進出色・後退色研究の新たな展開：軸上色収差説を修正して復活させる

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研究成果報告書

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はしがき

色立体視の新しいモデルとして、軸上色収差も考慮に入れた「重心説」を提唱し、定説となっている軸外収差説より優れていることを明らかとした。色依存の諸現象と、色が運動視に及ぼす影響の研究も進めた。

①研究組織

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②交付決定額

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③研究発表（★は本報告書に掲載）

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栗木一郎・仲泊聡・北原健二（2003）低酸素脳症の一症例における特異な色同時対比特性　*VISION,* **15,** 233-244.

④特許等

栗木一郎　立体画像呈示方法並びに立体視画像生成投影装置及び呈示システム装置　特願 2004–227421　特許出願 2004-227421（2004 年 8 月 4 日），特許公開 2006-47601 (2006 年 2 月 16 日)」

進出色・後退色研究の新たな展開：軸上色収差説を修正して復活させる
—概要—

1. 進出色と後退色

進出色・後退色と呼ばれる現象がある。一般的には、赤いものが近くに見え、青いものが遠くに見えるとされる。

しかしながら、進出色・後退色はひとつの現象ではないし、赤が手前・青が奥という考え方自体が先入観的なものであり、その見えには例外もある。たとえば、背景が黒の場合は確かに赤が青よりも手前に見える人が多いのであるが（図 1）、背景が白の場合はその比率が逆転する（図 2）。この原因としては少なくとも 2 つあり、1 つは本研究テーマの色立体視であり、もう 1 つはコントラストの効果である。コントラストの効果とは、コントラストが低い輪郭を持つ図形はコントラストが高い図形に比べて遠くに見える（図 3）という現象である（*e.g.* O'Shea et al., 1994, *Vision Reseach,* **34,** 1595-1604）。

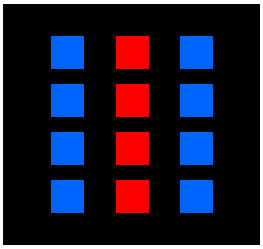


図 1 色立体視の例…赤が青よりも手前に見える人が多い。*

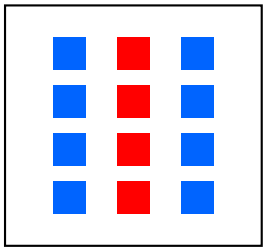


図 2 色立体視の逆転…青が赤よりも手前に見える人が多くなる。

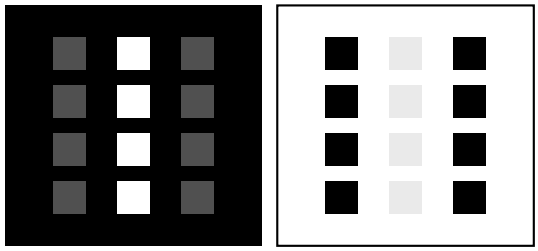


図 3 コントラストと遠近感…左図では白い正方形列が高コントラストで、手前に見えやすい。右図では黒い正方形列が高コントラストで、手前に見えやすい。

*以下、色立体視のデモ図は 1 メートル以上離れて見た方が効果が大きい。

2. 色立体視

みかけの距離で測定すると、健常者では赤は緑や青よりも手前に見え、赤と緑が区別できない色覚異常の人では赤は青より手前に見えるが、赤と緑には見えの距離の差はないという研究がある（Oyama and Yamamura, 1960, *Psychologia,* **3,** 191-194）。この研究では、本研究テーマである色立体視の色収差説を否定している。なぜなら、色覚異常の人も、眼の光学系に色収差はあるからである。

しかしながら、Oyama and Yamamura で測定されたものは絶対的距離知覚であり、単眼でも起こる現象である。一方、本研究がテーマとする色立体視は、色刺激の網膜像の水平方向の相対的位置ずれに基づく両眼立体視である。したがって、これらは別のものである。

色立体視（chromostereopsis）の定義としては、それが両眼立体視であること、単眼では色刺激の位置ずれが観測されること、の 2 点が必要である。本研究では、その位置ずれは光学系の色収差に依存するという考え方を踏襲する。しかし、以下に述べるように、色立体視の説明として広く受け入れられている「軸外収差説」を否定あるいは修正して、我々独自の「重心説」を新たに提唱する。

3. 軸上色収差説

色収差の考え方としては、軸上色収差と軸外色収差がある。

軸上色収差（longitudinal chromatic aberration）とは、眼の光学系は色収差を補正するメカニズムがないため、屈折率の大きい波長の短い光（青色光）は屈折率の小さい波長の長い光（赤色光）よりも、レンズに近い側で結像する（図 4）。この情報を脳が利用するのだと仮定すれば、青いものはより遠くに、赤いものはより近くに見えると言えるかもしれない。なぜなら、遠くのものは近くのものよりもレンズに近い側で結像するからである。

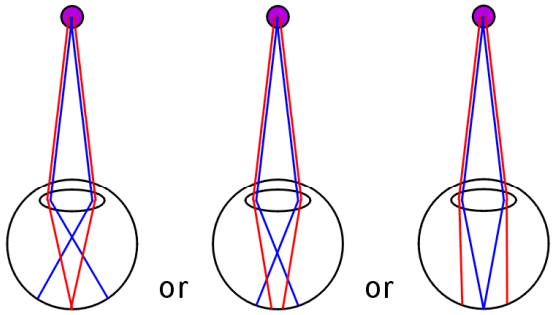


図 4 軸上色収差説…青は赤よりも相対的にレンズ寄りで結像するので遠くに見えると考える。

この考え方では、単眼でものを見ても色立体視が成立しなければならない。しかしながら、単眼では両眼で見た時のような強い効果は失われる。また、色立体視では、後述のように、青が赤よりも手前に見える人が少数ながらいるのであるが（第 6 項『色立体視の個人差』）、軸上色収差説では全く説明できないだけでなく、その事実は軸上色収差説の反証である。

4. 軸上色収差の観察

このように、色立体視の研究の中では、軸上色収差の考え方は真っ先に否定されるのであるが、そのため軸上色収差が色立体視に及ぼす影響の吟味は十分されてこなかったように思う。我々は、これに関して、2 つの問題設定を行い、詳細な現象観察を行なった。

問題設定の 1 つは、実際にこの色収差はあるのか、という点である。各種の教科書には当然のことのように書かれているが、日常において赤いものと青いものを見て、どちらか一方だけがぼけて見えるという経験はしない。この点を暗室で単波長光を用いて比較したところ、教科書通りの焦点ずれが観察された。赤にピントが合っているときは青がぼけて見え、青にピントが合っている時は赤がぼけて見えたのである。

おそらく、日常では色刺激は単波長光ではないことや、また背景からも光が来ることなどを利用して、この焦点ずれがわからないような知覚像を脳が積極的に作り出しているのであろう。つまり、脳としては軸上色収差による焦点ずれは厄介なものであるが、本研究においては、本研究の主張である重心説の論拠となる現象として、むしろ積極的にこの焦点ずれの存在を受け入れるものである。

観察者の報告を分析すると、赤の側にピントが合っている人が多く、青の側にピントが合っている人は少なかった。しかし、これについては遠視の人は青にピントが合いやすいようで、観察者に近視の人が多かったことがこの結果に影響しているようであった。なお、近視の人でも、刺激に目を近づけると、ピントが合う位置が赤から青に移動した。これは赤の屈折率が青より小さいため、赤にピントが合わなくなった時には、光学系がピントを合わせる位置を短波長側にシフトしたものと考えられる。遠視の人は屈折率の大きい青にピントを合わせておくのが楽なのかもしれない。

問題設定の 2 つ目は、ピントの好みが赤であるか青であるかということと色立体視の個人差（赤が手前に見える人と青が手前に見える人がいること）の関係である。もしこれらに関係があるならば、近視・遠視と色立体視の個人差（赤手前・青手前）が相関することになり、明快で興味深い結論が導き出される。しかしながら、今回の予備的研究で調べたのが 10 人程度と少数ではあったとは言え、何らかの関係を示唆するものを見出せなかった。研究代表者の大学の講義での調査（第 6 項『色立体視の個人差』）でも否定的結果であった。

5. 軸外色収差説

軸外色収差（transverse chromatic aberration）とは、ヒトの眼球は視軸が光学軸から 5 度も耳側にズレているため、中心窩に到達する光がプリズムを斜めに横切って来たのと同じこととなり、そのため屈折率の差で網膜に映る赤と青の位置がずれる、という考え方である（図 5）。具体的には、両眼とも、赤は青に比べて外側（耳側）に投影されることになる。これによって、赤が青より両眼立体視で手前に見える原因となる両眼視差が得られる、と考えるわけである。

人工瞳孔あるいはピンホールを通して刺激を見る場合、耳側にピンホールを置くと赤が手前に見え（図 6）、鼻側に置くと青が手前に見えるという現象がある（図 7）。これも、軸外色収差を支持する証拠とされた。

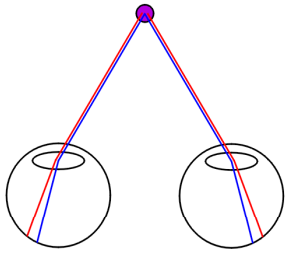


図 5 軸上色収差説…光学軸が視軸より外側に向いていることによって色収差が起こると考える。

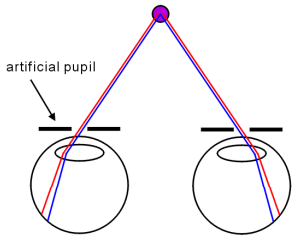


図 6 人工瞳孔による色立体視のコントロール（耳側配置）…この場合、赤が手前に見える。

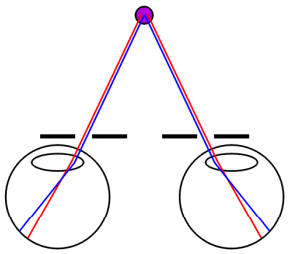


図 7 人工瞳孔による色立体視のコントロール（鼻側配置）…この場合、青が手前に見える。

ところが、この考え方では、青が赤より手前に見える観察者の眼球の解剖学的構造は、標準とは反対に、光学軸は視軸よりも鼻側にズレていることになる。そのような解剖学的証拠は知られてないし、ありえそうもない。これまでの研究において、このことは軽視され続けてきたわけであるが、ここに軸外色収差説の重大な脆弱性があることを強調したい。

6. 色立体視の個人差

背景が黒の場合、赤が手前に見え、青が奥に見える傾向にある（図 1）。これらの傾向は観察者の過半数に現れるが、残りの観察者は逆に、青が手前に、赤が奥に見える。この事実は先行研究に言及されてはいるものの、軸外色収差説には合わない現象であるためか、あまり広く知られていない。我々がこの研究テーマで学会発表をした時（**北岡明佳・栗木一郎・蘆田宏（2005）色立体視における個人差・視距離の影響・新しいモデル「重心説」　日本視覚学会 2005 年夏季大会**）、色研究の専門家にも青が手前に見える人が複数いて、「初めて知った。おもしろい」という反応であったほどである。

このように、色立体視には大きな個人差があるのであるが、数量化は意外となされていない。我々の公式データ（Kitaoka, Kuriki and Ashida, 2006, 文献添付）としては、20 人テストして、16 人が赤が手前に見える人、4 人が青が手前に見える人であったから、80%と 20%である。非公式データとしても、研究代表者が「知覚心理学」の講義で行なった調査（75 名）では、それぞれ 71%と 21%であった（残りは、赤と青は同じ奥行きに見えた）。色に関心のある観客が集まった講演会（**北岡明佳（2005）錯視における色の役割　ロレアル賞連続ワークショップ 2005・第 2 回「錯視　アート？サイエンス？心理学？脳神経科学？」・東京デザインセンター**）（約 200 名）で挙手を求めたケースでは、それぞれ 8 割、2 割程度と見積もられた。

これらを総合すると、約 4 対 1 で、赤が手前に見える人が多い、ということになる。もちろん、青が手前に見える人は少数派とは言え 100 人中 20 人もいるのだから、とりあえず無視しておいてよいというほどの少数でもない。

7. 色立体視に及ぼす視距離の効果

色立体視は、刺激を遠くから眺めた方が効果が大きいことが知られている。しかし、それは赤が手前に見える人による報告である。本研究でもその点は確認したが、青が手前に見える人も視距離が大きい方が色立体視効果が大きい（この場合は青がさらに手前に見える）ことを示した（Kitaoka, Kuriki and Ashida, 2006, 文献添付）（図 8）ことは、本研究の特色と言えよう。

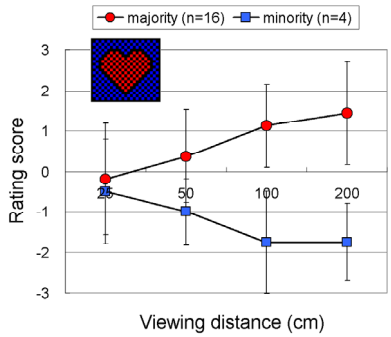


図 8　色立体視に及ぼす視距離の効果…視距離が大きいほど色立体視も大きい。

8. 白が背景の色立体視

赤が手前に見える人が 8 割、青が手前に見える人が 2 割である、という報告は、色刺激の背景が黒（図 1）の場合に得られるものである。それでは背景が白（図 2）になるとどうなるかというと、見えが逆転するのである。具体的には、赤が手前に見えていた人は青が手前に、青が手前に見えていた人は赤が手前に見える方向に変化する。ただし、奥行きの差の絶対量は減少し、同じ奥行きに見えると報告する例が増える。

この現象は、刺激の輝度と背景の輝度との関係で決まっているようである。例えば、図 9 において、上の列の右端の赤棒は 8 割の人には手前に見え、左端の黒棒は奥に見える。下の列でも左端の赤棒は 8 割の人には手前に見え、右端の黒棒は奥に見える。一方、2 割の人には逆の見え方をする。

この場合、黒棒は青としか接触していないから、青の刺激ということでよいが、赤棒は赤と青との境界で描かれている。この場合、赤の性質が優先しているようである。図 8 では、赤から黒へと棒の明るさが次第に変わっていくが、中ほどで急速に前後が入れ替わる場所がある。そのあたりはおそらく等輝度点と推定でき、そこを境により輝度の高い側の性質が優先されると考えることができる。

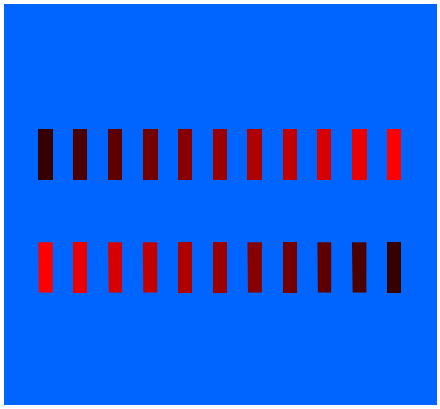


図 8　色立体視に及ぼす輝度の効果…明るい側が優先する。

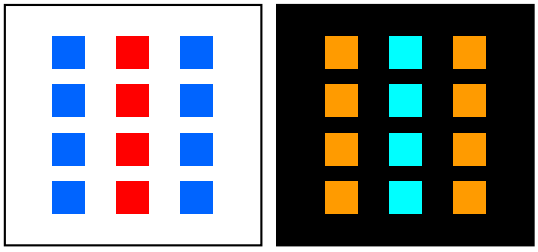


図 9　色立体視に及ぼす輝度の影響の一考察…左図の白背景の見えは、色反転した右図での色立体視の見えに等しいかもしれない。

もっとも、単純にこう考えるだけでは、図 2 が説明できない。明るい側優先というだけなら、赤の正方形も青の正方形も背景の白が優先なのだから、奥行きに差が出ないことになるが、そうではない。単なる明るい側優先ではなく、明るい側から暗い側を引き算した色で決まっているように思える（図 9）が、本研究では実験的な確認は行なっていない（*cf.* Winn, Bradley, Strang, McGraw and Thibos, 1995, *Vision Research,* **35,** 2675-2684）。

これらの性質が軸外色収差説では説明できるのかどうかは判然としない。なぜなら、等輝度点を境に見えが変化するというのであれば、色立体視は単純な光学系の現象というよりは、何らかの脳の処理も関わった高次の現象であることを示唆するからである。

なお、図は異なるが、現象としては同様のことを述べている先行研究はある（*e.g.* Faubert, 1994, *Vision Research,* **34,** 1165-1186; Faubert, 1995, *Vision Research,* **35,** 3161-3167）。しかし、その研究論文の著者は軸外色収差説を捨ててはいない。

9. 半視野遮蔽法

色立体視をコントロールする簡便法として、半視野遮蔽法がある。本研究を申請する以前に我々が独自で発見したものである。両眼の耳側を視野中心部を残して覆うと青が手前に、反対に両眼の鼻側を中心部を残して覆うと赤が手前に見える、というものである（図 10）。遮蔽物としては 2〜3cm 幅の厚紙がよいが、指でも十分である。

図 10 半視野遮蔽法…耳側の視野を遮ると青が手前に見える傾向が高まり（左図）、鼻側の視野を遮ると赤が手前に見える傾向が高まる（右図）。視野の中心まで遮る必要はないので、観察者にとって刺激の観察は楽である。

