (1995) also suggests that paying attention to the motion of an image defined by color and motion can enhance the responses of motion selective cells, but not those of cells which respond to motion and color.

Second, the results show that paying attention to color or luminance did not produce a different MAE than passive viewing of the stimulus, nor did it produce a different MAE than paying attention to motion. This finding suggests that processes specialized for the analysis of many features together are involved in the production of the MAE. Other psychophysical studies also indicate that multi-feature processes, such as cells which respond simultaneously to motion and to other features, can be involved in the production of the MAE (e.g. Derrington & Badcock, 1985; Mullen & Baker, 1985). Moreover, results suggest that these multi-feature processes are enhanced by attention. However, the exact influence of attention on the multi-feature processes remains unclear and possibilities which could account for the MAE results are discussed below. Physiological studies also indicate that attention can influence the responses of cells selective for many features (see review by Maunsell, 1995).

All together, the results show that attention influences the MAE. This conclusion is consistent with those of other studies which show that paying attention to a specific location (Chaudhuri, 1990; Giorgiades & Harris, 1996; Shulman, 1993; Takeuchi & Kita, 1994) or to one motion component of an image defined by two of them (Lankheet & Verstraten, 1995; Iordanova et al., 1996) influences the MAE. These findings are contrary to conclusions of others which indicate that attention does not influence the duration of MAEs induced by contraction/expansion (Takeuchi & Kita, 1994) and by rotation (Takeuchi & Kita, 1994; Wolgemuth, 1911). Moreover, a study using the same adaptation stimulus as the one used here indicates that the duration of the MAE is not influenced by attention (Boutet, Rivest & Intriligator, 1996). These findings suggest that attentional modulations are not involved in the duration of the MAE. It may be that duration is not a measure sensitive enough to evaluate the effect of attention; after all, duration of AEs are known to be unreliable (Anstis, 1986). Therefore, measuring the velocity of the MAE may be essential to determine whether or not it is influenced by attention. Finally, because the MAE transfers from one eye to the other, it has been attributed to the adaptation of binocular cells in cortical areas (for reviews see Brindley, 1970; Favreau & Corballis, 1976). The finding that the activity of these cortical cells can be influenced by attention supports the now accepted physiological view that cortical mechanisms can be modulated by attention (see review by Maunsell, 1995).

While the results of this experiment suggest that multi-feature processes are involved in the production of the MAE and that they are influenced by attention, the way in which attention influences them remains unclear. Possibilities which could explain why paying attention to color or luminance did not produce a different MAE than the ones produced by paying attention to color, and by not paying attention at all, are proposed and outlined in the following section.

Possibilities which could account for the MAE results

How can it be that paying attention to color or luminance did not produce a different MAE than the ones produced by paying attention to motion and by not paying attention at all? In this section, possibilities which could explain these results are presented. Moreover, whether or not these possibilities are supported by previous research is discussed.

It is possible that the multi-feature processes involved in the production of the MAE are not sufficiently enhanced by attention to color or luminance to change the MAE. This scenario would apply if the following attentional modulations were produced during adaptation. First, when attention is not devoted to any feature, a "baseline" MAE is produced. Second, paying attention to motion greatly enhances motion processes and weakly enhances multi-feature processes —this produces a significantly stronger MAE than the baseline MAE. Finally, paying attention to color or luminance naturally does not enhance processes specialized for the analysis of motion, but it weakly enhances multi-feature processes —this produces a greater MAE than the baseline MAE, and a weaker MAE than that produced when attention is devoted to motion; however, these differences may not be significant. This is what happened in this study.

This possibility implies that paying attention to motion greatly enhances motion processes, such as motion selective cells, whereas paying attention to either motion, color or luminance weakly enhances multi-feature processes, such as cells which respond to color, luminance and motion together. Physiological studies do not indicate whether paying attention to a specific feature produces a greater enhancement in cells specialized for the analysis of that feature than in cells specialized for the analysis of that feature as well as other features. For example, while a monkey was attending to the color or orientation of a stimulus defined by these two features, Maunsell and Hochstein (1985) recorded the responses of cells selective for color only, for orientation only, and for both features. The authors found that the responses of a majority of cells are enhanced when attention is devoted to a specific feature of the stimulus (e.g. color). However, they did not evaluate whether, for example, paying attention to color produces a stronger enhancement in the responses of color selective cells than in the responses of cells selective for both color and orientation.

