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Influences de la texture sur la perception du mouvement

Psychophysique et modélisation Bayésienne

par

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Cette thèse intitulée :

Influences de la texture sur la perception du mouvement : Psychophysique et modélisation Bayésienne

présentée par :
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Résumé

Afin d'interagir de façon adaptée avec son environnement, le monde phénoménologique construit par le système visuel doit correspondre raisonnablement bien avec le monde physique dans lequel l'observateur se trouve. Cependant, diverses expériences psychophysiques ont démontré que des observateurs humains commettent des erreurs lorsqu'ils estiment la vitesse et la direction de stimuli visuel simples et que divers facteurs peuvent influencer la vélocité perçue. Dans le premier article de cette thèse, nous avons investigué les effets de la superposition de texture de luminance statique sur la vitesse perçue d'un réseau en mouvement. Les résultats d'une tâche d'égalisation de vitesse démontrent que la vitesse perçue d'un réseau de luminance test augmente lorsqu'on augmentait le contraste de la texture. Nous attribuons ces résultats à la présence d'indices spatiaux fournis par la texture statique. Une expérience subséquente démontre que, bien que la texture de luminance n'interagisse avec le stimulus de mouvement que sur une échelle spatiale limitée, ces estimés locaux de vélocité sont ensuite intégrés sur une grande aire afin d'obtenir une estimation finale de vélocité. Dans une troisième expérience, nous avons étudié les effets de la texture dynamiques sur la vitesse perçue. Nos résultats démontrent que, contrairement à la texture statique, le contraste d'une texture de luminance dynamique ne produit aucun effet sur la vitesse perçue d'un réseau en mouvement. Ceci suggère que les composantes de mouvement du signal et du bruit sont ségréguées dans le processus d'agrégation menant à l'estimation de la vitesse. Les effets de la texture de luminance statique sur la vitesse perçue du mouvement sont discutés dans le contexte d'un modèle Bayésien de la vélocité perçue. Dans ce modèle, la vélocité perçue constitue une solution optimale (un « *best guess* ») étant donné un intrant sensoriel bruité et les connaissances *a priori* du système visuel que les vélocités lentes sont plus communes que les vélocités rapides.

Dans la deuxième section de cette thèse, nous discutons en plus de détails le modèle Bayésien de la vélocité perçue mentionné dans le premier article. Ici, nous tentons de décrire une implémentation possible de ce modèle en tenant compte des propriétés physiologiques de neurones de l'aire MT. Dans ce modèle, l'intrant sensoriel à la perception du mouvement était représenté par le patron d'activité d'unités accordées à la vélocité ayant des propriétés similaires aux neurones de l'aire MT. La connaissance du système visuel des propriétés statistiques du mouvement dans le monde physique était exprimée dans la pondération donnée aux réponses des unités accordées à la vélocité dans le calcul subséquent de la vélocité. La vélocité était calculée à partir de ces intrants pondérés selon une approche de moyennage de vecteurs. Dans sa forme originale, le modèle pouvait prédire l'augmentation de vitesse perçue lorsqu'on augmente le contraste du stimulus de mouvement. Similairement, nous avons trouvé que les effets de la texture sur la vitesse perçue pouvaient être expliqués par une augmentation dans le signal des unités accordées à la vélocité en présence de texture de luminance. Nous trouvons également qu'il est possible d'exprimer à l'intérieur du contexte Bayésien les hypothèses émises afin d'expliquer divers phénomènes dans la perception du mouvement, tel la suggestion que les effets consécutifs de mouvement sont le résultat d'une recalibration du système visuel.

Mots-clés : Texture, perception du mouvement, illusions de mouvement, modèle Bayésien

Abstract

In order to interact adaptively with his environment, the phenomenological world built by the visual system must correspond with reasonable accuracy with the physical world in which the observer is located. However, psychophysical experiments have demonstrated that human observers make a number of mistakes when estimating the direction and speed of simple visual stimuli and that a number of factors can influence perceived velocity. In the first section of this thesis, we investigated the effects of superimposing luminance texture on the perceived speed of a drifting grating. The results of a speed-matching task show that the perceived speed of a moving luminance-modulated test grating increases as the contrast of superimposed static luminance texture was increased. We attribute these results to the presence of the spatial cues provided by static texture. Further experimentation demonstrates that although static luminance texture only interacts with the motion stimulus over a limited spatial scale, these local velocity estimates are then integrated over a large spatial area. In a third experiment, we studied the effects of dynamic luminance texture on perceived speed. The results of this experiment show that, unlike static luminance texture, dynamic luminance texture contrast produces no change in the perceived speed of a moving grating. These results are consistent with previously reported effects of coherence level on the perceived speed of RDK stimuli. This suggests that the signal and noise motion components are segregated in the pooling process leading to the estimation of speed. The effects of static luminance texture on the perceived speed of a moving grating are discussed within the context of a Bayesian model of velocity perception, in which perceived velocity constitutes a best-guess given noise in the initial assessment of velocity and the visual system's *a priori* knowledge that slow motion velocities are more common than rapid ones.

In the second section of this thesis, we expand upon a Bayesian model of velocity perception discussed in the first article. Here, we attempt to describe a possible implementation of this model within a framework taking into account the physiological properties of neurons in area MT. In this model, the sensory input to motion perception was instantiated in the pattern of activity of velocity-tuned units sharing response properties similar to MT neurons. The visual system's prior knowledge about the statistical properties of motion in the physical world was expressed in the weight given to the responses of the velocity-tuned units in the subsequent computation of velocity. Velocity was computed based on these weighted outputs using a vector-averaging computation. In its original form, the model was capable of predicting the increase in the perceived speed of motion with higher contrasts of the motion stimulus. Similarly, we found that texture effects on perceived speed could be predicted by a proposed increase in the responses of velocity-tuned units in the presence of static texture. We also find that the proposals put forward to account for various phenomena in motion perception, such as the suggestion that a recalibration of the visual system underlies motion aftereffects, were expressible within this framework.

Keywords : Texture, motion perception, motion illusions, Bayesian models

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Introduction

Dans leur vie quotidienne, les organismes vivants doivent interagir de façon adaptée avec leur environnement afin d'assurer leur survie. La fonction primaire de notre système visuel ainsi que des autres modalités sensorielles est de nous fournir de l'information sur nos alentours dans le but de guider nos actions. Dans cette thèse, nous nous intéresserons à la perception du mouvement puiqu'on compte le mouvement parmi les attributs visuels importants à nos interactions avec le monde extérieur. Afin de pouvoir interagir de façon appropriée avec notre environnement, le monde phénoménologique construit à partir des intrants sensoriels doit correspondre raisonnablement bien avec le monde physique qui nous entoure. Par exemple, un oiseau de proie tentant de capturer un oiseau en plein vol doit, afin de réussir, être doté d'un système visuel capable de déterminer avec précision la vitesse et la direction à laquelle sa proie se déplace.

L'importance de la perception du mouvement à notre fonctionnement est également mise en évidence par les déficits observés chez des personnes ayant subi des lésions aux aires corticales sous-jacentes à la perception du mouvement. Il est en effet rapporté qu'une perte de la perception du mouvement suite à des lésions bilatérale des aires pariéto-occipitales chez une patiente (Rashbass, 1961; Zihl, von Cramon, & Mai, 1983) entraîne toute une gamme de déficits. Cette patiente démontrait, entre autres, des déficits dans la locomotion, dans le traitement d'objets en mouvement, dans les mouvements oculaires de poursuite visuelle et avait beaucoup de difficulté à se verser une tasse de café sans la faire déborder. En plus de fournir de l'information permettant de guider nos actions, le mouvement peut également servir d'indice afin de déterminer divers autres attributs visuels (Nakayama, 1985), tel la profondeur (parallaxe du mouvement) et la structure d'un objet. L'importance de la perception du mouvement à notre fonctionnement ainsi que son utilité en tant qu'indice pour d'autres attributs permettent d'expliquer pourquoi la perception du mouvement est presque universelle parmi les animaux dotés d'un système visuel.

Illusions de mouvement

Étant donné l'importance d'une perception véridique de la vélocité à notre fonctionnement, il semble raisonnable de s'attendre à ce que notre perception de la vitesse d'un stimulus soit véridique et robuste (i.e., non affectée par d'autres facteur que la vélocité du stimulus). Il est donc pour le moins surprenant que diverses expériences psychophysiques chez des observateurs humains aient démontré ceux-ci commettaient des erreurs dans l'estimation de la vélocité de stimuli visuels pourtant simples. Il est également démontré que des paramètres autres que la vitesse d'un stimulus en mouvement influencent la vitesse perçue. Au cours de la première partie de cette thèse, nous nous intéressera aux effets du contraste de la texture de luminance sur la vitesse perçue d'un réseau en mouvement. Diverses études ont rapporté que la présence de texture de luminance (Brown, 1931; Gogel & McNulty, 1983; Norman, Norman, Todd, & Lindsey, 1996; Blakemore & Snowden, 2000) produit une augmentation dans la vitesse perçue d'un stimulus en mouvement.

Brown (1931) fût le premier à rapporter que la texture de luminance produisait un effet sur la vitesse perçue du mouvement. Celui-ci compara la vitesse perçue d'un stimulus central lorsqu'un fond uniforme noir était présenté en périphérie, et lorsqu'un champ texturé (i.e., une tapisserie faite de carrés) était présenté en périphérie du stimulus de mouvement. Cet auteur fît la découverte que la vitesse perçue du stimulus de mouvement était plus lente lorsque le champ entourant le stimulus de mouvement était uniforme que lorsque le champ était texturé. Brown (1931) conclut donc que la vitesse phénoménologique du mouvement était déterminée dynamiquement par la structure et les propriétés du champ visuel dans lequel le mouvement se produit. Cet auteur ne propose cependant aucun mécanisme physiologique permettant d'expliquer cet effet. Gogel et McNulty (1983) étudièrent la relation entre la vitesse perçue d'un stimulus en mouvement et la vitesse physique du stimulus, l'étendue du mouvement, le nombre et la densité de points de référence. Parmi les paramètres testés, ils trouvèrent que le seul facteur ayant une influence sur la vitesse perçue autre que la vitesse du stimulus était la densité des points de références. Ces auteurs proposèrent donc que cet effet était attribuable à une plus grande contribution des indices de mouvement relatif à la perception de la vitesse lorsqu'on augmente la densité des points de références.

Les effets contextuels sur la perception du mouvement furent davantage investigués par Loomis et Nakayama (1973). Tel qu'illustré à la Figure 1, ces auteurs étudièrent les effets de la vitesse de points se déplaçant à différentes vitesses sur la vitesse perçue de deux points cibles se déplaçant à une vitesse identique. Les résultats de leur expérience démontrent que, même si les deux points cibles se déplaçaient à une vitesse identique, leur vitesse perçue était différente : le point cible entouré de points se déplaçant lentement semblait se déplacer plus rapidement que le point cible entouré de points se déplaçant rapidement. Afin d'expliquer ce phénomène, ces auteurs proposèrent un mécanisme de contraste de mouvement, répondant lorsqu'une différence importante de vélocité existe entre le centre et le pourtour du champ récepteur (Nakayama & Loomis, 1974). Un tel mécanisme répond optimalement lorsque le mouvement dans la région centrale est dans la direction opposée au mouvement dans la région périphérique. Cette proposition est supportée par la découverte de cellules répondant optimalement lorsque le mouvement dans le centre est dans la direction opposée du mouvement dans le pourtour du champ récepteur, peu importe la direction absolue du mouvement. Des enregistrements électrophysiologiques on trouvé de telles cellules dans l'aire tectale du pigeon (Loomis & Nakayama, 1973) ainsi que dans les aires MT (Lagae, Gulyas, Raiguel, & Orban, 1989) et MST (Tanaka et al., 1986) du singe.

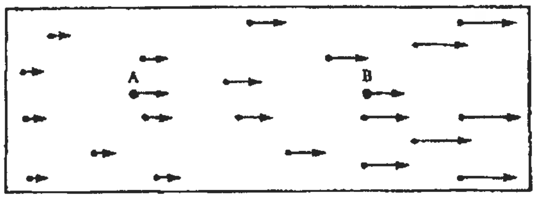

Figure 1. Illustration représentant un champ de points en mouvement. La longueur des flèches représente la vitesse à laquelle les points se déplacent. Bien que les points A et B se déplacent à la même vitesse physique, ce dernier semble se déplacer plus lentement que le point A. Figure empruntée de Loomis et Nakayama (1973).

Les effets de la texture de luminance sur la vitesse perçue du mouvement furent étudiés en plus de détails par Norman et al. (1996). Dans cette étude, la vitesse perçue du mouvement de points dans une région centrale était mesurée lorsque des points statiques ou en mouvement étaient ajoutés dans une région périphérique. Dans l'étude de Loomis et Nakayama (1973), tous les points se déplaçaient dans la même direction. Afin de tester le modèle de contraste de vélocité proposé par Nakayama et Loomis (1974), Norman et al. (1996) mesurèrent la vitesse perçue de points en mouvement dans une région centrale lorsque les points dans un anneau entourant cette région centrale étaient statiques ou se déplaçaient à diverses vélocités. Les points dans la région périphérique pouvaient se déplacer dans la même direction que les points dans la région centrale ou dans la direction opposée. Ces auteurs trouvèrent que la vitesse perçue du mouvement dans la région centrale était à son plus rapide quand les points dans la région périphérique étaient statiques. Lorsque les points dans la région périphérique étaient en mouvement, il se produisait une diminution dans la vitesse perçue des points dans la région centrale. Cette diminution se produisait peu importe si le mouvement dans les deux régions était dans la même direction ou dans des directions opposées. Ces résultats sont difficiles à expliquer par un mécanisme de contraste de vélocité puisqu'un tel mécanisme est optimalement activé lorsque le mouvement dans la région centrale est dans la direction opposée du mouvement dans la périphérie. Norman et al. (1996) soulèvent donc la possibilité que les signaux de mouvement du centre et du pourtour soient rectifiés avant le calcul de vitesse. Dans la première partie de cette thèse, nous étudierons les effets de la texture de luminance sur la vitesse perçue du mouvement.

La texture de luminance n'est pas le seul facteur ayant une influence sur la perception du mouvement. Parmi les paramètres influençant la vitesse perçue, on retrouve également l'absence de modulation de luminance dans un réseau chromatique (Cavanagh, Tyler, & Favreau, 1984), ainsi que le contraste d'un stimulus en mouvement (Thompson, 1982; Stone & Thompson, 1992; Blakemore & Snowden, 1999). Il est aussi rapporté que l'observation prolongée d'un stimulus se déplaçant à une vélocité constante produit une diminution dans la vitesse perçue du mouvement (Wohlgemuth, 1911; Gibson, 1937). De nombreuses études ont également démontré que cette période d'adaptation produit un percept de mouvement lors de la présentation subséquente d'un stimulus statique, une illusion connue sous le nom d'effet consécutif de mouvement (ECM). Ces phénomènes dans la perception du mouvement soulèvent une question : étant donné qu'une perception véridique du mouvement est importante à notre fonctionnement, pourquoi notre système visuel commet-il pourtant des erreurs dans l'estimation de la vélocité de stimuli visuels simples? Tout comme les phénomènes de perception visuelle en général, les modèles proposés afin d'expliquer les illusions dans la perception du mouvement sont généralement expliqués selon des modèles de traitement ascendant ou des modèles de traitement descendant. Dans les sections suivantes, nous nous pencherons sur ces deux approches à la perception visuelle.

Traitement ascendant

La première approche à la perception visuelle sur laquelle nous nous pencherons est l'approche du traitement ascendant L'approche ascendant conçoit le traitement de l'information visuelle comme un processus hiérarchique. Selon cette approche, la perception visuelle débute par un traitement simple de l'information visuelle et implique une série d'étapes accomplissant un traitement de plus en plus complexe de l'information visuelle. L'essor de cette approche dans le traitement de l'information de mouvement est en partie attribuable à la découverte de cellules sensibles à la direction du mouvement dans le cortex visuel primaire (Hubel & Wiesel, 1959) et dans l'aire corticale V2 (Hubel & Wiesel, 1965). Dans le traitement ascendant, chaque étape repose sur le traitement de l'information visuelle effectué par les étapes précédentes. Dans le cas du traitement du mouvement, l'approche ascendante propose que le système visuel procède à une extraction initiale de l'information de mouvement.

Différent modèles computationels ont été proposés quant aux mécanismes sous-jacents à l'extraction initiale de l'information de mouvement. Le premier modèle d'extraction d'information de mouvement élaboré fût le détecteur de mouvement de Reichardt (Reichardt, 1961), utilisé afin d'expliquer les réponses optomotrices chez les insectes. Ces détecteurs de mouvement calculent leur réponse sélective à la direction du mouvement en comparant les signaux décalés temporellement provenant de neurones ayant des champs récepteurs adjacents sur la rétine. Tel qu'illustré à la Figure 2, les signaux provenant de ces cellules convergent vers un site d'interaction, où ils sont multipliés et intégrés. Le délai temporel (Δt) imposé au signal provenant de la seconde cellule et la différence spatiale existant entre les champs décepteurs créent la sélectivité à la direction du mouvement des détecteurs Reichardt. Si on présente du mouvement vers la droite à un détecteur Reichardt ayant des propriétés similaires à celui illustré à la Figure 2, le signal provenant du champ récepteur gauche arrivera simultanément avec le signal provenant du champ récepteur droit au site de multiplication. Ceci produit une multiplication positive, signalant du mouvement vers la droite.

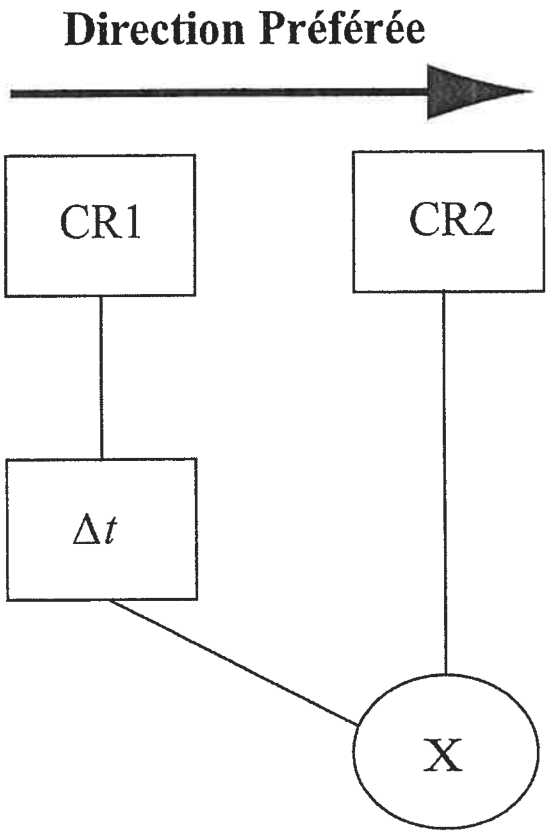

Figure 2. Représentation schématique d’un détecteur de mouvement de Reichardt (1961) élémentaire. Deux champs récepteurs (CR1 et CR2) convergent vers un site de comparaison. Un délai temporel *Δt* est imposé à l’intrant du CR1.

D’autres types de détecteurs de mouvement, tel le détecteur Reichardt élaborés (van Santen & Sperling, 1984) et les détecteurs d’énergie de mouvement (Adelson & Bergen, 1985) furent élaborés afin de modéliser l’extraction initiale de l’information de mouvement. Puisque ces mécanismes d’extraction ont pour but explicite de modéliser l’extraction initiale de l’information de mouvement, ces modèles doivent également être biologiquement plausibles. Dans cette optique les détecteurs d’énergie de mouvement constituent un bon modèle, puisqu’il a été démontré que ce modèle pouvait bien prédire les réponses de cellules complexes (Emerson, Bergen, & Adelson, 1992). Une caractéristique commune de ces modèles est que des stimuli statiques ne produisent pas d’activation chez ces détecteurs de mouvements. En effet, le test du piédestal profite de cette caractéristique afin d'étudier les mécanismes sous-jacents à la perception de différents types de mouvement (Lu & Sperling, 1995; Lu, Lesmes, & Sperling, 1999a).

Suite à l'extraction initiale de l'information de mouvement, ces modèles supposent une étape hypothétique subséquente d'intégration spatiale et temporelle (Barlow & Levick, 1965) présumément dans les aires corticales MT et MST (Nakayama, 1985). La suggestion que ces aires sont impliquées dans le traitement du mouvement est supportée par le fait que 90% des cellules dans l'aire MT sont sélectives à la direction du mouvement (Felleman & Van Essen, 1987; Merigan & Maunsell, 1993). Des enregistrements électrophysiologiques dans l'aire corticale MT ont également démontré l'existence de cellules accordées à la vitesse du mouvement, suggérant que cette aire corticale est impliquée dans le calcul de la vitesse (Maunsell & Van Essen, 1983; Lagae, Raiguel, & Orban, 1993; Perrone & Thiele, 2001). Cependant, de telles cellules sont incapables à elles seules de signaler la vitesse d'un stimulus de façon non-ambiguë puisqu'elles répondent à toute une gamme de vitesses et sont sensibles au contraste du stimulus.

Il est donc proposé que le système visuel détermine la vitesse d'un stimulus en mouvement à partir du patron d'activité d'une population de neurones sensibles à la vitesse (Priebe & Lisberger, 2004). Selon cette proposition, la présentation d'un stimulus en mouvement produit différents niveaux d'activation auprès des cellules sensibles à la vélocité du mouvement, produisant le plus haut niveau d'activation auprès des cellules dont la vélocité préférée correspond à la vélocité du stimulus de mouvement. Le système visuel calcule ensuite la vitesse du stimulus en mouvement à partir de ce patron d'activité. Le traitement des réponses de la population neuronale peut prendre la forme d'une approche « *winner-take-all* » (i.e., la vélocité perçue correspond à la vélocité préférée des cellules les plus actives), d'une somme vectorielle (i.e., la vitesse perçue correspond à la somme pondérée des vélocités préférées) ou d'une moyenne vectorielle (i.e., la vitesse perçue correspond à la moyenne pondérée des vélocités préférées).

Dans ces modèles, la vitesse d'un stimulus en mouvement est déterminée directement à partir du patron de réponse d'une population de cellules sélectives à la vitesse sans qu'il y ait contribution des connaissances *a priori* du système visuel sur les propriétés du mouvement. L'approche ascendante attribue généralement les illusions dans la perception du mouvement à des erreurs de la part du système visuel dans le traitement de l'information visuelle. Par exemple, il a été proposé par Stone et Thompson (1992) que les effets du contraste d'un stimulus en mouvement sur la vitesse perçue pouvaient être attribués à une erreur lors de la normalisation du signal d'énergie du mouvement. Cette hypothèse propose que, puisque le niveau de réponse des détecteurs d'énergie de mouvement (Adelson & Bergen, 1985) dépend à la fois de la vélocité et du contraste du stimulus en mouvement, ces unités ne peuvent pas signaler la vitesse du stimulus sans ambiguïté. Afin de signaler la vélocité d'un stimulus de mouvement de façon non ambiguë, il est donc nécessaire de normaliser (diviser) l'énergie de mouvement par un second signal d'énergie. Stone et Thompson (1992) proposent que le signal d'énergie de mouvement est normalisé par un signal de « contraste moyen » obtenu en intégrant l'extrant de cellules complexes sur une large aire du champ visuel (Heeger, 1992).

Il est proposé par Stone et Thompson (1992) que lorsqu'on présente simultanément un réseau test et un réseau standard, l'aire du champ visuel utilisée afin de normaliser le signal d'énergie de mouvement du réseau standard inclut les deux réseaux. Conséquemment, si le contraste du réseau standard est plus faible que le contraste du réseau test, le signal d'énergie de mouvement du réseau standard sera normalisé par un contraste moyen trop élevé, produisant une sous-estimation de sa vitesse. Inversement, si le contraste du réseau standard est plus élevé que celui du réseau test, le signal d'énergie de mouvement du réseau standard sera normalisé par un contraste moyen trop faible, produisant une surestimation de la vitesse de celui-ci. Lorsqu'on présente simultanément deux stimuli de mouvement de contraste différent, ce défaut dans la normalisation du signal d'énergie de mouvement produit ainsi une surestimation de la vitesse du réseau de haut contraste et une sous-estimation de la vitesse du réseau de bas contraste.

Similairement à la dépendance de la vitesse perçue sur le contraste du stimulus en mouvement, il a été suggéré que les effets consécutifs de mouvement (ECMs) étaient attribuables à un défaut du système visuel. En effet, il a été proposé que les effets consécutifs de mouvement soient attribuables à une fatigue sélective des neurones activés par le stimulus de mouvement présenté au cours de la période d'adaptation (Sutherland, 1961; Barlow & Hill, 1963). Tel que présenté dans la Figure 3, la présentation d'un stimulus en mouvement élicite une activité chez les neurones sensibles au mouvement durant la période d'adaptation, excitant davantage les cellules dont la direction préférée correspond à la direction du stimulus d'adaptation. Il est proposé que cette excitation fatigue les neurones activés par le stimulus d'adaptation, fatiguant davantage les cellules dont la direction préférée correspond à la direction du stimulus d'adaptation. Cette fatigue neuronale sélective des unités dont la direction préférée correspond à la direction du stimulus d'adaptation produit une diminution de leur activité spontanée lors de la présentation subséquente du stimulus test statique. Il est proposé que cette diminution dans l'activité spontanée de ces neurones produit un débalancement dans l'activité de la population neuronale. C'est à dire que, suite à la période d'adaptation, les neurones sélectifs au mouvement dans la direction opposée au stimulus d'adaptation auront un taux d'activité spontanée plus élevé que les neurones activés par le stimulus d'adaptation. Ce débalancement créée un percept de mouvement illusoire qui disparaît graduellement au fur et à la mesure que les neurones fatigués par la période d'adaptation récupèrent.

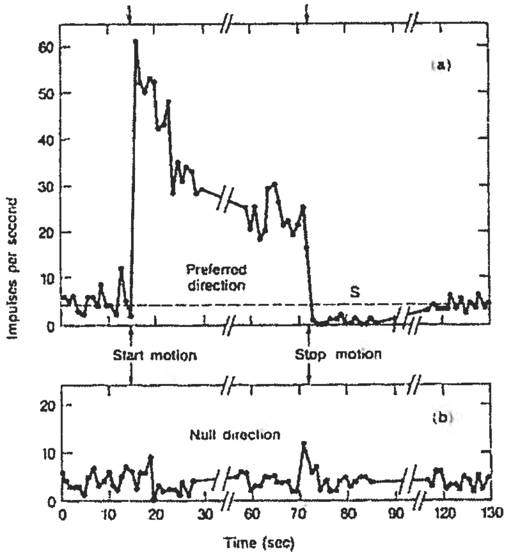

Figure 3. Taux de décharge d'une cellule ganglionnaire de la rétine d'un lapin avant, pendant et après le mouvement d'un disque de points aléatoire se déplaçant dans la direction préférée de la cellule (a) et dans la direction opposée à sa direction préférée (b). Figure empruntée de Barlow & Hill (1963).