半視野遮蔽法では中心の視野を遮らないので、光線の軸が変位したことを論拠とする軸外色収差説に不利である。もし軸外収差説の支持者が、知覚される光線の軸は刺激から網膜までの最短のもの 1 本ではなく、投射される複数の光線の位置の平均であるという考え方に修正するのならば、本研究がこれから主張する重心説と同じである。

ところで、半視野遮蔽法を考案したのは我々が最初であると主張したことは、勇み足であったかもしれない。Howard and Rogers (1995, *Binocular vision and stereopsis*. Oxford University Press) には同様の手法の言及があることを後に見つけたからである。唯一の違いは、我々の方法では中心部分の視野は遮らない、という点である。先行研究では半視野遮蔽法はピンホール研究法の同等物として位置されているから、中心部の視野を常に残してよいわけではない。

10. 重心説

半視野遮蔽法による知見を無理なく説明する考え方として、我々は重心説 (center-of-gravity model) を提起する。重心説においては、光点の知覚上の位置は光線の中心線が網膜に当たる部位ではなく、光線が投射する網膜領域の重心であると考える。

半視野遮蔽法では、視野の半分が中心視部分を残して遮蔽される。そうすると、遮蔽された部分の光線は網膜に達しないから、遮蔽されなかったところを通過した光線の情報を用いて、刺激の位置を脳は決めることになる。もし眼の光学系が色消しレンズとしてできていて、軸上色収差がないと仮定すれば、長波長光も短波長光も網膜の一点に収斂していることになるから、半視野遮蔽法で刺激のみかけの位置は変化しないと推論できる。しかし、実際には半視野遮蔽法で赤と青の相対的位置を変えられるのであるから、軸上色収差は存在することがわかる。

軸上色収差が存在するということは、赤にピントが合っている時には青にはピントが合っ

ていない、すなわち短波長光は網膜上である一定範囲に拡散して投射されていることになる。逆に、青にピントが合っている時には赤にはピントが合っていない、すなわち長波長光は網膜上である一定範囲に拡散して投射されていることになる。我々はこの点も確認している（第4項『軸上色収差の観察』）。

まず、赤にピントが合っていて、青にはピントが合っていない状態を考えてみよう。この場合、青はレンズに近い側で結像し、網膜には焦点を超えて交差して広がった光が到着することになる（図4の一番左の図）。ここで半視野遮蔽法で耳側を遮蔽すると、赤にはピントが合っているので光量が減じるだけで、網膜への投射位置は変わらない。ところが、青色光は光学系の前で耳側の光が遮蔽されるため、網膜上では鼻側の光が遮蔽される。結果として、青色光の投射は耳側に寄ることになる。

この耳側に寄った青色光の位置をどう決めるかという点において、重心説ではその重心を取ると考えるのである。そうすると、青の刺激のみかけの位置は耳側に寄ることになり、両眼とも耳側の遮蔽をしたのであれば、青の刺激に交差視差を与えたことと同じとなり、青は赤よりも手前に見えるようになると考えることができるのである。

青にピントが合っていて、赤にはピントが合っていない状態でも、論理は同じである。図11には、黄色（長波長寄りの中間の波長）にピントが合っていると仮定した場合の重心の移動を図示した。この場合は、耳側の遮蔽によって、網膜上は青は耳側に、赤は鼻側に重心が移動する。前者は交差視差、後者は非交差視差を与えるので、青はより手前に、赤はより奥に見えることになる。

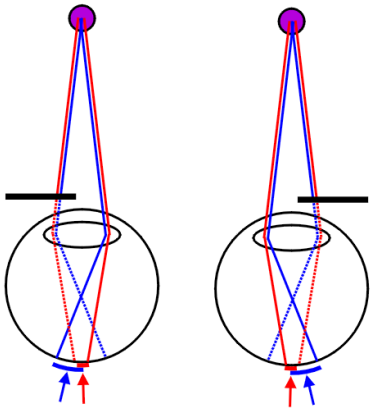


図11 重心説の模式図…拡散した光の重心をその光の位置とすると考える。

重心説は、軸外色収差説の証拠として評価されるピンホール研究（第5項『軸外色収差説』）の結果もそのまま説明できる。さらに、ピンホールが近接して2つあれば光点は2個見えるのであるが（我々自身でも確認済み）、これは重心説では簡単に説明できる。もっとも、軸外色収差説でも説明できると主張する人もいるかもしれない。そのような人は、重心説は軸外色収差説の一種であると考えるかもしれない。我々としては、重心説が「修正型軸外収差説」ということでも構わないと考える。ただし、重心説は軸上色収差の事実をモデルの中に必要不可欠なものとして組み入れており、この点が従来の軸上色収差説と異なることを強調して

おきたい。

11. 重心説は色立体視をどの程度説明できるか？

重心説は色立体視を説明するモデルとして、現在のところベストである、と我々は考える。それでは、重心説は色立体視の諸現象をどの程度説明できるのであろうか。結論を先に言うと、半分程度と思われる。

重心説が説明できない現象が 3 つある。1 つ目は光線の拡散と知覚のシャープさの不一致の問題、2 つ目は視距離が色立体視に及ぼす効果、3 つ目は明暗順応レベルと色立体視との関係である。なお、これらも従来の軸外色収差説で説明できるわけではない。

１つ目の問題であるが、軸上色収差によって投射光が拡散している場合、知覚上はシャープに見える場合とぼけて見える場合がある。日常生活において、赤と青が両方見えている状態でどちらかがぼけて見えるということはない。CRT や LCD モニターで示した色刺激でも同じである。この点は、ある範囲内のぼけは脳が修正して知覚上はクリアにみせかけるメカニズムがある、と仮定を加えて説明を補強できる。もちろん、「実際にぼかした刺激図形を見てシャープに見えることはない」という経験的事実があるが、これは「実際にぼかすと全波長をぼかすことになるので、その修正メカニズムでは修正しきれない波長が残ることになるためである」という説明が可能である。

2 つ目の問題は、視距離が大きくなると色立体視の効果が増す、という事実である（第 7 項『色立体視に及ぼす視距離の効果』）。どちらかというと、刺激に目を近づけると色立体視が失われる、という観点の方がわかりやすいかもしれない。これを説明するには、視差が同じなら、近くでものを見た時の奥行き量は計算上少なくなるから、という考え方が有力と思われる。

もっとも、単眼で観察した時には、色ずれそのものが失われているようでもあるから、最初に失われるのは立体視ではなく、色収差の可能性がある。色収差の考え方は光学系における光の屈折という事実にあるのだから、近くでものを見る時は屈折率は増すので色収差は増してもおかしくない。しかし、事実は反対である。

これを解決するために我々が提起した 1 つの憶測は、「近くを見るときの光学系はひずみが少なくできているが、遠くを見る時は原因不明のプリズム的作用が起こる」というものである（Kitaoka, Kuriki and Ashida, 2006, 文献添付））。その擬似プリズムの形の個人差に依存して、赤が手前に見える多数派と青が手前に見える少数派に分かれる、という考え方である。もちろん、この憶測を支持する解剖学的・生理学的知見は知られていない。

3 つ目の問題は、明暗順応レベルと色立体視との関係であるが、暗順応側になると（例えば夜になると）色立体視の効果は大きくなることが日常でも観察できる点と、赤が手前に見える人も暗順応レベルでは青が手前に見えるようになるという研究報告がある点である（*e.g.* Kishto, 1965, *Vision Research,* **5,** 313-329）。後者については、我々は実験的に確認できなかったが、これは我々の準備不足（暗室が完全ではなかったなど）が原因と考えられる。

夜になると色立体視の効果が大きくなるという観察は、重心説に合う。暗順応によって瞳孔径が大きくなると、軸上色収差が増すからである。一方、暗順応レベルで赤が手前に見え

る人が青が手前に見えるように変化するという報告は、重心説では説明し難い。

12. その他の関連した現象

眼鏡依存色収差錯視　たとえばマゼンタ色の光は赤と青の光からできているわけであるが、マゼンタ色の刺激を見ても、色収差があるはずなのに赤や青がはみ出して見えることはない。知覚上それに気が付かないのは、脳が補正しているためと考えるのが妥当である。その脳の補正を出し抜いた錯視として、眼鏡依存色収差錯視がある（図 12）。近眼で眼鏡をかけている人は、顔を右に向けて目は左でこの図を見ると、上半分のそれぞれの黒の正方形の左側は鮮やかな水色、右側は黄色（あるいはオレンジ色）に見える。この時、下半分の正方形の両側は緑色に見える。顔を左に向けた場合は、下半分のそれぞれの黒の正方形の左側は鮮やかな黄色（あるいはオレンジ色）、右側は水色に見える。この時、上半分の正方形の両側は緑色に見える。遠視あるいは老視の眼鏡をかけている人は、これらが逆に見える。これは眼鏡の端は光学的にはプリズムと同じであることから、脳の補正範囲を超えた色ズレを起こしたものと考えられる。眼鏡をかけていない人は、普通のプリズムを使って、同じ効果を見ることができる（*cf.* Faubert, Simonet and Gresset, 1999, *Opthalmic & Physiological Optics,* **19,** 336-346）。

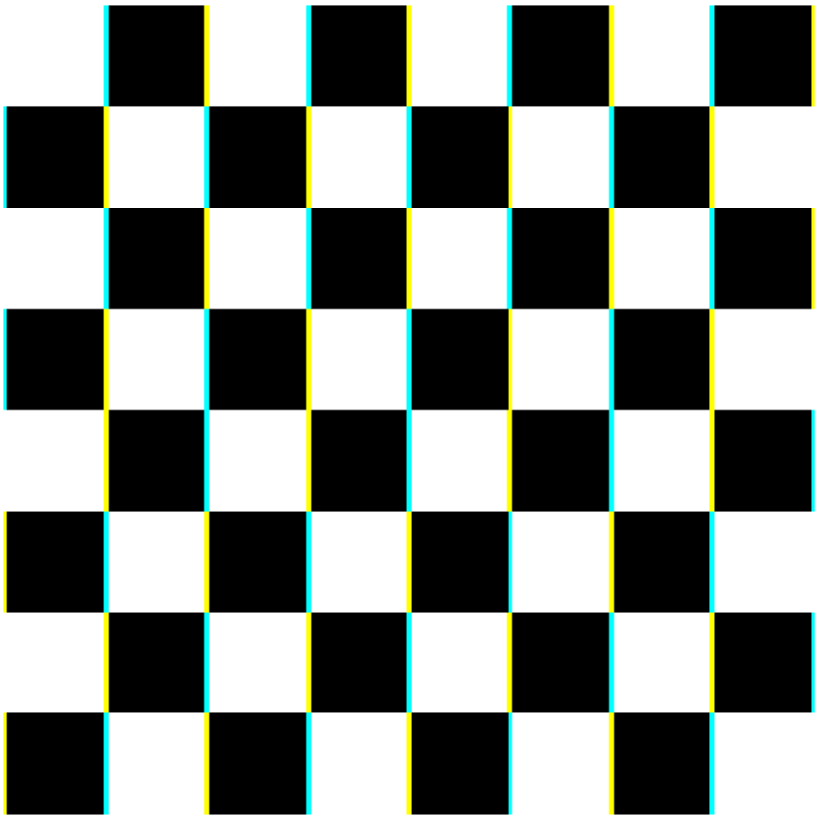


図 12　作品「色収差錯視チェッカーボード」(©Akiyoshi Kitaoka 2005)。眼鏡依存色収差錯視の一例である。説明については本文参照。

色依存の静止画が動いて見える錯視　ある刺激を波長の違う 2 色の境界として描画し、もう 1 つの刺激を 1 色と黒の境界として描画すると、前者の 2 色の輝度が近い時、後者が動いて見えるという錯視である。たとえば、図 13 は赤の背景の上に黒の正方形でできたハート形と、それを囲む緑の正方形でできている。ここで赤と緑の輝度が近い時、黒のハート形が動いて見える。この説明として、赤と緑は輝度が近いので、どちらの位置を優先するか（第 8 項『白が背景の色立体視』）が不安定となり、赤優先から緑優先、あるいはその逆に切り替わる時に位置ずれが起きるとともに、静止画が動いて見える錯視では参照枠（この場合は外側の緑の部分）は動かないように見ようとする性質があるから（Kitaoka, 2003, 文献添付）、内側の黒のハートの部分が誘導されて動いて見えると考えることができる。

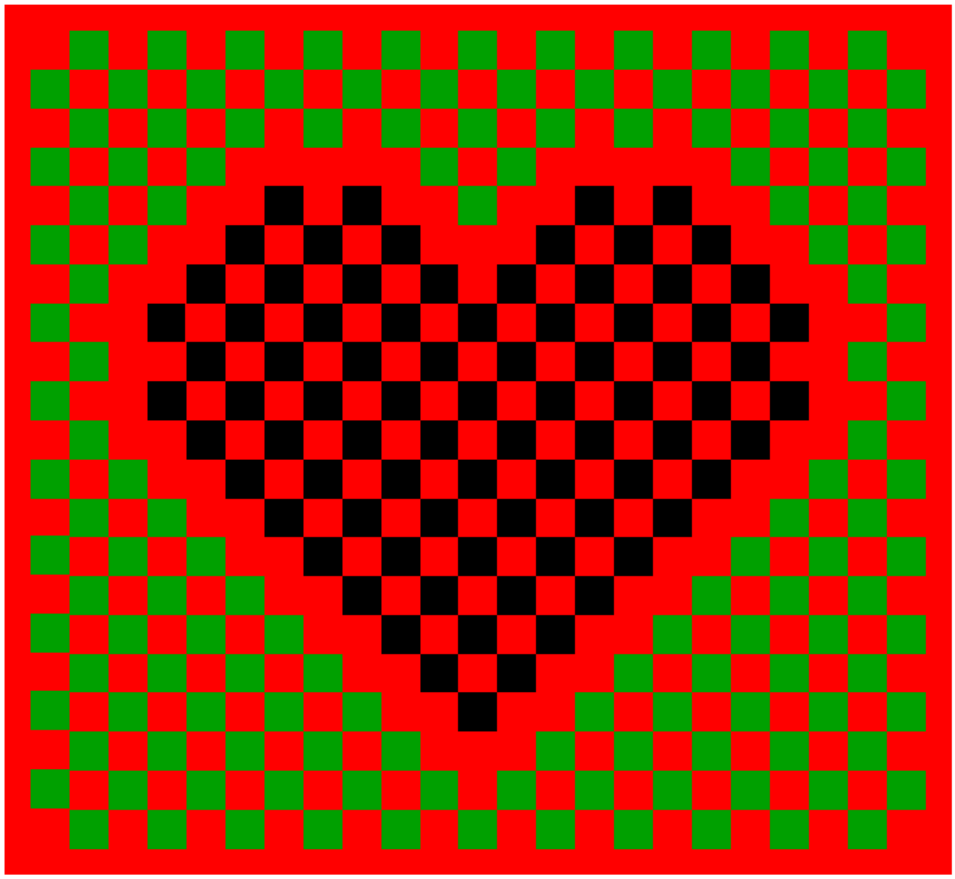


図 13　作品「踊るハート II」（©Akiyoshi Kitaoka 2005）。ただ眺めているだけで、黒いハートが動いて見える。説明については本文参照。

なお、この錯視については、等輝度に近い境界部分の知覚上の運動速度が相対的に遅いからである、という説明も可能である。今後の検討を要する。

さらに、我々は色の違いによる位置の計算の不安定性を仮定すると、静止画が動いて見える錯視のうち、色に依存性の認められるタイプのいくつかが説明できるのではないかと研究を続けてきた（*e.g.* Conway, Kitaoka, Yazdanbakhsh, Pack and Livingstone, 2005; Ashida, Sakurai and Kitaoka, 2005）。しかし、色収差が静止画が動いて見える錯視に及ぼす効果の決定的な証拠は、未だ得られていない。こちらも、さらなる検討が必要である。

線がずれて見える錯視　色収差を見るのに簡単な方法がある。図 14 のような刺激図がそれで、色収差に応じて一直線上に描かれた線がずれて見える。赤の正方形上に引かれた青線は、赤の輝度が青の輝度よりも高いので、みかけの位置は赤の色収差が優先となる（第 8 項『白が背景の色立体視』参照)。一方、緑の正方形上に引かれた青線は、緑の輝度が青の輝度よりも高いので、みかけの位置は緑の色収差が優先となる。そのため、引かれた線は青であるが、この線のみかけの位置は赤と緑の色収差の違いで決まるためと考えられる。