The possibility that paying attention to a specific feature influences processes specialized for the analysis of that feature to a greater extent than multi-feature processes could be due to the concept of "behavioral relevance". Psychologists (Ahissar et al., 1992; Thorndike, 1911) have argued that when an action is performed on a stimulus, the action must be relevant to the stimulus in order to produce modifications in the activity of cells responsible for the analysis of the stimulus. Interestingly, this idea could explain why paying attention to a specific feature could produce a greater enhancement in processes specialized for the analysis of that feature than in multi-feature processes. For example, it is possible that paying attention to motion maximally enhances motion processes because the attentional task —the behavior— perfectly matches the processes' specialization. In contrast, it is possible that paying attention to only one feature moderately enhances processes specialized for the analysis of color, luminance and motion because the attentional task is only partially relevant to the processes' specialization. It may be that a strong enhancement can only be produced when there is a "perfect match" between the attentional task and the processes' specialization —attention must be devoted to all three features in order to maximally enhance the processes specialized for the analysis of these three features. Such an effect could explain why paying attention to motion greatly influences processes specialized for the analysis of motion and weakly influences multi-feature processes.

Another possibility is that attention has an equivalent influence on motion and multi-feature processes, but that the involvement of multi-feature processes in the production of the MAE is minimal compared to that of motion processes. This possibility will be illustrated by assigning proportions to the involvement of motion and multi-feature processes in the production of the MAE (see Figure 10). First, lets assume that in all conditions, motion and multi-feature processes contribute to 3/4 and 1/4 of the production of the MAE, respectively. In this case, lets say that passive viewing of the adaptation stimulus will create an overall MAE of 1.00. Second, lets assume that paying attention to a specific feature doubles the activity of both types of processes. Thus, when attention is devoted to motion, both the 3/4 contribution of motion processes and the 1/4 contribution of multi-feature processes will double —this will create an overall MAE of 2.00. When attention is devoted to color or luminance, the 1/4 contribution of multi-feature processes will double, but not the 3/4 contribution of motion processes —this will create an overall MAE of 1.25. Therefore, under these assumptions, paying attention to color or luminance will produce a slightly stronger MAE (1.25) than passive viewing of the stimulus (1.00), and a slightly weaker MAE than paying attention to motion (2.00); however, these differences may not be significant. These results correspond to those obtained in the present experiment.