Comme nous pouvons le constater, les propositions avancées afin d'expliquer les effets du mouvement d'une texture de luminance périphérique sur la vitesse perçue d'un stimulus central (Nakayama & Loomis, 1974; Norman et al., 1996) s'inscrivent à l'intérieur du cadre ascendant. C'est à dire que ce modèles imputent ces effets strictement à une modification du signal de mouvement. Dans la première partie de cette thèse, nous nous intéresserons aux effets de la texture de luminance sur la perception du mouvement. Plus spécifiquement, nous nous intéresserons aux effets de la superposition de texture de luminance statique sur la vitesse perçue du mouvement. Ces phénomènes sont difficilement explicables par les propriétés des extracteurs de bas niveau de l'information de mouvement puisque ces détecteurs de mouvement sont insensibles à la texture de luminance statique. Il est plus probable que le modèle proposé par Nakayama et Loomis (1974) pour les effets du mouvement relatif sur la vitesse perçue de deux points cibles (Loomis & Nakayama, 1973) reflète les propriétés de cellules de l'aire MT (Lagae et al., 1989). Le mécanisme proposé a une organisation antagoniste centre-pourtour, produisant une réponse maximale lorsque le mouvement dans le centre est dans la direction opposée du mouvement dans le pourtour du champ récepteur. La réponse d'un tel mécanisme est minimisée lorsque le mouvement dans le centre et le pourtour du champ récepteur est uniforme. Ceci soulève donc des questions à la fois sur la vitesse perçue du mouvement et la réponse d'un tel mécanisme lorsque le stimulus de mouvement et la texture statique sont superposés l'un sur l'autre.

Traitement descendant

Une alternative au traitement ascendant de l'information visuelle est le traitement descendant. Cette approche met plutôt l'emphase sur l'influence exercée par l'information de haut niveau, tel les connaissances *a priori* d'un observateur, sur la perception. Cette approche est en accord avec la proposition que la perception visuelle implique un processus d'inférence inconsciente (Helmholtz, 1867). Cette suggestion provient de l'ambiguïté inhérente des images rétiniennes auxquelles le cortex visuel a accès afin d'évaluer son environnement : différents stimuli peuvent projeter une image identique sur la rétine (pour un exemple, voir Figure 4) et un même stimulus peut produire des images rétiniennes différentes (e.g., un objet tridimensionnel observé de différents points de vue). Afin de pouvoir résoudre les ambiguïtés de l'intrant sensoriel et d'être ainsi capable de faire des inférences sur notre environnement, Helmholtz (1867) propose que notre système visuel doive posséder des connaissances implicites sur le monde physique. Selon lui, le percept final est déterminé par le principe de vraisemblance : le percept final correspondra au stimulus pouvant le plus vraisemblablement être la cause de la stimulation sensorielle. Un descendant de cette approche est que la perception est gouvernée par un mécanisme de test d'hypothèse (Gregory, 1973). Cette approche suggère que l'intrant visuel fournit des données permettant de tester nos hypothèses sur l'état de notre environnement.

La psychologie de Gestalt a énoncé de façon informelle dans ses lois guidant la perception visuelle certaines des connaissances *a priori* du système visuel. L'exemple fourni à la Figure 4 illustre la loi perceptuelle de la simplicité. Cette loi dicte que si plusieurs interprétations sont possibles pour une image, le percept correspondant à l'interprétation la plus simple prévaudra. Bien que ces différentes loi perceptuelles soient bien démontrées par les divers exemples donnés afin d'illustrer ces lois, la psychologie de Gestalt est toutefois critiquée pour diverses raisons. Tout d'abord, certaines lois perceptuelles sont mal définies : par exemple, la loi de simplicité ne fournit pas de règles formelles permettant de déterminer laquelle parmi les diverses interprétations possibles constitue le percept plus simple. Une critique supplémentaire de l'approche Gestalt est que ses lois sont principalement descriptives : elles décrivent un phénomène perceptuel, mais font peu de prédictions pour des phénomènes visuels autres que celui qu'elles devaient expliquer à l'origine. En raison de l'absence d'un cadre formel, l'approche Gestalt a déjà été décrite comme la méthode « *look-and-see-for-yourself* » (regardez et voyez par vous même) (Pomerantz, 1981). Une approche davantage quantitative, permettant d'exprimer rigoureusement les principes guidant la perception visuelle, est donc nécessaire afin de décrire l'influence que les connaissances d'un observateur exercent sur la perception.

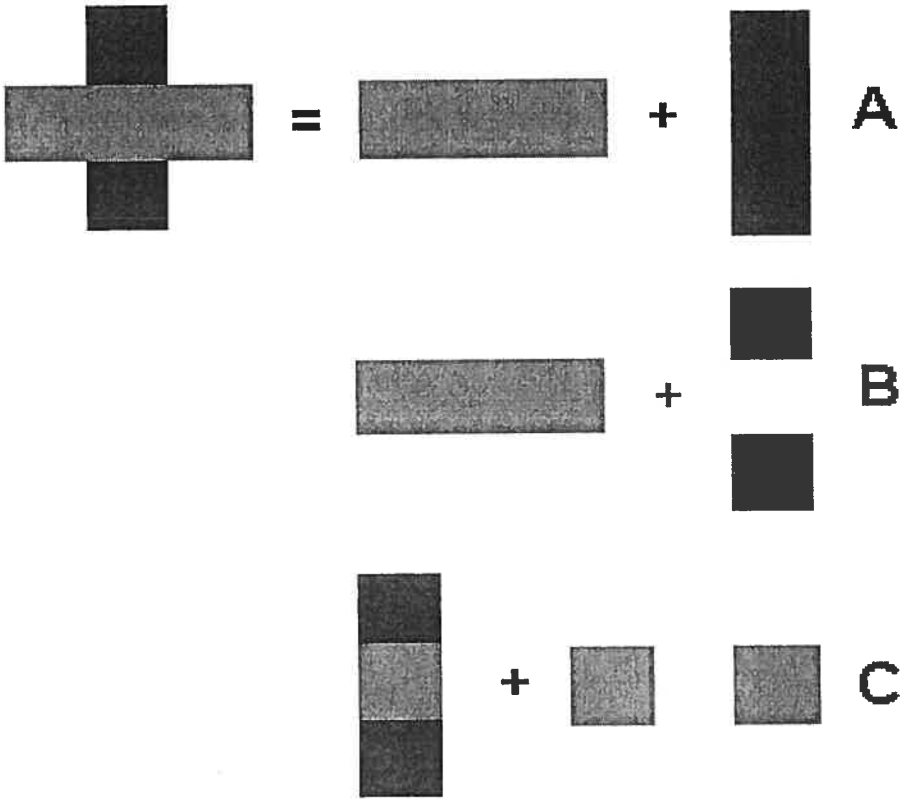

Figure 4. Illustration de la loi perceptuelle de simplicité. Nous percevons l'image présentée à gauche comme étant une barre horizontale grise superposée sur une barre verticale noire (A). Cependant, différentes configurations pourraient créer la même image sur la rétine (B et C).

Modèles Bayésiens

L'absence d'un cadre formel permettant d'exprimer les lois perceptuelles de la psychologie de Gestalt explique pourquoi le traitement descendant a généré moins d'intérêt de recherche que le traitement descendant. Cependant, il a récemment été proposé que la théorie de décision Bayésienne fournit un cadre théorique permettant d'exprimer de façon formelle les connaissances *a priori* qu'un observateur utilise afin d'interpréter l'intrant sensoriel. Dans le cadre Bayésien, le système visuel est construit afin d'exploiter les régularités présentes dans notre environnement (Geisler & Diehl, 2002). À l'intérieur de ce cadre formel, les lois perceptuelles énoncées par la psychologie de Gestalt existent car le système visuel exploite ses connaissances des propriétés statistiques des scènes naturelles afin de pouvoir interpréter l'intrant visuel. Par exemple, les lois perceptuelles de proximité et de bonne continuité existent car le système visuel « sait » que, dans les scènes naturelles, les éléments de bordure co-circulaires et situés à proximité l'un de l'autre ont tendance à appartenir au même contour physique (Geisler, Perry, Super, & Gallogly, 2001). Cette proposition est en accord avec les principes de la psychologie environnementale (Brunswik, 1956; Gibson, 1966; Gibson, 1979), qui mettait l'emphase sur le lien existant entre les régularités présentes dans l'environnement et notre perception.

Le modèle décrit dans la section précédente pour la dépendance de la vitesse perçue sur le contraste du stimulus de mouvement impute ce phénomène à une erreur computationelle dans la normalisation du signal d'énergie de mouvement. Cette suggestion diffère fondamentalement d'un modèle Bayésien de la vélocité perçue proposé récemment (Weiss, Simoncelli, & Adelson, 2002). Contrairement aux modèles attribuant les illusions dans la perception du mouvement à des erreurs computationelles, le modèle Bayésien suggère que ces illusions constituent plutôt des solutions optimales (i.e., un « *best guess* ») pour un système visuel conçu afin d'opérer en présence d'incertitude.

Similairement à la notion d'inférence inconsciente, dans les modèles Bayésiens, notre système visuel parvient à interpréter l'information fournie par l'intrant visuel afin de faire des inférences sur notre environnement parce qu'il possède des connaissances *a priori* des propriétés statistiques du monde extérieur. Par exemple, notre système visuel favorise l'interprétation A de l'image présentée à la Figure 4 parce qu'il « sait » qu'il est plus probable que l'image produite sur la rétine corresponde à un objet faisant occlusion sur un autre objet (interprétation A) qu'aux interprétations B et C. Dans le cadre Bayésien, les connaissances du système visuel sur les propriétés statistiques du monde extérieur sont exprimées dans la distribution de probabilité *a priori*. La première assomption du modèle Bayésien de la vélocité perçue est que les vélocités lentes sont plus communes que les vélocités rapides. La connaissance du système visuel de cette propriété statistique du mouvement résulte en un biais favorisant les vélocités lentes. La connaissance du système visuel de cette propriété statistique du mouvement dans le monde physique peut être exprimée de façon simplifiée sur un seul axe par une distribution de probabilité *a priori* (« *prior* ») Gaussienne dans laquelle la probabilité la plus élevée correspond à une vélocité de zéro. Bien qu'il n'existe présentement aucune preuve empirique que les vélocités physiques suivent une distribution Gaussienne, cette distribution permet d'exprimer formellement la suggestion que le système visuel ait un biais favorisant les vélocités lentes (Wallach, 1959; Ullman, 1979). Cette distribution peut être représenté par :

$$a\,priori = \text{Gaussienne}(0, \sigma_P), \tag{1}$$

dans laquelle σ_P correspond à l'écart-type de la distribution *a priori* et 0, à la vélocité moyenne de cette distribution.

L'information fournie par l'intrant sensoriel est représentée dans le cadre Bayésien par la fonction de vraisemblance (*likelihood function*). Cette fonction représente la probabilité d'une gamme de stimuli physiques, étant donné l'intrant sensoriel, sans qu'on tienne compte les connaissances *a priori* de l'observateur sur les propriétés du monde externe. Dans le contexte d'estimation de la vélocité, la fonction de vraisemblance représente la distribution de probabilité de la mesure initiale de vélocité (i.e., la probabilité qu'une vélocité physique corresponde à la mesure initiale de vélocité) sans que les propriétés statistiques du mouvement dans le monde physique aient été prises en considération. La seconde assomption du modèle Bayésien de la vélocité est que la mesure initiale de vélocité est bruitée. Il y a donc un certain niveau d'incertitude quant à l'exactitude de cette mesure : une mesure initiale de vélocité d'une certaine valeur peut en fait correspondre à toute une gamme de vélocités physiques. Conséquemment, il n'existe aucune règle déterministe permettant de déduire la vélocité physique d'un stimulus à partir de la mesure initiale de sa vélocité. Le système visuel doit donc utiliser une approche probabiliste, dans laquelle l'estimé final de vélocité constitue une solution optimale (un « *best guess* ») étant donné un intrant sensoriel bruité et les connaissances du système visuel sur les propriétés du mouvement dans le monde physique. Dans le modèle proposé par Weiss et al (2002), ce bruit dans la mesure initiale de vélocité prend la forme d'un bruit Gaussien dont l'écart type est connu. La fonction de vraisemblance peut être représentée par (Hurlimann, Kiper, & Carandini, 2002) :

$$\text{Vraisemblance} = \text{Gaussienne}(v_i, \sigma_L / c_m), \tag{2}$$

où v_i représente la valeur de la mesure initiale de vélocité, σ_L, l'écart type du bruit Gaussien et c_m, le contraste du stimulus en mouvement. Le type de bruit utilisé résulte en une fonction de vraisemblance dépendant du contraste : pour une valeur constante de σ_L, la fonction de vraisemblance sera plus étroite à des contrastes plus élevés du stimulus en mouvement qu'à des niveaux de contraste plus bas.

L'estimation finale d'un observateur idéal est basée sur la distribution *a posteriori*. Cette distribution est calculée en combinant la distribution *a priori* et la fonction de vraisemblance selon les règles de Bayes. La distribution de probabilité *a posteriori* représente l'estimation de la distribution de probabilité une fois qu'on ait pris compte de l'intrant visuel ainsi que des connaissances du système visuel sur les propriétés du monde extérieur. Cette distribution est obtenue par :

$$\text{a posteriori} \propto \text{a priori} \times \text{vraisemblance} \tag{3}$$

La dernière composante d'un modèle Bayésien est la règle de décision. Dans le modèle Bayésien de vélocité perçue, la règle de décision est une règle *maximum a posteriori* (MAP) où l'estimé final de vélocité de l'observateur idéal correspond à la vélocité ayant la plus haute probabilité dans la distribution *a posteriori*. Les différentes composantes du modèle Bayésien de la vélocité perçue sont illustrées à la Figure 5.

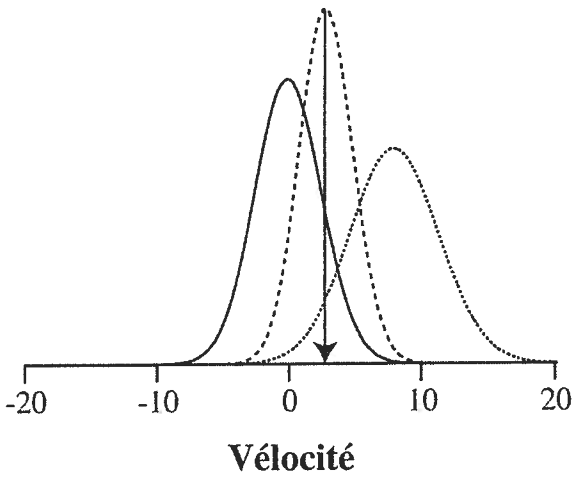

Figure 5. Modèle Bayésien de la vélocité perçue. La connaissance du système visuel que les vélocités lentes sont plus communes que les vélocités rapides est représentée par une distribution de probabilité *a priori* (courbe continue) où la probabilité la plus élevée correspond à une vélocité de zéro. La mesure initiale de vitesse est bruitée, produisant un « likelihood » (courbe pointillée) où la probabilité la plus élevée correspond à la mesure initiale de vélocité. On obtient la distribution *a posteriori* (courbe tiretée) en combinant la distribution *a priori* et le likelihood selon les règles de Bayes. L'estimé final de vélocité est obtenu en utilisant une règle de décision MAP, où l'estimé final correspond à la vélocité ayant la probabilité la plus élevée dans la distribution *a posteriori* (flèche pointant vers le bas).

La dépendance du bruit de la mesure initiale de vélocité sur le contraste du stimulus de mouvement permet de prédire l'augmentation de vitesse perçue se produisant lorsqu'on augmente le contraste de celui-ci (Weiss et al., 2002). Tel qu'illustré à la Figure 6, une fonction de vraisemblance largement distribuée produit une distribution *a posteriori* centrée plus près d'une vélocité de zéro qu'une fonction de vraisemblance étroitement distribuée.

Un observateur Bayésien idéal utilisant une règle de décision MAP rapportera donc un estimé final de vitesse plus rapide pour un réseau de haut contraste que pour un réseau de bas contraste. Le percept final de vélocité constitue un compromis entre le niveau d'incertitude de la mesure initiale de vélocité et les connaissances du système visuel sur les propriétés statistiques du mouvement dans le monde physique. En effet, le type de bruit utilisé produit une fonction de vraisemblance dépendant du niveau de contraste du stimulus en mouvement. Le percept final de vélocité peut donc être considéré comme un compromis entre le niveau d'incertitude de notre mesure initiale de vélocité et un biais favorisant les vélocités lentes.

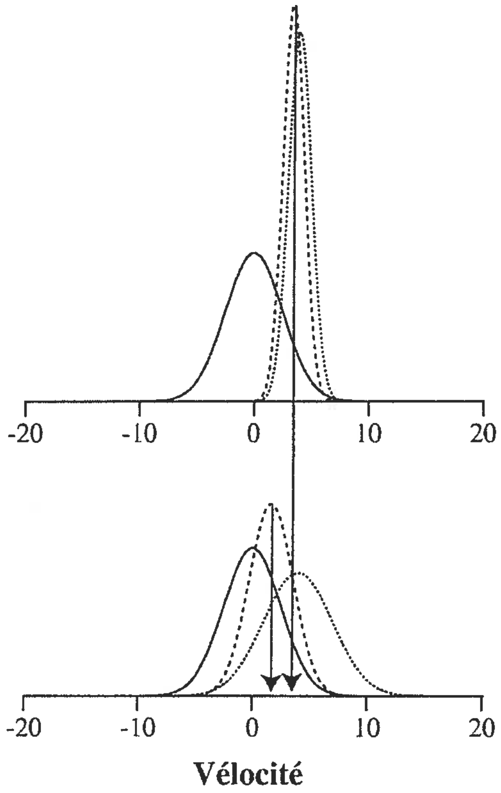

Figure 6. Distribution *a priori* (lignes pleines), fonction de vraisemblance (lignes pointillées), et distribution *a posteriori* (lignes hachurées) et estimation finale de vélocité d'un observateur Bayésien (flèches) lors de la présentation de stimuli de haut contraste (haut) et de stimuli de bas contraste (bas).

Dans la première partie de cette thèse, nous discuterons des effets de la texture de luminance statique sur la vitesse perçue du mouvement dans le cadre du modèle Bayésien de la vélocité perçue. Ce modèle sera davantage développé dans la seconde partie de cette thèse. Les modèles de bas niveau d'extraction de mouvement doivent tenir compte de la physiologie connue du système visuel. Bien que le modèle proposé initialement par Weiss et al. (2002) tienne peu compte de la physiologie du système visuel, des efforts ont été faits afin de tenir compte des propriété physiologiques du système visuel dans l'implémentation du modèle Bayésien (Ascher & Grzywacz, 2000; Hurlimann et al., 2002; Stocker &

Simoncelli, 2005). Nous discuterons de l'implémentation du modèle Bayésien de la vélocité perçue à l'intérieur d'un cadre tenant compte de la physiologie du système visuel. Dans cette section, nous discuterons également d'autres phénomènes dans la perception du mouvement, tel la lenteur perçue du mouvement chromatique et les ECMs à l'intérieur du contexte Bayésien. Nous nous pencherons également sur l'implémentation des hypothèses proposées pour divers phénomènes à l'intérieur du cadre Bayésien.

Les effets de la texture de luminance statique sur la vitesse perçue du mouvement

Ce chapitre est une reproduction exacte de l'article :

Nguyen-Tri, D. & Faubert, J. (soumis en 2004)

« Luminance texture increases perceived speed »

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Résumé

Dans la première expérience, nous démontrons que la superposition d'une texture de luminance statique sur un réseau en mouvement peut produire une augmentation dans la vitesse perçue du stimulus en mouvement. Ceci est en accord avec la suggestion que le système visuel puisse utiliser la texture de luminance statique comme point de référence spatiale afin d'évaluer la vélocité du réseau en mouvement. Nous discutons d'une implémentation possible de cette proposition à l'intérieur d'un cadre Bayésien. Les résultats de la seconde expérience démontrent que la vitesse perçue d'un réseau en mouvement dépend de l'aire couverte par la texture. Ceci suggère que l'interaction entre la texture de luminance et le stimulus de mouvement se produisait sur une échelle spatiale limitée afin d'obtenir des estimés de vélocité locaux et que ces estimé sont ensuite regroupés afin de déterminer la vitesse globale du stimulus. Dans la troisième expérience, nous démontrons que contrairement à la texture de luminance statique, la texture de luminance dynamique ne produisait pas d'effet sur la vitesse perçue d'un réseau en mouvement. Ces résultats démontrent une différence fondamentale entre la texture de luminance dynamique et statique.

Luminance texture increases perceived speed

Abstract

Previous research has demonstrated that factors other than velocity itself can exert a considerable influence on the perceived velocity of visual stimuli. In Experiment 1, we demonstrated that superimposing static luminance texture on a drifting luminance modulated grating can produce an increase in perceived speed. This suggests that the visual system could use static luminance texture as a landmark to assess the speed of a drifting grating. This explanation can be expressed formally within a Bayesian model of velocity perception. The results of Experiment 2 demonstrated that perceived speed depends on the size of the area covered by texture. This suggests that luminance texture and the motion stimulus only interacted with each other over a small spatial scale to obtain local speed estimates. These local speed estimates are then pooled to determine the speed of the motion stimulus. In Experiment 3, we showed that contrary to static luminance texture, dynamic luminance texture did not alter perceived speed. These results demonstrate a fundamental difference between static and dynamic luminance texture: the former can be used as a landmark to aid the initial assessment of speed whereas the latter cannot.

Keywords: Motion, perceived speed, position tracking, spatial uncertainty

Introduction

Our interactions with the external world require a visual system that is capable of accurately assessing of the velocity of the motion present in our environment. For instance, catching a ball thrown in our direction requires a reasonably precise estimate of the ball's velocity. Motion velocity can also serve as a cue to determine other visual attributes such as depth (motion parallax). Given our dependency on a precise estimation of velocity, it is surprising that a number of factors other than speed itself can exert a significant influence on our perception of a visual stimulus' speed. For example, psychophysical experiments have demonstrated that the absence of luminance modulation in drifting chromatic gratings (Cavanagh et al., 1984), a luminance-modulated grating's spatial frequency (Campbell & Maffei, 1981; Smith & Edgar, 1990; Priebe & Lisberger, 2004), and luminance contrast (Campbell & Maffei, 1981; Thompson, 1982; Stone & Thompson, 1992; Blakemore & Snowden, 1999) all alter perceived speed. These factors affecting perceived velocity can even have consequences on behaviour, such as a tendency to drive faster in foggy conditions (Snowden, Stimpson, & Ruddle, 1998).

The presence of luminance texture is also found among the stimulus parameters known to influence the perceived speed of motion. Previous research has reported increases in perceived speed in the presence of static luminance texture relative to when there is no luminance texture (Brown, 1931; Norman et al., 1996; Blakemore & Snowden, 2000).Additionally, the perceived speed of a center region populated by random dots is contingent upon the speed, but not the direction, of the dots in a surrounding annulus: the perceived speed of motion in the central region is greatest when the surrounding annulus is static (Norman et al., 1996). Motion in the surrounding annulus decreased the perceived speed of motion in the central region. Moreover, it has been found that the perceived speed of a uniform moving disk increases with increasing levels of background texture contrast (Blakemore & Snowden, 2000).These authors also report that textured backgrounds can even eliminate the contrast-dependency of perceived speed. Finally, static luminance texture facilitates other aspects of motion perception, such as motion detection (Bonnet, 1984) and motion integration (Lorenceau & Boucart, 1995).

In order to account for the increase in perceived speed that occurs when texture is added in the background, it has been suggested that the landmarks provided by static luminance increase the relative motion cues. This increase in relative motion cues in turn, alters perceived speed (Gogel & McNulty, 1983). It has also been suggested that second-order processes could account for the decrease in contrast dependency of perceived speed that occurs with increasing levels of texture contrast (Blakemore & Snowden, 2000). Simply put, a uniform moving disk that has a luminance close to the mean luminance of the background on which it is presented appears more visible when the background is textured than when the background also has a uniform luminance.

One way to determine if textured backgrounds increase perceived speed by providing a spatial referent or solely by increasing the visibility of the motion stimulus is by superimposing static texture with the motion stimulus. This is the case because in these conditions, increasing texture contrast decreases the visibility of the motion stimulus. If the decrease in the contrast dependency of perceived speed in the presence of texture is solely attributable to an increase in the visibility of the motion stimulus, then perceived speed should decrease with increasing levels of texture contrast. On the other hand, if the effects of texture on perceived speed occur because the visual system uses static luminance texture as a landmark in the assessment of perceived speed, then perceived speed should increase when the contrast of the static luminance texture increases. The purpose of Experiment 1 was therefore to investigate the effects of a superimposed static luminance texture's contrast on the perceived speed of a drifting grating.

Experiment 1

Methods

Observers

Three experienced psychophysical observers participated in the study. All observers had normal visual acuity. Two of the observers (JF and DN) were authors on this paper and the third observer was naive to the hypotheses of the experiments.

Apparatus and stimuli

An Apple PowerMac G3 computer was used in order to generate stimuli and collect the data. Stimuli were presented on an Apple studio display monitor with a mean luminance of 38 cd/m^2 and a 120 Hz frame rate. Lookup tables were used to gamma-correct gun outputs. Stimuli were generated and the data were collected using MATLAB and the extensions provided in the Psychophysics Toolbox (Brainard, 1997) and low-level Videotoolbox (Pelli, 1997).

A representation of the stimulus is presented in Figure 7. A central fixation point was present at all times during testing. On each trial, two vertical sinewave luminance-modulated gratings (the standard grating and the test grating) were simultaneously presented directly below and above fixation. Each grating had a spatial frequency of 0.5 cycles/degree and was centred at 2.5 degrees of eccentricity through square apertures subtending 4 degrees of visual angle in width and height. The standard grating drifted at a speed of 8 degrees/sec (4 Hz temporal frequency), either leftward or rightward, and the test grating drifted in the opposite direction. Both the test and the standard gratings were modulated at 10% Michelson contrast. A stationary plaid pattern, composed of two luminance-modulated sinewave gratings was added to the standard grating. One plaid component was vertically oriented and the other was horizontally oriented. Perceived speed was measured at component spatial frequencies of 0.5, 1, 2, and 4 cycles/degree. The contrast of the individual plaid components was 0, 5, 10, or 15% Michelson contrast.