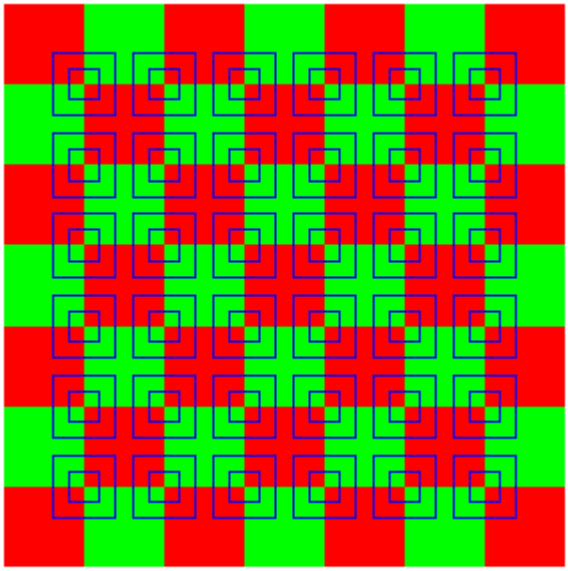


図 14　作品「額がガクガク」(©Akiyoshi Kitaoka 2003)。青の線画の正方形が赤と緑の正方形の境界を超えるところでズレて見えることがある。

この図を見ると、人によっては縦方向にも色収差があることがわかる（横線がズレて見える)。これは、軸外収差説では説明できず、重心説で説明できる現象である。

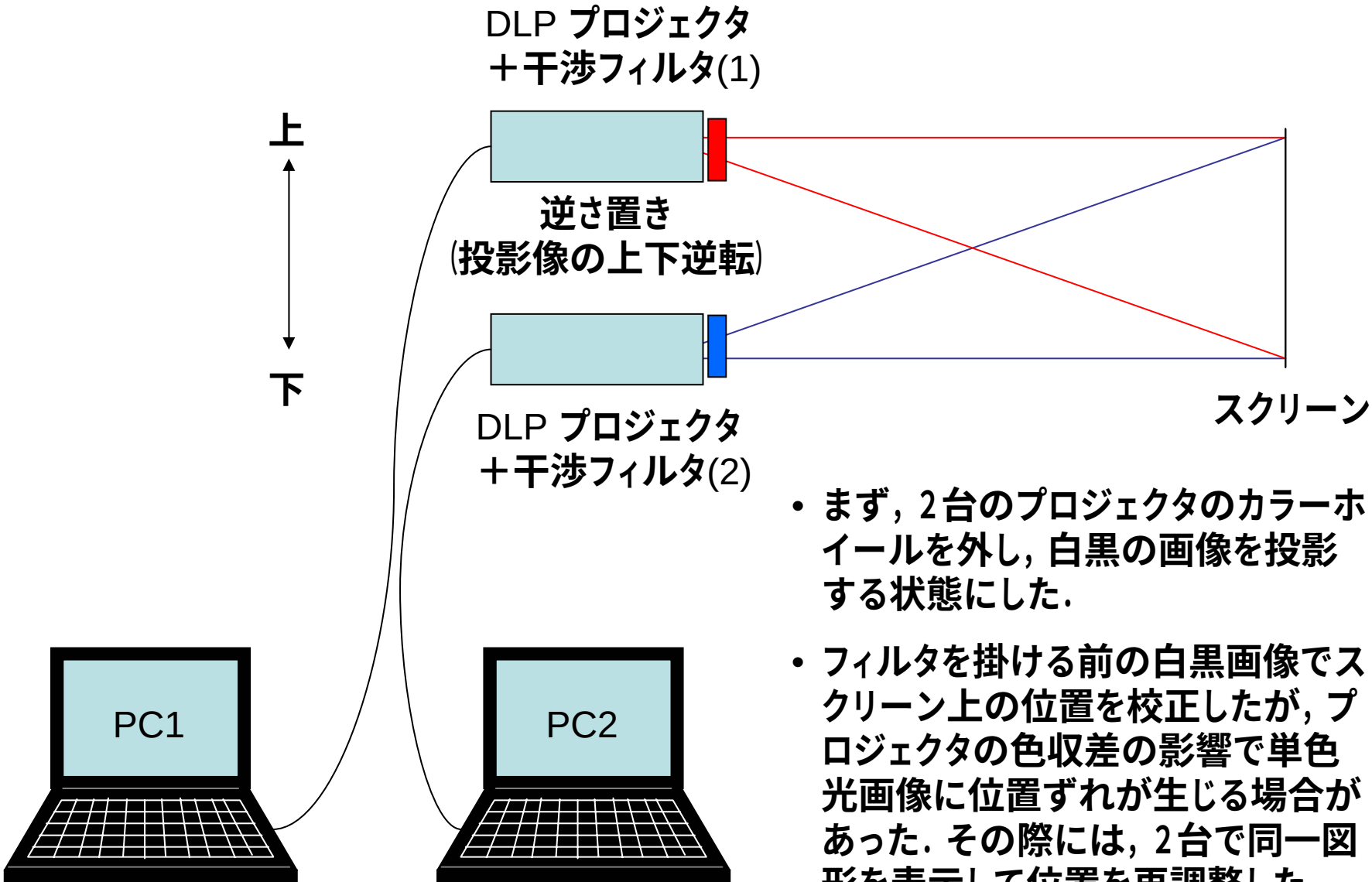
13. 展望

「赤は進出色、青は後退色」という紋切り型の「常識」に疑問を感じてスタートした本研究であったが、色立体視とその周辺に限定したにもかかわらず、これほど多くの実りのある発見と知識の体系化ができたことは、本研究の現時点での成功を意味する。将来的には、高次のレベルをも含めた進出色・後退色の包括的な知識の体系化に努めたい。

北岡明佳・栗木一郎・蘆田宏

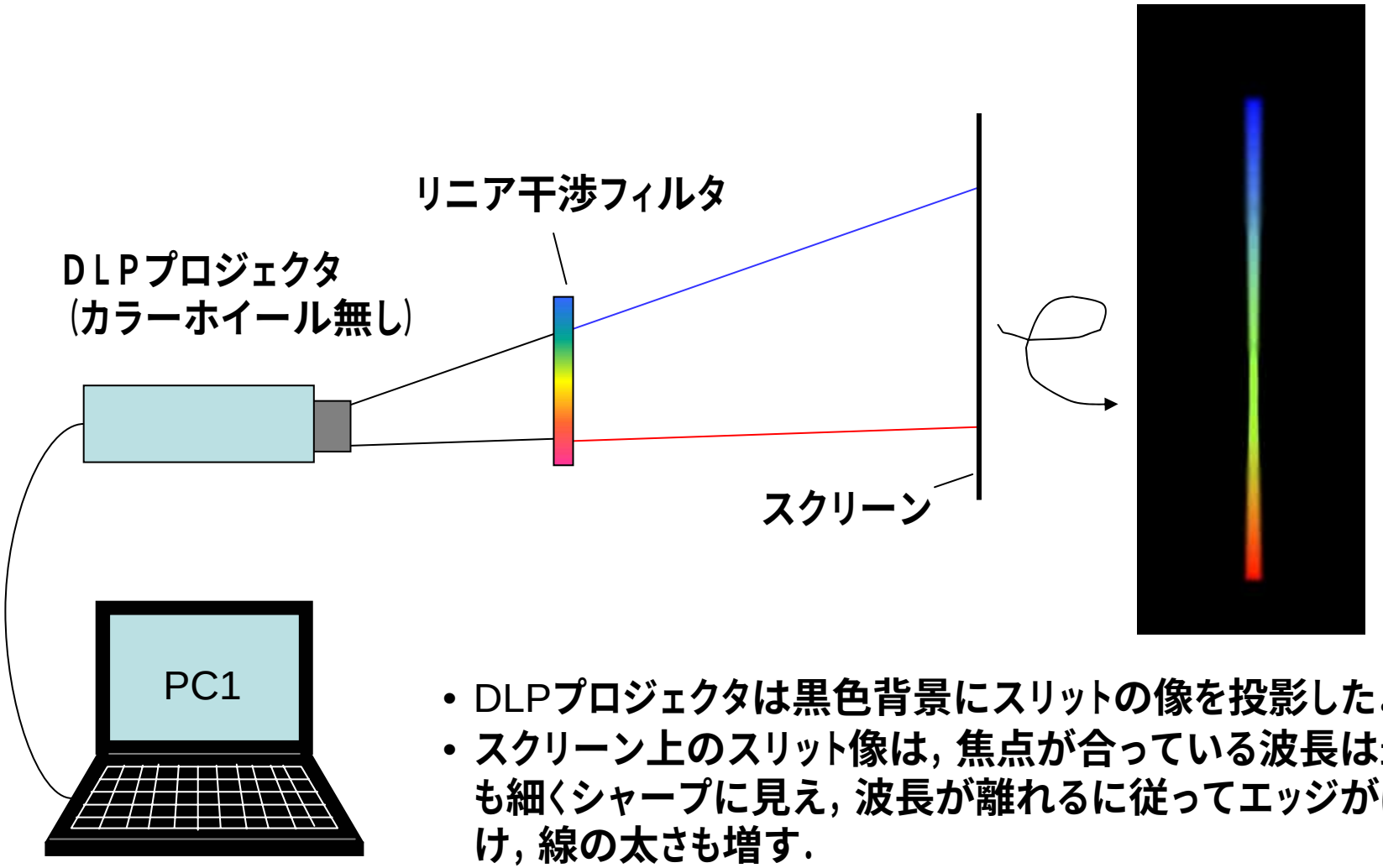
2006 年 3 月 1 日

単色光による色立体視実験系（概略図）



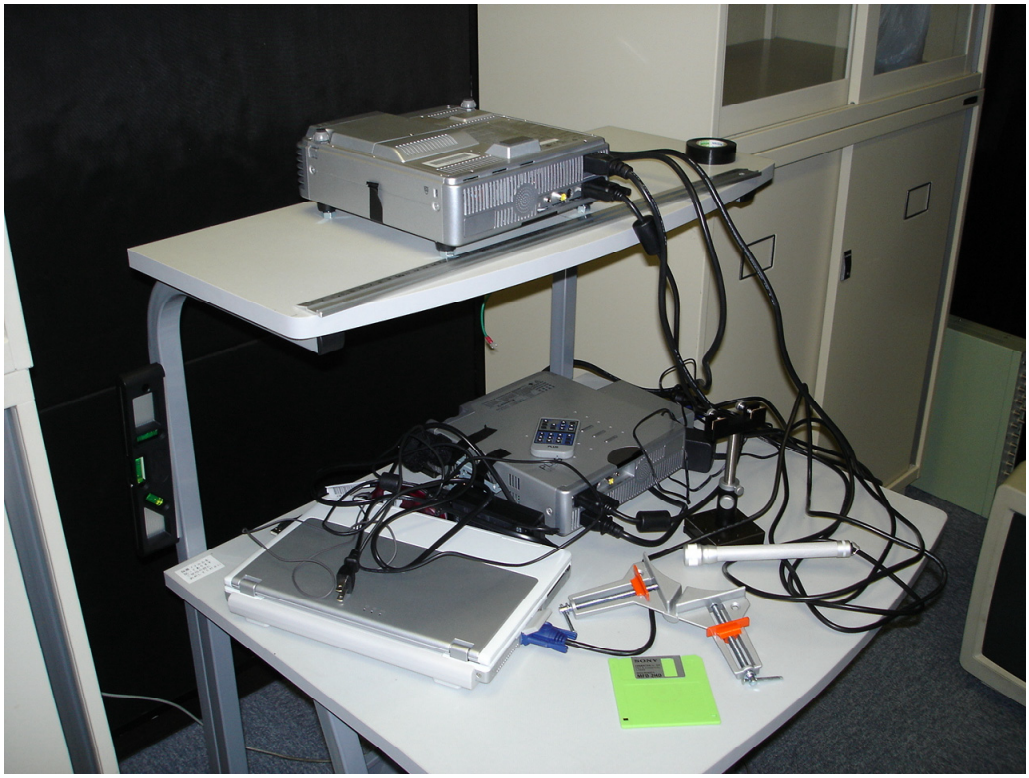
- まず，2台のプロジェクタのカラーホイールを外し，白黒の画像を投影する状態にした．
- フィルタを掛ける前の白黒画像でスクリーン上の位置を校正したが，プロジェクタの色収差の影響で単色光画像に位置ずれが生じる場合があった．その際には，2台で同一図形を表示して位置を再調整した．

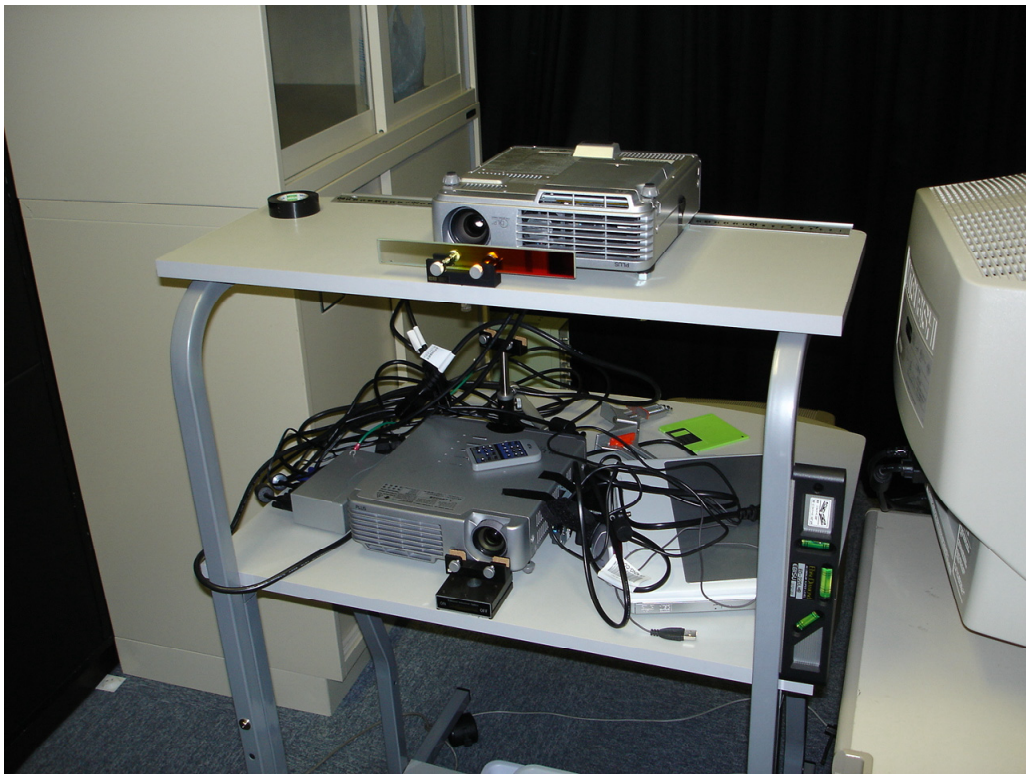
自然瞳孔での焦点波長を観察するための実験系（概略図）



- DLPプロジェクタは黒色背景にスリットの像を投影した．
- スクリーン上のスリット像は，焦点が合っている波長は最も細くシャープに見え，波長が離れるに従ってエッジがぼけ，線の太さも増す．
- 焦点が合う波長は，屈折矯正が行われている状態で500〜550 nm と思われ，遠視の観察者がスクリーンに近づくと，調節限界により合焦波長が徐々に短くなる．

主な実験装置





Research note

The Center-of-gravity Model of Chromostereopsis

KITAOKA Akiyoshi[1], KURIKI Ichiro[2], and ASHIDA Hiroshi[3]

We propose the center-of-gravity model to explain chromostereopsis. This new model assumes that we perceive each color position at the center of gravity of diffusely projected color light, and that these positions gives binocular disparities to generate binocular stereopsis. This model fits the paradoxical pieces of findings on chromostereopsis better than do the previous two models.

Key words : chromostereopsis, longitudinal chromatic aberration, transverse chromatic aberration, center-of-gravity model

Introduction

Chromostereopsis is a binocular stereoscopic phenomenon that for many observers red stimuli appear to be in front of blue ones even if they are placed in the same frontoparallel surface (Figure 1). There is, however, a minority in which observers see blue in front of red (Hartridge, 1947; Howard and Rogers, 1995). Our preliminary surveys suggested that about 80% of observers see red in front of blue while about 20% see blue in front of red.

Moreover, chromostereopsis is a function of viewing distance, as suggested by Faubert (1994). We confirmed this function that the longer the viewing distance the stronger the effect. This function held true for both the majority and the minority (Yamauchi, 2004) (Figure 2).

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Furthermore, it has been reported that the red-in-front-of-blue stereopsis reverses to the blue-in-front-of-red stereopsis at low illumination (Kishto, 1965; Sundet, 1972, 1976; Simonet and Campbell, 1990a). We have failed to detect this effect clearly in our casual setting. Inversely, we observed that chromostereopsis tends to be enhanced under dark adaptation, possibly depending on dilated pupils.

The longitudinal chromatic aberration model

There are two major models to explain chromostereopsis. One is the model based upon the longitudinal chromatic aberration, while the other is the one depending on the transverse chromatic aberration.

The longitudinal chromatic aberration refers to the optical phenomenon that in the eye's optic system the focus of blue light (short-wavelength light) is inevitably nearer to the lens than that of red light (long-wavelength light) even if they are projected

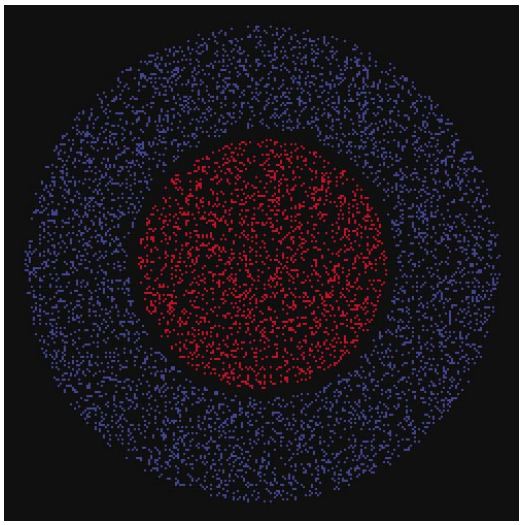

Figure 1. Chromostereopsis, a binocular stereopsis based upon the difference in color. The majority sees the circle of red random dots in front of the surrounding annulus of blue random dots. There is, however, the minority in which observers see blue in front of red. Chromostereopsis is strong when observers watch this image from more than 1 meter apart.