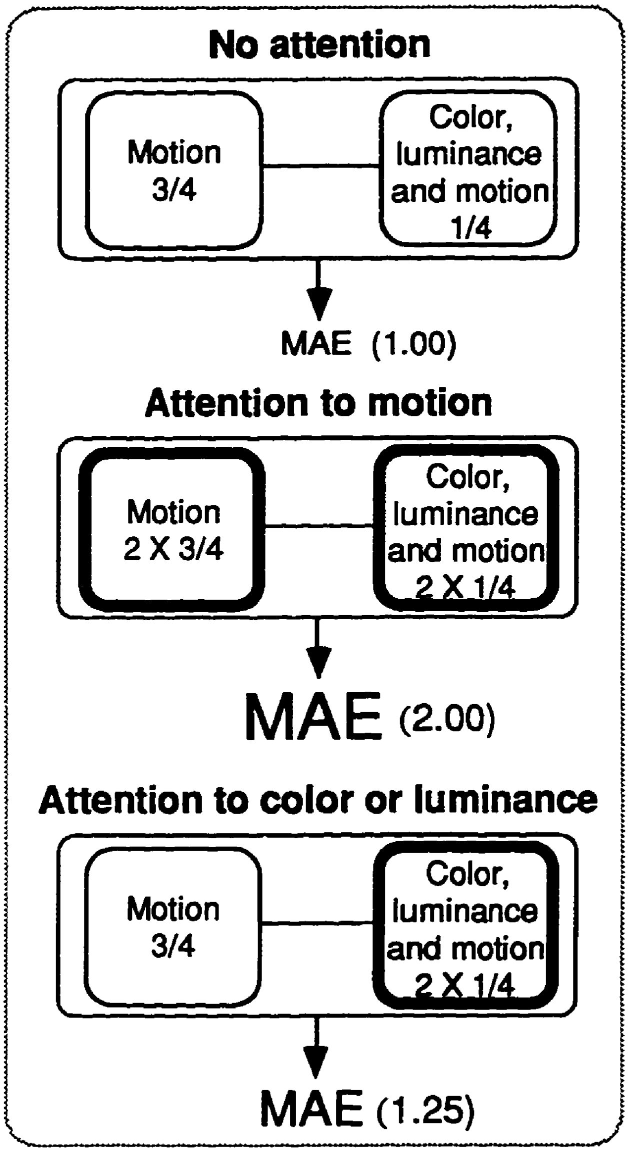

Figure 10. A schematic illustration of the possibility that attention has an equivalent influence on motion and multi-feature processes, but that the involvement of multi-feature processes in the production of the MAE is minimal compared to that of motion processes. Each third of the figure illustrates whether, during adaptation, there was no attention, attention to motion, or attention to color or luminance. The letter size of "MAE" illustrates the strength of the MAE (also indicated in parenthesis). The small boxes illustrate the processes involved in the production of the MAE: motion processes and processes specialized for the analysis of color, luminance and motion together (multi-feature). The proportion of the contribution of each type of processes to the production of the MAE is also indicated. The thick contours illustrate an influence of attention which doubles the activity of both types of processes. See text for more details.

This possibility could account for the MAE results if the MAE was produced in one area where motion cells are found, and another one where cells which respond to many features are found, and if the former area contributes more to the production of the MAE than the latter. The three following observations suggest that this possibility is plausible. First, it has been shown that different areas of the visual system can be involved in parallel in the production of the MAE (e.g. Favreau, 1976; Wenderoth, Bray & Johnstone, 1988). Second, physiological research indicates that among all the areas which could be involved in the production of the MAE, some have motion selective cells, and others have cells selective for motion as well as other features. For example, because areas MT, MST and IT are selective for the type of motion used to induce the MAE in this study (i.e. contraction) (Tootel et al., 1995b), these areas may be involved in the production of the MAE. The majority of cells in MT and MST are exclusively selective for motion (e.g. Maunsell & Van Essen, 1983 for MT; Tanaka & Saito, 1989 for MST) while some cells in IT are selective for motion as well as other features (e.g. Sàry, Vogels & Orban, 1993). Third, physiological research also indicates that different visual areas contribute differently to the production of a MAE induced by contraction (Tootel et al., 1995a). Using fMRI, Tootel et al. (1995a) showed that MAE activation in area MT is 70%, MAE activation in area V2 is 23%, and MAE activation in area V3 is almost 0%. A MAE activation was also observed in MST. All together, these observations suggest that the MAE may depend on the activity of motion cells in, for example, areas MT and MST, and cells selective for motion and other features in, for example, area IT. However, it is possible that because areas MT and MST contribute more to the production of the MAE than area IT, an influence in the former may change the MAE whereas an influence in the latter may not.

As in this study, Chaudhuri (1990) found that paying attention to the color of a moving colored stimulus did not produce a greater MAE than passive viewing of the stimulus. In one of his experiments, a stimulus defined by color and motion was presented during adaptation and the duration of the MAE was measured under the following two conditions: when observers paid attention to the color of the adaptation stimulus and when they passively viewed it. These two conditions did not produce a different MAE. The aforementioned possibilities could also account for Chaudhuri's results. Indeed, in his experiment, the MAE could have been produced by processes specialized for the analysis of color and motion, and attention to color could have enhanced these processes. However, it is possible that these processes were not sufficiently enhanced, or that their involvement in the production of the MAE was not sufficient to change the duration of the MAE.