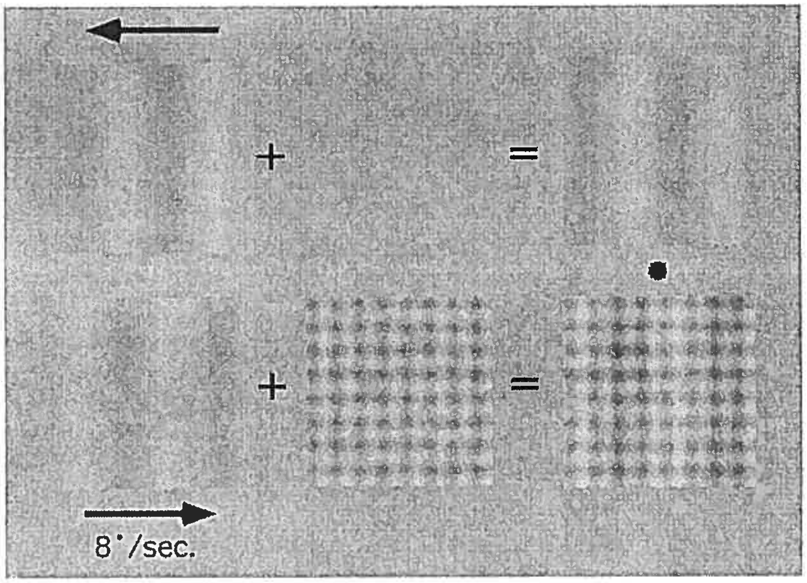

Figure 7. Schematic illustration of the speed matching stimulus. (Top) A 10% Michelson contrast 0.5 cycles/degree sinusoidal test grating. (Bottom) A standard grating of identical spatial frequency and contrast was also presented. The standard grating drifted at 8°/sec. in a direction opposite to that of the test grating. A static luminance plaid was added onto the standard grating.

Procedure

A chin rest and forehead bar were used in order to ensure a 57 cm viewing distance. Observers were instructed to keep their gaze centered on the fixation point. A speed-matching task (Thompson, 1982; Cavanagh et al., 1984; Nguyen-Tri & Faubert, 2002) was used in order to determine the effects of luminance texture on the perceived speed of the standard grating. In order to complete the task, observers were instructed to use the mouse to adjust the speed of the test grating until both the test and the standard grating appeared to drift at a similar speed. Observers indicated a match by clicking the left mouse button. No time limit was given for responding. At the end of each trial, the relative speed of the test grating ($speed_{test}/speed_{standard}$) which perceptually matched the speed of the standard grating was recorded. Observers completed a total of 128 trials, eight measurements for each combination of plaid spatial frequency and contrast.

Results

The results of the speed matching task used in Experiment 1 are shown in Figure 8 for each observer. At plaid spatial frequencies of 1, 2 and 4 cycles/degree, increasing the contrast of the static plaid produced an increase in the relative speed match results, indicating that adding a static plaid to a drifting grating increased the perceived speed of the standard grating. This increase in perceived speed is present for every observer: at the highest tested contrast, the physical speed of the test grating was always faster than the physical speed of the standard grating which it perceptually matched. At plaid spatial frequencies of 1 and 2 cycles/degree, the speed match was approximately 30% faster at the maximum tested texture contrast than when no texture was added to the standard grating.

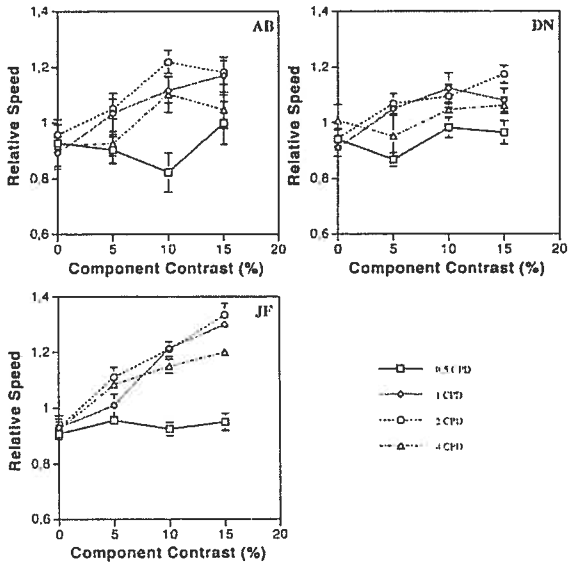

Figure 8. Relative speed of matches for individual observers. Relative speeds are shown as a function of the contrast and spatial frequency of the components of a static plaid. Results are shown for plaid spatial frequencies of 0.5 (full line with squares), 1 (dotted line with diamonds), 2 (dashed line with circles), and 4 (dash-dotted line with triangles) cycles/degree. Error bars represent ± 1 SEM.

The increase in the perceived speed of the standard grating that occurred at the higher plaid spatial frequencies was not found at texture spatial frequencies of 0.5 cycles/degree. At this plaid spatial frequency, increasing texture contrast did not reliably produce either a significant increase or decrease in the perceived speed of the standard grating.

Discussion

Because computational models emphasizing bottom-up processing of motion represent the prevailing approach to modelling motion perception, motion illusions have also tended to be explained using a similar approach. The bottom-up approach generally attributes motion illusions to flaws by the visual system in the computation of motion. For instance, it is pointed out that because energy-based motion detectors are sensitive to both the contrast and the velocity of a motion stimulus (Adelson & Bergen, 1985), their responses cannot unambiguously encode stimulus speed. It is therefore necessary to normalize (i.e., divide) the motion energy signal by an average contrast signal in order to obtain an unambiguous estimate of a moving stimulus' speed. It has been suggested that a flaw in the normalization process can account for the contrast dependency of perceived speed (Stone & Thompson, 1992). These authors suggest that the average contrast signal is obtained by pooling the responses of complex cells over a wide spatial area. If a test and a standard grating of different contrasts are presented simultaneously, this will produce errors in the estimation of the two gratings' velocity because the area from which the average contrast signal is obtained encompasses both gratings. In these conditions, the motion energy signal of the low contrast grating will be normalized by an inappropriately high average contrast signal, and the motion energy signal of the high contrast grating will be normalized by an inappropriately low average contrast signal. This normalization error will ultimately produce an overestimation of the high contrast grating's speed and an underestimation of the low contrast gratings' speed.

The proposed flaw in the normalization of the motion energy signal fails to account for results of previous research on the effects of static luminance texture on the perceived speed of a moving stimulus (Norman et al., 1996). That is, it has been proposed that the motion energy signal is normalized by an average contrast signal obtained over a wide area of the visual field (Stone & Thompson, 1992). If this is indeed the case, the motion energy signal would presumably be normalized by a greater average contrast signal when there is texture present in the area surrounding the motion stimulus than when the background is uniform. This would predict a slower perceived speed in the presence of texture than when the background is uniform. Furthermore, the lower perceived contrast of a central region in the presence of texture in the surrounding region (Chubb, Sperling, & Solomon, 1989; Cannon & Fullenkamp, 1991; Snowden & Hammett, 1998) would also predict a slower perceived velocity, given that at low luminance contrasts, motion stimuli tend to yield a slower percept of motion (Stone & Thompson, 1992). It has been proposed that the average contrast signal is obtained by pooling the outputs of all complex cells over a wide area (Stone & Thompson, 1992). If, as suggested, these cells are unresponsive to static stimuli, then static luminance texture should not influence the perceived speed of a drifting stimulus. In either case, the proposed flaws in the normalization of the motion energy signal fail to account for the increase in perceived speed that occurs in the presence of static luminance texture.

Previous research has found that a uniform moving disk with a luminance close to the mean luminance of a textured background seems to move faster at higher levels of background contrast (Blakemore & Snowden, 2000). The authors have proposed that this increase in perceived speed is due to an improvement in the visibility of the moving disk through second-order processes. In Experiment 1, the visibility of the standard grating diminished when the contrast of the superimposed static luminance texture increased. Therefore, the concomitant increase in perceived speed cannot be attributed to an improvement in the visibility of the standard grating with increasing levels of texture contrast. It appears more likely that static luminance texture increased the perceived speed of the standard grating by providing a spatial reference to assist the assessment of position changes.

Within the spatial frequencies tested in Experiment 1, the increase in perceived speed observed with increasing texture contrast depended on the spatial frequency of the texture. This suggests that previous reports of texture effects on perceived speed (Brown, 1931; Gogel & McNulty, 1983; Norman et al., 1996; Blakemore & Snowden, 2000) may also be dependent on the spatial frequency of the luminance texture. This selectivity of the increase in perceived speed on the spatial frequency of texture also suggests that the mechanism underlying the speed increase does not utilise all spatial frequencies equally. If it did, because there is more spatial information at higher spatial frequencies, perceived speed should increase as the spatial frequency of the static texture increases, provided that sensitivity to the texture spatial frequency remains high. Given that the sensitivity to luminance-modulated stimuli is high at 4 cycles/ degree (Mullen, 1985), it is unlikely that the smaller increase in perceived speed at this texture spatial frequency is attributable to a diminished contrast sensitivity of the visual system at this spatial frequency per se. Rather, it appears more likely that the smaller increase in perceived speed at this spatial frequency is the result of spatial or temporal resolution limits specific to the system underlying the increase in perceived speed, which, of course, may depend on the speed parameter.

The Bayesian model of velocity perception (Weiss et al., 2002) differs fundamentally from approaches which suggest that motion illusions are the result of flaws in the computation of motion. According to this model, perceived velocity represents an optimal solution (i.e., a best guess) for a visual system designed to function in the presence of uncertainty, given its prior knowledge about the external world. Motion "illusions" thus occur because these percepts represent optimal solutions. The use of the Bayesian framework in visual perception is in agreement with the notion of unconscious inference (Helmholtz, 1867): the idea that the visual system possesses implicit prior knowledge about the external world that it uses in order to interpret what would otherwise be ambiguous visual information. Gestalt psychologists expressed some of the visual system's prior knowledge about the external world informally in the form of rules dictating perceptual grouping and organization. However, these informal rules were sometimes ill-defined and often failed to make predictions beyond the phenomenon that they were originally intended to explain.

The results of Experiment 1 support the proposal that the visual system uses static luminance texture as a spatial reference to make the initial assessment of the moving grating's velocity. This proposal is similar to the suggestion offered by a Bayesian model of velocity perception (Weiss et al., 2002) for the contrast dependency of perceived speed; that there is more information about the exact velocity at which a stimulus is moving at high contrasts of the motion stimulus than at low contrasts. The following section will attempt to integrate the proposal that the visual system uses static luminance texture as a landmark to assess motion velocity within the framework of a Bayesian model of velocity estimation. Thus, the Bayesian framework presented in the following section does not constitute a competing account, but rather an attempt at formally representing the proposal that static luminance texture is used as a landmark in the assessment of motion. The Bayesian model also presents a considerable advantage over the informal proposal that the visual system uses static texture as a landmark to assess motion velocity. Whereas the landmark hypothesis makes no predictions about motion perception other than for the phenomenon that it was originally intended to explain, the Bayesian model provides a theoretical framework that allows one to make predictions about the influence of texture on the perception of visual motion in various conditions.

Landmarks and Bayesian models

Recently, a Bayesian model of velocity perception has been proposed (Weiss et al., 2002) to account for phenomena in the perception of motion. The Bayesian model differs from a variety of computational models by suggesting that motion "illusions" occur because these percepts represent optimal solutions (i.e., a best guess) for a visual system designed to operate in the presence of uncertainty with implicit prior knowledge about the external world rather than being the result of a miscalibration or some other form of computational error.

The Bayesian model of velocity estimation makes two basic assumptions: 1- that there is noise in the initial assessment of velocity and 2- that slow velocities are more common than fast ones.

As a consequence of the assumed noise in the initial assessment of velocity, the initial measurement of velocity can, in fact, correspond to a range of physical motion velocities. This assumption is expressed in the likelihood distribution in the form of Gaussian noise. This noise takes the form of a Gaussian-shaped likelihood distribution in which the highest probability corresponds to the veridical speed of the stimulus. The broadness of the likelihood distribution is determined by σ, the known standard deviation of the noise. For one-dimensional motion stimuli, this can take the form of:

$$P\langle I(x_i,t)|v_i\rangle \propto \exp\left[-\frac{(I_x v - I_t)^2}{\sigma_t^2}\right]$$

in which I_x and I_t are the derivatives of the image in space and time respectively, and σ_t, noise in this initial assessment of velocity.

The likelihood was expressed by Hurlimann et al. (2002) as:

$$\text{Likelihood} = \text{Gaussian}\left[v_{real}, \sigma/c\right]$$

where c represents the contrast of the moving grating and v_{real}, the veridical velocity of the motion stimulus. The division of the noise standard deviation by motion stimulus contrast produces the contrast dependency of perceived speed: it results in a narrowly distributed likelihood at high contrasts and a broadly distributed likelihood for low contrasts. This makes sense intuitively, as there is more information about the velocity of the motion stimulus at high contrasts than at low contrasts.

The tendency of images to move at slow velocities rather than rapid ones is included in the visual system's implicit prior knowledge about the properties of motion. In a Bayesian context, this prior knowledge is represented formally in the form of a Gaussian prior distribution in which slow velocities have a higher probability than fast ones. Although there is no empirical evidence that motion velocities follow a Gaussian distribution, the proposed bias towards slow velocities is in agreement with previous suggestions that human observers have a preference for "shortest path" solutions (Wallach, 1935; Ullman, 1979). For example, when viewing drifting gratings through a circular window, the resulting motion percept is consistent with the slowest velocity that is consistent with the visual information (i.e., along an axis orthogonal to the orientation of the drifting grating), although many motion velocities could also be consistent with the motion stimulus. The prior can be represented by:

$$P(v) \propto \exp\left(-v^2/2\sigma_p^2\right),$$

where v represents velocity and σ_P, the previously known standard deviation of the prior distribution.

The posterior distribution is obtained by combining the prior and likelihood distributions using Bayes' rules and is proportional to the product of the prior and the likelihood:

$$\text{Posterior} \propto \text{Prior} \times \text{Likelihood} \tag{4}$$

The components of the Bayesian model of velocity perception are depicted in Figure 9. The prior distribution, indicating the visual system's implicit knowledge that slow speeds are more likely to occur than fast one, is shown in Figure 9A. Figure 9B and C represent the likelihood distribution: panel B, in the case of a high contrast motion stimulus and panel C, in the case of a low-contrast motion stimulus. In both cases, the highest probability in the likelihood distribution corresponds to the same velocity. However, the higher uncertainty in low contrast conditions results in a broadly distributed likelihood whereas at high contrasts, the likelihood is relatively narrow. Figure 9D and E show the posterior distribution obtained by combining the prior and likelihood distributions following Bayes' rules respectively for high contrast and low contrast stimuli. We can see that the posterior distribution is shifted towards a velocity of zero for low-contrast stimuli. By comparison, for the high-contrast stimulus, the highest probability of the posterior distribution is closer to the veridical speed of motion. As depicted in Figure 9, an ideal observer that estimates perceived speed by selecting the speed that follows a *maximum a posteriori* (MAP) decision rule, in which the final estimate of velocity corresponds to the velocity that has the highest probability in the posterior distribution will estimate faster speeds at high contrast, and slower ones at low contrasts.

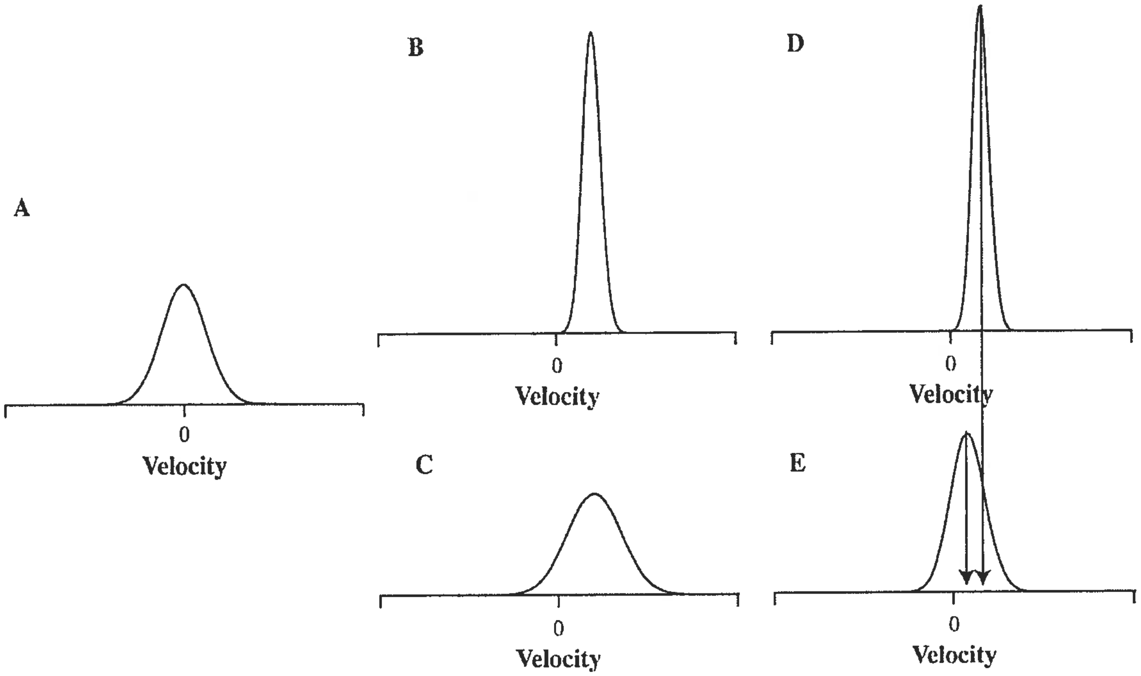

Figure 9. Schematic depiction of the Bayesian model of velocity perception. Panel A represents a prior favoring slow speeds. Panels B and C depict the likelihood obtained by the initial assessment of speed for high contrast and low contrast stimuli respectively. Panels D and E represent the posterior obtained by combining the prior and likelihood shown in panels B and C respectively according to Bayes' rules. The arrows represent the final velocity assessments of and ideal observer using a MAP decision rule.

It was found that the Bayesian model of velocity perception can account for a wide variety of phenomena reported previously in the motion literature (Weiss et al., 2002), including the dependency of perceived speed on motion stimulus contrast (Thompson, 1982; Stone & Thompson, 1992; Blakemore & Snowden, 1999).The Bayesian model's use of Gaussian noise in the initial assessment of speed produced a likelihood that is dependent on contrast. According to the authors, this makes sense intuitively, as there is less information about the exact speed of a moving stimulus at low contrasts than at high ones. This results in higher levels of uncertainty at low contrasts, producing a more broadly distributed likelihood (Weiss et al., 2002). It is this relationship between stimulus contrast and the uncertainty of the initial assessment of velocity, rather than flaws in the computation of motion velocity, which accounts for the dependency of perceived speed on stimulus contrast. Thus, the Bayesian model's explanation for motion illusions differs fundamentally from the proposal that these phenomena are due to flawed motion computations.

This explanation for the dependency of perceived speed on motion stimulus contrast is in agreement with the accounts proposed for the increase in perceived speed in the presence of luminance texture: it has been suggested that static luminance texture increases the perceived speed of motion by providing a spatial reference to measure the relative motion (Gogel & McNulty, 1983). As is the case for luminance contrast, such an explanation appears intuitively correct: there is more spatial information to evaluate the velocity of a drifting grating in the presence of static luminance texture than in its absence. When no luminance texture is added, the best spatial referent is the edges of the window through which the drifting grating is viewed. As we can see, the accounts for the contrast dependency of perceived speed and for the increase in perceived speed in the presence of static luminance texture are very similar.

Here, we propose that the suggestion that luminance texture increases perceived speed by providing additional information in the initial assessment of speed can be expressed formally within the Bayesian model of perceived velocity. It should be emphasized that the Bayesian model and the landmark account do not constitute competing hypotheses for the increase in perceived speed in the presence of luminance texture. Rather, the Bayesian model provides a framework that allows the proposal that static luminance texture is used as a landmark by the visual system to be expressed in a formal manner. In the Bayesian model, the additional spatial information provided by static luminance texture decreases the amount of noise in the initial assessment of speed by providing a spatial referent to make that assessment. This decreased uncertainty results in a narrower likelihood distribution. Instead of being merely dependent on stimulus contrast, the broadness of the likelihood would also depend on the contrast of the stationary luminance texture. This could take the form of:

$$\text{Likelihood} = \text{Gaussian}\left\{ v_{real}, \frac{\sigma}{\left[c_s(1 + c_t)\right]} \right\}, \tag{5}$$

where c_s represents the contrast of the motion stimulus relative to the mean background luminance, and c_t, the contrast of a static luminance texture.

As in the original model, the posterior, upon which the final speed assessment is based, is determined by combining the likelihood and posterior distribution according to Bayes' rules. The final assessment of velocity was determined using a MAP decision rule.

The informal proposal that the visual system uses static luminance texture as a spatial reference to assess the velocity of a moving grating makes no predictions beyond the phenomenon that it was originally intended to explain. However, its formal expression within a Bayesian framework allows us to make predictions about the effects of texture beyond the initial phenomenon that texture increases perceived speed. For instance, we used this model in order to determine how an ideal observer might behave in a speed matching task in which the observer is required to adjust the speed of a test stimulus of known contrast to match the speed of a standard grating drifting at a known constant velocity at various levels of standard grating and texture contrasts. No texture was present to facilitate the initial measurement of the test grating's speed. The posterior was obtained by combining the likelihood and prior distributions according to Bayes' rules. The final assessment of the test and standard gratings' speed was determined using the maximum probability of the posterior distribution. The physical speed of a 10% Michelson contrast test grating which would produce an identical perceived speed was then determined.

Finally, the relative speed of the ideal observer's match was obtained by dividing the physical speed of the test grating by the physical speed of the standard grating.

The relative speed matching results of this Bayesian ideal observer are shown in Figure 10. We have no doubt that not every detail of this model is correct. For instance, it predicts high perceived speeds at a motion stimulus contrast of zero when texture contrast is high. Nevertheless, it can qualitatively predict the decrease in the contrast-dependency of perceived speed with increasing levels of texture contrast (Blakemore & Snowden, 2000), provided that motion stimulus contrast remains suprathreshold. In the presence of static luminance texture, because the spatial information provided by the texture has already diminished the uncertainty in the initial assessment of speed, changing the contrast of the moving stimulus doesn't affect the broadness of the likelihood distribution as much as it does in the absence of luminance texture. This in turn changes the posterior distribution: in the presence of texture, increasing the contrast of the stimulus will not produce a large shift the highest probability of the posterior towards the veridical speed of motion as it would in the absence of texture. An ideal observer following a MAP decision rule would therefore estimate a speed that is largely dependent on stimulus contrast at low texture contrasts, but would gradually become less and less dependent on the contrast of the motion stimulus as texture contrast increases. It should also be noted that according to the Bayesian model, the faster velocity estimates occurring at high motion stimulus contrasts and in the presence of static luminance texture also correspond to a final assessment of speed that is closer to the veridical speed of the stimulus.

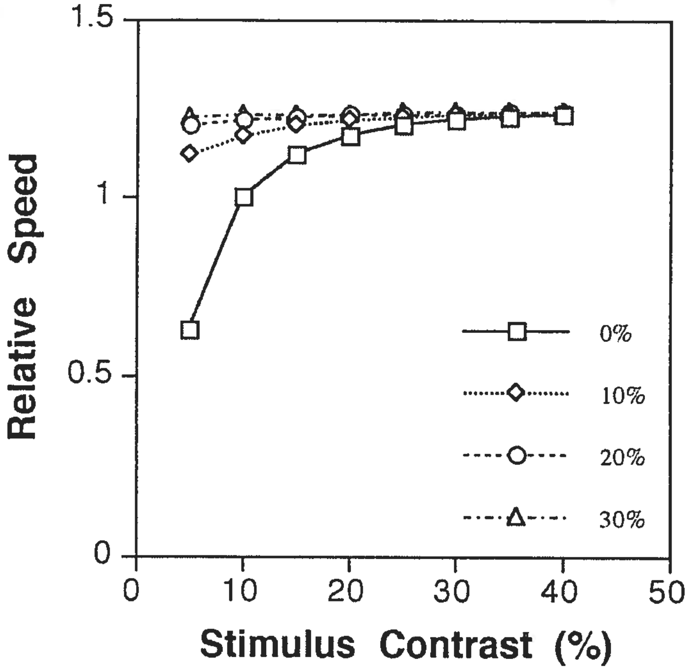

Figure 10. Relative speed matches of a test stimulus according to a Bayesian ideal observer as a function of stimulus and texture contrast. The abscissa values represent stimulus contrast and the different curves represent speed matching results for the various levels of texture contrast. The different curves represent the speed matching results a texture contrasts of 0 (solid line with squares), 10 (dotted line with diamonds), 20 (dashed line with circles), or 30% (dash-dotted line with triangles) Michelson contrast.

Experiment 2

In Experiment 1, we demonstrated that superimposing static luminance texture on a drifting grating could increase the perceived speed of motion. The purpose of Experiment 2 was to evaluate how the visual system uses luminance texture in the assessment of velocity. It has been suggested that landmarks and moving stimuli only interact with each other over a small spatial scale (Norman et al., 1996; Blakemore & Snowden, 2000). If this suggestion is correct, then superimposing static luminance texture over only part of the area covered by the motion stimulus could alter perceived velocity in a number of ways.

The first question that we seek to answer in Experiment 2 is how the final assessment of velocity is influenced by the spatial extent covered by the static luminance texture. If landmarks interact with the motion stimulus over a large spatial scale in the initial assessment of velocity, then one might expect perceived speed to increase very rapidly with the area of the motion stimulus covered by static texture, reaching an asymptote fairly rapidly. On the other hand, if the interactions between the static texture and the standard grating only occur over a small spatial scale, the perceived speed of a drifting grating may be determined using a number of possible strategies. Local velocity estimators able to use landmarks over a small and a large scale are shown in Figure 11.

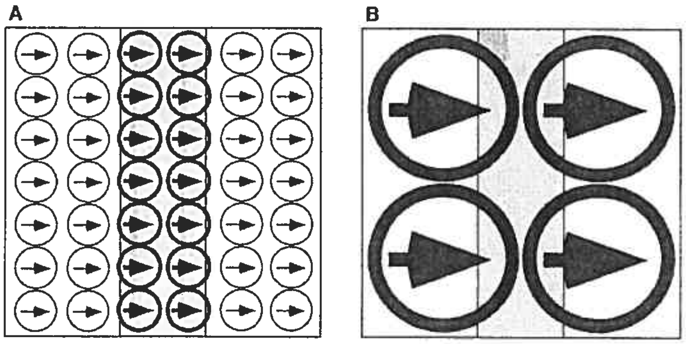

Figure 11. Schematic illustration of a stimulus where local "speed estimators" interact with static luminance texture over a small scale (A) or over a large scale (B). The grey area represents the area of a rightward drifting grating covered by texture and the white area represents the area of the drifting grating where there is no static luminance texture. Circles represent the area over which a local "speed estimator" can use texture in order to assess speed. Circles with thin outlines and arrows represent the local "speed estimators" that did not use texture in speed assessment, speed judgements. Circles with thick outlines and arrows represent local "speed estimators" that used static luminance texture in the assessment of speed.

The first possible strategy that we will discuss is a "region of lowest uncertainty" approach, in which only the section of the image with the lowest level of uncertainty in the initial measurement of velocity would be used by the visual system to determine perceived speed. In such a case, given that there would be less variance between the local speed estimates over and near the textured area, this implies using only these initial estimates to determine velocity and dismissing those that didn't use static luminance texture to facilitate the initial assessment of speed. Simply put, this would involve only using the part of the image that contains the least uncertainty to assess speed. In such a case, one would expect speed perception to be unaffected by the size of the area covered by luminance texture, provided that the area remains large enough to be visible. The expected results for such a proposed scheme would resemble those expected if the motion stimulus and texture interact over a large scale. That is, perceived speed would increase rapidly as soon as texture is added and would not be affected by the size of the area occupied by texture.