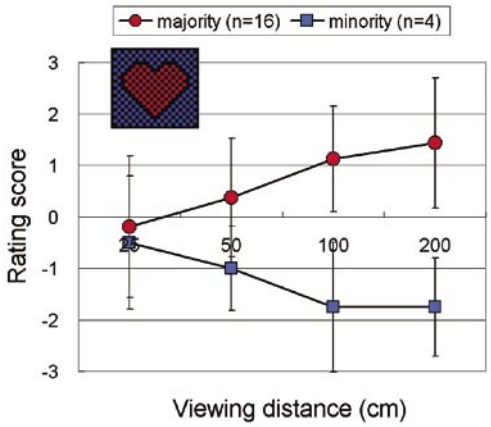

Figure 2. Chromostereopsis as a function of viewing distance (Yamauchi, 2004). Rating score 3 was given when "red appears to be in front of blue strongly" ; score 2 was given when "red appears to be in front of blue" ; score 1 was given when "red appears to be in front of blue slightly" ; score 0 means no chromostereopsis; score -1 was given when "blue appears to be in front of red slightly" ; score -2 was given when "blue appears to be in front of red"; score -3 was given when "blue appears to be in front of red strongly". The used stimulus is superimposed. The "majority" means the observers who usually see red in front of blue while the "minority" refers to those who usually see blue in front of red. For both groups, the longer the viewing distance the stronger the effect.

from the same place (Figure 3). This phenomenon depends on the difference in the refractive index, in which the index for short wavelengths is about 1.5 or 2.0 diopters greater than that for long wavelengths (Uozato, 2000). The model using the longitudinal chromatic aberration is that this foci inconsistency informs that the blue source should be farther than the red source. It is because the farther the source the nearer the focus to the lens if the refractive index is constant.

This model, however, has been discarded because chromostereopsis has to occur monocularly in this model but it actually needs binocular viewing (Howard and Rogers, 1995). Moreover, this model cannot explain why there is the minority of the blue-in-front-of-red stereopsis.

The transverse chromatic aberration model

The transverse chromatic aberration refers to the optical phenomenon that in binocular viewing blue light is projected to a more nasal part of the retina than does red light because the optical axis of the eyeball is slightly (about 5° from the visual axis: angle alpha) shifted in the outward direction from the

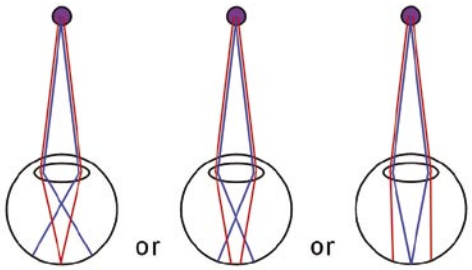

Figure 3. The longitudinal chromatic aberration. Blue has the focus nearer to the lens than red because of the difference in the refractive index depending on wavelengths of light.

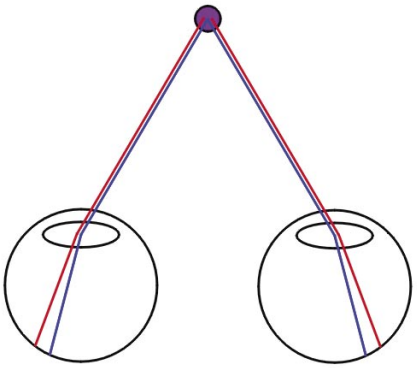

Figure 4. The transverse chromatic aberration. Blue light is projected to a more nasal part of the retina than does red light because of the difference in the refractive index depending on wavelengths of light. Note that the optical axes disagree with and are diverged from the visual axes.

visual axis (Uozato, 2000) (Figure 4). The model using the transverse chromatic aberration is that this angular difference gives binocular disparities to generate binocular stereopsis (Hartridge, 1918).

This model has widely been supported. In particular, the pinhole study has repeatedly supported it. When pinholes or artificial pupils are placed just in front of the eyeballs, chromostereopsis depends on the position of the pinholes (Terada, Yamamoto and Watanabe, 1935; Vos, 1960, 1966; Owens and Leibowitz, 1975; Simonet and Campbell, 1990b; Ye, Bradley, Thibos and Zhang, 1991). When they are placed on the temporal sides, chromostereopsis is red-in-front-of-blue (Figure 5a). On the other hand, when they are placed on the nasal sides, chromostereopsis is blue-in-front-of-red (Figure 5b). These effects have been regarded as evidence for the critical role of the transverse light projection.

This model, however, cannot fully explain why there is the minority of the blue-in-front-of-red stereopsis. If this model tries to explain this, it should be assumed that in the eyeballs of the minority the optical axis is rotated in the inward direction from the visual axis. This assumption is not plausible because it requires too much anatomical distortion.

This model cannot explain the effect of viewing distance, either. If this model tries to explain this, it should be assumed that the crystalline lens changes its orientation to make the optical axis agree with the visual axis when observers see stimuli close up. This assumption is not plausible, either, because it also requires too much anatomical transformation.

Furthermore, this model cannot explain the following phenomenon (Howard and Rogers, 1995). When the temporal half of each visual field (the nasal half of each retina) is mostly occluded, with the foveal vision being intact, blue tends to be perceived nearer than red (Figure 6a). Even the majority can see blue in front of red in this method. On the other

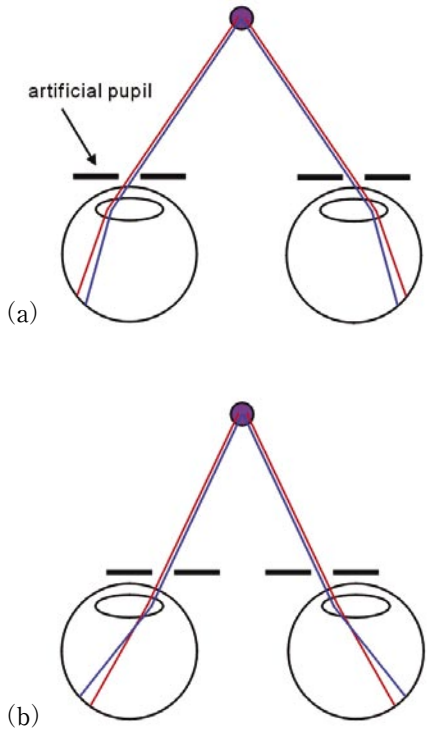

Figure 5. The effect of the position of pinholes or artificial pupils. (a) When they are placed on the temporal sides, chromostereopsis is red-in-front-of-blue. (b) When they are placed on the nasal sides, chromostereopsis is blue-in-front-of-red.

hand, when the nasal half of each visual field (the temporal half of each retina) is mostly occluded, with the foveal vision being intact, red tends to be seen nearer than blue (Figure 6b). Even the minority can see red in front of blue in this method. Since these methods do not disturb the central path of projected light, little or no changes in chromostereopsis are expected in the transverse chromatic aberration model, but this is not the case.

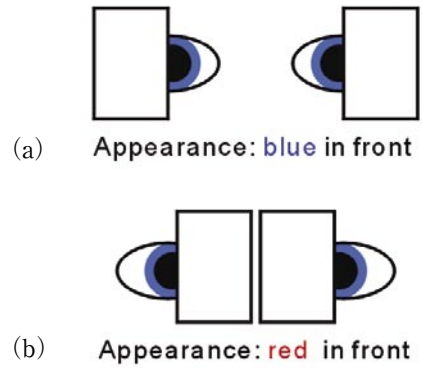

Figure 6. The effect of occlusion of half of visual fields. (a) When the temporal half of each visual field is mostly occluded, with the foveal vision being intact, blue tends to be perceived nearer than red. (b) When the nasal half of each visual field is mostly occluded, with the foveal vision being intact, red tends to be observed nearer than blue.

The center-of-gravity model

To explain these half-occlusion effects, we propose the center-of-gravity model of chromostereopsis. This model hypothesizes that the position of color is determined at the center of gravity in the range of each projected light onto the retina.

If red light is just in focus, blue light is projected diffusely. In this case, the position of the red image is in focus while the center of gravity of the diffused blue light represents the position of the blue image. On the other hand, if blue light is just in focus, red light is projected diffusely. In this case, the position of the blue image is in the focus while the center of gravity of the diffused red light represents the position of the red image.

In general, when the temporal half of each visual field (the nasal half of each retina) is

mostly occluded, with the foveal vision being intact, the center of gravity of red light shifts in the nasal direction while that of blue light deviates in the temporal direction (Figure 7). These shifts give binocular disparities to generate the blue-in-front-of red stereopsis. When the nasal half of each visual field (the temporal half of the retina) is mostly occluded, the positional shifts are the reversal and the appearance is red-in-front-of-blue. The center-of-gravity model therefore can explain the phenomenon observed with half-occluded pupils.

Moreover, this model is perfectly consistent with the pinhole study (Figure 5) because the retinal position of the projected light through the pinhole equals the center of gravity of the light. Furthermore, the center-of-gravity model has an advantage to take into account the longitudinal chromatic aberration (Figure 3). However, the center-of-gravity model could also be regarded as a modified version of the transverse chromatic aberration model.

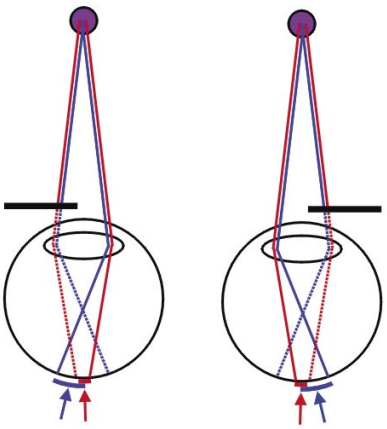

Figure 7. The center-of-gravity model. It is hypothesized that the position of color is determined at the center of gravity in the range of each projected light onto the retina. When the temporal half of each visual field (the nasal half of each retina) is mostly occluded with the foveal vision being intact, the center of gravity of red light shifts in the nasal direction while that of blue light deviates in the temporal direction. These shifts give binocular disparities to produce the blue-in-front-of-red stereopsis.

Speculation

Although the center-of-gravity model explains chromostereopsis much better than the simple longitudinal or transverse chromatic aberration models, it cannot explain the effect of viewing distance or why there are the majority and the minority. One or two independent mechanisms are then necessary to explain chromostereopsis fully.

Our speculation is that there might be individual differences in the changes in possible off-axis-viewing effects, like viewing through prism, in the optical characteristics of the overall ocular media, when observers change the viewing distance, especially when observers see into the distance. It is assumed that there are two types of off-axis-viewing effects, one being like prisms tapered in the temporal direction while the other being like prisms tapered in the nasal direction. The majority might depend on the former while the minority might reflect the latter.

There is no physiological evidence for this speculation at present because of difficulty to correctly measure the optical characteristics of ocular media in vivo. However, in our preliminary study, we observed switches in the depth order by using prisms in an

ophthalmic corrective-lens set, as mentioned in Howard and Rogers (1995). This may support our speculation for the explanation of individual differences in the chromostereopsis.

Acknowledgements

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MEG recording from the human ventro-occipital cortex in response to isoluminant color stimulation

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Abstract

In contrast to PET and fMRI studies, color-selective responses from the ventro-occipital area have rarely been reported in MEG studies. We tried to minimize the stimulation to all areas in the visual system except the color-processing ones by using a color space based on psychophysical and physiological knowledge in order to maximize the signal-to-noise ratio for MEG responses from the ventro-occipital area. MEG obtained from long intermittent reversals (2.0–3.5 s) of isoluminant chromatic gratings showed two major peaks at the latencies of approximately 100 and 150 ms. The estimated location of the equivalent-current dipole for response at 100-ms latency was in the calcarine sulcus and that of the dipole for the response at 150 ms was in the collateral sulcus in the ventro-occipital area. The response around 150 ms was uniquely observed in MEG elicited by chromatic reversals. The average of lags between MEG responses from the calcarine sulcus and ventro-occipital area was 43 ms, which suggests sequential processing of color information across the visual cortices.

Keywords: Color vision, MEG, Ventro-occipital cortex, Calcarine sulcus, Temporal lag

Introduction

The locations and functions of the cortical areas that selectively respond to chromatic stimulations have been extensively studied in monkey (Zeki, 1973) and humans (Lueck et al., 1989; Sakai et al., 1995; Zeki & Marini, 1998; Bartels & Zeki, 2000). The majority of the studies on human subjects measured the regional cerebral blood flow or the level of blood oxygenation using positron emission tomography (PET) or functional magnetic-resonance imaging (fMRI) techniques, respectively, to visualize active areas in the human visual cortex.

Electroencephalograms (EEGs) and magnetoencephalograms (MEGs) have advantages for studying the temporal characteristics of the cortex because they record electromagnetic changes with high temporal resolution. Some MEG studies with color stimuli have reported responses from the occipito-parietal regions (Regan & He, 1996) or cuneus (Koike et al., 1996). However, none have reported MEG responses from ventro-occipital areas, which have been suggested to play significant roles in color-information processing in various PET and fMRI studies (Lueck et al., 1989; Sakai et al., 1995; Bartels & Zeki, 2000). It is curious that MEG has not been able to record responses from ventro-occipital areas, while fMRI and PET studies have.

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Many EEG studies have reported the characteristics of visually evoked potential (VEP) with changes in chromatic characteristics of the stimulus (Rabin et al., 1994; Buchner et al., 1994; Crognale et al., 1997). A study by Buchner et al. (1994) succeeded in showing that some of the responses arise from the ventro-occipital area after elaborate signal processing. Therefore, we used relatively longer interstimulus intervals (ISIs), which is expected to improve the clarity of MEG response from the ventro-occipital area.

Another important factor in recording clear MEG responses to locate the focus of brain activity is to minimize the number of cortical areas that are stimulated in each trial. There are two major possible reasons previous MEG studies were unsuccessful in recording responses to color stimuli in the ventro-occipital area. One is that the intensity of the MEG responses to chromatic stimuli from the ventro-occipital area was not strong enough to cope with the responses from other cortical areas. The response from cortex, which is closer to the sensor than the ventro-occipital area, might have masked the response from the ventro-occipital area. The second is that MEG response from the ventro-occipital area to different feature of visual stimulus masked the response to chromatic stimulation. Since a blank screen can be thought as a figure, the procedures with both the appearance (onset) and disappearance (offset) of stimulus pattern from a blank screen stimulate the part of the visual system that selectively responds to figural changes in the stimuli. The candidate area for the figural information processing is the fusiform gyrus in the ventro-occipital area (Zeki & Marini, 1998;

Grill-Spector et al., 2004). This area is very close to the color-sensitive area in the ventro-occipital cortex. Therefore, to improve the signal-to-noise ratio of MEG response to chromatic stimulation from the ventro-occipital cortex, we presented long-intermittent color reversals as the only change across MEG triggers.

The primary purposes of the present study were to record responses to chromatic stimuli from the ventro-occipital area of the human visual cortex with a whole-head-type MEG sensor and clarify the temporal characteristics of the information processing in the visual areas.

Materials and methods

MEG recordings and analysis

We used a whole-head MEG sensor-array system (CTF, Canada) whose 64 axial sensors are equally spaced around the surface of the subject's head. Data were recorded at 625 Hz for a 1000-ms interval that started 200 ms before the stimulus trigger and ended 800 ms after the trigger. The data were stored in a computer through an analog/digital (A/D) converter without any hardware filtering. Data were recorded at least 100 times for one stimulus condition. Epochs with strong artefacts from eye blinks or eye movements were omitted from the analysis, but the total number of epochs for each condition was not less than 90.

The data were averaged across the epochs, and a low-pass filter was applied with the cut-off frequency at 40 Hz. Up to the third gradient and the DC component of the data were removed. Equivalent-current dipole (ECD) estimation was performed using software supplied by the manufacturer of the MEG system. A conductive sphere was used to estimate the ECD. The radii for the three subjects were 7.5, 7.3, and 7.25 cm. The size and the center of each sphere was determined from a structural (T1) MR image for each subject to minimize the distance error from the surface of sphere to the cortical surface. The T1 images were taken with a clinical magnetic resonance imaging (MRI) scanner (Siemens Magnetom Vision, 1.0T, Munich, Germany), and the resolution was 1 mm in voxel size. In this paper, we will show ECDs that met the following criteria: (1) Goodness of fit (GOF) of not less than 80%, (2) no significant residual error in the occipital cortex, (3) persistence of longer than 10 ms, and (4) the 95% confidence volume of the ECD smaller than 4 cm^3. The GOF is defined as follows:

$$\mathrm{GOF}\,[\%] = \left(1.0 - \frac{\sum_{i=1}^{64}(m_i - m_i^e)^2}{\sum_{i=1}^{64} m_i^2}\right) \times 100,$$

where m_i and m_i^e are the measured and estimated outputs of ith sensor, respectively.

The estimated ECD was superimposed on a T1 structural image for each subject. The subject wore three positioning coils during MEG data acquisitions, one at the nasion and two at periauricular points. To be more exact, the two coils at the periauricular points were placed at the small flat space near the bottom end of the helix and the tragus of the left and right ears. Before every session, we recorded the locations of the three positioning coils relative to the positions of the MEG sensor coils. To spatially align the MEG data and the anatomical MR image, liver-oil droplets were applied at the same location as the MEG-positioning coils during MR structural image acquisition. The locations of the MR image and MEG data were aligned by minimizing the deviations at these three points.