Finally, an alternative explanation for the MAE results is that spatial attention produced the enhancement in the MAE that was observed in the different-conditions. Indeed, in order to perform the attentional task during adaptation, observers had to pay attention to the spatial location of the adaptation stimulus. It is possible that whenever attention is devoted to one feature of the adaptation stimulus, spatial attention is also modulated and therefore has an influence on the MAE. Thus, in the different-condition, the MAE may not be enhanced because attention to color or luminance influences multi-feature processes. Rather, it could be that the MAE was enhanced because paying attention to the location of the adaptation stimulus influences processes which exclusively analyze motion. In this case, paying attention to motion would greatly enhance the MAE because here, motion processes are not only influenced by attention to motion, but also by spatial attention. In contrast, paying attention to color or luminance would weakly enhance the MAE because here, motion processes are only influenced by spatial attention.

The aforementionned possibilities are non-exclusive and all could be at play. The possibility that paying attention to a specific feature better enhances the responses of cells selective for that feature than the responses of cells selective for many features remains to be explored. In contrast, the possibility that populations of motion cells contribute more to the production of the MAE than populations of cells selective for motion and other features is supported by previous research. Finally, several psychophysical and physiological studies have shown that spatial attention can influence motion processes.

Future research may aim at determining whether or not these possibilities can account for the MAE results.

As previously suggested, populations of motion selective cells in areas MT and MST and populations of cells selective for motion as well as other features in area IT may be involved in the production of the MAE. Another area which could be responsible for the production of the MAE is V3a. Indeed, using fMRI, Tootel et al. (1995a) have shown that this area is activated when observers experience a MAE. The results of this study suggest that neural processes in these areas could be influenced by attention. Past research indicates that this is the case for areas MST and IT (see review by Maunsell, 1995). However, as far as I know, whether similar modulations exist in MT and V3a has not yet been determined.

To conclude, this study suggests that paying attention to motion influences the motion processes involved in the production of the MAE. It appears that multi-feature processes are also involved in the production of the MAE and that they are influenced by attention. However, this exact influence remains to be determined. In contrast, paying attention to a feature does not influence the production of the CAE and BAE, respectively.

In light of the conclusions reached in this study, one must ask why paying attention to a feature can influence visual processes involved in the analysis of that feature. It is clear that segregating features accurately is essential for object recognition. Indeed, different objects can be identified because they are defined by different features and because their features differ from the background. Feature-specific attention may play an important role in object recognition. Indeed, paying attention to one feature of an object may increase the processing of that feature and as a result, facilitate object recognition. Accordingly, this study suggests that paying attention to motion can increase the processing of motion information.

Finally, this study brings about several questions for future research which, if addressed, would increase our understanding of the role that feature-specific attention plays in visual processing and of its effect on cortical activity and AEs. First, whether paying attention to one feature of an image influences processes specialized for the analysis of that feature to a greater extent than multi-feature processes remains to be determined. If these two types of processes were equally influenced by attention, another issue which should be examined is whether or not they are equally involved in the production of the MAE. Finally, more research is needed to test whether the present finding that the BAE and CAE are not influenced by attention is reliable.