The perceived speed of the motion stimulus could also be determined by integrating the local speed estimates obtained over the whole image. In a Bayesian model, the variance of the local speed estimates taken across a population diminishes as the area covered by static luminance texture grows. In other words, for a given texture contrast, the proportion of local speed estimates yielding an assessment of speed at or near veridical speed grows as the area subtended by the texture increases. This results in a narrower likelihood distribution as the area of the motion stimulus covered by static texture grows. In the Bayesian model of velocity perception, a narrow likelihood produces a posterior where the maximum probability is closer to the veridical assessment of speed than a broad likelihood (see Figure 9 for an illustration). This predicts that the final assessed speed of an ideal observer using a MAP decision rule will increase as a function of the area covered by texture.

Methods

Stimuli

A depiction of the standard grating stimulus used in Experiment 2 is shown in Figure 12. As in Experiment 1, both the standard and test grating had a 0.5 cycles/degree spatial frequency. The standard grating drifted at a speed of 8°/sec. In order to assess how texture was used by the visual system to increase perceived speed, a horizontal or vertical window of texture was added to the standard grating. The texture was a 2 cycles/degree vertically oriented sinusoidal grating, modulated at 15% Michelson contrast. We opted to use this spatial frequency and contrast because Experiment 1 demonstrated that an increase in the perceived speed of the standard grating occurred reliably under these conditions.

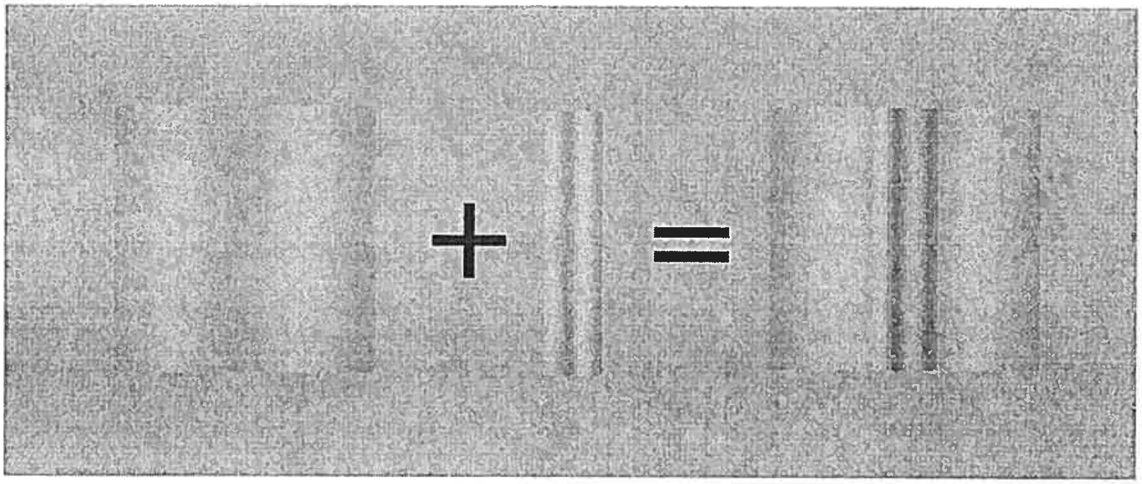

Figure 12. Demonstration of the standard grating motion stimulus. The standard grating was a 0.5 cycles/degree 10% sinusoid grating drifting at a speed of 8°/sec. and was modulated at 10% Michelson contrast. A window of static luminance texture waas added to the standard grating. The texture was modulated at 15% Michelson contrast grating with a spatial frequency of 2 cycles/degree. The texture window could be either vertically oriented or horizontally oriented.

Procedure

The speed-matching procedure used in order to determine the perceived speed of the standard grating in Experiment 2 was the same as in Experiment 1.

Results

The results of Experiment 2 are shown in Figure 13. For both types of windows, the speed of the test grating needed to match the perceived speed of the standard grating increased as a function of the area covered by texture. This indicates that the perceived speed of the standard grating increased with the area of the motion stimulus covered by texture. The increase in perceived speed was gradual. Observers did not show a sudden increase in perceived speed when texture was added: their speed estimates were slower when texture only subtended a small part of the motion stimulus than when it subtended the entire stimulus. Observers also did not show a systematic difference between vertically oriented and horizontally oriented texture windows.

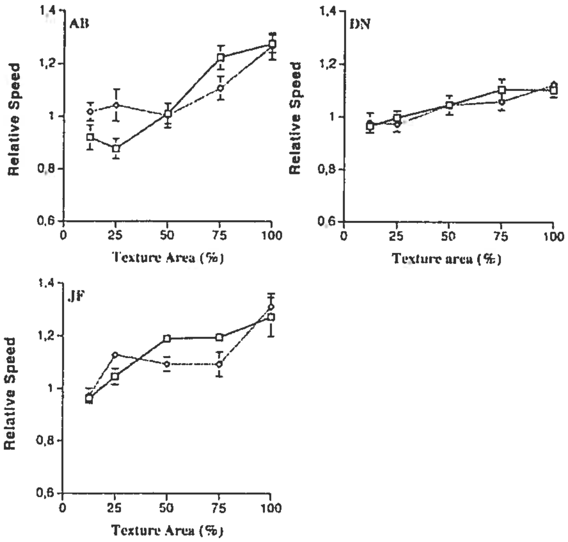

Figure 13. Relative perceived speed of a standard grating as a function of the proportion of the standard grating's area covered by static luminance texture for individual observers. Results are shown for horizontally oriented (dotted lines with squares) and vertically oriented (lines with diamonds) windows of static luminance texture. Error bars show ±1 SEM.

Discussion

The results of Experiment 2 show that a gradual increase in the perceived speed of the standard grating occurs as the static luminance texture window covered more area. This increase in perceived speed also indicates that the area over which landmarks can be used in order to facilitate motion is fairly limited: if the various local velocity estimators were able to use texture regardless of its location for local speed estimates, then perceived speed should have peaked rapidly, as opposed to the gradual increase reported here. This is consistent with earlier suggestions that the spatial area over which relative motion can influence perceived speed is limited (Norman et al., 1996). Although they favoured the interpretation that second-order processes explained the loss of contrast-dependency of perceived speed in the presence of texture, Blakemore and Snowden (2000) also considered that spatial referents may only interact with the motion stimulus over a small scale.

The gradual increase in perceived speed in Experiment 2 also rules out a "region of lowest uncertainty" mechanism in which perceived speed is determined by using solely the area where local speed estimates show less uncertainty. Rather, it appears that the local speed estimates are integrated over the entire image prior to the final assessment of speed. The gradual increase in perceived speed can be accounted for by a gradual decrease in the uncertainty across the local velocity estimate population as the area of the motion stimulus covered by static texture increases.

Experiment 3

The proposal that static luminance texture is used as a reference point by the visual system in the initial assessment of velocity raises questions about the effects of luminance texture on the perceived velocity of motion when the texture does not represent a reliable spatial reference. One possibility is that the visual system continues to use luminance texture as a reference mark to make the initial assessment of velocity even when the texture does not constitute an appropriate spatial reference. In this case, superimposing dynamic luminance noise on a drifting grating should produce a noisier initial assessment of velocity, ultimately resulting in a slower percept of motion with increasing levels of noise contrast. It is also possible that the visual system stops using luminance texture when it does not provide a reliable spatial reference. If this is indeed the case, the perceived speed of a drifting grating should be unaffected by the contrast of a superimposed dynamic luminance noise. The purpose of Experiment 3 was to assess the effect of dynamic luminance noise on the perceived speed of a drifting grating. The rationale for this experiment is that whereas the static luminance texture used in Experiments 1 and 2 can provide a reliable spatial reference, dynamic luminance noise cannot, because it contains no luminance spatial structure. Additionally, the use of dynamic luminance noise will allow us to investigate the proposal that signal and noise motion components are largely, but not completely, segregated in the computation of speed (Zanker & Braddick, 1999).

Methods

Observers

Four psychophysical observers completed Experiment 3. As in Experiments 1 and 2, all observers had normal or corrected to normal visual acuity. One of the observers (DN) is an author on this paper and the others were naïve as to the hypotheses of this experiment.

Stimuli

As in the previous experiments, on each trial, observers were presented a standard grating drifting at a speed of 8°/sec. and a test grating drifting in opposite directions. Both the test and the standard grating had a spatial frequency of 0.5 cycles/degree and 10% Michelson contrast. Dynamic luminance noise was added to the standard grating. The contrast of the noise was 5, 10, 15, or 20% Michelson contrast. The dynamic binary noise had a grain size of two pixels (four minutes of arc). A new noise field was generated every four frames (noise refresh rate of 30 Hz).

Procedure

The method of constant stimuli was used to determine the effects of dynamic noise on the perceived speed of the standard grating. Observers initiated each trial with a keypress. On each trial, the test and the standard grating were presented simultaneously to observers, one above and the other below fixation. Stimuli were presented for 500 msec. (2 cycles). The observer's task was to indicate which of the two gratings seemed to drift faster. No time limit was given for responding. The observers' responses were used in order to determine the point of subjective equality (PSE), that is, the speed of the test grating at which the test and the standard grating appeared to drift at the same speed. A pilot study also used flickering and jittering gratings as dynamic luminance texture, but these data are not shown here because the results were very similar to those obtained when using dynamic luminance noise.

Results

The relative speed of the PSE as a function of dynamic noise contrast is shown in Figure 14. These results show that increasing the contrast of dynamic luminance texture produces no change in the perceived speed of the standard grating. The speed of the test grating which matched the perceived speed of the standard grating remained close to the physical speed of the standard grating regardless of noise contrast.

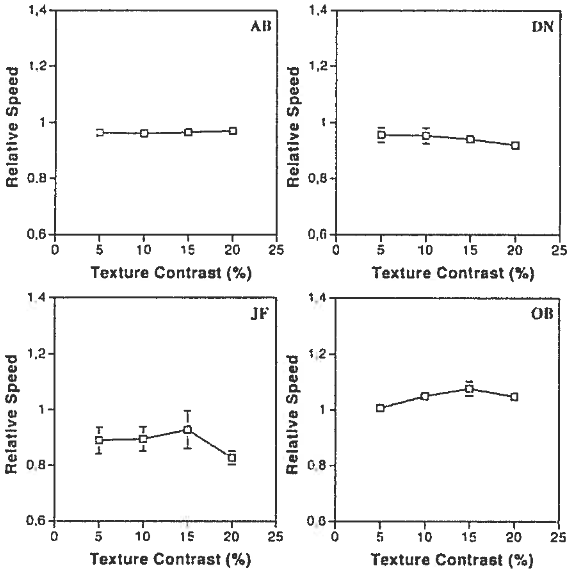

Figure 14. Relative speed of the PSE as a function of dynamic noise contrast. Error bars show ±1 SEM.

Discussion

The results of Experiment 3 demonstrate that increasing the contrast of dynamic luminance noise did not produce any significant change in the perceived speed of the standard grating. This supports the proposal that an unreliable spatial reference, such as dynamic luminance noise, is not used by the visual system to make the initial measurement of velocity. Taken together, the results of Experiments 1 and 3 are in agreement with those of Norman et al. (1996). These authors showed that while an annulus of static luminance dots produced an increase in the perceived speed of moving dots in a central area, increasing the speed in the surrounding annulus did not cause as large an increase in perceived speed, regardless of direction in the two regions.

The failure of dynamic luminance noise to produce a change in the perceived speed of the standard grating in Experiment 3 is also in agreement with previous results obtained with RDKs (Zanker & Braddick, 1999). These authors suggest that the failure of coherence level to affect the perceived speed of motion in RDKs is due to a large, but incomplete, segregation between the signal and noise motion components in the pooling process leading to the final speed estimate. It is suggested that the independence of the speed percept from noise level in RDKs is achieved in two steps. The first step involves determining the direction of RDK motion. In the second step, perceived speed is determined by averaging exclusively from the units signalling the correct direction and dismissing the input of other units. This proposal can account for the failure of coherence level to produce a change in the perceived speed of RDKs as well as the failure of dynamic luminance noise contrast to affect perceived speed in Experiment 3. However, by itself, this account fails to explain the increase in perceived speed with increasing static luminance texture contrast reported in Experiments 1 and 2. Indeed, according to this proposal, static luminance texture should have had no effect on the perceived speed of the standard grating.

Here, we suggest that the reason for the apparent partial segregation between the noise and signal motion components in RDKs may come from a surface segregation mechanism. It has been mentioned that when drifting plaid patterns give rise to a percept of transparent motion, observers perceive the individual component gratings as two surfaces drifting one on top of the other (von Grünau, Dubé, & Kwas, 1993). We propose that this surface segregation mechanism produces two perceived surfaces when luminance texture is superimposed on a drifting grating: one surface for the texture and the other for the drifting grating. This proposal is by no means at odds with the previously described explanation for the independence of perceived speed on the coherence level of RDKs. Indeed, the initial step of determining direction of motion may very well form the basis on which the visual system identifies the texture and the motion components as belonging to two different surfaces. In the case of static luminance texture, the surface formed by the static texture can then be used as a spatial reference in order to assist the assessment of the drifting grating's velocity. In the presence of dynamic luminance texture, the segregation of signal and noise motion components allows the visual system to dismiss the luminance noise component because it does not provide a useful spatial reference to assess the position changes of the drifting grating.

The failure of dynamic luminance noise to produce a change in the perceived speed of a superimposed drifting grating in Experiment 3 also indicates that the visual system does not use dynamic luminance texture as a landmark in the assessment of motion. This seems to make sense intuitively, as dynamic luminance texture cannot provide a reliable spatial reference. In the Bayesian model, the proposed dismissal of the visual system on dynamic luminance texture would produce an identical likelihood in the absence of texture as in its presence. The original proposal that signal and noise motion components are segregated in the computation of speed (Zanker & Braddick, 1999) would also produce a likelihood for the motion signal that is unaffected by the level of noise contrast. The independence of the likelihood distribution from dynamic luminance texture contrast would produce a posterior that is also independent of texture contrast. This posterior distribution would be identical to the posterior produced by a grating of identical contrast to which no dynamic luminance texture had been added. This proposal also makes the prediction that the perceived speed of a moving stimulus should depend on its contrast, regardless of dynamic luminance texture contrast, because the visual system cannot rely on landmarks in the luminance texture to provide additional spatial information. However, in the presence of static luminance texture, the dependency of perceived speed on the contrast of the moving stimulus should decrease as texture contrast increases.

General Discussion

The increase in perceived speed with increasing levels of texture contrast reported in Experiment 1 is in agreement with previous reports of increases in perceived speed in the presence of texture (Brown, 1931; Gogel & McNulty, 1983; Blakemore & Snowden, 2000). However, because the visibility of the standard grating diminished with increasing levels of texture contrast, the concomitant increase in perceived speed cannot be attributed to an increase in the visibility of the standard grating through second order processes. Rather, it seems that the visual system uses static luminance texture as a landmark to facilitate the initial assessment of the standard grating's velocity. This proposal can be integrated within a Bayesian model of velocity perception in which static luminance texture provides additional information to make the initial assessment of velocity (Hurlimann et al., 2002). This is in agreement with the suggestion that the visual system uses luminance texture to assess velocity (Gogel & McNulty, 1983). It was found that such a model was able to account for the previously reported decrease in contrast-dependency of perceived speed with increasing levels of static texture contrast (Blakemore & Snowden, 2000).

It is also interesting to note that Experiment 1 found that perceived speed increased with the contrast of static texture. This raises questions about the mechanism underlying the increase in perceived speed. That is, texture could be used by the visual system as a landmark so long as it is supra-threshold. Thus, if, as suggested, static luminance texture produces increases in perceived speed by serving as a landmark to assess relative motion, then our results show that the visibility of these landmarks is an important factor in determining motion velocity.

The increase in perceived speed with increasing size of the area occupied by texture in Experiment 2 demonstrates that texture only facilitates the initial assessment of speed over a small spatial scale. These results also rule out a "region of lowest uncertainty" scheme in which only the area covered by texture would be used to determine perceived speed. Rather, it appears that the final assessment of velocity is based on an integration of these local velocity estimates over the area covered by the motion stimulus. This produces an overall initial assessment of speed that becomes less noisy as the area of the motion stimulus covered by texture increases. For the ideal observer discussed in this article, the narrower likelihood representing this effect of texture ultimately results in a faster final assessment of speed as the area of the motion stimulus covered by texture grows.

The failure of dynamic luminance noise to alter the perceived speed of motion in Experiment 3 is in agreement with the findings of previous research, which found a similar failure of coherence level to affect perceived speed in RDKs (Zanker & Braddick, 1999). These authors proposed a two-step model to account for the failure of coherence levels to influence perceived speed. Although this model can account for the failure of dynamic luminance noise to influence perceived speed, by itself, it is insufficient to explain the increase in perceived speed with increasing levels of static texture contrast. Taken together with the results of Experiment 1, the results of Experiment 3 demonstrate that a fundamental difference exists between static and dynamic luminance texture: whereas the former can be used as a spatial referent to facilitate the initial assessment of speed, the latter is not. A surface segregation mechanism may simultaneously explain the increase in perceived speed at higher levels of texture contrast in Experiment 1 and the failure of dynamic luminance noise to affect perceived speed in Experiment 3. Further experimentation will be necessary to obtain a more complete understanding of the computations underlying speed perception and how they take texture into account.

Another possibility for the effects of static luminance texture contrast on perceived speed is that the texture increases the overall contrast of the compound stimulus. That is, the luminance difference between the darkest and brightest parts of the texture plus motion stimulus was greater than when the motion stimulus was presented alone. This proposal, however, is at odds with current computational models of low-level motion extraction. For instance, motion energy detectors are insensitive to static stimuli (Adelson & Bergen, 1985). The pedestal test takes advantage of this feature in order to investigate the mechanisms underlying motion perception (Lu & Sperling, 1995; Lu, Lesmes, & Sperling, 1999). Further, the contrast between the light and dark parts of the motion stimulus increases whether we superimpose static or dynamic luminance texture, yet we found that only the former produces increases in perceived speed. Additionally, the increased contrast proposal cannot account for the effects of texture on perceived speed when it is located adjacent to the motion stimulus.

In conclusion, we demonstrate that perceived speed is influenced by the spatio-temporal characteristics of luminance texture. The faster perceived velocities at higher levels of static luminance texture contrast supports the proposal that the visual system uses the texture as a landmark to assess motion velocity (Gogel & McNulty, 1983). We suggest integrating this proposal within a Bayesian framework of velocity perception. The formal expression of this proposal within a Bayesian context has the benefit of allowing us to make predictions beyond the phenomenon that the landmark account was originally intended to explain.

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Un modèle Bayésien biologiquement plausible pour expliquer les phénomènes de mouvement.

Ce chapitre est une reproduction exacte de l'article :

Nguyen-Tri, D. & Faubert, J. (soumis en 2005)

« A biologically plausible Bayesian model to explain motion phenomena »

Psychological Review

Résumé

Bien que nos interactions avec notre environnement nécessitent une estimation relativement précise de la vélocité du mouvement, diverses expériences psychophysiques ont démontré que les observateurs humains font des erreurs dans l'estimation du mouvement de stimuli visuels simples. Un cadre Bayésien a été proposé afin d'expliquer ces illusions de mouvement. Ce modèle présuppose que 1- les vitesses lentes sont plus communes que les vitesses rapides 2- il y a du bruit dans la mesure initiale de vélocité. Dans ce chapitre, nous nous pencherons sur une implémentation biologiquement plausible du cadre Bayésien.

Abstract

Although interacting with our environment requires an accurate assessment of motion, psychophysical experiments show that human observers make mistakes in assessing the velocity of simple visual stimuli. Different models, generally attributing these illusions to flaws in the computation of motion, have been proposed to account for these various individual findings. In the current article, we attempt to explain some of these findings and hypotheses within the conceptual framework of a Bayesian model of velocity perception (Weiss et al., 2002) which suggests that motion illusions constitute optimal solutions for a visual system designed to function in the presence of uncertainty. We find that this framework can account for a wide range of phenomena reported in the motion literature.

Introduction

The primary purpose of the visual system and the other sensory modalities is to provide our brain with the information necessary to guide our actions. Consequently, in order to interact adaptively with our surroundings, it is imperative that the percepts obtained by analyzing the various sensory inputs represent a reasonably accurate assessment of the physical world. For instance, catching a ball or avoiding collisions when walking in a crowd requires a visual system that is capable of accurately estimating the speed and direction of the motion present in our environment. Given our dependency on an accurate assessment of velocity, it is therefore surprising that a number of psychophysical experiments have demonstrated that human observers commit a number mistakes in assessing the speed and direction of simple moving visual stimuli.

The currently prevailing approach to motion processing emphasizes bottom-up processing. The impetus for the bottom-up framework to motion processing originates from the discovery of motion sensitive neurons in the striate cortex and in visual area V2 (Hubel & Wiesel, 1959; Hubel & Wiesel, 1965). In this approach, processing of motion information is considered to begin with basic units, such as direction-selective cells in the striate cortex (Nakayama, 1985) and to involve increasingly complex computations, with each additional step relying on the foundation laid by earlier computations. A number of computational models, such as the Reichardt detector (Reichardt, 1961), elaborated Reichardt detectors (van Santen & Sperling, 1984; van Santen & Sperling, 1985) and motion energy detectors (Adelson & Bergen, 1985) have been developed on the basis of physiology to describe the low-level extraction of motion information. Following this, a hypothetical integration stage is proposed where the various initial local motion measurements are used in order to obtain a more global description of motion. This integration is generally believed to occur in extrastriate areas, presumably in cortical areas MT and MST. The models developed within this framework to account for motion illusions generally attribute these motion phenomena to computational errors by the visual system. These models also tend to be illusion specific.

An alternative approach to bottom-up processing emphasizes top-down processing, in which "higher level" information, such as an observer's prior knowledge, influences perception. This is consistent with the notion of unconscious inference (Helmholtz, 1867): the suggestion that the human visual system must rely on prior knowledge about the physical world in order to be able to interpret incomplete or otherwise ambiguous visual information. Gestalt psychologists expressed some of the visual system's prior knowledge about the physical world informally in their "laws" guiding perceptual grouping and organization. The perceptual principles formulated by Gestalt psychologists suffered from a number of shortcomings. Firstly, unlike the computational models developed within the bottom-up approach, some of these principles were ill-defined. For instance, the law of simplicity states that if a number of competing interpretations are possible for an image, the simplest one will prevail perceptually. However, this law fails to provide well-defined guidelines for determining which among a set of possible interpretations constitutes the simplest one. Another shortcoming of the Gestalt approach is that it provides mainly after-the-fact explanations for our percepts. For example, the Gestalt law of proximity states that items close to one another tend to be grouped together, but it makes no predictions beyond the phenomenon that it was originally intended to explain. What is needed then is a quantitative framework, which allows the principles guiding perception to be expressed in a formal manner that makes predictions about what should be perceived in different conditions.

Bayesian decision theory provides a theoretical framework that allows the expression of an observers' prior knowledge about the properties of the physical world in a formal manner. In the Bayesian framework, a correspondence is expected between the design of the visual system and the properties of the environment: the physical world exhibits certain regularities, and the visual system should be built to exploit them (Geisler

& Diehl, 2002). For instance, within a Bayesian framework, the Gestalt laws of "good continuation" and "proximity" exist because the visual system exploits the statistical property of natural scenes that close and co-circular (tangent to the same circle) edge elements tend to belong to the same physical contour (Geisler et al., 2001). This framework is consistent with environmental psychology (Brunswik, 1956; Gibson, 1966; Gibson, 1979), which emphasized the relationship between environmental regularities and perception.

Recently, a Bayesian model of motion perception (Weiss et al., 2002; Hurlimann et al., 2002) has been developed in order to account for various motion illusions. In contrast with "computational error" models of motion illusions, the Bayesian model suggests that motion illusions occur because these percepts represent optimal solutions (i.e., best guesses) for a visual system designed to function in the presence of uncertainty, given its prior knowledge about the statistical properties of motion in the physical world. In the context of velocity estimation, this model makes two assumptions: 1- that slow velocities are more common than fast ones and 2- that there is noise in the initial assessment of velocity. The proposal that the human visual system has knowledge that slow velocities are more common than fast ones is consistent with suggestions that it has a bias favouring slow motion velocities (e.g., (Wallach, 1959; Ullman, 1979)). In Bayesian modelling of human visual perception, the observer's knowledge about the properties of his environment is expressed in the prior (Mamassian, Landy, & Maloney, 2002). Weiss et al. (2002) formally instantiated the visual system's knowledge that slow velocities are more common than fast ones in the prior by a Gaussian probability distribution in which the highest probability corresponds to a velocity of zero.

In Bayesian modelling, the likelihood distribution represents the probability of a range of possible visual stimuli that can give rise to the initial assessment of velocity. The second assumption of the Bayesian model of velocity perception is that there is noise in the initial assessment of velocity. This is instantiated in the Bayesian model with Gaussian noise. As a result of this uncertainty, a gamut of physical velocities can bring about the initial assessment of velocity. For a for a stimulus moving at a velocity of v_{real}, this uncertainty is formally expressed by Weiss et al. (2002) with a Gaussian likelihood distribution in which the mean is equal to the value of the initial assessment of velocity. This was expressed by Hurlimann et al., (2002), simplified to one-dimension, as:

$$\text{Likelihood} = \text{Gaussian}\left(v_a, \sigma_L / c_m\right)$$

where σ_L is a constant representing the known standard deviation of the Gaussian noise in the initial measurement of velocity and c_m, the contrast of the moving stimulus. The division of σ_L by c_m, results in a greater uncertainty in the initial assessment of velocity at low contrasts than at high contrasts. This makes sense intuitively: there is more information about the exact velocity at which a stimulus is moving at high contrasts than at low contrasts of the motion stimulus.

The posterior distribution, upon which the percept of an ideal observer is established, is computed from the prior and likelihood distributions using Bayes' rules. The posterior is obtained by:

$$\text{Posterior} \propto \text{Prior} \times \text{Likelihood}$$

The Bayesian observer's final assessment of velocity corresponds to the velocity that has the highest probability in the posterior distribution (MAP decision rule). The components of the Bayesian model and their contribution to attaining a final estimate of velocity are illustrated in Figure 15. It was found by Weiss et al. (2002) that this model of velocity perception was able to account for an impressive array of phenomena previously reported in the motion literature, including reports of dependency of perceived speed on the luminance contrast of the motion stimulus (Thompson, 1982; Stone & Thompson, 1992; Blakemore & Snowden, 2000). In this theoretical paper, we will investigate whether this Bayesian model can account for a number of phenomena observed in the motion literature and to cast already existing hypotheses for motion illusions within the framework provided by the Bayesian model of velocity perception. We will also attempt to elaborate a biologically plausible framework through which the visual system can implement its knowledge about the statistical properties of motion in the physical world.