Visual stimuli

Apparatus and chromatic calibration

Visual stimuli were generated with a VSG 2/3 visual stimulus generator graphic board (Cambridge Research Systems, U.K.). The luminance and chromaticity were carefully calibrated with a SR-1 spectroradiometer (TOPCON, Japan). The stimulus was presented from a DLA-G10 LCD projector (JVC, Japan) placed outside of the shielded MEG room to a screen placed right in front of the subject. The distance from the subject to the screen was 1.4 m, and the screen subtended 40 deg × 30 deg in visual angle. The screen was placed in the shielded room and the door of the shielded room was kept open to introduce the projector image to the screen. A previous study confirmed that the recording of MEGs with this system yields reliable results with repeated recordings over 50 epochs (Takeda et al., 1996).

Definition of chromatic modulations

To minimize the activation of areas other than the color-processing ones, the direction of modulation must be precisely reproduced on the screen to restrict the channels stimulated. Stimuli were modulated in two directions in the equiluminant plane and in the achromatic direction.

The directions of chromatic modulation were defined by the so-called cardinal axes of color space (Krauskopf et al., 1982; Derrington et al., 1984). The cardinal axes consist of two chromatic axes (L−M and S−(L+M)) and one achromatic axis (L+M+S). Electrophysiological studies of monkeys (Derrington et al., 1984; Lee et al., 1988; Kremers et al., 1992; Hanazawa et al., 2000) have confirmed that each axis corresponds to the selectiveness of the luminance and chromatic channels in the color space. Taking the similarity between the monkey and human visual systems into consideration, we expected that the stimulation in the directions of the cardinal axes would selectively stimulate each channel (Valberg et al., 1992). This has already been reported in previous VEP studies (Rabin et al., 1994; Kulikowski et al., 1996), and we used the same axes to define the chromatic stimulus.

The cone response was calculated using Smith-Pokorny cone fundamentals (Smith & Pokorny, 1975). The center of the cardinal axis was the metamer of equal-energy white, whose chromatic coordinates in the CIE xy color space were $(x, y) = (0.333, 0.333)$.

Fig. 1 shows the chromaticities in the sinusoidal grating at the maximum amplitude. The amplitude of the chromatic modulation in the L-M direction was determined from the maximum extent of the color gamut. The extents of chromatic modulation were 0.08 in L-cone contrast ($= \Delta L/L_{\mathrm{white}}$) for the L-M direction condition, 0.80 in S-cone contrast ($=\Delta S/S_{\mathrm{white}}$) for the S-(L+M) direction condition, and 1.0 in cone contrast for the achromatic-direction condition (MacLeod & Boynton, 1979). The detection threshold in each chromatic direction was measured in a preliminary experiment with a 0.5-s flash of a 3.2 cycle/deg (cpd) grating, and the ratio of thresholds was used to determine the ratio between $\Delta L/L_{\mathrm{white}}$ and $\Delta S/S_{\mathrm{white}}$. The chromatic modulation in the MEG experiment was magnified by a factor of approximately 70. In the achromatic-direction (luminance) condition, the contrast of the stimulus was 100%.

Equal luminance of the chromatic stimuli was confirmed by heterochromatic flicker photometry (HFP) at the center of the screen. Two lights with different chromaticities were presented

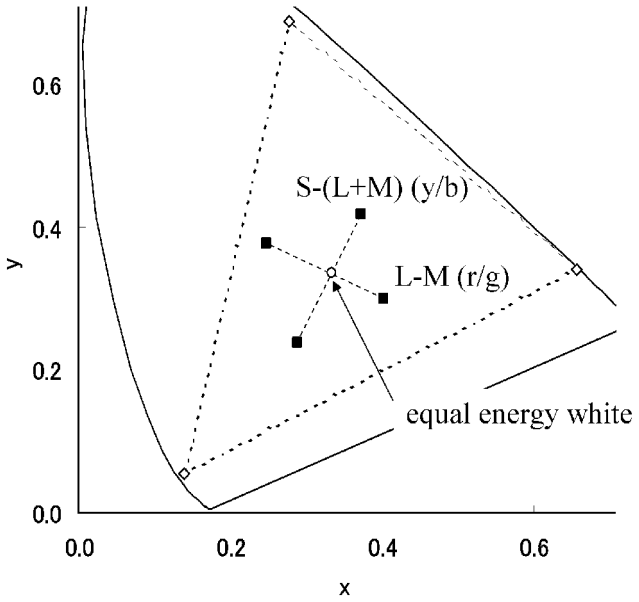

Fig. 1. Chromaticities of chromatic and achromatic stimuli in CIE *xy* color space. The chromaticity for background grey was a metamer of equal-energy white $(x, y) = (0.333, 0.333)$. The directions of chromatic modulation in L−M and S−(L+M) were determined to selectively stimulate differences between L and M cones (L−M) and the S cones, respectively. See text for details.

alternatively at 20 Hz in a square (2 deg × 2 deg) at the center of the screen with uniform grey (equal-energy white metamer, 25.0 cd/m^2) surround while the observer fixated at the center of this stimulus. This HFP setting reduced the luminance artefact, which was caused mainly by the difference in the spectral luminous sensitivities between the photometer and each subject. To be more precise, the point of equal luminance gradually changes across the visual field from center to the periphery. This is mainly because of the gradual changes in macular pigment density with the retinal eccentricity and because of the nonuniformity of neural circuitry across the retina. The effect of macular pigment density appears mainly in the form of luminance nonuniformity across the visual field. If this nonuniformity seriously affected the result, one would expect the MEG responses to the chromatic reversals to show the same pattern as the MEG response to luminance reversals, or the luminance-reversal result to contain the same waveform component as the chromatic-reversal result with a much stronger intensity. But it turned out that the MEG response, whose ECD was estimated to locate in ventro-occipital area, appeared only in the chromatic reversals. Therefore, our method of separating chromatic and luminance stimulation was effective enough and sufficient for the purpose of this study.

To find the individual S-cone direction, we slightly tilted the direction of the S-cone axis around the calculated S-axis direction based on Smith-Pokorny cone fundamentals (1975). It is known that the S cones do not contribute to luminance sensitivity (Eisner & MacLeod, 1981). On the other hand, by searching color pairs that do not allow the subject to conduct the HFP task under isoluminance, it is possible to search S-cone axis. If there were any residual stimulation to L and M cones, the subject would be able to carry out HFP adjustments. The hue directions in which the subjects were not able to carry out HFP adjustments had a certain range around the calculated S-cone axis, but the range was not small enough to determine an axis. We performed another kind of test where we presented one color (yellowish green) as a background and the other (bluish purple) as text and rated the subject's performance (Mullen & Kingdom, 2002) while varying the hue of the text. The result was basically the same as the HFP tests. We finally took the S-cone axis determined by Smith-Pokorny cone fundamentals as the S-cone direction stimulus. Since we presented the stimulus in a full half-screen, it was not possible to define an ideal S-cone stimulus for both the foveal and peripheral visual field according to the difference in the density of macular pigment between fovea and periphery. To be precise, our S-cone direction stimulus mainly stimulates the S cones but it is not possible to say this is an exact S-cone axis for each subject in overall screen. In the formal sessions, we conducted HFP with a red–green pair (L-M direction condition) before each session.

Temporal and spatial configurations

The stimuli were reversals of a sinusoidal grating, which stimulates the visual system only at the instance of reversal in the chromatic grating phase at random intervals between 2.0–3.5 s. The minimum length of the intervals (2 s) of stimulus alternations was decided so as to provide the observers with a more convincing color perception than in previous studies (Rabin et al., 1994; Regan & He, 1996; Koike et al., 1996). In terms of contrast sensitivity near threshold (Kelly, 1983), color alternation at around 1 Hz seems to be optimal to differentially stimulate parvocellular and mangocellular streams, which might be similar to the characteristics revealed in the electrophysiological study of monkey lateral geniculate nucleus (LGN) (Merigan & Maunsell, 1993). However, the aim of the present study was to record the response from the ventro-occipital cortex, which might process higher-order information (presumably closer to color appearance, rather than detection or discrimination) than the LGN. We performed informal observations of stimuli by presenting various intervals of chromatic reversals to naïve graduate students in our laboratory. When the students were asked to name colors of light alternately presented for less than 2 s for each color, they yielded a "cluttering" percept and the task was very difficult. The same kind of phenomenon would be observed, if subjects were asked to match one of the colors in a flickering square with a static one. Subjects may not be convinced of the target color to be matched at higher temporal frequency, and the difficulty of perceiving it would increase under higher temporal frequency. The subjects will not be able to make convincing matches at the temporal frequency above 0.25 Hz or so. It should be noted that *color percept* is used in this manuscript to mean color appearance at the suprathreshold level. We pay more attention to *percept* in order to stimulate the higher-order color appearance system. Interval randomization was used to prevent subjects anticipating the next reversal, which would happen if the reversals had taken place at an even pace.

The long interval of 2.0–3.5 s between the grating reversals also prevents apparent-motion perception. According to the results of studies on chromatic motion perception (McKeefry, 2002; Dobkins & Albright 1994; Baker et al., 1998), an isoluminant chromatic grating can evoke continuous "signed" motion perception, and this should be avoided. A faster reversal of the grating might evoke continuous apparent motion, if the visual system tracks the peaks and troughs of the chromaticity or luminance.

The screen subtended 40 deg × 30 deg. Since object edges may activate many parts of the visual system, which processes figural information, we did not vary shapes across the MEG triggers. In

addition, we tried to remove figural changes during the course of a session, because the appearance and disappearance of a figure would also affect the visual system. According to the results of a preliminary experiment, there were no prominent differences between stimulus presentation in the left and right half of the visual field. Therefore, we precisely examined the left hemifield (right hemisphere). We used three spatial-frequency conditions for the grating, 0.025, 0.4, and 3.2 cpd, to examine whether the color sensitive area has any specific selectivity in spatial frequency. The 0.025 and 3.2 cpd were determined from the overall size of the screen and the spatial resolution limit of the projector, respectively.

Procedure

The subject sat in the shielded room and preadapted to a uniform grey screen (equal-energy white metamer; in CIE *xy* coordinates, $x = 0.333$ and $y = 0.333$) with the luminance of 25.0 cd/m^2 for at least 5 min to prevent unexpected chromatic adaptation and dark adaptation. Before starting a session, a subject conducted ten repetitions of HFP settings to a pair of two extreme chromaticities in an L-M grating. The equiluminance pairs for chromatic gratings were determined based on this result. During a session, a subject was asked to fixate on a dot presented at the center of the screen with a slight (0.5 deg) horizontal offset from the exact center in the right half (uniform grey). Within a session, the direction of chromatic (or achromatic) modulation and the spatial frequency of the grating were kept constant. Therefore, only the reversals of the polarity of chromatic modulations stimulated the visual system during the MEG recordings (Fig. 2).

An epoch of MEG recording started 200 ms prior to the grating reversal, and the recording continued until 800 ms posterior to the reversal; overall recording duration was 1000 ms. This was repeated for 100 trials, and a complete session took approximately 20 min.

fMRI data acquisition and analysis

To confirm the location of the activity estimated from the ECD analysis, we conducted a supplemental experiment using the functional MRI (fMRI) technique. MR images were recorded using a Siemens Magnetom Vision Plus (1.5T) clinical scanner with an external trigger input. The visual stimulus was generated with a Macintosh PowerBook G3 computer with a C-language library for psychophysical stimulus presentation (Vision Shell, MicroML, Inc., Canada). The stimulus was presented on a plastic screen placed in the shielded room with a liquid crystal projector (TH-L777J, Panasonic, Japan). Subjects lied supine in the MRI gantry and viewed the stimuli through an oblique mirror mounted on a head coil.

The observer viewed chromatic and achromatic gratings presented in the left hemifield of the screen. The stimuli were presented with a block design, in which five rest scans and five task scans were presented alternatively. In task scans, either chromatic or achromatic gratings were presented in the left hemifield of the screen. The definitions of achromatic and chromatic gratings were the same as those in the MEG experiment. The polarity of gratings reversed at random ISI between 2.0–3.5 s. To suppress artefacts from the stimulus presentation order, the task stimuli were designed to present chromatic and achromatic grating conditions in a random order. The total number of scans was 160; 40 for the chromatic grating condition, 40 for the achromatic grating condition, and 80 for the rest (uniform grey screen) conditions. The screen subtended 20 deg × 15 deg in visual angle, and the spatial frequency of the grating was 0.4 cpd.

Functional images were taken with the T2* weighted protocol (Ogawa et al., 1990), with 45 slices of scans, 3-mm thickness with 64 × 64 pixels in-plane resolution for the field of view (FoV) of 192 mm × 192 mm (Voxel size was 3 × 3 × 3 mm). Acquired functional images were preprocessed (motion correction and smooth-

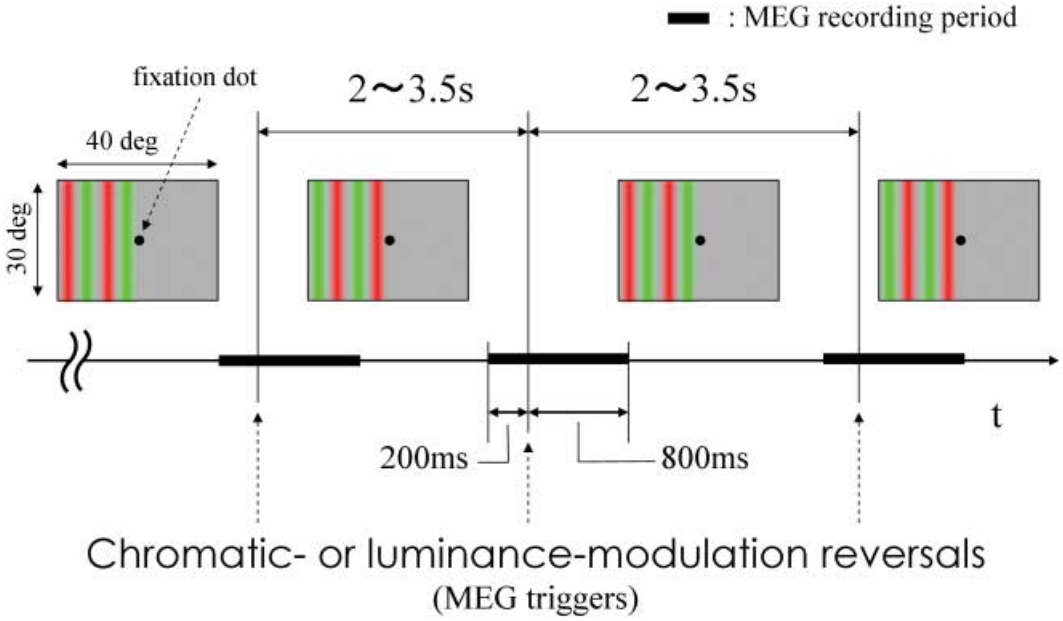

Fig. 2. Time course of stimulus presentation. The stimulus was presented continuously, but the polarity of the grating modulation was reversed across the MEG recording trigger. MEG recording started 200 ms before the trigger and finished 800 ms after it. Inset at the left top of the chart shows the size of the screen in visual angle.

ing) with SPM 99 software (Friston et al., 1995). Statistical images (*t*-test) were generated using our in-house software. The threshold of the level of statistical significance was set at $P < 1.0 \times 10^{-4}$. The isolated dots disappeared at this significance level. To compare the focus of activated points in the fMRI data and the estimated ECD location in the MEG data, the level of statistical significance was set as low as 1.0×10^{-6}. The Talairach coordinates for the focus of fMRI activity were consistent with previous fMRI studies (summarized in a table in Bartels and Zeki, 2000).

Subjects

Subjects were two undergraduate students (KS, KA, both aged 22 years) and the first author (IK, aged 32 years). Two of them had normal visual acuity and one had corrected-to-normal visual acuity. All of the subjects were right handed. Subjects KS and IK participated in both the MEG and fMRI experiments.

Results

Fig. 3(a) shows a typical time chart with a stuck plot of MEG from the 64 sensor channels under the chromatic reversal condition. There are two prominent peaks. The first peak appears at around 100 ms of latency and the second at around 150 ms.

The MEG peak at around 150-ms latency was specific for the chromatic stimulus conditions. Fig. 3(b) shows the MEG time chart from a typical luminance reversal condition for the same subject. The magnetic field map at the latency of the most prominent peak, at around 100 ms, shows a clear dipole near the occipital pole.

The MEG corresponding to each peak that persisted for more than 10 ms and whose pattern shows a clear dipole configuration was analyzed by equivalent-current dipole (ECD) estimation. Fig. 4 shows typical MEG patterns from a chromatic condition [Fig. 3(a), 158 ms] used for ECD estimation.

Fig. 5 shows the locations of the ECDs estimated for the recording from subject KA with L-M direction stimulation with 3.2-cpd grating. The ECD estimated from the latency of around 100 ms was located in the calcarine sulcus, which means the estimated location of the activity was the primary or secondary visual cortex (V1/V2). The second ECD was estimated from the map around 150 ms and the estimated location was in the ventro-occipital area. After a precise examination, this ECD was found to be located within the fusiform gyrus. The ECD estimated from the MEG at the latency of around 100 ms was generally located in the calcarine sulcus, and the one from the MEG at the latency of around 150 ms was located generally in the ventro-occipital area.