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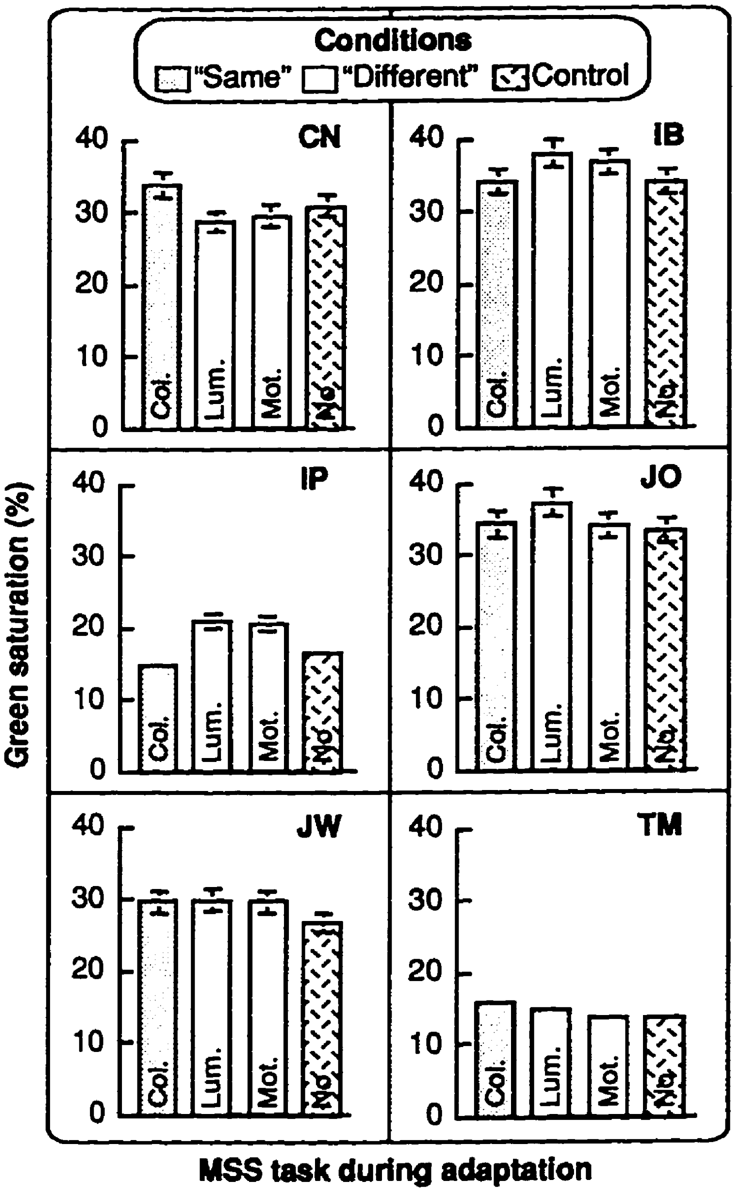
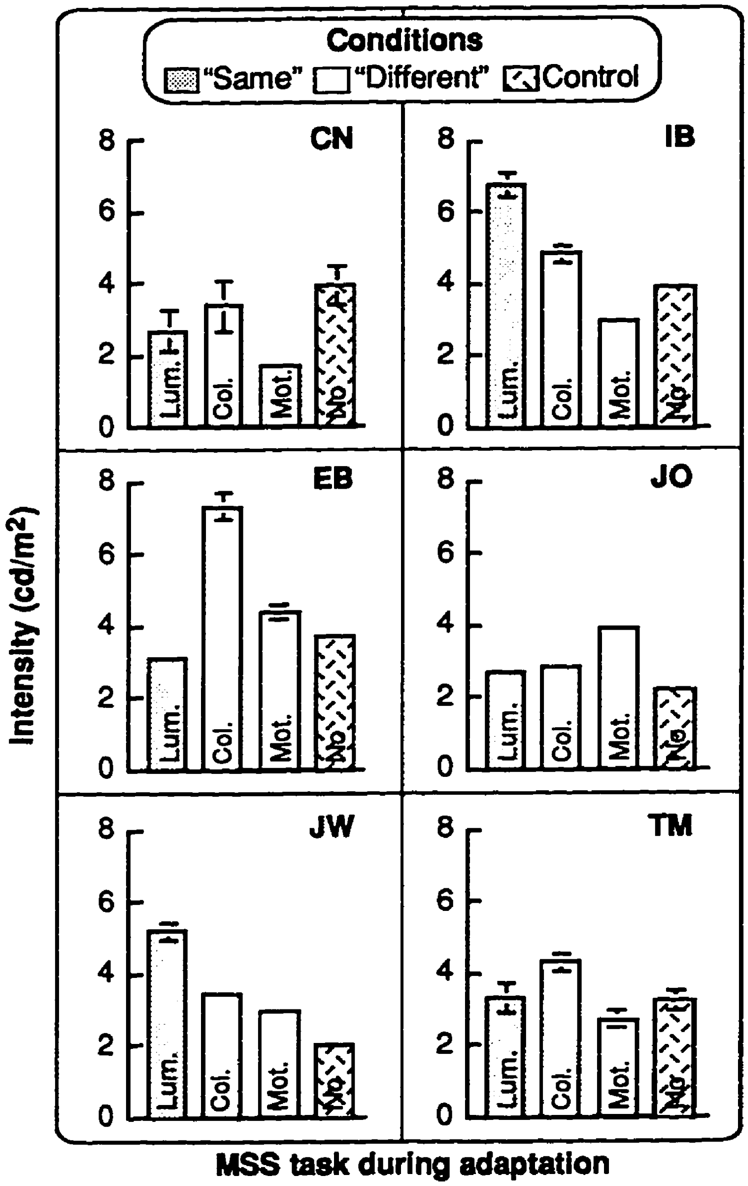
APPENDIX A