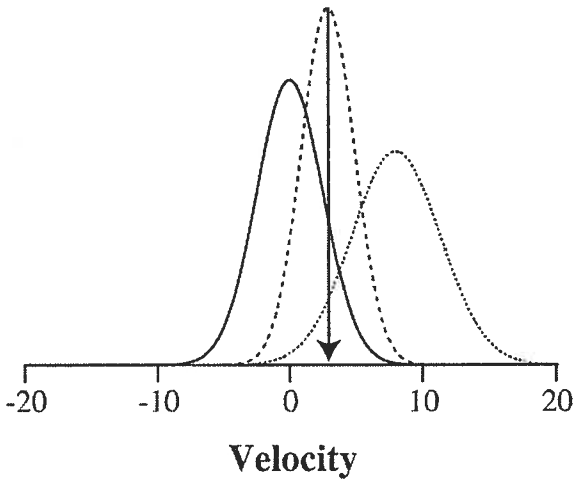

Figure 15. Prior, likelihood and posterior probability distributions as a function of velocity. The solid line represents a prior favouring slow velocities. The dash-dotted curve represents the initial assessment of a static test grating's velocity. The continuous curve represents the resulting posterior. The arrow indicates the final velocity assessment of a Bayesian observer using a MAP decision rule.

Contrast dependency of perceived speed

It has been demonstrated that perceived speed is influenced by the contrast of the motion stimulus. It is generally found that, at identical physical speeds, high contrast stimuli seem to move faster than low contrast stimuli (Thompson, 1982; Stone & Thompson, 1992; Blakemore & Snowden, 2000). In some cases, this may even produce a complete loss of the motion percept (Campbell & Maffei, 1981). This contrast dependency of perceived speed can even produce behavioural effects, such as a tendency to drive faster in foggy conditions (Snowden et al., 1998).

Stone and Thompson (1992) have proposed that the contrast dependency of perceived speed occurs because the units sensitive to motion energy (Adelson & Bergen, 1985) are sensitive to both the velocity and the contrast of the motion stimulus. As a result of this, motion-energy sensitive neurons cannot unambiguously encode the velocity of a stimulus. Stone and Thompson (1992) suggest that, in order to obtain an unambiguous estimate of velocity, the output of motion-energy sensitive cells had to be normalized (i.e., divided) with an average contrast signal. This signal is obtained by pooling the output of all complex cells over a wide spatial area. In speed-matching experiments, a test and a standard stimulus are generally presented simultaneously. The speed of the standard grating remains constant and the speed of the test grating is manipulated. The observer is instructed to indicate which of the two stimuli appears to drift at a faster speed. If the pooling takes place over an area of the visual field large enough to encompass both the test and standard gratings, then normalization errors will happen when the two gratings do not have equal contrasts. If the standard grating has a higher contrast than the test grating, the motion energy signal generated by the former will be normalized by an inappropriately low average contrast. Conversely, if the standard grating has a lower contrast than the test grating, the standard grating's motion energy signal will be normalized by an inappropriately high average contrast. This normalization error ultimately produces an overestimation of the speed of the standard grating at high contrasts and an underestimation of speed at low contrasts. As we can see, this suggestion holds that a flaw in the computation of velocity can account for the contrast dependency of perceived speed.

The Bayesian model differs fundamentally from the proposal that normalisation errors account for the contrast dependency of perceived speed. That is, rather than being the consequence of flaws in the computation of motion velocity, the Bayesian model (Weiss et al., 2002; Hurlimann et al., 2002) suggests that this illusion occurs because perceived velocity constitutes an optimal solution (i.e., a best guess) for a visual system designed to operate in the presence of uncertainty. As we can see in Equation 1, the type of noise used by Weiss et al. (2002) produces a likelihood that is dependent on the contrast of the motion stimulus: a low contrast motion stimulus results in a more broadly distributed likelihood than a high contrast one. As illustrated in Figure 16, this contrast-dependence of the likelihood distribution ultimately produces a posterior distribution in which the highest probability will correspond to a slower speed as the contrast of the motion stimulus decreases. Consequently, a Bayesian observer using a MAP decision rule will report slower velocities at low motion stimulus contrasts than at high contrasts.

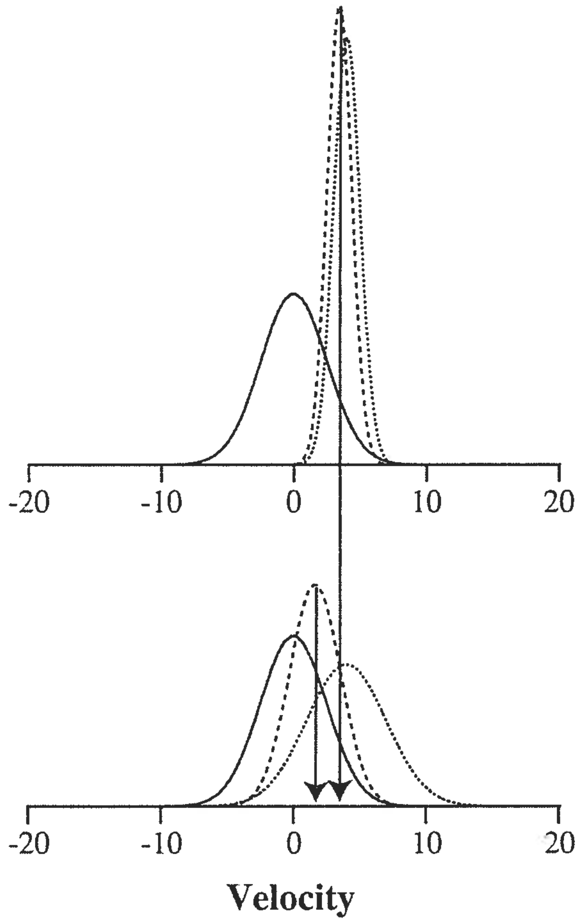

Figure 16. Schematic depiction of the Bayesian model of velocity perception proposed by Weiss et al. (2002). The prior, likelihood, and posterior probability distributions are represented respectively by the full, dotted and dashed curves. The top panel show these distributions in the presence of a high contrast motion stimulus and the bottom panel, in the presence of a low contrast motion stimulus. The arrows represent the final speed assessments of and ideal observer using a MAP decision rule.

In the theoretical framework of the Bayesian model, the final assessment of velocity represents a trade-off between an ideal observer's prior knowledge about the statistical properties of motion in the physical world (i.e., that slow velocities are more common than fast ones) and the amount of uncertainty in the initial assessment of velocity. At low levels of uncertainty, the final estimate of velocity will be similar to the velocity having the highest probability in the likelihood function. At high levels of uncertainty, the visual system will rely more on its prior knowledge about the properties of motion, producing a final assessment of velocity that is significantly slower than the velocity having the highest probability in the initial assessment of velocity. It is worth noting that within the Bayesian framework, the faster percept of velocity at higher contrasts of the motion stimulus also corresponds to a more veridical assessment of speed, rather than an overestimation of the speed of the motion stimulus. The effects of contrast on the perceived speed of a drifting stimulus were accounted for within Weiss et al.'s original proposal (2002). In the following sections, we expand their original suggestion to account for a wider variety of phenomena reported in the motion perception literature.

One of our main objectives is to provide a biologically plausible model for how the human visual system can implement a Bayesian framework. In order to do so, we will try to integrate units having response properties similar to those of speed-tuned neurons discovered in area MT: These neurons respond optimally to stimuli moving at their preferred velocity, and less, or not at all, to stimuli moving at a different velocity (Maunsell & Van Essen, 1983; Perrone & Thiele, 2001). As a result of their velocity tuning, these MT neurons will be responsive to a gamut of stimulus speeds and consequently, a single neuron cannot unambiguously signal that a stimulus is moving at a given speed. Perrone & Thiele (2001) conclude that an estimate of actual speed would have to be derived at a neural stage after MT, based on some form of population code.

Efforts emphasizing computation of speed based on the population responses of speed sensitive neurons in area MT have been made to comprehend how velocity is encoded within the visual system (Priebe & Lisberger, 2004). As a result of the tuning of velocity sensitive neurons, the presentation of a motion stimulus activates many of these velocity-tuned neurons, with the most active cells being the ones whose preferred velocity matches that of the motion stimulus. Based on population responses, the visual system can then determine stimulus velocity using a number of computational methods, such as vector averaging, winner-take-all, and vector summation (Robinson, 1972; Salinas & Abbott, 1994; Pouget, Zhang, Deneve, & Latham, 1998; Groh, 2001), which all emphasize the preferred velocity of the most active neurons in the computation of the final estimate of speed. Priebe & Lisberger (2004) conclude that perceived speed is determined using a vector averaging computation. However, because a low contrast motion stimulus reduced the overall population response without changing which speed sensitive neurons responded preferentially to the motion stimulus, vector averaging, by itself, could not account for the previously reported effects of stimulus contrast on perceived speed (Campbell & Maffei, 1981; Thompson, 1982; Stone & Thompson, 1992; Blakemore & Snowden, 1999).

The authors correct this shortcoming by introducing a bias parameter favouring slow speeds at low stimulus contrasts. However, why this bias is present and why it manifests itself more at low contrasts remain unanswered. A crucial element, namely noise in the initial assessment of velocity, is left out of the model proposed by Priebe & Lisberger (2004). That is, were it not for neural noise, the most active neuron in a population of velocity-tuned neurons would always correspond to the cell whose preferred velocity matches that of the motion stimulus, regardless of stimulus contrast. The perceived speed obtained by a winner-take-all, vector sum or vector average computational approach would still yield a correct assessment of velocity, regardless of contrast. Thus, without noise, the visual system's bias towards slow speeds would constitute a computational flaw, given that it introduces error in the assessment of velocity.

Here, we suggest a biologically plausible implementation of a Bayesian velocity estimator based on the population responses of velocity-tuned neurons. In this model, each action potential coming from a velocity-tuned neuron counts as a "vote" in favour of the cell's preferred velocity. For the purposes of this model, we modeled the response of 460 velocity-tuned units, tuned to 26 different preferred velocities, to a motion stimulus drifting at a velocity of 4 deg./sec. Half of these units were responsive to motion in one direction and the other half were responsive to motion in the opposite direction. The slowest preferred velocity of the receptors was set to 0.0625 deg./sec., and the preferred velocity of each subsequent velocity-tuned unit was equally spaced on a logarithmic axis between this minimum speed and a maximum preferred speed of 256 deg./sec. This representation of preferred speed has the added advantage of being parsimonious: it is possible to express a broad range of velocities with units tuned to a limited number of velocities. This is similar to colour vision, in which a multitude of colour percepts is based on the activity of just three retinal photoreceptors. In this article, we adopted the convention that the direction selectivity of motion-sensitive units is expressed as either a positive or a negative the absolute velocity value represents their preferred speed. For instance, for movement along a horizontal axis, the preferred velocity of a unit responding optimally to 4 deg./sec. leftward motion would be described by a value of –4 deg./sec., and a preferred velocity of 4 deg./sec. would correspond to a unit responding optimally to rightward motion at a speed of 4 deg./sec.

A significant difference between previous neural models of velocity estimation and our current proposal is the emphasis on the presence of stochastic noise in the responses of velocity sensitive neurons. This noise in the initial assessment of velocity in the responses of velocity sensitive neurons was instantiated in the form of additive Gaussian noise with a known mean and standard deviation. This noise introduces an uncertainty in the assessment of speed based on initial responses. As a result, the visual system cannot compute the speed of a visual stimulus using a deterministic approach. Rather, it must use a probabilistic approach, in which perceived speed represents a best guess, given a pattern of activation in MT speed-tuned cells and the visual system's prior knowledge about the properties of motion. We modelled the response of velocity-tuned units to a motion stimulus based on the response properties of speed-tuned MT neurons. These units are unresponsive to static stimuli and to motion in the direction opposite to their preferred direction of motion. We modelled the response properties of velocity-tuned units with a Gaussian in a logarithmic space. When presenting a stimulus moving at velocity *v* in unit *i*'s preferred direction, its response level can be represented as:

$$R_i = SA + N + c_m^q \times (1 - SA) \times \exp\left\{ - \frac{\left[\log 2|v| - \log 2|PV_i|\right]^2}{\sigma_v^2} \right\},$$

where PV_i corresponds to the unit's preferred velocity, *SA*, to its level of spontaneous activity, σ_v to a parameters representing the unit's velocity-tuning width, c_m to the contrast of the moving stimulus, and *N*, to Gaussian noise in the responses of these speed-tuned cells. The parameter *q* corresponded to an exponent that a compressive nonlinearity in unit response. This is similar to MT cells, which show clear response saturation as the contrast of a stimulus increases (Sclar, Maunsell, & Lennie, 1990). We set *q* to a value of 0.4 based on the values for this parameter calculated by Hürlimann et al. (2002). The standard deviation of the Gaussian noise was set to 0.025 and its mean, to 0. The response curves of a series of speed-tuned cells are depicted in Figure 17. As a result of these units' velocity tuning, the presentation of a The response properties of such units reflect well the response properties of MT cells, which are well described by a Gaussian over a lognormal space (Anderson, Nover, & De Angelis, 2003).

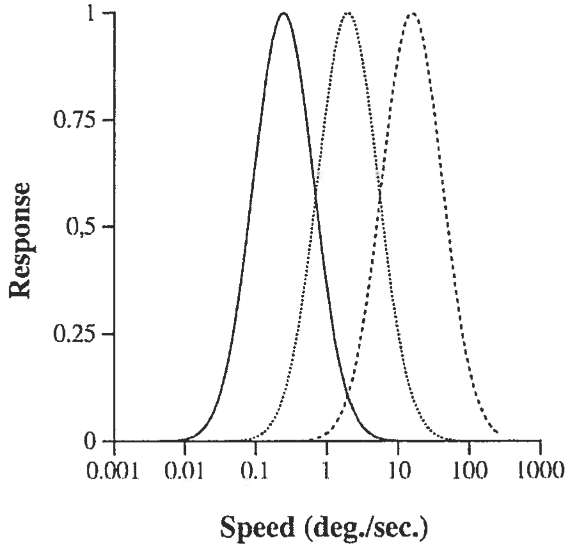

Figure 17. Response level of three velocity-tuned units to stimuli drifting at different speeds in their preferred direction. The full, dotted and dashed line respectively represent the response level of units tuned to speeds of 0.25, 2, and 16 deg./sec.

We have no doubt that, in its current form, this formal portrayal grossly oversimplifies the computations underlying velocity perception and contains a number of flaws. For instance, the level of noise remains constant regardless of stimulus contrast, and all velocity-tuned units had the same contrast-dependency of response level. Nevertheless, as we will show, this framework is sufficient to account for contrast effects on perceived velocity.

As a result of these units' velocity tuning, the presentation of a motion stimulus drifting, say, rightward at a velocity of 4 deg./sec. will produce different levels of activity among a population of velocity-tuned units. Units whose preferred velocity most closely corresponds to the velocity of the motion stimulus will be the most activated. No change will occur in the response level of units tuned to motion velocities in the opposite direction. Units whose preferred velocity differs markedly from the presented motion will only be slightly activated, or not at all (i.e., they will maintain their spontaneous firing rate). This distribution of activity is similar to the likelihood function in Bayesian modelling in that activity reflects an initial assessment of velocity, made without taking the statistical properties of motion into account. This population response may form the basis on which an initial assessment of velocity may be founded.

Within this approach, the contrast of the motion stimulus changes the activity of motion sensitive units. The effect of contrast on the responses of a population of velocity-tuned unit is plotted as a function of their preferred velocity. The value of v_0 was chosen so that the weight given to the velocity-tuned unit with the slowest preferred velocity corresponded to a value of 1. Figure 18 illustrates velocity-tuned unit responses to a high and a low-contrast motion stimulus drifting at 4 deg./second as a function of unit preferred velocity. As shown in Figure 18 similarly to a likelihood distribution, the responses of a population of speed-tuned units can be represented as a distribution, in which the response level of speed-tuned units can be plotted as a function of their preferred velocity. At low contrasts, units whose preferred velocity corresponds closely to the velocity of the motion stimulus are less activated than at high contrasts, producing a weaker signal of stimulus velocity within the population. Units that are unresponsive to the motion stimulus at high contrasts due to the difference between stimulus velocity and their preferred velocity remain unresponsive at low contrasts. That is, these cells will, on average, maintain their spontaneous firing rate even in the absence of their preferred velocity. As a consequence, even though a high contrast and a low contrast motion stimulus both preferentially activate the same velocity-tuned neurons, the decrease in the activation of these neurons in the low contrast condition produces a lower signal to noise ratio within the neuronal population signalling velocity.

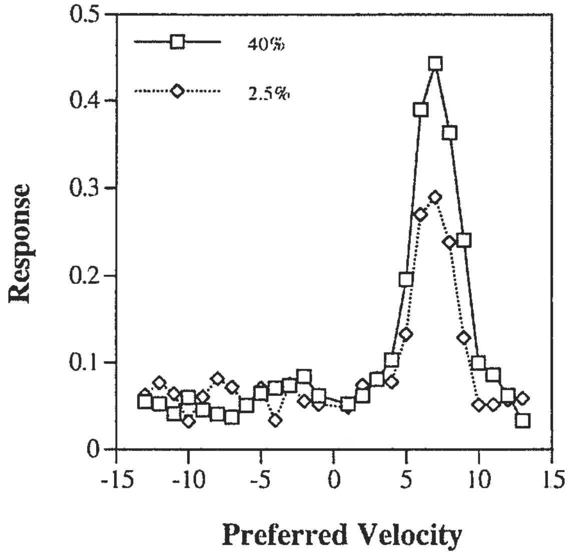

Figure 18. (a) Response level of velocity-tuned units as a function of their preferred velocity $\left[{PV_i}/{|PV_i|} \times \log 2 \left| {PV_i}/{v_0} \right| \right]$ and stimulus contrast. Please note that positive and negative velocity values correspond to an equal preferred speed of motion, but in opposite directions.

If, as suggested, the visual system possesses knowledge about the properties of motion in the physical world that it uses in processing the motion velocity signal, then implementation of this knowledge requires some type of modification of the initial velocity signal. The visual system's prior knowledge that slow velocities are more common than fast ones can be implemented in a number of ways. We propose that the visual system implements its knowledge that slow velocities are more common than fast ones by giving the neurons signalling slow velocities a greater weight in the computation of motion velocity. That is, the visual system's prior knowledge that slow velocities are more common than fast one is expressed in the form of weights, with slow velocities being given a greater weight than rapid ones in the computation of velocity. This bias favouring slow velocities was originally modelled to follow a Gaussian distribution (Weiss et al., 2002). However, subsequent research has found that the prior has significantly heavier tails than a

Gaussian and follows a power law function (Stocker & Simoncelli, 2005). The function describing the relationship between the weights given to a velocity-tuned unit in the subsequent computation of velocity as a function of the unit's preferred velocity can thus be described by:

$$w_i = a|PV_i|^n ,$$

in which n was given a negative value, producing a smaller neural weight for units having a faster preferred velocity. This value was set to –0.15, considerably smaller than Stocker and Simoncelli's value of –1.4. We opted to do this because using their value would have almost completely eliminated the responses of the fastest velocity-tuned units in the subsequent computation of motion velocity.

The resulting neural weight is illustrated in Figure 19 as a function of preferred velocity. The greater probability for slower velocities in the prior is reflected by the greater weight given to units tuned to slow velocities than to units tuned to rapid velocities.

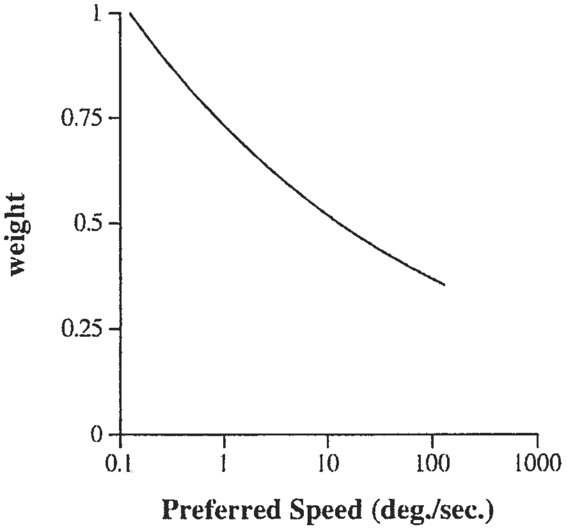

Figure 19. Weight given to a speed-tuned unit in a subsequent representation of velocity as a function of the unit's preferred speed.

Taken together, the responses of the initial velocity assessment and the neural weights can be used to compute responses at a subsequent stage that reflects both the initial assessment of velocity and the visual system's prior knowledge that slow speeds are more common than fast ones. The response of a velocity-tuned unit at this subsequent stage of processing is obtained by:

$$R'(PV) = R(PV) \times w(PV)$$

The pattern of weighted outputs is similar to the posterior distribution in Bayesian modelling: it takes both the sensory input and the visual system's prior knowledge about the world into account. Figure 19 depicts the pattern of activity resulting from the presentation of a 4 deg./sec. (see Figure 18 for the initial pattern of activity) high or low contrast motion stimulus at this subsequent stage of representation.

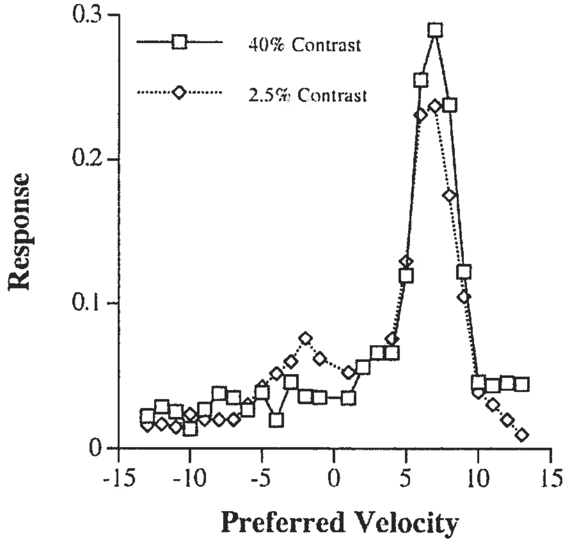

Figure 20. Weighted output of velocity-tuned units as a function of unit preferred velocity $\left[\frac{PV_i}{|PV_i|} \times \log 2\left|\frac{PV_i}{v_0}\right|\right]$ and motion stimulus contrast.

In the model initially proposed by Weiss et al. (2002), the Bayesian observer's final estimate of velocity was determined by a *maximum a posteriori* (MAP) decision rule, in which the final velocity estimate corresponds to the velocity that has the highest probability in the posterior distribution. The visual system's equivalent of the maximum *a posteriori* decision rule would correspond to a "winner-take-all" mechanism in which perceived velocity corresponds to the preferred velocity of the most active units. Alternative computational approaches proposed for the processing underlying the perception of visual velocity have taken the form of vector summation and vector averaging. Rather that a winner-take-all computation, we opted to use a vector averaging computation to determine the Bayesian observer's final assessment of velocity (v') because this computational approach allows the expression of a vast range of perceived velocities with a limited number of preferred velocities. The final assessment of velocity was thus obtained by:

$$v' = \frac{\sum_i R'_i \times PV_i}{\sum_i R'_i}$$

We simulated the performance of a Bayesian observer in a speed-matching task. On each trial, the Bayesian observer computed the speed of two stimuli drifting at a speed of 4 deg./sec.: a test stimulus, whose contrast was varied, and of a 10% Michelson contrast standard motion stimulus. The "perceived" speed of the variable contrast stimulus relative to the perceived speed of the 10% contrast stimulus was recorded at the end of each trial. The mean relative perceived speed of the test stimulus is shown in Figure 21. As we can see, this model can qualitatively predict the increase in perceived speed with increasing levels of motion stimulus contrast. This is consistent with the previous reports that the final speed estimate of a Bayesian observer, like those of human observers, are contrast dependent (Hurlimann et al., 2002; Weiss et al., 2002).

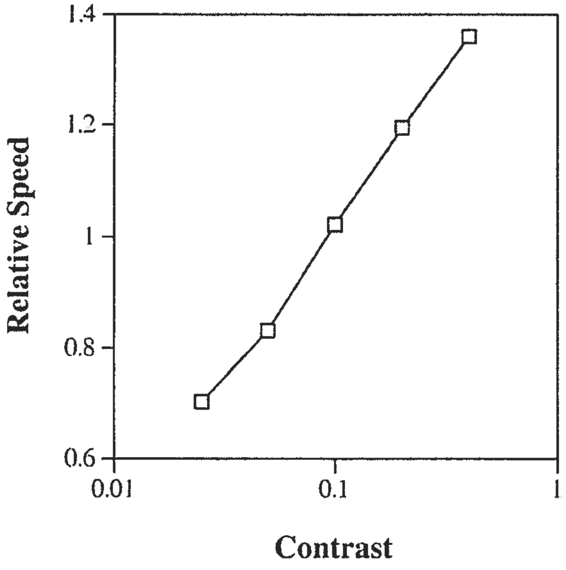

Figure 21. Speed of a test motion stimulus reported by a Bayesian observer relative to a 10% Michelson contrast stimulus drifting at the same physical speed as a function of test stimulus contrast.

Texture effects on perceived speed

In the previous section, we discussed the effects of luminance contrast on perceived speed within the context of a Bayesian model of velocity estimation. Another factor that has been shown to influence the perceived speed of a moving stimulus is the presence of static luminance texture (Brown, 1931; Gogel & McNulty, 1983; Norman et al., 1996; Blakemore & Snowden, 2000; Nguyen-Tri & Faubert, 2004). Similarly with increasing the contrast of the motion stimulus, these studies have reported that increasing the contrast of static luminance texture increases the perceived speed of a moving stimulus. Blakemore and Snowden (2000) also report a decrease in the dependency of perceived speed on motion stimulus contrast with increasing levels of static luminance texture contrast. This effect is mainly due to the fact that increasing the contrast of static luminance texture increased perceived speed at low motion stimulus contrast, but not at high motion stimulus contrasts. The proposal that normalization errors cause the contrast dependency has difficulty explaining these effects of static luminance texture on the perceived speed of a drifting grating.

A motion contrast model, based on the response of velocity sensitive neurons, has been proposed for induced motion and related phenomena (Nakayama & Loomis, 1974). This model is supported by the discovery of cells sensitive to relative motion between its central and surround areas in the pigeon tectal area (Frost & Nakayama, 1983), the cat suprasylvian visual area (von Grünau & Frost, 1983) as well as monkey cortical areas MT (Lagae et al., 1989) and MST (Tanaka et al., 1986). These cells respond optimally when the motion present in the center of its receptive field is in the direction opposite to the motion present in its surround, regardless of the absolute direction of motion. When presenting motion in the same direction, but at different speeds, to the center and surround region of such cells, they become more responsive as the speed difference between the two regions increases. Thus, this proposal can potentially explain the reported difference in the perceived speed of two dots moving at identical velocities depending on the speed of surrounding dots moving in the same direction (Loomis & Nakayama, 1973). However, the motion contrast proposal cannot account for the finding that increasing the speed of drifting dots in an annulus produced a decrease in the perceived speed of drifting dots in a central region, regardless of whether the dots in the annulus drifted in the same direction as the central region or in the opposite direction (Norman et al., 1996). These authors mention the possibility that the velocity signals are rectified, essentially suggesting that the mechanism underlying texture effects on perceived speed may be a speed-contrast mechanism.