The latencies of the peaks at around 100 and 150 ms were reexamined after the locations of the ECDs were specified in the structural MRI image. The latencies of the MEG amplitude peak that corresponds to ECDs in the calcarine sulcus (V1/V2) and in the fusiform gyrus (ventro-occipital area) are plotted with different symbols in Fig. 6. There are clear latency differences between the MEG amplitude peaks with ECDs in the calcarine sulcus and fusiform gyrus. The average difference in the latency was 43 ms. We varied spatial frequency among the three conditions. However, we found no common tendency among observers in peak latency, MEG amplitude, and the location of ECD

For two of the three subjects, the locations of fMRI responses were compared with the estimated ECD locations. Fig. 7 shows the result of the fMRI experiment and the estimated ECD location in the same slice from one subject. Since the stimulus was presented in the right half of the screen, most of the voxels with high BOLD signal locate in the occipital cortex in the left hemisphere. The location of ECD in the calcarine sulcus and the V1/V2 activity in the fMRI show good coincidence. The ECD in the ventro-occipital area was within the fusiform gyrus, as were the foci of fMRI activity.

According to the studies by McKeefry and Zeki (1997) and Bartels and Zeki (2000), the response to stimulus presentation in the top and bottom half of a screen distribute over the collateral sulcus. As shown in Fig. 7, foci from both fMRI and MEG measurements appear to locate medially to the collateral sulcus (i.e. lingual gyrus). Our data are consistent with previous results, in that the fMRI response would span across the collateral sulcus if the significance level were raised. The results for both modalities of measurement are summarized in Table 1, which includes as a reference the focus of fMRI response in the right hemisphere obtained by McKeefry and Zeki (1997) when they presented the stimulus in the full field of the screen.

Table 1. *Summary of ECD locations and fMRI activity foci*[a]

		x (mm)		*y* (mm)		*z* (mm)	
Data source/subject	Modality	avr	S.D.	Avr.	S.D.	avr.	S.D.
McKeefry & Zeki (1997): Right hemisphere, full field	fMRI	30		−78		−18	
KS	fMRI	24.4		−68.3		−17.7	
	MEG	23.3	2.28	−74.25	1.99	−16.5	2.45
IK	fMRI	18		−81		−18	
	MEG	15.9	1.3	−71.1	4.8	−20.1	2.1
KA	MEG	30.0	2.4	−67.2	2.1	−15.4	1.7

[a]ECD locations were summarized by taking average and standard deviations (S.D.) across MEG experiment sessions. The foci of fMRI activity for subjects KS and IK were determined by using high significance level ($p < 1.0 \times 10^{-6}$). As a reference, the top row shows a data of fMRI focus in the right hemisphere from McKeefry and Zeki (1997), which was obtained under full-field stimulation condition.

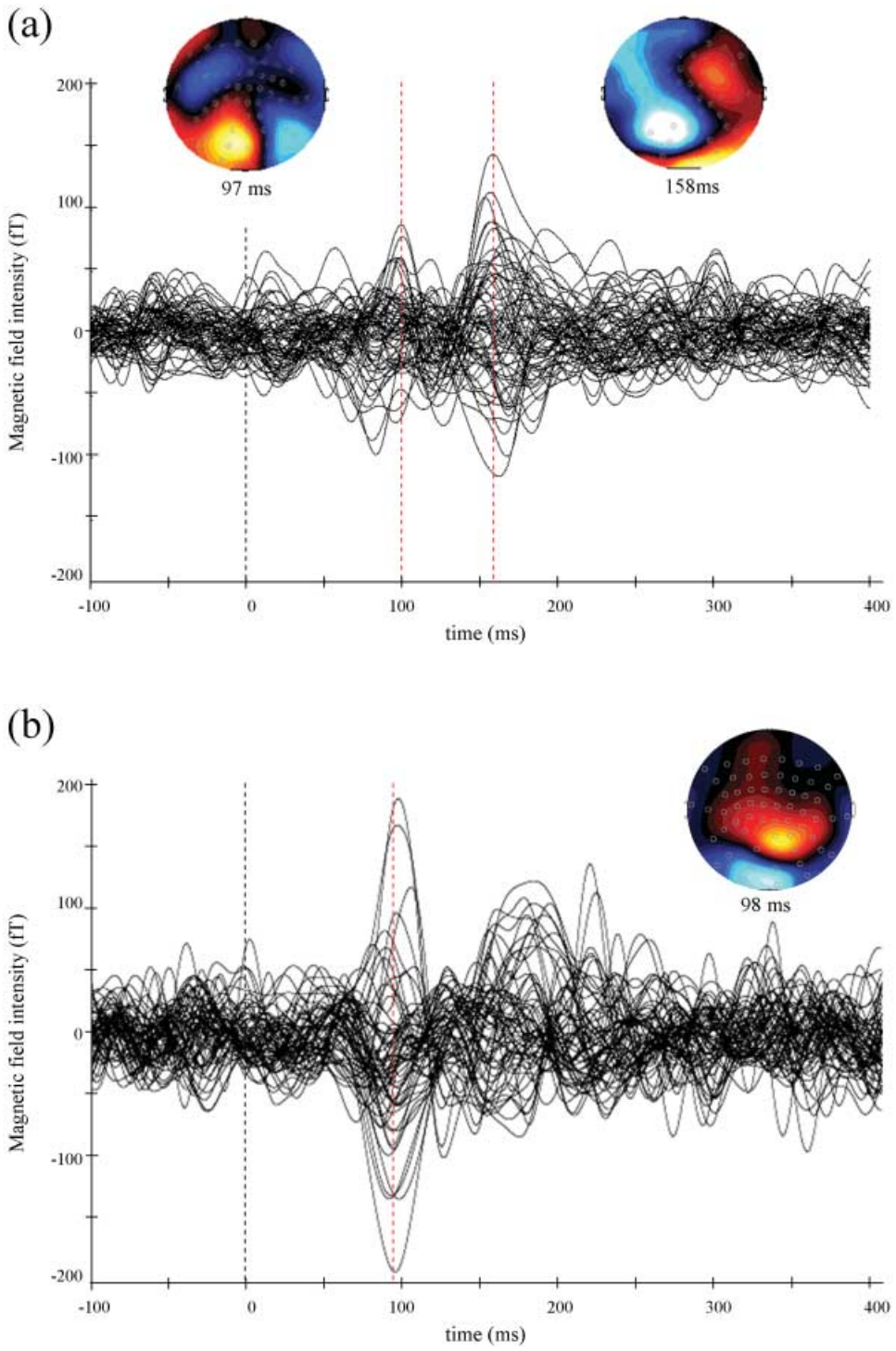

Fig. 3. Typical stack plots of the 64 MEG channels. (a) Result for subject KA from L-M reversal of the 3.2-cpd grating. The first peak appears at 93 ms, and the second at 158 ms. Insets show MEG field maps corresponding to each peak. (b) Result for the same subject for luminance reversal of the 3.2-cpd grating. A prominent response is found only at the latency of around 100 ms.

General discussions

Efficiency of long-intermittent color reversal stimulus

The present study has successfully recorded MEG responses to chromatic stimuli whose ECDs located in the ventro-occipital area. This source location was confirmed by fMRI with the same visual stimulus and is consistent with the previous PET or fMRI studies (Lueck et al., 1989; Sakai et al., 1995; Zeki & Marini, 1998; Bartels & Zeki, 2000). The latencies of MEG peaks in the present study are consistent with those in previous EEG studies, although

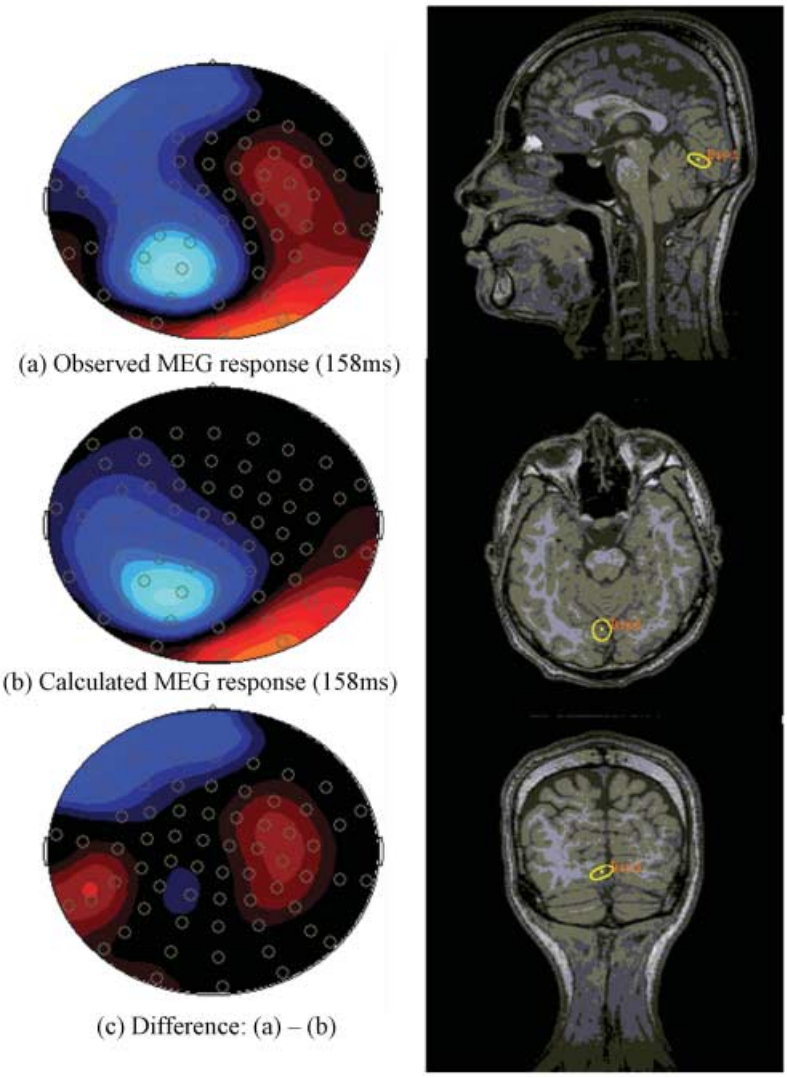

Fig. 4. The left column shows maps derived from the second-peak data. (a) Recorded MEG data; (b) calculated magnetic-field map for ECD estimation displayed in right column; (c) the difference between (a) and (b). The goodness of fit (GOF) was 84.4% for this result; residual errors are small and restricted to the frontal area. The MRIs show sagittal, transverse, and coronal views (top to bottom) of subject KA at slices including the location of the estimated ECD. The small ellipses in the ventro-occipital area show the 95% confidence volume for the ECD, the estimated location of which is shown by a small dot at the centre of each ellipse.

with one exception (Buchner et al., 1994), these studies did not attempt to localize the ECD (Crognale et al., 1993; Rabin et al., 1994; Gerth et al., 2003). Our stimulus was slightly different from conventional ones, and our result suggests that our method was effective for recording MEG responses to color stimulus from the ventro-occipital area. The second peak at around 150 ms of latency in the present study, with ECD in the ventro-occipital area, has not been successfully observed in the previous MEG studies with conventional visual stimuli (Regan & He, 1996; Koike et al., 1996). It is known that the electric current source for MEG and EEG are common, but because of the geometric and electromagnetic difference between the evoked potential and magnetic field, some brain activities are not always recorded by both modalities (Hämäläinen et al., 1993). From previous MEG and EEG studies, it can be inferred that recording the activity in the ventro-occipital cortex, stimulated by conventional onset-offset or reversal stimulus, is advantageous for EEG.

As an aid in discussing the reason for our success, we would like to introduce the result of our preliminary experiment. In this preliminary experiment, we recorded MEG responses while presenting two chromatic stimulus conditions (r/g and y/b) and one luminance stimulus condition within a session in a random order. Each stimulus was presented with the stimulus onset (the appearance of a grating from uniform a grey screen) preceding by 1.0–1.5 s (randomly perturbed between trials) the single polarity reversal of sinusoidal grating. The grating was modulated in either color or luminance with a spatial frequency of 0.4 cpd. In the color conditions, gratings were modulated under isoluminance, and in the luminance condition the average luminance was kept the same as the uniform grey background. The stimulus went back to a uniform grey screen at 1.0 s after the single reversal of chromatic or luminance polarity. The other details of the stimulus were the same as in the main experiment. MEG responses were recorded from −200 ms to +800 ms of latency with respect to the instance of reversal, and the data were analyzed by taking the average of more than 40 epochs for each stimulus condition. During the MEG recording period, the stimulus condition was completely the same as in the main experiment. However, the result showed peaks only at 80–100 ms of latency, and the ECD was estimated to locate in calcarine sulcus. Unlike in the main experiment, no peak response was observed at around 150 ms of latency. This was consistent among the three subjects in both hemispheres (6 samples).

This preliminary result suggests that the MEG response to the onset of chromatic stimulus, which changed in color and shape but

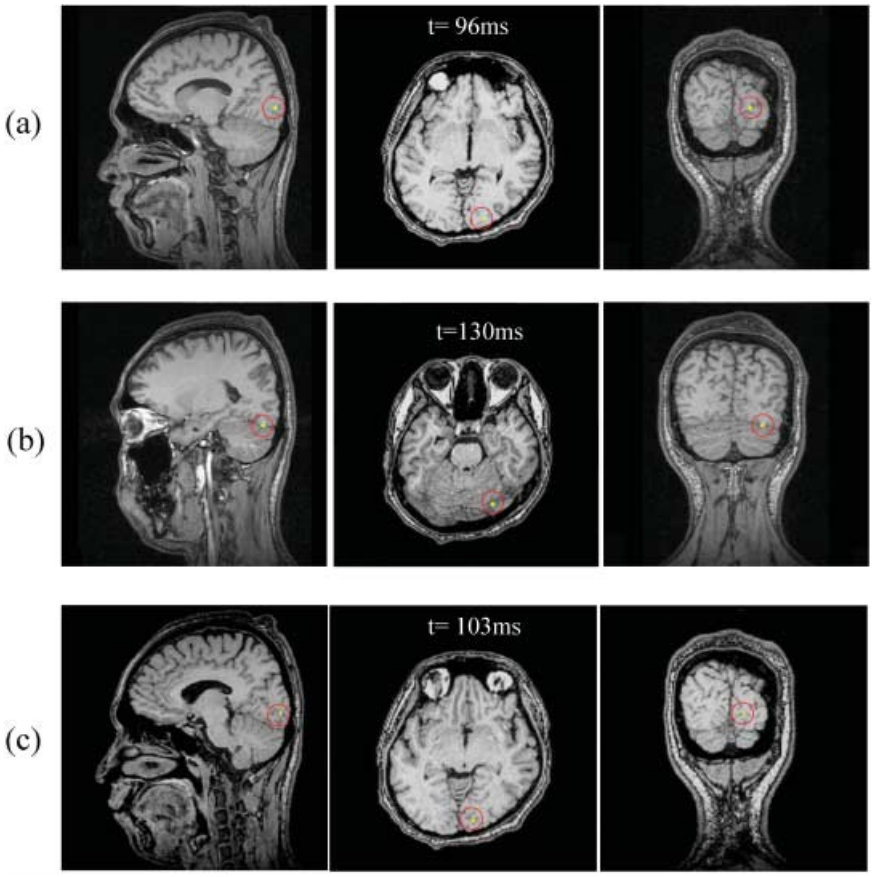

Fig. 5. The results of ECD estimations. Rows (a) and (b) show the results for the first peak and the second peak for subject KS, S−(L+M), 0.4 cpd, in the left hemifield stimulation. Rows (a) and (b) show the location of the estimated ECD at 96 and 130 ms, respectively. GOF for each ECD fit was 84% for the first peak and 83% for the second. The three panels in row (c) show results of ECD estimation from the same subject under the luminance reversal condition (0.4 cpd, 103 ms). GOF was 91%.

not in luminance, was strong enough to evoke brain activity that interferes with the recording of MEG response from the ventro-occipital area, which is evoked only by a color reversal 1.0–1.5 s after the onset. At the same time, this implies that the MEG response from the ventro-occipital area at the latency of about 150 ms is not robust and easily disappears with the changes in preceding stimulus condition. Since the fusiform gyrus in the ventro-occipital area is estimated to process figural information

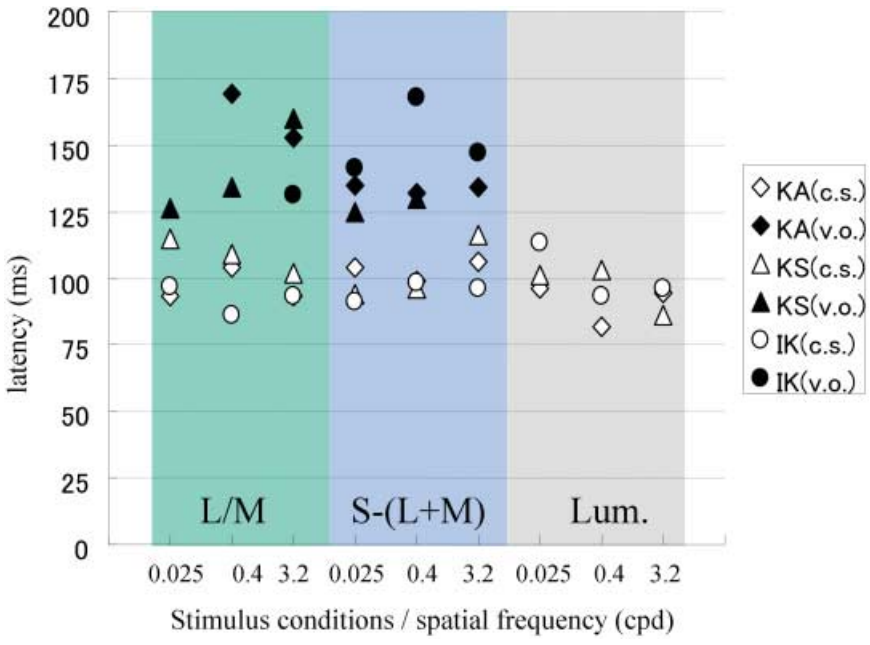

Fig. 6. Latencies of the first and second peaks in each stimulus condition for the three subjects that allowed the estimation of ECDs satisfying the constraints listed in the text. The three shaded areas represent different stimulation conditions, such as the L−M, S−(L+M), and luminance conditions (from left). The open symbols represent latencies for the first peak (located in the calcarine sulcus; abbreviated c.s.) and the filled symbols represent latencies for the second peak (located in the ventro-occipital area; abbreviated v.o.).