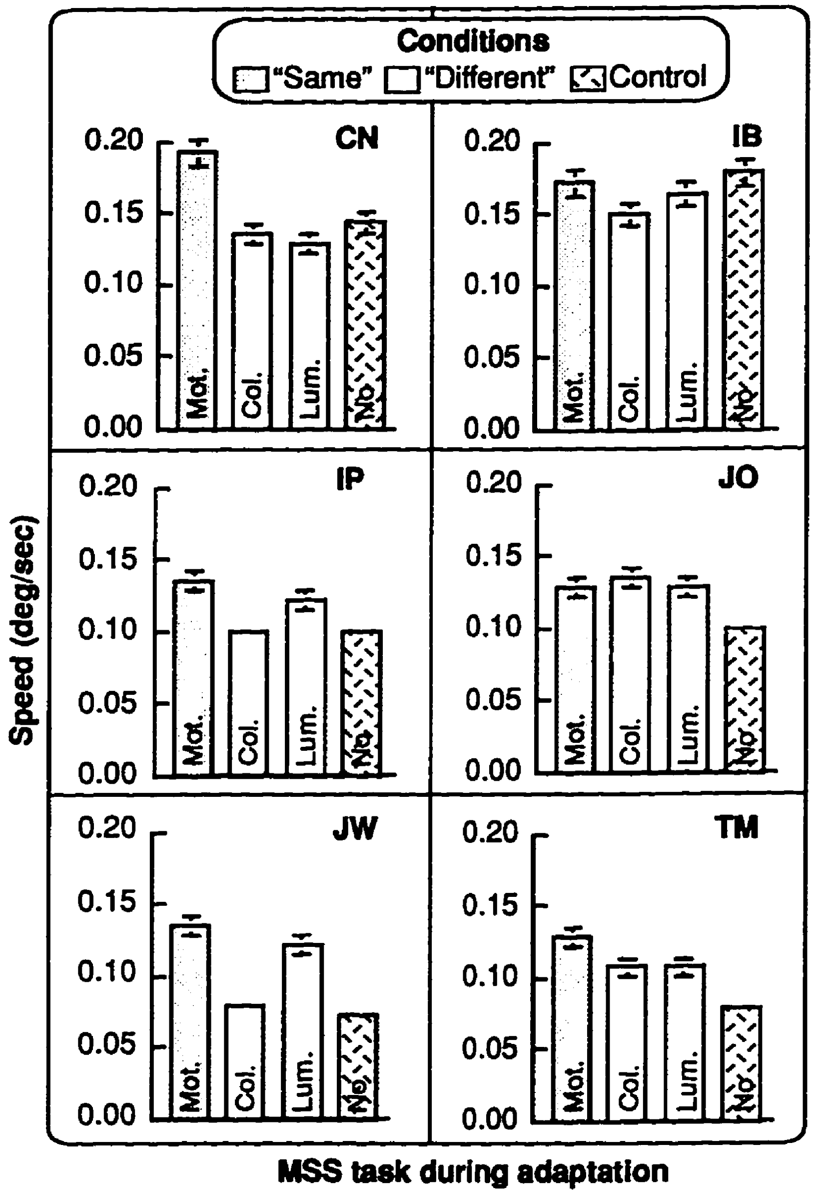
Green saturations obtained by each observer in the four adaptation conditions —MSS color, MSS luminance, MSS motion and no MSS— for the CAE. The three attentional conditions —same-, different- and control— are represented by different shadings. One error bar represents one standard error.

APPENDIX B



Intensities obtained by each observer in the four adaptation conditions —MSS luminance, MSS color, MSS motion and no MSS— for the BAE. The three attentional conditions —same-, different- and control— are represented by different shadings. One error bar represents one standard error.

APPENDIX C



Speeds obtained by each observer in the four adaptation conditions —MSS motion, MSS color, MSS luminance and no MSS— for the MAE. The three attentional conditions —same-, different- and control— are represented by different shadings. One error bar represents one standard error.