In the previous section, we have proposed that a Bayesian framework in which perceived speed constitutes an optimal solution for a visual system operating in the presence of uncertainty provides a suitable theoretical framework to express the effects of contrast on perceived velocity. Similarly, we also believe that the effects of static luminance texture on perceived velocity can be modeled in a Bayesian context. While Gogel and McNulty's (1983) suggestion that luminance texture increases perceived speed by increasing relative motion cues for the effects of texture on perceived speed seems reasonable, it lacks a way to computationally represent the effects of texture on perceived speed.

Here, we suggest that the addition of static luminance texture increases the responsiveness of velocity-tuned units to motion in their preferred direction. As mentioned above, previous research has demonstrated that texture properties could modulate cell responses in area MT (Lagae et al., 1989) and MST (Tanaka et al., 1986) of the monkey. Norman et al. (1996), suggested, based on their psychophysical findings, that a rectification occurred in the motion signals of the center and surround areas. This "speed-contrast" mechanism would be maximally active when the texture surrounding the motion stimulus is stationary. In addition to the increase in perceived speed in the presence of texture, this model should also be able to explain the reported decrease in the contrast dependency of perceived speed with increasing levels of texture contrast (Blakemore & Snowden, 2000). Given that the velocity-tuned units described in the previous section are unresponsive to static luminance texture, this texture can only change perceived speed either by amplifying the signal of velocity-tuned cells. This is consistent with Norman et al's proposal (1996). We instantiated the proposed amplification of the motion response by making the exponent q (see Equation 3) dependent of the contrast of static luminance texture. This takes the form of:

$$q = {}^{q_0}\!/_{k^{c_t}}$$

where c_t represents the luminance contrast of a static luminance texture.

In this approach, increasing the contrast of static luminance texture amplifies the responses of the velocity-tuned units activated by the motion stimulus. This increase in unit activity is most noticeable at low contrasts than at high motion stimulus contrasts, where the responses of velocity-tuned units saturate. An interesting feature of this proposal is that static luminance texture will not affect the activity of motion sensitive units in the absence of a moving component.

The relative perceived speed reported by a Bayesian observer is illustrated in Figure 22 as a function of motion stimulus and static luminance texture contrast. As can be observed, in the absence of static luminance texture, a Bayesian observer's final assessment of speed will become faster as the contrast of the motion stimulus increases. Furthermore, the relative perceived speed reported by a Bayesian observer were faster with increasing levels of texture contrast. This is in agreement with previously reported effects of static luminance texture on perceived speed (Brown, 1931; Norman et al., 1996; Blakemore & Snowden, 2000; Nguyen-Tri & Faubert, 2004). However, increasing luminance texture contrast did not produce a uniform increase in perceived speed: larger increases in perceived speed occurred at low contrasts of the motion stimulus than at high motion stimulus contrasts. As a result of this, the relative velocity assessment tended to converge to similar values as motion stimulus and static luminance texture contrast increased. This produced a decrease in the contrast dependency of perceived speed with increasing levels of texture contrast. Thus, in addition to the increase in perceived speed, the model is capable of predicting the decrease in the contrast dependency of perceived speed with increased levels of static luminance texture contrast (Blakemore & Snowden, 2000). Within the Bayesian framework, this occurs because both texture contrast and stimulus contrast are used by the visual system to obtain a final estimate of velocity that it closer to the veridical velocity of the motion stimulus.

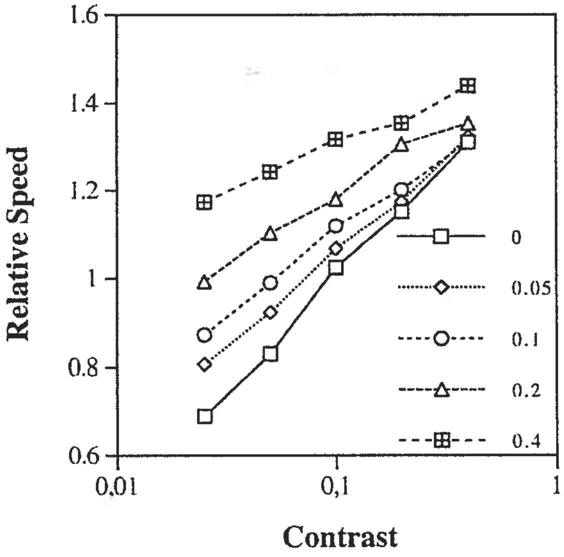

Figure 22. A Bayesian observer's reported perceived speed of a test stimulus relative to the perceived speed of a 10% contrast standard stimulus as a function test stimulus contrast and the contrast of the static luminance texture superimposed on the test grating.

Previous research on the effects of texture has also taken interest on the effects of dynamic texture on perceived speed. The studies have discovered that it produces different effects than static luminance texture. That is, it has been found that the perceived speed of a drifting grating is unaffected by the contrast of dynamic luminance noise (Nguyen-Tri & Faubert, 2004). These results are in agreement with the previous finding that the perceived speed of motion in RDKs is unaffected by coherence levels, provided that they remain well above direction discrimination thresholds (Zanker & Braddick, 1999). These authors attribute the failure of coherence levels to strongly influence perceived speed to a large, but incomplete segregation between the signal and noise motion components in the pooling process leading to the estimation of speed. It is proposed that a two-step strategy can account for this independence. In this strategy, the direction of RDK motion is first determined, and then the visual system relies exclusively on the units signalling the correct direction for the computation of speed. Although this proposal can account for the failure of noise contrast and coherence levels to alter the perceived speed of a moving stimulus, by itself, it is insufficient to explain the increase in perceived speed with increasing levels of static luminance texture contrasts (Brown, 1931; Gogel & McNulty, 1983; Norman et al., 1996; Blakemore & Snowden, 2000; Nguyen-Tri & Faubert, 2004).

We have suggested that the segregation of signal and noise motion components in the pooling process leading to the final estimate of speed may reflect a surface segregation mechanism. This is consistent with the observation that when drifting plaid patterns give rise to a transparent motion percept, observers see the component gratings as two surfaces drifting one on top of the other (von Grünau et al., 1993). This proposal is not inherently at odds with Zanker and Braddick's (1999) suggested strategy: it is possible that direction discrimination may form the basis for the surface segregation. If static luminance texture is added to a drifting grating, the surface formed by the static texture can be used as a spatial reference in the initial assessment of the drifting grating's velocity. In the case of dynamic luminance noise, the surface segregation mechanism allows the visual system to dismiss the dynamic noise in the assessment of speed because is does not provide a useful spatial reference to facilitate the initial assessment of the drifting grating's velocity. The proposed segregation between signal and noise motion components would result in a likelihood that is largely independent of the contrast of dynamic luminance noise because it does not provide any useful information to the initial assessment of velocity.

Motion Aftereffects

In the previous sections, we took interest in the factors that influence the perceived velocity of moving stimuli in the context of a Bayesian model of velocity perception. More particularly, we have taken interest in the effects of motion stimulus and texture contrast on perceived speed. In the present section, we will investigate the effects of texture on another motion phenomenon. It is reported that after prolonged viewing of a continuously moving stimulus, a subsequently presented stationary test stimulus appears to drift in the direction opposite to the adapting motion (Wohlgemuth, 1911). This illusory motion gradually slows down, until stopping completely. This phenomenon, known as the motion aftereffect (MAE), is one of the most extensively studied phenomena in motion perception. In this section, we present the results of an experiment on MAEs, and discuss them in the context of the Bayesian approach described in earlier sections.

Early explanations for the MAE argued that selective fatigue of direction-selective neurons during the adaptation period caused the illusory motion percept (Sutherland, 1961; Barlow & Hill, 1963). This account proposes that motion adaptation produces a selective fatigue of neurons whose preferred direction matches the direction of the adaptation stimulus. It is suggested that, as a result of this, these neurons will respond below their spontaneous level of activity upon presentation of a static test stimulus, whereas neurons tuned to the opposite motion direction will maintain their spontaneous firing rate. As a result of this imbalance in responding, an illusory percept of motion will occur. Alternative explanations for have also been proposed MAEs, such as recalibration (Dodwell & Humphrey, 1990), as well as the proposal that MAEs are the result of an error-correcting mechanism (Andrews, 1964).

Previous experiments on texture effects have found that adding static luminance texture in the area surrounding the adaptation and test stimuli increases the strength of MAEs (Day & Strelow, 1971). Based on these findings, the authors conclude that the MAE is essentially a relative motion phenomenon. In the current experiment, we will investigate the effects of luminance texture on MAE duration when it is superimposed on the motion stimulus. If, as suggested, MAEs are essentially a relative motion phenomenon, then superimposing static luminance texture should yield an increase in MAE strength. We also investigated the effects of static luminance texture on MAE duration because one of the key distinctions between first- and second-order (texture defined) motion is the failure of adaptation to second-order motion to generate static MAEs (Turano & Pantle, 1985; Derrington & Badcock, 1985; McCarthy, 1993).

Explanations for this difference between first- and second-order motion have focused on either the properties of the motion stimulus as well as differences in the properties of the motion systems underlying the perception of these two types of motion. For instance, it has been proposed that second-order motion is primarily encoded by a feature-tracking mechanism, since adaptation to stimuli considered to favour such processes does not generate compelling static MAEs (Anstis & Mather, 1985). It now looks unlikely that this is the case, given that second-order motion stimuli support a number of phenomena that rule out feature-tracking strategies (Cavanagh & Mather, 1989). It has also been proposed that, given the poor sensitivity to second-order motion, a stationary carrier may reinforce the immobility of the test stimulus or override weak motion signals (Ledgeway, 1994). We believe that it is unlikely that static texture prevents MAE build-up by overriding weak motion signals, given that psychophysical experiments have found that static luminance texture increases perceived motion speed (Brown, 1931; Gogel & McNulty, 1983; Norman et al., 1996; Nguyen-Tri & Faubert, 2004) and that this increase in perceived speed is greater at low motion stimulus contrasts (Blakemore & Snowden, 2000), when motion signals are weakest. In the current experiment, we investigated the extent to which differences between first- and second-order motion adaptation in generating MAEs was attributable to texture itself, given that second-order stimuli necessitate the presence of a carrier luminance texture.

Methods

Observers

Three observers participated in the study. All observers had normal or corrected to normal visual acuity. One of the observers (DN) was also an author on this article. The remaining observers were naïve regarding the hypotheses of the experiments.

Apparatus and stimuli

An Apple PowerMac G3 computer was used in order to generate stimuli and collect the data. Stimuli were presented on an Apple studio display monitor with a mean luminance of 38 cd/m^2 and a 120 Hz frame rate. Lookup tables were used to gamma-correct gun outputs. Stimuli were generated and the data were collected using MATLAB and the extensions provided in the Psychophysics Toolbox (Brainard, 1997) and low-level Videotoolbox (Pelli, 1997).

Stimuli were presented through a hard-edged circular aperture subtending four degrees of visual angle in diameter. On all trials, a vertically oriented 0.5 cycles/degree sinusoid grating drifting at a speed of 8 deg./sec along the horizontal axis (4 Hz temporal frequency) was presented during the adaptation period. Grating contrast was set to 15% Michelson contrast. Two types of binary luminance noise could be added to the motion stimulus: static or dynamic luminance noise. During the test period, the sinusoid grating always remained static.

In the first-order conditions, the drifting grating presented during the adaptation period was luminance-modulated at 15% Michelson contrast. In one condition, no noise was added to the drifting grating. In the other two conditions, static or dynamic luminance noise was added to the drifting grating. The luminance noise had a grain size of two pixels (4 minutes of arc) and was modulated at 30% Michelson contrast. In the dynamic conditions, a new noise field was randomly generated every four frames (noise refresh of 30 Hz). In the static condition, the luminance noise remained static throughout the adaptation and test period. In the dynamic conditions, the luminance noise was dynamic for both the adaptation and the test period.

In the second-order condition, a static carrier noise was multiplied with a 0.5 cycles/degree sinusoidal modulation. Because these second-order gratings require carrier noise to be visible, there was no “noise absent” condition for these stimuli. The contrast modulation depth of the second-order stimuli was 100%, with a maximum local luminance contrast of 30% Michelson contrast and a minimum local contrast of 0% Michelson contrast. In the dynamic condition, the same noise refresh rate (30 Hz) was used for second-order motion as for first-order motion. A schematic depiction of the various noise (static vs. dynamic) and grating (first-order vs. second-order) combinations used during adaptation and testing is provided in Figure 23.

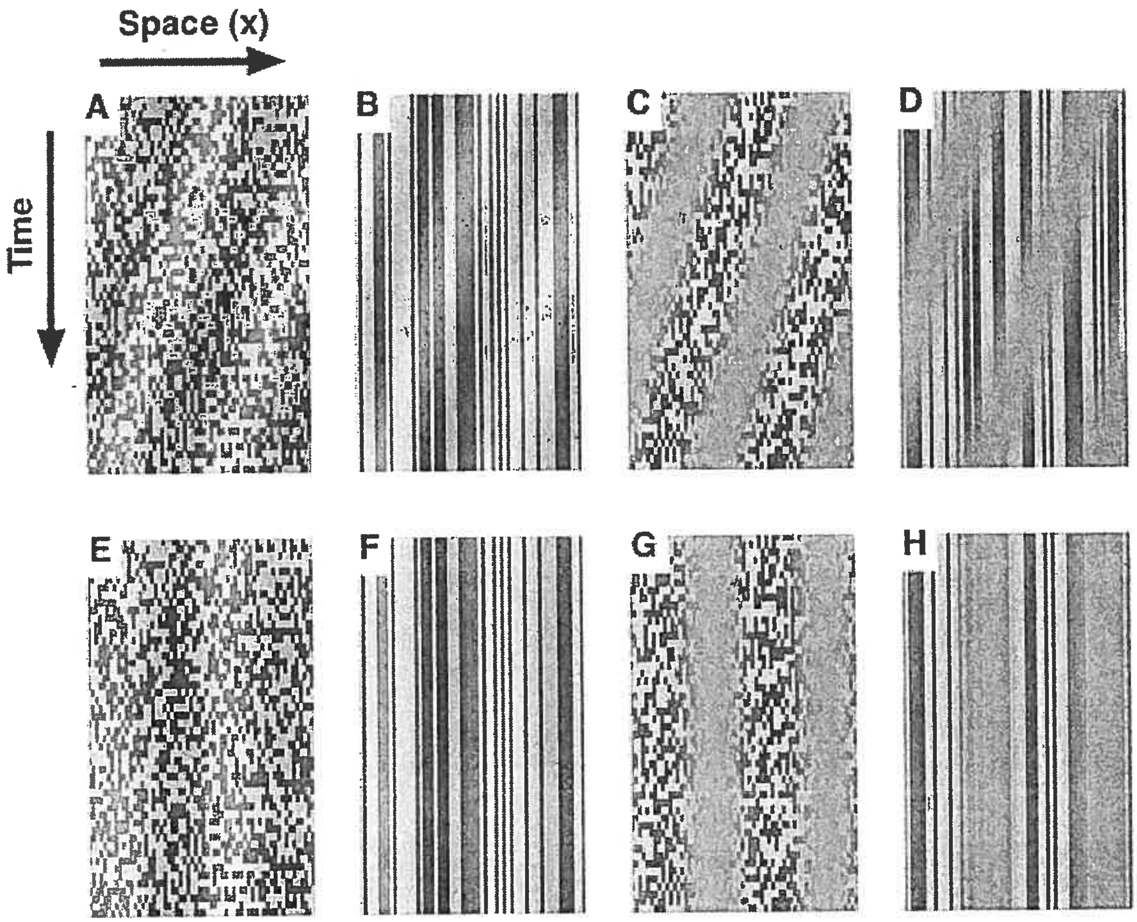

Figure 23. Space-time illustration of the various conditions tested in Experiment 1. Panels A-D represent the adaptation period and panels E-H represent the test period. Panel A: adaptation to a drifting first-order grating to which dynamic luminance noise is added, follwed by the test period, in which the luminance grating stops (panel E). Panel B: adaptation to a drifting first-order grating to which static luminance noise is added, followed by the test period (panel F). Panel C: Adaptation to a drifting second-order grating with a dynamic luminance-noise carrier, followed by the test period, during which the second-order grating is stationary, but the carrier remains dynamic (panel G). Panel D: adaptation to a drifting second-order grating with a static carrier, followed by a test preiod during which both the grating and the noise are static.

Procedure

Observers viewed the stimuli from a 57 cm viewing distance. Viewing was binocular. Observers initiated the first trial of each block with a key press and the remaining trials were run automatically.

A trial consisted of a 30 second adaptation period, immediately followed by presentation of the test stimulus. A fixation point was presented at all times during testing to indicate to observers where to focus their gaze during trials. During the adaptation period, observers were shown a luminance-modulated or a contrast-modulated sinusoid grating drifting along a horizontal axis. The direction of drift (left or right) varied randomly from trial to trial. The adaptation period was immediately followed by the test period, during which the sinusoid grating remained stationary. The observer's task was to indicate when the MAE was no longer visible by clicking a mouse button. Observers were further instructed to respond as rapidly as possible if no MAE occurred. The test stimulus was removed immediately after the observer reported no longer seeing a MAE. MAE duration was recorded after each trial. A 15 second inter-trial interval separated the end of each trial with the beginning of the next one.

Results

The duration of MAEs are shown in Figure 24 as a function of motion type (first-order or second-order) and noise type (static, dynamic, or no noise). For all observers, MAE duration was longest in the absence of a superimposed luminance texture. When static luminance texture was added to the motion stimulus, all observers reported a significant decrease in MAE duration for first-order motion stimuli. When using static texture, no significant difference in MAE duration existed between first and second-order motion.

When using dynamic luminance texture, observers reported longer MAE durations than with static luminance texture. This was the case for both the luminance and the contrast modulated noise. As with static luminance texture, we found no systematic difference in MAE duration between first and second-order stimuli in the dynamic luminance texture conditions.

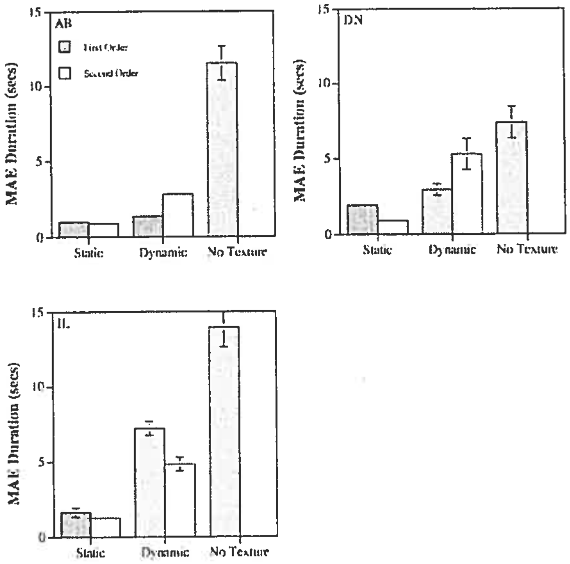

Figure 24. MAE duration as a function of noise and motion stimulus type. Grey bars represent the results for first-order motion stimuli and white bars, for second-order motion. Error bars show ±1 SEM.

Discussion

The results of this experiment demonstrated that superimposing luminance texture decreases MAE duration. This decrease in MAE duration in the presence of static luminance noise in Experiment 1 is in agreement with the previously reported effects of texture when the texture and motion stimulus occupy the same spatial location (Smith, Musselwhite, & Hammond, 1984). Because the adaptation stimulus used by Smith et al. (1984) contained both first- and second-order modulation, it could be argued that the effect of static texture on MAE duration was due to the presence of second-order motion during adaptation, which does not generate compelling MAEs. The results of this experiment suggest otherwise. That is, it is the presence of static luminance texture itself that produces a decrease in MAE duration when it is superimposed on the adaptation and test stimuli.

The results reported here also demonstrate that texture produces different effects on MAE when it is superimposed and when it is presented adjacently to the adaptation and test stimuli. That is, whereas superimposing texture produces a reduction in MAE duration, it has been previously reported that adding static texture in the area surrounding the motion stimulus increases MAEs (Day & Strelow, 1971; Strelow & Day, 1975). These different effects of texture on the MAE, depending on where it is located in relation to the adaptation and test stimuli, stand in contrast with the effects of texture on perceived speed, where texture increases perceived speed both when it is superimposed on the motion stimulus (Nguyen-Tri & Faubert, 2004) and when it is located in the near periphery of the moving stimulus (Brown, 1931; Norman et al., 1996; Blakemore & Snowden, 2000). Smith et al. (1984) suggest that the discrepancy between the effects of stationary luminance texture when it is located peripherally to the motion stimulus and when it occupies the same spatial location as the motion stimulus may be due to induced movement. That is, the moving bars might cause induced motion in the static texture in the direction opposite to the direction of the moving bars. Following the adaptation period, the induced motion would produce a MAE that would partially cancel out the main MAE.

Previous experiments in the MAE literature have reported that, contrary to luminance-modulated stimuli, adaptation to second-order motion fails to produce static MAEs (Turano & Pantle, 1985; Derrington & Badcock, 1985; McCarthy, 1993). In this experiment, we found that adaptation to a drifting luminance-modulated grating fails to elicit compelling MAEs when static luminance texture is superimposed on the adaptation and test stimuli. This suggests that the previously reported failure of second-order motion stimuli to elicit a compelling static MAE may stem from the presence of the stationary carrier necessary to generate second-order stimuli rather than a difference between the mechanisms underlying the perception of first- and second-order motion.

It seems unlikely that the decreased MAE durations in the presence of static luminance texture is due to a greater fatigue of motion-energy detectors in the absence of texture: motion energy detectors (Adelson & Bergen, 1985) are unresponsive to static stimuli. Further, static texture produces an increase in MAE duration when it is presented adjacently to the adaptation and test stimuli (Day & Strelow, 1971). Given that static luminance produces similar effects on perceived speed regardless of whether it is superimposed or presented contiguously with the motion stimulus, it also appears highly improbable that the decrease in static MAE duration in the presence of static luminance texture was attributable to its effects on the perceived velocity of the adaptation stimulus. It also appears unlikely that the decrease in MAE duration when static luminance texture is added to a first-order adaptation and test grating is due to a decrease in the visibility of the test grating, because MAEs decrease with increasing levels of test pattern contrast (Keck, Palella, & Pantle, 1976; Ishihara, 1999).

Early explanations for MAEs suggested that neuronal fatigue was responsible for MAEs (Sutherland, 1961; Barlow & Hill, 1963). However, the neural fatigue explanation encounters a number of shortcomings. For instance, some neurons do not show signs of fatigue with continuous stimulation (van de Grind, Grûsser, & Lukenheimer, 1973). Furthermore, electrophysiological studies on the effects of motion adaptation have reported that adaptation to motion produces no change in the subsequent spontaneous activity of complex cells upon presentation of a blank field or of a stationary pattern (Hammond, Mouat, & Smith, 1988), although psychophysical studies found that these conditions elicit MAEs. Additionally, some visual aftereffects need only a brief adaptation period to be observed (Wolfe, 1984; Harris & Calvert, 1989). Finally, the time course of recovery doesn't match what would be expected from neural fatigue: some aftereffects may occur hours or even days after the end of adaptation (Stromeyer 3rd, 1978). It thus seems improbable that MAEs occur due to the selective fatigue of motion detectors whose preferred direction matches that of the adaptation stimulus.

As a result of these shortcomings, alternative hypotheses have been suggested to account for MAEs. For instance, it has been proposed that the MAE could be accounted for by an error-correcting perceptual mechanism (Andrews, 1964) or a recalibration (Dodwell & Humphrey, 1990) of the visual system. The recalibration hypothesis, based on earlier work by Andrews (1964) and by Helson (1964), suggests a functional role for aftereffects. That is, the recalibration hypothesis proposes that rather than being the result of neural fatigue or some other flaw in the computation of motion velocity, MAEs constitute the result of an attempt by the visual system to maintain the phenomenological world in agreement with the statistical properties of motion in the physical world. It is suggested by Andrews (1964) that an error-detecting mechanism detects discrepancies between the properties of the perceptual world and the known statistical properties of the physical world.

In the case of the MAE, it is proposed that the statistical property that the visual system attempts to maintain in the perceptual world is that, on average, motion velocity is zero (Andrews, 1964). This, however, constitutes a long-term statistical property of motion: it is frequently being violated in the short-term. The error-detecting device must therefore ignore these short-term violations. However, if we present motion at a constant velocity in one part of the visual field, as occurs during motion adaptation, a consistent discrepancy will arise between the percept of continuous motion and the long-term statistical properties of motion in the physical world. Andrews (1964) has proposed that an error-detecting device notices this discrepancy and attempts to bring our percept of motion back in line with the long-term statistical properties of the physical world by performing an inverse transformation on its input. This produces a reduction in the motion percept of the adaptation stimulus, thereby reducing the discrepancy between the perceived motion and the long-term statistical properties of motion. After the adaptation period, the subsequent presentation of a static test stimulus will produce a motion percept, this time in the direction opposite to the direction of adaptation. The error-correcting device will again detect the discrepancy between this illusory motion percept and the long-term statistical properties of the physical world, and will recompute a transfer function until the illusory motion disappears.

The recalibration (Dodwell & Humphrey, 1990) and the adaptation level (Helson, 1964) hypotheses hold that a shift in the visual system's metric during adaptation is responsible for the MAE. In this proposal, stationarity is thought of as a null point lying along a continuum ranging from, say, rapid leftward motion to rapid rightward motion. However, the brain has no metric to represent the physical world that is independent from its own activity. As a result, the visual system must monitor its own activity in order to determine if the metric is well calibrated. Similar to the error-correcting account (Andrews, 1964) the recalibration hypothesis proposes that a consistent discrepancy between a continuous percept of motion and the assumption of average zero motion in the physical world during the adaptation period will be detected by an error-detecting mechanism. In response to this discrepancy, the visual system will shift its internal metric in order to maintain the motion percept in agreement with the statistical properties of motion. As a result of this metric shift, the subsequent presentation of a stationary test grating will produce a velocity measurement that doesn't lie on the internal metric's null point, producing an illusory motion percept in the direction opposite to the adapting motion. As the test period progresses, the discrepancy between the illusory motion and the statistical properties of motion will again be detected by the error-detecting mechanism, and the visual system will again shift its internal metric until the illusory motion percept comes to a stop.

According to both the error-correcting (Andrews, 1964) and the recalibration (Dodwell & Humphrey, 1990) hypotheses, the statistical property of motion in the physical world that the visual system attempts to maintain in the perceptual world is that, on a continuum ranging from, say, rapid motion to the left to rapid rightward motion, the average motion velocity is zero (i.e., stationary). This statistical property is strikingly similar to the Bayesian model's formal representation of the assumption that slow speeds are more common than fast ones (Weiss et al., 2002). The visual system's prior knowledge of this property was represented formally in the prior by a Gaussian probability distribution, in which both the velocity with the highest probability and the average velocity corresponded to a velocity of zero. The presentation of continuous motion in one part of the visual field during the adaptation period produces a violation of this assumption.