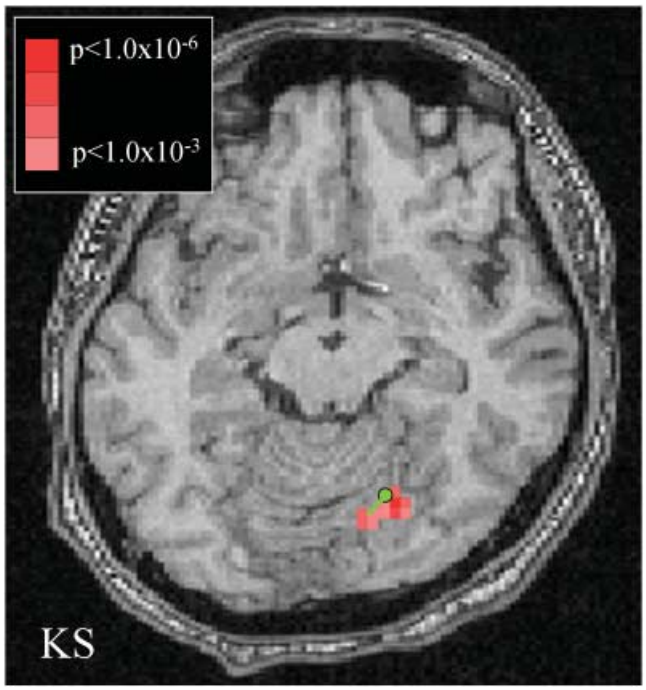

Fig. 7. Comparison of ECD location with a fMRI statistical map. The ECD location and statistical map from fMRI analysis are superimposed on the same plane of the transverse section of an anatomical MR image. The ECD was derived from the magnetic map recorded from subject KS at the latency of 130 ms (Fig. 5, bottom row). The green circle represents the location of the ECD from MEG and the red blob represents the fMRI result (t-test, $P < 1.0 \times 10^{-3}$–1.0×10^{-6}). Talairach coordinates for the focus of fMRI activity are shown in Table 1. Both the ECD and fMRI activity locate on the ventral surface of the occipital lobe.

(Zeki & Marini, 1998; Grill-Spector et al., 2004), the response to figural changes in this area somehow disturbed recording clear MEG responses to color-information processing area in the ventro-occipital cortex. This might be the reason previous MEG studies using the conventional method of visual stimulation were not successful in recording responses from the ventro-occipital area.

The present study and an EEG study by Buchner et al. (1994) recorded current source activity in the ventro-occipital area at the latency of around 150 ms. Although Buchner et al. used a color stimulus with luminance distributions, both their and our studies presented no figural changes across the color stimulations. This indicates that our attempt to avoid presenting any figural changes in the main experiment prevent the occurrence of any disturbance from stimulating the cortical area sensitive to changes in the figural configuration. In our stimulus, we also made the screen isoluminant in chromatic conditions to prevent stimulating subsystems of human vision, which obtain information mainly from luminance distribution, such as shape, motion and so on, from the subject's involuntary eye movements. This is because responses from these subsystems seem to disturb recording response to color from the ventro-occipital area, especially in MEG recordings.

Another similarity between this study and Buchner et al.'s is that the length of ISI was relatively longer. This might be another important factor in successful recording of MEG responses from the ventro-occipital area. Gerth et al. (2003) presented either onset or reversals in multifocal stimulating procedure in a random order (12 bits m-sequence) and concluded that a color-onset stimulus was more effective than color reversals. The multifocal stimulation is based on assumptions that linear summation of each evoked response is equivalent to the recorded waveform and that the response to each stimulus presentation in a rapid sequence is robust. Several studies suggested that this method would be successful also in MEGs (Wang et al., 2001; Tabuchi et al., 2002), but the source of the responses were mainly in the calcarine sulcus. The robustness of responses from the calcarine sulcus at around the latency of 100 ms seems to hold. However, as our preliminary experiment showed, the robustness does not seem to hold for MEG responses from the ventro-occipital area with a rapidly changing stimulus. Therefore, we infer that the use of the relatively longer ISI (2.0–3.5 s) in the present study was effective for observing relatively weak MEG responses from the ventro-occipital area.

The presentation of a long-intermittent single reversal of a grating may evoke an apparent-motion percept. However, this was not the case in our experiment. Two of the three subjects did not perceive the apparent-motion percept in any condition. Subject KA reported an apparent-motion percept for a few times in the highest spatial-frequency condition (3.2 cpd). Especially in the case of 0.025 cpd, one half of a grating was shown in a full half-field of the screen; therefore, the color reversal did not appear as motion at all. If the motion percept had strongly disturbed the MEG response, the resulting MEG would have shown some systematic change due to spatial frequency of the stimulus.

About the MEG response latencies between visual areas

A recent study presented a series of electrophysiological recordings from monkey visual cortex and reported a series of differences in the latencies (Schmolesky et al., 1998). In that study, the latency between V1 and V4, which are considered to be homologues of the ECD locations estimated as V1/V2 and ventro-occipital foci in the present study, was approximately 20 ms at the very first instance of activation. According to the difference in the time course of cell activity growth, the latency became about 45 ms at the level of 75% cell activity (Fig. 2 in Schmolesky et al., 1998). However, since their results are recordings of single-cell activity and ours is a MEG of the human brain, these data have to be compared carefully.

The difference of 43 ms in MEG latency from the calcarine and collateral sulci (Fig. 6) is not unusually long for the following reason. The latencies of the ECDs located in the calcarine sulcus at around 80–100 ms have been observed frequently in various MEG studies using a visual stimulus. However, the source of the MEG signal has been estimated to be a result of the synchronized activation of hundreds of thousands of neurons (Hämäläinen et al., 1993). According to the inherent characteristics of nerve-cell membrane, the temporal-frequency limit of the nerve impulse could reach about 200 Hz. In general, the frequency range of the firing rate is about several ten to 100 Hz. Basically, a nerve impulse itself does not carry specific information; the frequency of the spike codes the intensity of the signal in a neuron. In addition, each neuron has spontaneous discharge when idle, which is expected to be ignored, and the frequency of the spike train itself randomly fluctuates (Teich, 1989). Therefore, the receivers of the pulse, probably synapses or postsynaptic neurons, have to analyze the incoming pulse train for at least several milliseconds to determine whether the incoming spikes contain signal (Teich et al., 1990). Taking the above discussion into consideration, a neuron in the following stage of information processing has to wait more than a few milliseconds after the first nerve impulse with some signal

reaching the synapse terminal. The mechanism of transition from single neuron activation to mass activation is still unknown, but it may take more than several ten milliseconds (the time to decode the strength of incoming signal) after the arrival of the *first* impulse. This can be easily imagined from the difference in the time between the estimated time of arrival of the first impulse (40–50 ms) and the first prominent peak of MEG/EEG activity in the primary visual cortex (70–100 ms) (Schmolesky et al., 1998). Therefore, the major factor in the difference between electrophysiological single-cell recordings and the MEG response may be the time needed to initiate the synchronized activation by a huge number of cells (Hämäläinen et al., 1993), and this should be taken into consideration when reading MEG data.

Temporal characteristics of color vision in MEG and psychophysical studies

It is commonly known among color-vision researchers that the fast alternation of lights (about 10 Hz and up) of different chromaticity does not provide convincing perception of color. However, the difference in the luminance between two lights is visible in the form of flicker. This phenomenon is thought to originate from differences in the temporal-response characteristics of the human visual system.

In psychophysical studies, one way to study temporal response characteristics of the chromatic system is to measure contrast sensitivity to flicker (Kelly, 1983). Another is to use chromatic double pulses while changing the stimulus onset asynchrony (SOA) to measure subthreshold summation. Uchikawa and Yoshizawa presented two short chromatic pulses (20-ms duration) with a certain SOA and asked the observer to report whether any pulse was visible. By varying the SOA and the intensities of the pulses, a time course of detection threshold was derived (Uchikawa & Yoshizawa, 1993). The results showed that the additive effect between two pulses lasts about 0–200 ms after the onset of the first pulse, which means the pulse coming 200 ms after the onset of the first pulse was treated as an independent one. This implies that the chromatic mechanism has to wait more than approximately 200 ms to complete a series of information processes for a single event.

Ohtani et al. have studied MEG responses to chromatic double-pulse presentations (Ohtani et al., 2002). The focus of the response was estimated to locate in the calcarine sulcus (at V1/V2, according to their expression). Their result showed that the temporal summation effect in the MEG lasted as long as 50 ms with the SOA at the level of response at the V1/V2. This means that, at V1/V2, a series of information processes is treated as a unit during the first 50 ms after the emergence of the first chromatic stimulus. However, this length of time is significantly shorter than that estimated in a psychophysical study: 200 ms.

The psychophysical data tell us that somewhere in the visual system, which is closely related to the percept of chromatic pulses, there is an accumulating period of 200 ms. A pair of two independent pulses with 100 ms of SOA is treated separately in V1/V2, but they are treated as a single pulse when the signals for each pulse pass a stage within the visual system. This accumulation of visual signal for more than 200 ms must occur at a stage after the V1/V2. At least, the present study suggests that the ventro-occipital area is a possible site; our data indicate that the ventro-occipital area selectively responds to chromatic stimuli after V1/V2. However, it is not possible to argue that the ventro-occipital area is a possible site of temporal summation from the data in the present study.

Conclusions

We have succeeded in recording MEG responses of the human visual system specific to chromatic stimulation from the ventro-occipital area by using the single reversal of color grating with ISIs of 2.0–3.5 s as the visual stimulus. The difference in latency between V1/V2 and ventro-occipital area (presumably human V4 homologue) was approximately 40–50 ms (43 ms on average), which was consistent between subjects.

Acknowledgments

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Action-specific extrapolation of target motion in human visual system

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Abstract

Neuropsychological studies have indicated two distinct visual pathways in our brain, one dedicated to conscious perception and one to visuomotor control. Some psychophysical results support this idea with normal subjects, but they are still controversial. This study provides new psychophysical evidence for the dissociation by showing action-specific extrapolation of the visual target trajectory. When a moving target disappears, the perceived final position is liable to be shifted forward (representational momentum). In experiment 1, larger and more robust forward shifts were found when the position was directly touched without seeing the screen (open-loop pointing) than when the position was judged perceptually. The most striking dissociation was that fixation did not affect the forward shift in open-loop pointing while it almost abolished the shifts in perceptual judgements. In experiment 2, this action-specific result was found to disappear after a response delay of 4000 ms. Experiments 3 and 4 confirmed that the results were not affected by the external reference frames. The specific forward shifts found in open-loop pointing suggest that the visuomotor system compensates for the neural delays by extrapolating the target motion. The results, together with earlier findings, lead to a psychophysical double dissociation of the two visual pathways.
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Keywords: Representational momentum; Visuomotor; Reaching; Action; Visual motion

1. Introduction

Neuropsychological studies on brain damage patients have indicated that the human brain has distinct visual pathways for action control and for detailed visual perception, a conclusion which is also supported by monkey neurophysiology (Milner, 1999; Milner & Goodale, 1995). For example, a patient with 'visual form agnosia' was able to post a plaque into a slot without being able to report its orientation. Together with the knowledge that damage in the parietal cortex can lead to visuomotor disorders (Bálint syndrome), there seems to be a double dissociation in terms of both function and physical pathways. Psychophysical studies on intact observers, however, have not shown such a clear picture. One line of evidence for separate functional pathways comes from results where the grasping action resists visual geometrical illusions such as the size contrast effect in Titchner–Ebbinghaus circles (Aglioti, DeSouza, & Goodale, 1995). However, there are possible artefacts (Franz, 2001), and dissociation in the results might not be evidence of two pathways (Bruno, 2001; Franz, Bulthoff, & Fahle, 2003). Given that a dissociation between perception and action has been reported in many other cases (e.g. Bridgeman, Peery, & Anand, 1997; Burr, Morrone, & Ross, 2001; Dyde & Milner, 2002), the weakness seems to be that action is always more immune to illusion, a claim which has no a priori justification.

Yamagishi, Anderson, and Ashida (2001) provided the counterpart to complete the double dissociation. Using drifting Gabor patches, they demonstrated that the positional bias due to carrier motion (Anstis & Ramachandran, 1995; De Valois & De Valois, 1991) is more pronounced in an immediate open-loop reaching task than in perceptual judgement, showing that action can be more prone to illusion. The time taken for visual processing is a problem when determining the location of a moving target, and one possibility is that our visual system anticipates the target's true location on the basis of the motion signal (Anstis & Ramachandran, 1995). If so, it is not surprising that a larger extrapolation should be found in a real-time reaching action in order to avoid missing the target. This idea, however, remains speculative because anticipation is not a real requirement in the case of motion-related positional biases because the envelope pattern does not move. We need to test the anticipa-

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tory effect for a moving target in a more straightforward situation.

While anticipatory mechanisms in the retina of rabbits and salamanders have been reported (Berry, Brivanlou, Jordan, & Meister, 1999), it is unclear if primates or humans, with their more complex visual systems, have a similar function. Discussion on anticipatory visual coding has been active in psychophysics since the rediscovery of the flash-lag illusion (Nijhawan, 1994), in which a continuously moving target is perceived ahead of a flashed stimulus when the two are physically aligned in space and time. Nijhawan (1994) argued that the visual system extrapolates the moving object's instantaneous location to compensate for the processing delay. Although it is an intriguing idea, later results are more favourable to other factors as the cause of the flash-lag illusion, for example, processing delay for the flashed target (Whitney & Murakami, 1998) or time averaging of the position of the moving object (Eagleman & Sejnowski, 2000), and discussion on the flash-lag continues (see Nijhawan, 2002). Since anticipation is particularly important in direct action (Nijhawan, 1994, 2002), it is notable that Nijhawan and Kirschfeld (2003) found a similar flash-lag phenomenon between visual and motor domains. They showed that perception of a flashed visual target lagged behind the position of an unseen rod that was manually controlled. While they argued for analogous delay-compensating mechanisms in visual and motor processing, they did not provide clear evidence either against the other theories of visual flash-lag or against the possibility that all compensation is accomplished in the motor system.

Here we address two main questions: firstly, whether the brain operates purely visual extrapolation to compensate for the neural delays, and secondly whether such extrapolation selectively affects direct visuomotor co-ordination. To answer these questions, this study investigated the judged final position of a linearly moving target after it suddenly disappeared. The perceived final position is apt to be shifted forward, an effect referred to as "representational momentum" (RM), because it seems as if the inner representation has momentum (Freyd, 1983). There are two major advantages to using this phenomenon. First, the target actually moves and the forward shift is more straightforwardly explained in terms of extrapolation than in the case of the Gabor stimuli. Second, since observers are not asked to point to the target itself, compensation for motor delays is not required. A substantial shift in the motion direction would therefore be a signature of visual extrapolation along the target path. The main interest is in the way in which forward shift occurs in perceptual and motor responses.

While RM has been found for several kinds of motion, a linear and smooth motion as tested by Hubbard and Bharucha (1988) is the most desirable for the current purpose. Two main and two control experiments revealed a distinct pattern of results for open-loop action, evidence of specific visual extrapolation for the immediate control of action. The results also provide another piece of evidence for the distinct visual processing for perception and action.

2. General method

2.1. Observers

HA was the author, and MN was a senior researcher. NY participated as an undergraduate course requirement. Naïve observers (RS, SY, HM, and TI) participated in the two main experiments with payment by the standard of Kyoto University. All the participants except the author himself gave their informed consent before starting the experiment. All were right-handed and had normal or corrected-to-normal vision. Their age ranged between 21 and 34 years.

2.2. Apparatus and procedure

Stimuli were generated by a framebuffer system (Cambridge Research Systems, VSG 2/3) and were presented on a CRT monitor (SONY, GDM-F400) that was equipped with a four-wire resistive touchscreen (Touch Panel Systems, Inc., AccuTouch). A pair of liquid crystal shutter goggles was used to restrict the observers' view during the responses. The transmittance of the shutter was about 30% when open, and was reduced by more than 10 dB when closed. The screen was turned off when the shutter was closed, and nothing remained visible in a dim room. A trackball (by Logitech Inc.) was used for perceptual cursor adjustment, which, unlike a mouse, neither required arm and wrist movement nor allowed unconscious feed-forward control because the observers did not use it daily. A chin rest was used to restrict the viewing distance to 40 cm.