In the case of the Bayesian model, the prior distribution expresses the visual system's internal representation that slow velocities are more common than fast ones in the physical world. However, like the metric proposed in the recalibration (Dodwell & Humphrey, 1990) and adaptation level (Helson, 1964) hypotheses, the visual system has no means to determine whether or not this internal representation is well calibrated that is independent from its own activity. The prior must therefore be calibrated based on the visual system's own activity in order to maintain a percept of motion that is consistent with the statistical properties of motion in the physical world.

For instance, let us suppose that an observer is presented continuous rightward motion in one part of the visual field for an extended time period, as occurs during the adaptation period of MAE experiments. The resulting motion percept and neural activity are discrepant with the assumption that zero motion velocity is the most prevalent (and average) velocity in the physical world. This percept of continuous motion could originate from two possible sources: 1- continuous physical motion in this area of the visual field or 2- a miscalibrated prior. Because the visual system has no way to measure motion velocity that is independent of its own activity, it also has no means to determine which of these two factors is the primary contributor to the percept of continuous motion. Given that the Bayesian model assumes that a velocity of zero constitutes both the most probable and the average velocity in the physical world, the visual system will attempt to bring the perceptual world in agreement with these statistical properties.

We have proposed earlier in this paper that the visual system's bias towards slow velocities is expressed in the relative weights of velocity-tuned neurons in the subsequent computation of velocity, with neurons signalling slow velocities being given a greater weight than neurons signalling rapid velocities. Here, we suggest that the visual system recalibrates these weights on the basis of a comparison between the weighted output of velocity-tuned units and an output template (*O*), representing their normal output when motion velocity of zero. During sustained viewing of a motion stimulus moving at a constant velocity, a consistent discrepancy occurs between the neural activity elicited by the motion stimulus and the activity predicted by the template. As a result of this consistent discrepancy between the pattern of activity among velocity-tuned neurons and their expected activity, the neural weight of these neurons changes in order to minimize the discrepancy between perceived velocity and the long-term statistical properties of motion in our environment. The neural weight w_i at iteration j can be represented by:

$$w_i(j) = w_i(j-1)^p + CR[R'_i - O_i],$$

where *CR* denotes the change rate of the weights. The effects of continuous adaptation to a motion stimulus drifting at a velocity of 4 deg./sec. on the weight given to velocity-tuned units in the subsequent computation of velocity is shown in Figure 25. As can be observed, the recalibration of the weights produces a reduction in the weight of the units signalling the velocities closest to the stimulus velocity following the continuous presentation of a stimulus moving at a constant velocity during the adaptation period.

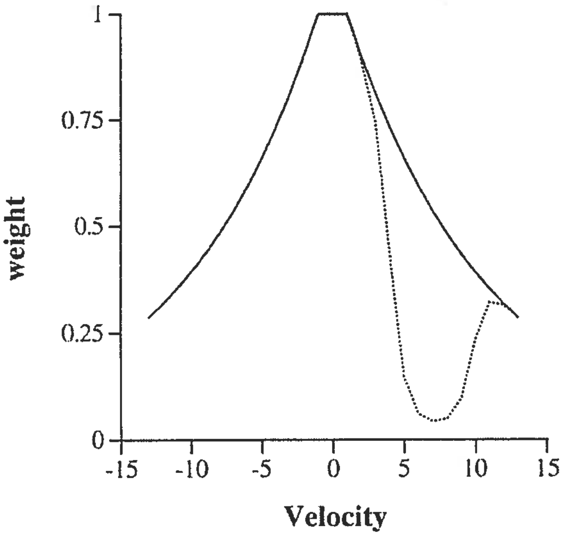

Figure 25. Weight given to the responses of velocity-tuned units in the subsequent computation of velocity prior to adaptation (full line) and after 100 iterations of adaptation to motion at 4 deg./sec. (dotted line) as a function of unit preferred velocity

$$\left[PV_i \big/ \left| PV_i \right| \times \log 2 \left| PV_i \big/ v_0 \right| \right].$$

As a result of this recalibration of the weights given to velocity-tuned units, adaptation to continuous motion at a constant velocity changes the posterior distribution produced by the presentation a static test stimulus. The weighted unit responses produced by the presentation of a stationary test following adaptation to a motion at 4 deg./sec. are illustrated in Figure 26 as a function of unit preferred velocity. As we can observe, the weighted unit outputs are higher for motion in the direction opposite to the direction of motion, especially at speeds equal to the speed of the adaptation stimulus. As indicated by the arrow, the vector average resulting perceived velocity is in the direction opposite to the direction of motion. Thus, the proposal that the visual system shifts its prior during adaptation is able to account for the static MAE.

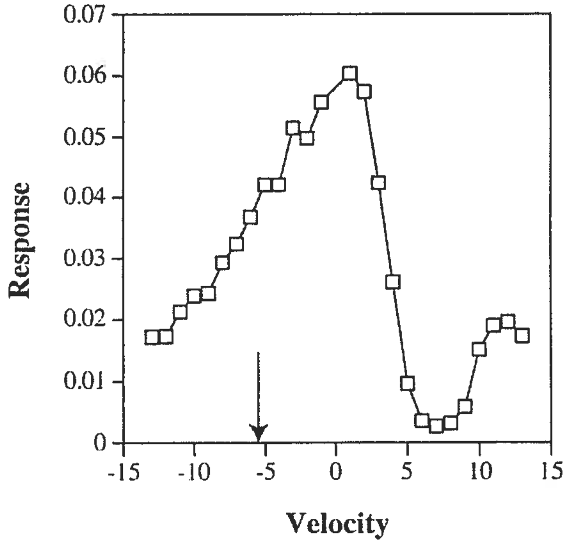

Figure 26. Mean weighted output of velocity-tuned units as a function of their preferred velocity $\left[{PV_i}/{|PV_i|} \times \log 2 \left| {PV_i}/{v_0} \right| \right]$. The arrow represents the perceived velocity determined from these weighted unit outputs using a vector-average computation.

We simulated the performance of a Bayesian observer in an MAE duration task. We simulated the effects of 500 iterations to motion at 4 deg./sec. on the weight of velocity-tuned units. Following this "adaptation period," we simulated the responses of velocity-tuned units to a subsequently presented static test stimulus. We then computed the number of iterations necessary for the perceived velocity to fall below a threshold velocity value. This value was set to 0.0625 deg./sec. (the slowest preferred velocity of our model's velocity-tuned units) in the direction opposite to the motion adaptation stimulus. We simulated the effects of motion adaptation at 5, 10, 20 and 40% Michelson contrast on "MAE duration". The effect of adaptation stimulus contrast on the number of iterations necessary for the motion percept to fall below the threshold velocity is illustrated in Figure 27. As we can observe, "MAE duration" increased with increasing adaptation stimulus contrasts. This is in agreement with previous reports in the literature (Nishida, Ashida, & Sato, 1997; Ishihara, 1999). Within the context that we have proposed, it is the greater activation of the velocity-tuned units responsive to the motion stimulus that produces the faster perceived velocity at higher motion stimulus contrasts (Thompson, 1982; Stone & Thompson, 1992; Blakemore & Snowden, 1999). This greater activation of velocity-tuned units at high motion stimulus contrasts also creates a greater discrepancy between the activity template, which resembles the activity of the velocity-tuned units in the absence of motion, and the weighted output of these units. As a result, the weight of these units has to be decreased by a greater amount in order to bring the weighted output pattern back in line with the activity template. As illustrated in Figure 29, this also has the effect of bringing the motion velocity reported by the Bayesian observer closer to a velocity of zero, which is in agreement with what is proposed by the recalibration hypothesis (Dodwell & Humphrey, 1990).

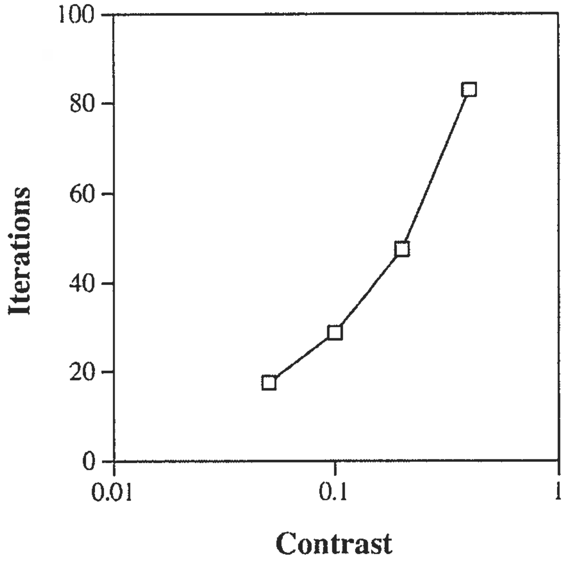

Figure 27. Number of iterations necessary for the percept of velocity reported by a Bayesian observer to be below the preferred velocity of the slowest velocity-tuned unit in the direction opposite to the direction of adaptation.

In addition to the reports that static MAE duration increases with higher contrasts of the adaptation stimulus, it is also reported that higher adaptation stimulus contrasts increase the perceived speed of the MAE (Ishihara, 1999). As well as being able to qualitatively predict the classic static MAE and the dependence of MAE duration on adaptation stimulus contrast, the proposal that a shift in the prior distribution occurs during the adaptation period can also account for the dependence of perceive speed of MAEs on motion stimulus contrast, as shown in Figure 28. As with MAE duration, the increase in the perceived speed of the MAE with increasing adaptation stimulus contrast is attributable to the greater discrepancy between the weighted outputs of the velocity-tuned units responding and their expected output at high motion stimulus contrasts.

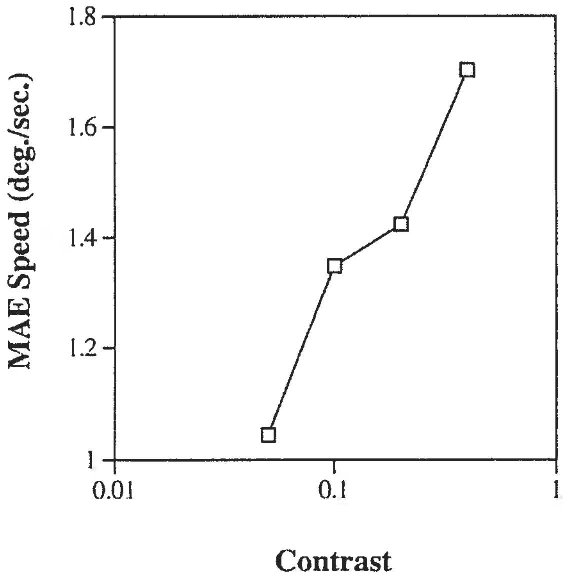

Figure 28. Initial speed of the MAE (deg./sec.) reported by a Bayesian observer as a function of adaptation stimulus contrast.

In addition to being able to account for the classic static MAE, the proposal that a shift in the prior distribution occurs during the adaptation period can also account for various findings in the MAE literature. For instance, it is reported that MAE strength is contrast dependent: static MAE duration and perceived speed increase with higher contrasts of the adaptation stimulus and decrease as the contrast of a static test stimulus increases (Nishida et al., 1997; Ishihara, 1999). As was modelled in Equation 3, the response level of velocity-tuned units is dependent on stimulus contrast. As discussed in the previous sections, within a Bayesian context, it is this higher level of responding that causes drifting high contrast patterns to appear to move faster than low contrast patterns (Thompson, 1982; Stone & Thompson, 1992; Blakemore & Snowden, 1999). Because of the higher level of activity among the velocity-tuned units, a greater discrepancy exists between the expected weighted output of velocity-tuned units and their actual weighted output for high contrast motion adaptation stimuli than for low contrast motion stimuli. The weight of the velocity-tuned units responsive to the motion stimulus would therefore have to undergo a greater shift in order to bring the final percept of velocity back in line with the long-term statistical properties of the physical world.

It has been suggested that static luminance texture produces an increase in perceived speed increasing the relative motion cues (Gogel & McNulty, 1983). In the theoretical framework provided by the Bayesian model, this was represented as an increase in the responses of velocity-tuned units in the presence of luminance texture, producing a stronger velocity signal. This proposal can account for the increase in perceived speed in the presence of static luminance texture as well as previous reports of a reduction in the contrast dependency of perceived speed with increasing levels of texture contrast (Blakemore & Snowden, 2000). Depending on its location, static luminance texture produces different effects on MAEs. That is, whereas static luminance texture increases MAE strength when it is located adjacent to the adaptation and/or test stimulus (Day & Strelow, 1971), it leads to a reduction in MAE strength when it is spatially coextensive with these stimuli (Smith et al., 1984). Static luminance texture must therefore produce different effects depending on where it is located relative to the adaptation and test stimuli.

One possibility is that superimposed static texture prevents the build-up of the MAE by minimizing the prior shift during the adaptation period. The proposed cause for the prior shift during adaptation is that the visual system attempts to maintain the percept of continuous motion in line with the long-term statistical property that the average motion velocity in the physical world is zero. It accomplishes this by changing the weight of the velocity-tuned units responsive to the motion stimulus so that their output resembles their output in the absence of motion. We have proposed that static luminance texture and the motion stimulus are represented as two distinct surfaces, which produce two different velocity assessments. If static luminance texture is superimposed on the adaptation grating, the pattern of activity in the velocity-tuned units assessing the static texture's velocity does not violate the long-term statistical properties of the physical world. Because it is in agreement with the long-term statistical properties of motion in the external world, this second assessment of velocity may therefore reduce or completely prevent the prior shift from occurring during the adaptation period. As a result of this minimized prior shift, a subsequently presented test stimulus will produce a weaker MAE in the presence of static luminance texture.

Within this framework, a decrease in the uncertainty of the initial assessment of velocity in the presence of static luminance texture may account for the failure of adaptation to second-order motion, such as contrast-modulated noise, to generate a MAE when tested with static second-order patterns (Ledgeway & Smith, 1994). Given that the presence of static luminance texture is necessary to generate second-order stimuli, it is possible that it is static luminance texture itself, rather than a fundamental difference between first- and second-order motion mechanisms, that explains the failure of adaptation to second-order motion to elicit a MAE.

The suggestion that the MAE can be explained in a Bayesian framework of perceived velocity by a shift in the prior in the direction opposite to the direction of adaptation can account for the decrease in the perceived speed of a motion stimulus drifting at a constant velocity following prolonged viewing (Wohlgemuth, 1911; Gibson, 1937). This occurs as a result of the decreased weight of velocity-tuned units responding to the motion stimulus during prolonged viewing. As illustrated in Figure 29, the prior shift occurring during the prolonged viewing of a grating drifting at a constant velocity will produce a decrease in the perceived speed reported by the Bayesian observer. Further, a test stimulus drifting in the same direction but at a slower speed than the stimulus presented during adaptation will also produce a slower perceived speed (Carlson, 1962; Scott, Jordan, & Powell, 1963; Rapoport, 1964; Thompson, 1981; Ledgeway & Smith, 1997).

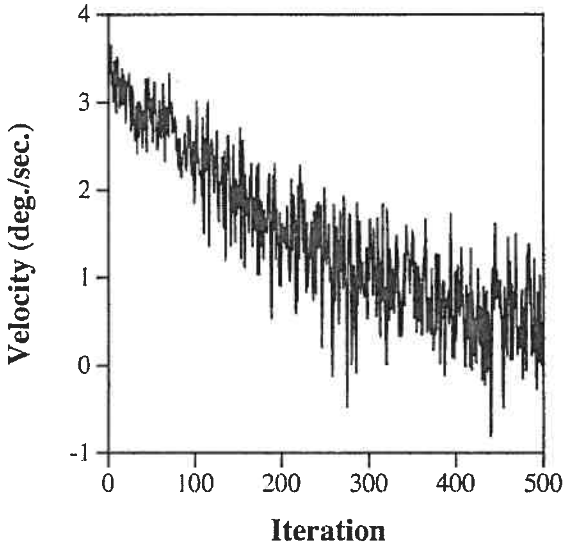

Figure 29. Velocity reported by a Bayesian observer of a motion stimulus drifting at 4 deg./sec. as a function of iteration number.

General discussion

In the previous sections, we have described a possible implementation of the Bayesian model of velocity perception based on the activity of velocity-tuned units with properties similar to the velocity-tuned neurons found in area MT (Maunsell & Van Essen, 1983; Perrone & Thiele, 2001; Anderson et al., 2003). In the model originally proposed by Weiss et al., (2002), noise in the visual system's initial assessment of velocity made it impossible to use a deterministic approach to accurately compute motion velocity. Consequently, in addition to the sensory input, the visual system had to rely on its prior knowledge about the statistical properties of motion in the external world in order to compute the most probable motion velocity. Hence, unlike previous models proposed for motion illusions, these phenomena are not the result of flawed computations. Rather, motion illusions are considered to be optimal solutions for a visual system designed to operate in the presence of uncertainty, given its prior knowledge about the statistical properties of motion in the physical world and the pattern of activity elicited by the sensory input.

In the implementation that we proposed for the Bayesian model, the likelihood function, representing the visual system's initial assessment of velocity, is expressed in the pattern of activity in a population of velocity-tuned units possessing different preferred velocities. The visual system's prior knowledge that slow velocities are more common than rapid ones is expressed in the weight given to the responses of velocity-tuned units in the subsequent computation of velocity. That is, units tuned to slow velocities are given a greater weight than units tuned to fast velocities. The final estimate of velocity was determined based on these weighted responses using a vector-averaging computation. This constitutes a departure from the MAP decision rule, whose neural equivalent is a "winner-take-all" computation, in which perceived velocity corresponds to the preferred velocity of the unit with the maximum weighted output. We opted for vector averaging because it allows the expression of a broad range of velocities with relatively few velocity-tuned receptors. As demonstrated in previous sections, this model was capable of explaining illusions such as the contrast-dependency of perceived speed (Thompson, 1982; Stone & Thompson, 1992; Blakemore & Snowden, 1999). We also find that this model makes it possible to express a number of previously made proposals for various motion phenomena, such as the proposal that static texture increases perceived speed by increasing relative motion cues (Gogel & McNulty, 1983), or the proposal that MAEs occur due to a recalibration of the visual system during motion adaptation (Dodwell & Humphrey, 1990).

Principles in neurophysiology can be expressed within this model. For instance, although the model originally proposed by Weiss et al. (2002) performed poorly when trying to quantitatively predict the perceived velocity of human observers, implementing contrast gain control in the form of a compressive nonlinearity in the representation of contrast significantly improved the match between predicted and experimental data (Hurlimann et al., 2002). Here, we also showed that explanations previously proposed to account for various phenomena in motion perception could be cast within the Bayesian framework. For instance, the principles of the recalibration (Dodwell & Humphrey, 1990) and error-correcting (Andrews, 1964) hypotheses for MAEs were expressible within a Bayesian framework. Within this context, rather than the visual system's metric, it is our internal representation of the statistical properties of motion in the physical world that are recalibrated in order to maintain the perceptual world in agreement with the properties of the physical world. This recalibration occurs because the only cue that the visual system is well calibrated is the weighted output of velocity-tuned units. The proposal that static luminance texture could be used as a reference to assess motion was also found to be expressible within a Bayesian framework: the effect of static luminance texture contrasts on the perceived speed of a moving stimulus could be explained in terms similar to those used to model the effects of contrast on perceived speed. That is, texture increases the perceived speed of a motion stimulus by increasing the signal within the velocity-tuned units responsive to the motion stimulus.

The Bayesian model of velocity perception could also potentially explain other phenomena reported in the motion perception literature. For instance, it has frequently been reported that chromatic motion perception is degraded relative to the perception of luminance-modulated motion stimuli: isoluminant chromatic motion stimuli seem to move more slowly (Moreland, 1982; Cavanagh et al., 1984; Mullen & Boulton, 1992; Nguyen-Tri & Faubert, 2002) and less smoothly (Mullen & Boulton, 1992) than luminance-modulated stimuli drifting at equal physical speeds. In some cases, the decrease in the perceived speed of isoluminant chromatic stimuli can even produce "motion standstill", in which visible moving chromatic stimuli do not appear to move (Ramachandran & Gregory, 1978; Cavanagh et al., 1984; Livingstone & Hubel, 1987; Lindsey & Teller, 1990; Mullen

& Boulton, 1992; Lu, Lesmes, & Sperling, 1999b; Nguyen-Tri & Faubert, 2002). Another aspect in which the chromatic motion percept is degraded relative to the percept of achromatic motion is in direction discrimination thresholds: whereas detection and direction discrimination thresholds are nearly identical for luminance-modulated stimuli, it has been reported that detection thresholds are significantly lower than direction discrimination thresholds for moving chromatic gratings (Lindsey & Teller, 1990; Mullen, Yoshizawa, & Baker, 2003).

Various tentative explanations have been put forward in order to account for the slower perceived speed of chromatic motion at isoluminance. It has been suggested that drifting chromatic stimuli appear to move more slowly than achromatic stimuli because their neural coding is similar to that of low-contrast luminance stimuli and that isoluminant motion stimuli don't isolate chromatic mechanisms (Troscianko & Fahle, 1988). An alternative explanation for the slow perceived speed of chromatic motion at isoluminance is the proposal that there is a miscalibration in velocity decoding units for chromatic motion (Cavanagh & Anstis, 1991). This explanation is similar to the explanation proposed by Stone and Thompson (1992) for the contrast dependency of perceived speed: these authors propose that a normalization error accounts for the percept of slowed chromatic motion at isoluminance. That is, because direction sensitive cells are sensitive to both the contrast as well as the velocity of a chromatic motion stimulus, they cannot unambiguously encode its velocity. As a result of this, the input of a second type of cells sensitive to the contrast of the drifting stimulus, but not to its velocity, is necessary in order to obtain an unambiguous estimate of velocity. This input allows the assessment of the contribution of contrast to directional-cell responses. It is suggested that these non-directional units are more sensitive to contrast than the directional units signalling chromatic motion, causing an overestimation of the contribution of colour modulation to the responses of these directional units. Consequently, the visual system will underestimate the speed of chromatic motion.

The Bayesian model of velocity perception, which proposes that motion illusions occur because these percepts represent optimal solutions for a visual system designed to operate in the presence of uncertainty, stands in sharp contrast with the miscalibration hypothesis for the slow perceived speed of chromatic motion. Rather than errors in the computation of chromatic motion velocity, the slower perceived speed of chromatic motion at isoluminance could constitute the result of a greater uncertainty in the initial assessment of velocity for chromatic stimuli than for luminance-modulated stimuli. This is compatible with the suggestion that luminance provides a strong input to the motion system, whereas the *L-M* (red-green) and *S* (blue-yellow) colour mechanisms provide weaker inputs to the motion system (Dougherty, Press, & Wandell, 1999; Nguyen-Tri & Faubert, 2002). This proposal is supported by fMRI recordings in human observers (Wandell et al., 1999) and electrophysiological recordings (Seidemann, Poirson, Wandell, & Newsome, 1999). Both of these studies find that isoluminant patterns stimulating the *S*-cones, generated a weaker signal than luminance in area MT. In a Bayesian context, this weaker signal would produce a slower perceived for chromatic stimuli than luminance-modulated ones.

In its current form, the model proposed in this article cannot account for a number of phenomena reported in the motion literature. One of these phenomena is the decrease in static MAE duration with increasing test stimulus contrast (Keck et al., 1976; Ishihara, 1999). This failure occurs because the velocity-tuned units described in this article were unresponsive to static stimuli as well as to stimuli moving in their non-preferred direction. As a result, the contrast of static stimuli did not elicit any change in the activity of velocity-tuned units. However, the informal proposal that there is more information about the exact position and velocity of the test stimulus at high test stimulus contrasts is consistent with the observed effects of test stimulus contrast on the MAE.

In its current form, the Bayesian model also cannot account for the effects of stimulus structure on MAE duration (Fang & He, 2004). These experimenters measured static MAE duration with three types of wave forms: a sine wave, a square wave with an identical fundamental frequency, and the square wave components with scrambled phases. It was found that the longest MAEs were obtained with the sine wave stimulus. The scrambled phase stimulus resulted in a somewhat shorter MAE durations and the square wave stimulus produced the shortest MAEs. A cross adaptation experiment demonstrated that the determining factor of MAE duration was the type of test pattern, not adaptation. The authors argue that position reliability contributed to the minimized MAE duration when using square wave test patterns. This suggestion posits that if a stationary test stimulus provides reliable spatial position cues, then it will be harder to generate illusory motion. A square wave pattern, with its sharply localized boundaries, presumably provides such cues, which has the effect of minimizing MAE duration. This proposal is similar to the explanation given in the Bayesian framework for the dependency of perceived speed on pattern contrast: that there is more information about the exact speed of a stimulus at low contrasts than at high ones, yielding a more reliable initial assessment of speed.

As demonstrated earlier, although our model predicts the decrease in perceived speed following prolonged viewing of the motion stimulus. In general, this model predicts slower perceived speeds for test stimuli drifting in the same direction as the adaptation stimulus and faster ones for test stimuli drifting in the opposite direction. However, it has been reported that adaptation to motion in a given direction, produced a slower perceived speed for subsequently presented test stimuli drifting in the opposite direction (Carlson, 1962; Rapoport, 1964; Smith, 1985). The results of adaptation when the test grating is drifting in the same direction as the adaptation grating, but at a faster speed than are less clear: there are reports that the perceived speed of the test grating decreases of remains unchanged after adaptation (Scott et al., 1963; Thompson, 1981; Smith, 1985), while others report a faster percept of speed in these conditions (Carlson, 1962; Rapoport, 1964; Ledgeway & Smith, 1997). Thompson (1981) suggests that previous reports of increases in perceived speed may reflect a reduction in the apparent contrast of the moving grating following adaptation. Further, although Carlson (1962) reported that adaptation to motion produced a decrease in the perceived speed of a stimulus drifting in the same direction as the test stimulus, others have found an increase in perceived speed (Rapoport, 1964). While these contradictory results may be difficult to explain using any model, the clear result that perceived speed decreases sustained viewing of a motion stimulus is qualitatively predicted in this model.

In the current article, we have proposed a computational model of velocity perception in which the direction and speed of motion are encoded together. However, it has been proposed that a mechanism encodes speed without regards to motion direction (Smith & Edgar, 1994). If this is indeed the case, it is likely that the visual system's knowledge of the statistical properties of motion speed in the physical world are also implemented in the encoding of speed and that the statistical properties of motion direction are taken into account in the mechanism encoding direction. As suggested by Hurlimann et al. (2002), the elegant model proposed by Weiss et al. (2002) will have to lose some of its simplicity in order to account for human data. We have no doubt that the same can be said of the implementation of the Bayesian model that we discussed in the previous sections.

For instance, in the model described here, we accounted for static MAEs solely through a change in the weights given to velocity-tuned units in the subsequent computation of velocity. Thus, in its current form, the model did not take into account the desensitization of motion sensitive neurons that occurs as a result of motion adaptation (Hammond et al., 1988). Furthermore, in the model described in this paper, we simulated the effects of adaptation at a single site. However, it is likely that motion adaptation entails adaptation at multiple sites (Mather & Harris, 1998). This view is consistent with the differences found between static and dynamic MAEs (e.g. (Nishida, Ashida, & Sato, 1994)). In the model described here, we implemented a compressive nonlinearity in the responses of velocity-tuned units with increasing contrasts. However, the representation of contrast likely includes both an expansive nonlinearity near threshold and a compressive nonlinearity above threshold (Boynton, Demb, Glover, & Heeger, 1999). In the current model, the presence of noise in unit responses was instantiated in the form of additive

Gaussian noise with a known standard deviation. This stochastic noise in unit responses was independent of the unit's level of responding and of the unit's preferred velocity. However, a number of studies have argued that a more realistic representation of neural noise includes multiplicative noise as well as additive noise (Lu & Dosher, 1999; Kontsevich, Chen, & Tyler, 2002).

In conclusion, the Bayesian context provides a suitable theoretical framework to formally express top-down influences on perception. In the current article, we have proposed a model through which the visual system may implement its knowledge that slow velocities are more common than fast ones in the computation of velocity. The model proposed here had the advantage of casting the computations underlying perceived velocity within a biologically plausible framework. It was capable of explaining a number of phenomena in the motion literature. Further, it was found that various hypotheses given for motion phenomena were formally expressible within this framework. We also believe that higher-order effects, such as the effects of attention on motion perception (Cavanagh, 1992; von Grunau, Bertone, & Pakneshan, 1998), could also potentially be cast within the Bayesian framework discussed in this article.

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Conclusion

Dans le premier chapitre de cette thèse, nous nous sommes intéressés aux effets de la superposition de texture de luminance statique et dynamique sur la vitesse perçue d'un réseau en mouvement. Il a été proposé que l'augmentation dans la vitesse apparente d'un disque uniforme en mouvement lorsqu'on augmente le contraste de la texture de luminance sur laquelle le disque se déplace était attribuable à une augmentation dans la visibilité du disque en présence de texture à travers un traitement de deuxième ordre (Blakemore & Snowden, 2000). Dans notre expérience, il semble peu probable que la superposition de texture de luminance sur un stimulus de mouvement ait produit une augmentation dans la visibilité du stimulus de mouvement. En effet, il est rapporté que la visibilité d'un stimulus de luminance diminue lorsqu'on augmente le contraste d'une texture de luminance superposée (Gegenfurtner & Kiper, 1992). De plus, diverses expériences ont démontré que l'ajout de texture de luminance dans une région adjacente à un stimulus de mouvement produit un augmentation dans la vitesse perçue du mouvement (Brown, 1931; Gogel & McNulty, 1983; Norman et al., 1996). Or, il est rapporté que l'ajout de texture de luminance dans l'aire entourant un stimulus produit une diminution dans le contraste perçu du stimulus central (Chubb et al., 1989). Ceci n'exclut pas la possibilité qu'une augmentation dans la visibilité du stimulus de mouvement à travers des mécanismes de deuxième ordre ait pu contribuer aux résultats obtenus par Blakemore et Snowden (2000). Cependant, il semble peu probable que les effets de la texture de luminance statique sur la vitesse perçue d'un stimulus en mouvement soient strictement attribuables à une augmentation dans la visibilité du stimulus de mouvement.

Une hypothèse alternative proposée afin d'expliquer les effets de la texture de luminance sur la vitesse perçue est que la texture statique serve de point de référence afin de juger le mouvement relatif (Gogel & McNulty, 1983). Nakayama et Loomis (1974) ont proposé un mécanisme de contraste de vélocité ayant un antagonisme centre-pourtour afin d'expliquer les effets du mouvement relatif sur la vitesse perçue d'un stimulus de mouvement (Loomis & Nakayama, 1973). L'augmentation dans la vitesse perçue d'un stimulus en mouvement lorsqu'on augmente le contraste d'une texture de luminance statique est difficile à expliquer avec un tel le modèle puisque la texture statique et le stimulus de mouvement occupaient le même espace. Il est cependant possible que le centre ait répondu au réseau en mouvement et le pourtour, à la texture de luminance statique. Ce modèle a également de la difficulté à expliquer pourquoi la vitesse de points en mouvement dans une région centrale semble plus rapide lorsque les points dans une région périphérique sont statiques, peu importe les directions relatives du mouvement dans ces deux région (Norman et al., 1996). Ces auteurs proposent donc une rectification du signal de vélocité, de sorte que le mécanisme sous-jacent aux effets de la texture sur la vitesse perçue du mouvement est un mécanisme de contraste de vitesse. Bien que cette hypothèse parvienne à expliquer pourquoi la direction relative du mouvement dans les deux régions n'a pas d'effet sur la vitesse perçue, Norman et al. (1996) concèdent qu'elle peut difficilement expliquer pourquoi l'ajout de la texture de luminance statique produit une augmentation dans la vitesse perçue du mouvement.

Il est intéressant de noter que la vitesse perçue du réseau en mouvement augmentait lorsqu'on augmentait le contraste de la texture de luminance statique. Ceci soulève des question quant au mécanisme sous-jacent à l'augmentation de vitesse perçue, puisque la texture pourrait servir de point de référence peu importe son contraste, pour autant que le niveau de contraste demeure supra-seuil. Conséquemment, si, tel que suggéré, la texture de luminance statique produit une augmentation dans la vitesse perçue en servant de point de référence pour juger le mouvement relatif, nos résultats démontrent que la visibilité des ces points de références est un facteur important pour déterminer la vélocité.

Nous discutons de l'implémentation possible de la suggestion que l'indice de mouvement relatif fourni par la texture statique augmente la vitesse perçue dans le contexte d'un modèle Bayésien (Weiss et al., 2002) proposé afin d'expliquer divers phénomènes dans la perception du mouvement. Dans ce modèle, les illusions de mouvement surviennent car ces percepts constituent une réponse optimale, étant donné un intrant sensoriel bruité et les connaissances *a priori* du système visuel sur les propriétés statistiques du mouvement dans le monde externe. Ceci diffère fondamentalement des approches proposant que les illusions de mouvement soient le résultat d'erreurs computationelles dans le traitement de l'information de mouvement (e.g., Stone & Thompson, 1982). Il est à noter que dans ce cadre théorique, l'augmentation dans la vitesse perçue lorsqu'on élève le contraste du stimulus de mouvement ou lorsqu'on ajoute de la texture de luminance correspond à une vitesse perçue plus près de la vitesse véridique du stimulus. Le cadre Bayésien proposé dans la discussion de cette expérience est davantage élaboré dans la deuxième section de cette thèse.

Dans la seconde expérience du chapitre 1, nous avons investigué l'étendue spatiale sur laquelle la texture de luminance interagit avec le stimulus de mouvement ainsi que le schème d'intégration utilisé par le système visuel. Les résultats de cette expérience démontrent que la vitesse perçue d'un stimulus en mouvement augmente graduellement au fur et à la mesure qu'on augmente l'aire du stimulus en mouvement couverte par la texture statique. Ces données indiquent donc que la texture de luminance et le stimulus de mouvement interagissent sur un espace limité afin d'obtenir un estimé local de vélocité. Ceci est en accord avec des suggestions similaires dans la littérature (e.g., Norman et al., 1996). De plus, ces résultats nous permettent d'éliminer la possibilité que la vitesse perçue est déterminée en utilisant exclusivement la région texturée du stimulus en mouvement. Nous concluons donc que la texture de luminance interagit avec les mesures initiales de vitesse locales sur une relativement petite échelle spatiale et que ces mesures locales de vélocité sont ensuite intégrées afin d'obtenir une mesure globale de vélocité.

Dans la troisième expérience du premier chapitre, nous avons étudié l'effet de la texture de luminance dynamique (i.e., du bruit de luminance dynamique) sur la vitesse perçue du mouvement. Les résultats de cette expérience démontrent que, contrairement à la texture statique, le contraste d'une texture de luminance dynamique ne produit aucun effet sur la vitesse perçue d'un stimulus en mouvement. Ces résultats sont congruents avec l'absence d'effets que produit le niveau de cohérence d'un stimulus RDK (random dot kinematogram) en mouvement sur la vitesse perçue du mouvement (Zanker & Braddick, 1999). Ces auteurs expliquent leurs résultats en suggérant que les composantes de mouvement du signal et du bruit sont largement séparées dans le processus d'agrégation menant à l'estimation de la vitesse. Cette explication est compatible avec l'absence d'effets du contraste du bruit de luminance dynamique sur la vitesse perçue d'un réseau en mouvement. Cependant, cette proposition ne peut pas, à elle seule, expliquer l'augmentation de vitesse perçue d'un réseau en mouvement lorsqu'on augmente le contraste d'une texture de luminance statique superposée sur le stimulus de mouvement.

Nous avons suggéré que le mécanisme sous-jacent à l'indépendance de la vitesse perçue du mouvement sur le contraste d'une texture de luminance dynamique est un mécanisme de ségrégation de surface. Cette proposition est en accord avec l'observation qu'on perçoit deux surfaces distinctes lorsqu'on perçoit du mouvement transparent. lors de la présentation de stimuli de type « plaid » (von Grünau et al., 1993). Ce mécanisme permet une ségrégation des composantes de signal et de bruit de mouvement lorsqu'on superpose du bruit dynamique sur le stimulus de mouvement. Cette ségrégation de la composante de mouvement du signal (réseau en mouvement) et du bruit (bruit dynamique) a pour conséquence que le contraste du bruit ne produit pas d'effet sur la vitesse perçue du réseau en mouvement. Cependant, nous avons proposé que la superposition de texture de luminance statique entraîne une amplification du signal de vélocité en fournissant un référence spatiale pour juger le mouvement relatif.

Un mécanisme possible pour les effets de la texture de luminance statique sur la vitesse perçue est que la texture augmente le contraste total du stimulus composite. C'est à dire que la différence de luminance entre les régions les plus claires et les plus sombres du stimulus était plus importante lorsque de la texture de luminance statique était superposée sur le stimulus de mouvement que lorsqu'on présentait uniquement le stimulus de mouvement. Cependant, cette proposition diverge des modèles existants d'extraction de mouvement. Par exemple, les détecteur d'énergie de mouvements sont insensibles aux stimuli statiques (Adelson & Bergen, 1985). Le test du piédestal tire avantage de cette propriété des détecteurs d'énergie de mouvement afin d'étudier les mécanismes sous-jacents à la perception de différents types de mouvement (Lu & Sperling, 1995; Lu, Lesmes, & Sperling, 1999). De plus, le contraste entre les zones claires et sombres d'un stimulus augmente peu importe si on superpose de la texture statique ou dynamique à un réseau en mouvement. Cependant, nous avons trouvé que seul le contraste de texture statique produit une augmentation dans la vitesse perçue. Finalement, cette explication ne peut pas expliquer les effets de la texture de luminance lorsque celle-ci est située à une location adjacente au stimulus de mouvement (Brown, 1931; Gogel & McNulty, 1983; Norman et al., 1996) puisque cette texture ne change pas le contraste du stimulus de mouvement.

Dans le chapitre 1, nous avons suggéré d'intégrer la proposition que la texture de luminance statique augmente la vitesse perçue du mouvement en servant de référence spatiale pour juger le mouvement relatif à l'intérieur du cadre Bayésien. Cette proposition comporte l'avantage de pouvoir modéliser de façon formelle les effets de la texture de luminance sur les mécanismes sous-jacent au calcul de la vitesse. Dans ce modèle, la vélocité perçue d'un stimulus constitue une solution optimale, étant donné un intrant sensoriel bruité et les connaissances *a priori* du système visuel sur les propriétés statistiques du mouvement dans son environnement. La seconde partie de cette thèse met l'emphase sur le développement d'une implémentation du modèle Bayésien de la vélocité perçue à l'intérieur d'un cadre tenant compte de la physiologie du système visuel. Le modèle que nous proposons se base sur un intrant sensoriel bruité fourni par le patron de réponse d'unités sélectives à la vélocité afin d'estimer la vélocité à laquelle un stimulus de mouvement se déplace. Ces unités sélectives à la vélocité étaient modélisées afin d'émuler les propriétés des réponses des cellules sensibles à la vélocité qu'on retrouve l'aire MT (Anderson et al., 2003). Nous avons exprimé les connaissances *a priori* du système visuel sur les propriétés statistiques du mouvement dans le monde physique en donnant un plus grand poids aux unités signalant les vélocités lentes dans le calcul subséquent de la vélocité. Nous avons démontré que ce modèle était capable de prédire la dépendance de la vitesse perçue sur le contraste d'un stimulus en mouvement (Thompson, 1982; Stone & Thompson, 1992; Blakemore & Snowden, 1999).

Nous nous sommes également intéressés aux effets de la texture de luminance sur la vitesse perçue à l'intérieur de ce cadre Bayésien. Il a été suggéré que l'augmentation de vélocité perçue en présence de texture de luminance statique était attribuable à une augmentation des indices de mouvement relatif (Gogel & McNulty, 1983). Nous avons formalisé cette suggestion par une amplification du signal de vélocité en présence de texture de luminance statique. Cette proposition était en mesure d'expliquer les effets de la texture de luminance statique sur la vitesse perçue d'un stimulus en mouvement (Brown, 1931; Gogel & McNulty, 1983; Norman et al., 1996; Blakemore & Snowden, 2000; Nguyen-Tri & Faubert, 2004). Nous avons également démontré que cette suggestion pouvait prédire la diminution dans la dépendance de la vitesse perçue d'un stimulus en mouvement sur le contraste de celui-ci lorsqu'on augmente le contraste d'une texture de luminance (Blakemore & Snowden, 2000).

Dans le chapitre 2, nous présentons également les résultats d'une expérience sur les effets de la superposition de la texture de luminance sur la durée des ECMs (effets consécutifs de mouvement). Ces résultats démontrent que la superposition de texture de luminance produit une diminution marquée dans la durée des ECMs : ces conditions ne généraient pas d'ECMs ou des ECMs plus courts qu'en l'absence de texture de luminance. Aucune différence systématique dans la durée des ECMs n'était observable entre les stimuli de premier-ordre auquel on avait ajouté de la texture de luminance et les stimuli de deuxième-ordre. Nos résultats suggèrent donc que l'échec de l'adaptation au mouvement de deuxième-ordre à produire des ECMs statiques (Turano & Pantle, 1985; Ledgeway & Smith, 1993; McCarthy, 1993) est peut-être attribuable à la texture de luminance nécessaire afin de générer des stimuli de deuxième-ordre. La diminution dans la durée des ECMs lors de la superposition de texture de luminance est en accord avec les résultats rapportés précédemment dans la littérature (Smith et al., 1984). Il est cependant rapporté que l'ajout de texture de luminance statique dans la périphérie du stimulus d'adaptation et du stimulus test produit une augmentation de la force des ECMs (Day & Strelow, 1971). Il semble donc que la texture de luminance influence les ECMs statiques différemment quand elle est superposée sur le stimulus d'adaptation et quand elle est située dans un location adjacente au stimulus de mouvement.

Différentes hypothèses ont été proposées afin d'expliquer les ECMs. Parmi ces hypothèses, on retrouve la suggestion que ce phénomène est le résultat d'un mécanisme détectant les erreurs (Andrews, 1964) ou d'une recalibration du système visuel (Dodwell & Humphrey, 1990) au cours de la période d'adaptation. Dans ces modèles, le système sous-jacent à la perception du mouvement est recalibré en se basant sur la « diète perceptuelle » de mouvement. La raison proposée pour la changement dans la calibration du système visuel est une incongruité entre le mouvement perçu et l'assomption qu'à long terme, la vélocité moyenne du mouvement est de zéro (Dodwell & Humphrey, 1990). Cette supposition sur les propriétés statistiques du mouvement est en accord avec les propriétés de la distribution *a priori* proposée par Weiss et al., (2002). Nous avons trouvé que ces propositions étaient exprimables à l'intérieur du contexte Bayésien décrit dans le chapitre 2. Nous attribuons les effets consécutifs de mouvement à une recalibration de l'*a priori* au cours de la période d'adaptation. L'*a priori* ne constitue donc pas une représentation interne immuable des propriétés du mouvement, mais est constamment recalibrée afin de maintenir un percept de mouvement en accord avec les propriétés statistiques à long terme du mouvement dans le monde physique. Ceci implique un processus itératif surveillant l'extrant pondéré des unités accordées à la vélocité et changeant les poids afin de maintenir un certain patron d'activité. Cette implémentation permet de prédire non seulement l'ECM statique classique, mais également la dépendance de la durée et de la vitesse de l'ECM sur le contraste du stimulus d'adaptation (Keck et al., 1976; Nishida et al., 1997; Ishihara, 1999). Dans ce contexte, nous proposons que, puisque la texture de luminance superposée ne contrevient pas à l'assomption que la vélocité moyenne du mouvement est de zéro, elle minimise la recalibration du système visuel au cours de la période d'adaptation, minimisant ainsi l'ECM lors de la période test.

Parmi les phénomènes que le modèle Bayésien décrit dans le chapitre 2 pourrait potentiellement expliquer, on retrouve également la lenteur du mouvement perçu des stimuli chromatiques isoluminants (i.e., définis uniquement par des différences de couleur) relativement à la vélocité perçue de stimuli de luminance (Moreland, 1982; Cavanagh et al., 1984; Mullen & Boulton, 1992; Nguyen-Tri & Faubert, 2002). Similairement aux effets du contraste sur la vitesse perçue, il a été proposé que la différence de vitesse perçue entre le mouvement chromatique et le mouvement de luminance est attribuable à une erreur dans la normalisation du signal de mouvement de stimuli chromatiques (Cavanagh & Anstis, 1991). Une hypothèse alternative pour ce phénomène de mouvement est que l'intrant sensoriel fourni par les mécanismes chromatiques aux mécanismes sous-jacents à la perception du mouvement est plus faible que l'intrant sensoriel fourni par les mécanismes sensibles au contraste de luminance (Dougherty et al., 1999; Nguyen-Tri & Faubert, 2002). Ceci peut être représenté par une réponse plus faible des unités sélectives à la vélocité du mouvement pour les stimuli de mouvement chromatiques isoluminants que pour les stimuli ayant une modulation de luminance. Cette proposition est en accord avec des enregistrements électrophysiologiques chez le singe (Seidemann et al., 1999) ainsi qu'avec les données fMRI chez l'humain (Wandell et al., 1999) démontrant que des stimuli chromatiques isoluminants produisent une activité plus faible dans l'aire MT que des stimuli de luminance. Dans le modèle discuté dans le chapitre 2, une réponse plus faible des unités accordées à la vélocité émulant les propriétés de cellules dans l'aire MT produit une estimation finale de vélocité plus lente.

Comme nous l'avons démontré dans le chapitre 2, le contexte Bayésien fournit un cadre théorique permettant d'exprimer formellement les diverses hypothèses proposées afin d'expliquer des phénomènes dans la perception du mouvement. Cependant, diverses modifications pourraient être apportées au modèle afin de mieux tenir compte de la physiologie du système visuel et afin que le modèle puisse expliquer davantage de phénomènes dans la perception du mouvement. Par exemple, le modèle présenté dans le chapitre 2 était unidimensionnel : la vélocité préférée des unités sélective à la vélocité était représentée sur un seul axe. La direction préférée d'une unité sélective à la vélocité était exprimée par la polarité de la vélocité préférée. Une représentation plus réaliste du mouvement dans le plan fronto-parallèle implique une représentation bidimensionnelle des vélocités préférées de mouvement. Un tel modèle pourrait potentiellement prédire les effets de différents paramètres sur notre tendance à percevoir du mouvement cohérent ou du mouvement transparent lors de la présentation de stimuli « plaids ».

Dans le chapitre 2, nous avons expliqué les ECMs par un changement au niveau des poids donné aux diverses unités sélective à la vélocité dans le calcul subséquent de la vélocité du mouvement au cours de la période d'adaptation. En réalité, l'adaptation au mouvement implique fort probablement plusieurs sites d'adaptation (Mather & Harris, 1998). Il est à noter que le modèle décrit dans le deuxième chapitre pourrait également potentiellement prédire les ECMs dynamiques observables lors de la présentation d'un stimulus test directionnellement ambigu (McCarthy, 1993; Ledgeway & Smith, 1994). Par exemple, la présentation d'un réseau test papillotant en contrephase produirait un patron d'activité bimodal auprès des unités sensibles à la vélocité. Cependant, tel qu'illustré à la Figure 30, l'extrant pondéré des unités sensibles à la direction opposée au stimulus d'adaptation sera plus important, produisant un percept de mouvement dans la direction opposée au stimulus d'adaptation.

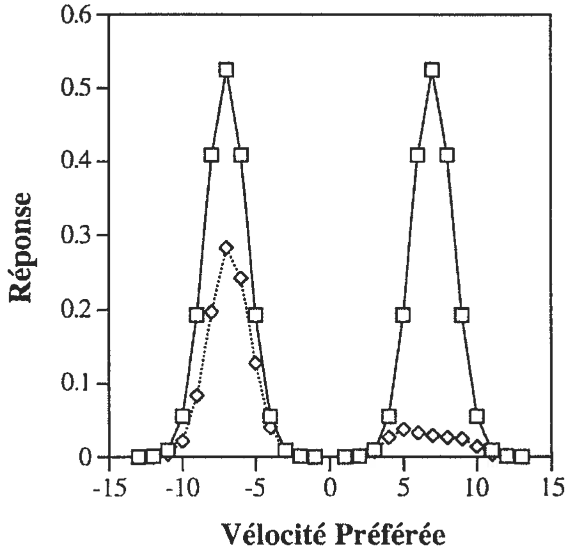

Figure 30. Taux de réponse (ligne pleine avec carrés) et taux de réponse pondéré (ligne pointillée avec losanges) d'unité accordées à la vélocité en fonction de leur vélocité préférée $\left[{}^{PV_i}\!/_{|PV_i|} \times \log 2 \left| {}^{PV_i}\!/_{v_0} \right| \right]$ lors de la présentation d'un réseau papillotant en contrephase suite à une période d'adaptation au mouvement.

Les ECMs dynamiques pourraient même être mieux expliqué que les ECMs statiques dans le cadre proposé au chapitre 2. En effet, il est proposé que les ECMs dynamiques constituent le résultat d'une adaptation au niveau de l'aire corticale MT, tandis que les ECMs statiques reflètent davantage une adaptation au niveau du cortex visuel primaire (Mather & Harris, 1998). Ceci est en accord avec la découverte que l'ECM dynamique démontre des propriétés similaires aux cellules de l'aire MT. Par exemple, il a été trouvé un transfert interoculaire complet a été trouvé pour les ECMs dynamiques (Nishida et al., 1994), tandis que les ECMs statiques produisent seulement un transfert interoculaire partiel (Moulden, 1980). De plus, les ECMs dynamiques sont accordés à la vélocité (Ashida & Osaka, 1995) tandis que les ECMs statiques sont accordés à la fréquence temporelle (Pantle, 1974; Wright & Johnston, 1985). Il est à noter qu'une désensibilisation des unités sélectives à la vélocité du mouvement au cours de la période d'adaptation contribue probablement à l'ECM dynamique (Petersen, Baker, & Allman, 1985).

Dans le modèle proposé afin d'expliquer les ECMs, nous avons suggéré que le système visuel comparait le patron d'activité des unités sensibles à la vélocité du mouvement avec un « template » d'activité. Ceci produisait un changement dans les poids des unités dans le calcul subséquent de vélocité, de sorte que le patron d'extrants pondérés des unités ressemblait plus au « template ». Cependant, le « template » lui-même ne changeait pas. Il est cependant possible que le « template » d'activité change au cours de la période d'adaptation. Il est également possible que ce soit la vélocité perçue elle-même, plutôt qu'un « template d'activité » qui influence le poids donné aux unités sensibles à la vélocité du mouvement dans le calcul subséquent de la vélocité du mouvement.

Dans le modèle discuté dans le chapitre 2, la seule propriété du mouvement dans le monde physique que le système visuel utilisait afin d'estimer la vélocité du mouvement est que les vélocités lentes sont plus communes que les vélocité rapides. Cependant, le mouvement dans le monde physique possède également d'autres propriétés que le système visuel doit fort probablement utiliser afin d'interpréter un intrant sensoriel bruité. Par exemple, une propriété du mouvement que le système visuel pourrait potentiellement utiliser dans le calcul de la vélocité est l'inertie : la tendance d'un objet à maintenir une vélocité uniforme à moins qu'une force extérieure n'intervienne.

Nous avons proposé dans le chapitre 2 que la texture de luminance statique cause une augmentation dans la vitesse perçue d'un stimulus en amplifiant les réponses des unités accordées à la vélocité. Cependant, bien que des études électrophysiologiques aient démontré que la réponse de cellules sensibles au mouvement est influencée par les propriétés de la texture de luminance (Frost & Nakayama, 1983; von Grünau & Frost, 1983; Tanaka et al., 1986; Lagae et al., 1989), nous n'avons pas trouvé d'études ayant simplement comparé la réponse cellulaire en présence de texture statique et d'un champ uniforme. De telles études seraient en mesure d'évaluer la proposition que la texture de luminance cause une augmentation dans la vitesse perçue du mouvement en changeant la réponse d'unités encodant à la vitesse d'un stimulus en mouvement. De telles études permettraient également de comparer les effets de la texture de luminance statique et dynamique sur la réponse cellulaire à un stimulus en mouvement ainsi que d'évaluer les effets du contraste de la texture de luminance sur ces réponses.

Dans sa forme présente, le modèle que nous avons décrit dans le chapitre 2 ne peut expliquer certains phénomènes dans la perception du mouvement. Par exemple, ce modèle est incapable d'expliquer la diminution, voire l'inversion, de la dépendance de la vitesse perçue du mouvement sur le contraste du stimulus en mouvement lorsque le stimulus de mouvement se déplace rapidement (Thompson, 1982). Cependant, cet auteur a été incapable de reproduire cet effet lors d'une expérience subséquente et a conclu que les résultats originaux étaient attribuables à un artéfact lors de la première expérience (Stone & Thompson, 1992). Un autre phénomène que ce modèle ne permet pas d'expliquer est les effets du contraste du stimulus test sur les ECMs statiques (Keck et al., 1976; Nishida et al., 1997; Ishihara, 1999). Ceci se produit parce que les unités sélectives à la vélocité du stimulus en mouvement sont insensibles aux stimuli statiques.

En conclusion, il semble que les effets de la texture de luminance sur la vitesse perçue du mouvement puissent être modélisés dans un contexte Bayésien par un changement dans le signal d'unités accordées à la vélocité. Le modèle Bayésien du mouvement perçu propose que les illusions dans la perception du mouvement ne sont pas le résultat d'erreurs dans le traitement de l'information visuelle. Ces phénomènes se produisent plutôt parce que ces percepts constituent des solutions optimales pour un système visuel conçu afin d'opérer en présence d'incertitude. Divers aspects du modèle sont certainement modifiables afin de mieux tenir compte de la physiologie du système visuel, des propriétés du mouvement que le système visuel utilise afin d'interpréter l'intrant sensoriel et d'expliquer un plus large éventail de phénomènes. Cependant, nous sommes confiant que le principe central du modèle Bayésien (i.e., que le système visuel se base sur le propriétés du mouvement dans le monde physique afin d'interpréter un intrant sensoriel ambigu ou bruité) demeurera inchangé.

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