In experiments 1, 2, and 3, the monitor was positioned in front of the observer. In experiment 4, the monitor was positioned on the left side of the observer, who viewed the stimuli through a front-silvered mirror that was placed at an angle of 45°. In that case, the touchscreen was placed behind the mirror at the same position as in the other experiments, so that the observers touched the screen without seeing their hand and arm while the stimulus screen remained visible.

The display resembled that of Hubbard and Bharucha (1988). As shown in Fig. 1, a black disk (1.0° in diameter) was presented as a target on a white (45 cd/m^2) rectangular background that subtended 25.8° horizontally and 17.3° vertically. The target moved horizontally from the middle of the left or the right edge of the white area at a constant speed, and disappeared at a random horizontal position. The observers judged the final position of the target and responded with their right hand.

Three types of responses were tested: cursor adjustment, closed-loop pointing, and open-loop pointing. For cursor adjustment, the observers adjusted a screen cursor to the re-

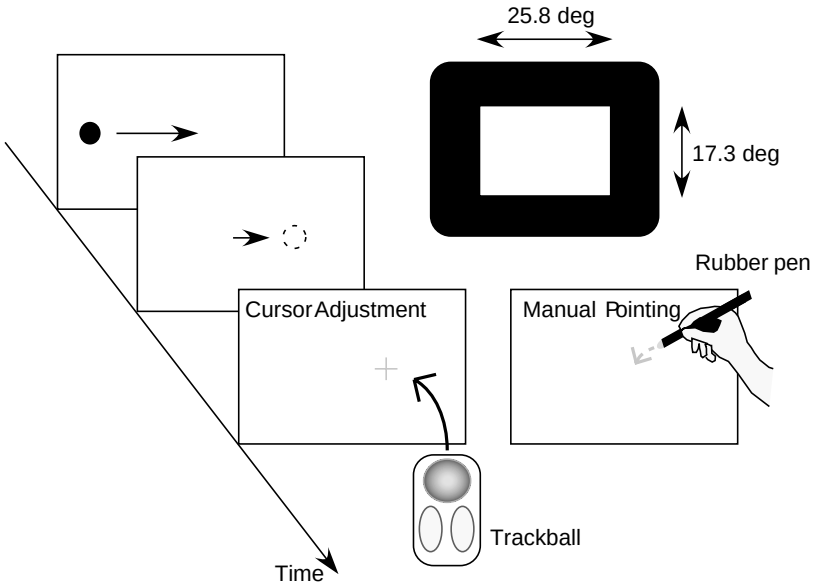

Fig. 1. A schematic illustration of the procedure. A black target disk appeared at the left or the right edge of a white rectangular area, and moved horizontally to the right or to the left at a constant speed. The participants judged the final position where it disappeared and responded either by adjusting a screen cursor or by touching the screen with a pen. See text for more details.

membered final position of the target, as in previous studies (Hubbard & Bharucha, 1988; Kerzel, Jordan, & Musseler, 2001) but using a trackball instead of a mouse. For this test, the shutter was always open. For closed-loop pointing, the observers touched the screen with a rubber pen. The shutter was always open and the screen, the hand, and the arm remained visible, thus providing visual feedback for the pointing action while adjusting the pen toward the remembered position. For open-loop pointing, the observers touched the screen with a rubber pen, with the shutter closed before they started the pointing action. The whole visual field was invisible when the shutter was closed. Shutter timing varied across experiments. Under all these conditions, fixation was either free or maintained at a fixation mark that was presented 4.0° below the centre of the screen. The fixation mark, if any, disappeared during the judgement. Eye movement was not measurable due to the shutter goggle.

The observers initiated each trial by pushing a button with their right hand so that the reaching action started from the same position. The direction and the speed of the target were always randomised within a session. Four sessions were conducted for each condition, resulting in 20 responses in each direction.

2.3. Data analysis

The horizontal shift of each response from the physical position of the target disappearance was analysed. As there was no consistent effect of motion direction, the results were collapsed across motion direction so that a positive value indicates shift in the motion direction. The 40 measurements were then averaged for each condition and each speed.

3. Experiment 1

3.1. Method

Cursor adjustment, close-loop pointing, and open-loop pointing were tested with and without fixation. Three speeds were tested (10, 19, or 35°/s). For open-loop pointing, the shutter was closed just when the target disappeared. In this experiment, the observers were not required to follow the target strictly when there was no fixation mark, but all the observers tried to do so according to their later verbal report.

As a more genuinely perceptual judgement, a control condition was tested. Target presentation was the same as in the other conditions. After the target disappeared, a probe disk of the same size and colour was presented just below the target path with a delay of 500 ms. The observer judged whether the probe disk appeared to the left or the right of the final position of the target. The probe was presented at five positions relative to the target's final position. Data were collapsed across motion direction and the final position of the target, and the relative position that gave 50% responses, estimated using probit analysis, was used as the amount of forward shift.

3.2. Results and discussion

The left panel of Fig. 2 shows the forward shift averaged across four observers. A three-way (response type × fixation × speed) repeated measure analysis of variance (ANOVA) revealed significant effects of response type [$F(2, 6) = 14.9$, $P < 0.01$] and fixation [$F(1, 3) = 57.3$, $P < 0.01$]. Open-loop pointing yielded more shifts than

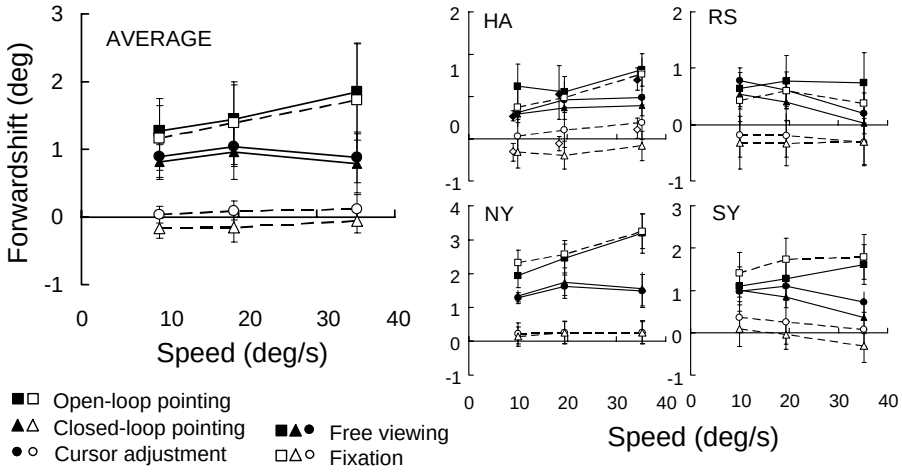

Fig. 2. The results of experiment 1. Mean horizontal shift in the motion direction is plotted as a function of the target speed for open-loop pointing (squares), closed-loop pointing (triangles), and cursor adjustment (circles). Filled symbols with solid lines represent the free viewing condition, and open symbols with dashed lines represent the fixation condition. The left panel shows averaged results from the four participants, with error bars indicating standard error of the mean. The right panels show the results for individual participants, with error bars showing 95% confidence intervals. For observer HA, the diamonds show the results of the control condition (probe judgement), which are horizontally shifted by 1°/s for clarity.

closed-loop pointing and cursor adjustment ($P < 0.05$ by Tukey's HSD test, $P < 0.01$ by Fisher's LSD test), but closed-loop pointing and cursor adjustment did not yield a significant difference ($P > 0.1$ either by HSD or LSD). Interactions were significant between response type and fixation [$F(2, 6) = 13.0$, $P < 0.01$], and between response type and speed [$F(4, 12) = 9.43$, $P < 0.01$]. The simple main effect of response type was significant under both fixation conditions [free viewing: $F(2, 12) = 18.4$, $P < 0.001$; fixation: $F(2, 12) = 26.7$, $P < 0.001$]. Simple main effect of fixation was significant under closed-loop pointing [$F(1, 12) = 45.4$, $P < 0.001$] and cursor adjustment [$F(1, 12) = 34.5$, $P < 0.001$] conditions, but not under the open-loop pointing condition [$F(1, 12) = 0.0007$]. The right panels of Fig. 2 show the results of individual observers, with all showing similar tendencies.

The results of the control condition, using the probes, are shown in the panel of Fig. 2 for observer HA. The shifts were nearly as large as those for open-loop pointing, but they were reduced to almost zero by fixation as found in cursor judgement and closed-loop pointing. Large reduction by fixation is therefore common to all the three methods and is considered a signature of perceptual judgement, whereas, larger shifts in open-loop pointing alone may not be so. Reduction of forward shift by fixation was also confirmed by a naïve observer (YW) who was tested only for the highest speed. The amount of shift was 1.36° (the 95% confidence interval: 1.02–1.64°) without fixation and 0.82° (0.65–0.02°) with fixation. The naïve observer showed substantial forward shift with fixation, but this could be an artefact of unstable fixation, at least to some extent, because the observer had no prior experience of psychophysical experiments. The shifts became smaller in later sessions, but the numbers of measures were insufficient for formal proof.

Neither fixation nor speed had a significant effect on response time. The average response time from the offset of the target was 2.16 s for cursor adjustment, 1.24 s for closed-loop pointing, and 1.16 s for open-loop pointing. The cursor responses were slower than the pointing responses by about 1 s, which is probably due to slower control of the trackball, but the very close results for cursor and close-loop conditions suggest that the timing of judgement was similar in these conditions. The small difference between the close-loop and open-loop conditions might suggest additional feedback control for closed-loop pointing, but it is not statistically significant. The difference in the judged position is therefore more likely caused by different initial visual representations.

The results are summarised in three points. First, close-loop pointing and cursor adjustment yielded very similar results. Second, fixation greatly reduced the forward shift for close-loop pointing and cursor adjustment, confirming the results of Kerzel (2000). Finally, the forward shift under the open-loop pointing condition, which was the largest and varied most linearly with speed, was not affected by fixation. These results indicate that the open-loop pointing relied upon a different representation from that used under the other two conditions. A different output gain in the open-loop pointing may explain the larger shifts, but it cannot explain the divergent effects of fixation. These results suggest that the open-loop pointing was supported by the direct visuomotor system while the others were possibly supported by the perceptual system.

One could argue that cursor judgement and closed-loop pointing were not genuinely perceptual. The former case is then crucial because the latter is considered perceptual on the basis of its similarity with the former. As to the forward shift, it has been shown that mouse pointing is differ-

ent from relative judgement (Kerzel, 2002) but is similar to manual pointing (Kerzel, 2003). Also, correction of mouse control was shown to be as fast as that of manual pointing (Brenner & Smeets, 2003). Pointing using a mouse cursor could therefore be regarded as a more or less direct action. In the present case, however, a crucial difference is that the cursor was controlled by a trackball, which is different from a mouse in two major ways: its control does not include arm and wrist movement and the observers were not trained in its use. Its control with an index finger (or possibly the middle finger) is far less direct as a reaching action, which normally requires more deliberate correction. It is unlikely that the observers in this experiment, including the author, were able to control the cursor in a fast and efficient way. Furthermore, the reduction of forward shifts by fixation in the probe judgement, which is considered more purely perceptual, supports the idea of a common perceptual representation underlying these conditions.

4. Experiment 2

It has been suggested that the visuomotor system works in real time, and delayed responses must rely on stored information in the perceptual system (Hu, Eagleson, & Goodale, 1999; Hu & Goodale, 2000; Yamagishi et al., 2001). If so, delayed open-loop pointing would not show the specific pattern of forward shifts. As experiment 1 confirmed that closed-loop pointing does not yield action-specific responses but relies on perceptual information, only closed-loop and open-loop responses were tested in this experiment.

One problem with open-loop pointing in experiment 1 was that the shutters were closed just when the target disappeared, which implies that target disappearance event was not visible. This was not crucial in experiment 1 because the task of judging the final position was the same. However, this can produce a significant artefact then the results are compared with and without delays, because the target disappearance is clearly perceived in the latter. A short delay was therefore involved in the immediate condition in this experiment.

4.1. Method

Closed-loop and open-loop responses were tested in separate sessions, for three speeds (10, 19, or 28°/s). Response delays of 200 and 4000 ms that were tested in separate sessions. Fixation was always maintained. During the response delay, the fixation mark remained on the screen. The observers kept fixation until a sound notified the start of response. The shutter was closed at the end of the delay period for open-loop response. The maximum speed was reduced because the naïve observers in this experiment claimed difficulty of judgement at 35°/s during practice.

4.2. Results and discussion

The averaged results (Fig. 3, left panel) showed that the open-loop pointing yielded significant shifts with a 200 ms delay but not with a 4000 ms delay. It was supported by the statistical test; a two-way (response type × speed) repeated measures ANOVA, performed separately for each delay conditions, revealed a significant effect of response type with a 200 ms delay [$F(1, 3) = 106.7$, $P < 0.01$] but not with a 4000 ms delay [$F(1, 3) = 0.063$]. No other effects were significant ($P > 0.1$).

Neither response type nor speed had a significant effect on the response time. The average response times from the

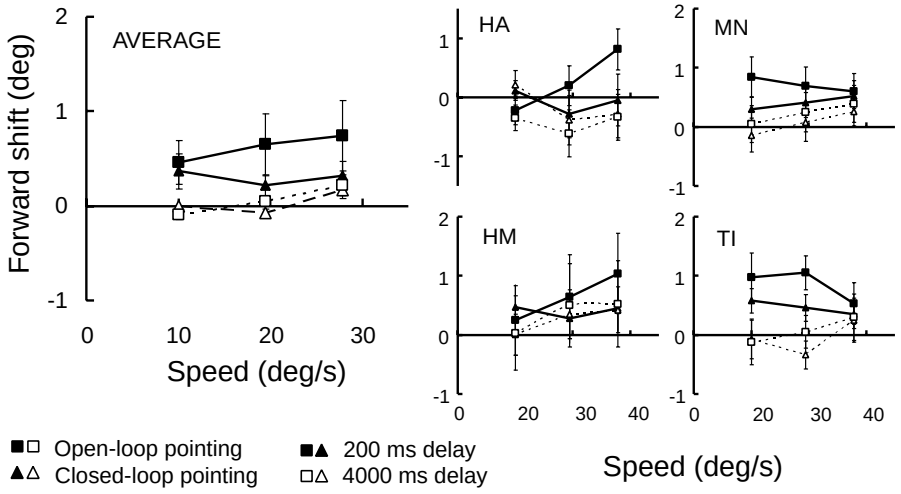

Fig. 3. The results of experiment 2. Mean horizontal shift in the motion direction is plotted as a function of the target speed for open-loop pointing (squares), and closed-loop pointing (triangles). Filled symbols with solid lines represent the 200 ms delay condition, and open symbols with dashed lines represent the 4000 ms delay condition. The left panel shows averaged results from the four participants, with error bars indicating standard error of mean. The right panels show the results for individual participants, with error bars indicating 95% confidence intervals.

end of the delay period were 0.95 s with a 200 ms delay and 1.15 s with a 4000 ms delay, the difference being only marginally significant by a three-way repeated measures ANOVA [$F(1, 3) = 7.54$, $P < 0.1$].

Of primary interest was that the difference between the open-loop and closed-loop conditions. The difference was clear with the delay of 200 ms, but disappeared with the delay of 4000 ms, as would be expected given the real-time operation of the visuomotor system. This indicates that two different representations were used for open-loop and closed-loop pointing only for a 200 ms delay. A single representation, which serves conscious perception, was presumably used with a 4000 ms delay.

The significant effect of the response type at 200 ms confirmed that the results specific to open-loop pointing was not predominantly due to an artefact of missing the target disappearance event. However, as the difference between open-loop and closed-loop responses was much smaller than that in experiment 1, such an artefact might have some effect. Or even a delay as short as 200 ms might reduce the effect of direct visuomotor responses. With different observers groups, firm conclusion cannot be drawn on this point, which is anyway not essential for the main discussion.

Closed-loop responses yielded somewhat larger shifts with a 200 ms than with a 4000 ms delay. Although a three-way ANOVA only showed marginal interaction between the response type and the delay [$F(1, 3) = 6.99$, $P < 0.1$], the simple main effect of the delay was significant for closed-loop pointing [$F(1, 6) = 6.63$, $P < 0.05$]. This indicates that the closed-loop condition yielded significant, though small, forward shifts when there was a 200 ms delay, which was not the case in experiment 1. As we see in the right panels of Fig. 3, this effect mostly reflects the results of observer TI. A speculation is that this observer performed the pointing action less carefully (i.e. using less feedback control) so that there was more effect of visuomotor responses, but this is not supported by the fact that the averaged response time under this condition was slightly longer for TI (1161 ms) than for the others (766–1033 ms). We cannot draw firm conclusion since this observer did not participate in experiment 1, but note that even for this observer there was clear difference between the open-loop and closed-loop responses with a 200 ms delay but not with a 4000 ms delay. The discrepancy between open-loop and closed-loop condition is thus evident for all the observers with a 200 ms delay but not with a 4000 ms delay.

5. Experiment 3

There remains the possibility that the open-loop effect was caused by the lack of a spatial frame of reference and we do not need to consider the visuomotor responses (Bruno, 2001). According to this hypothesis, fixation would lead to more reliable positional coding of the target against the background and thus to suppression of the illusory forward shift. This would apply to cursor adjustment and closed-loop pointing but not to open-loop pointing as the background was not visible during responses, and the discrepancy in the results could therefore be explained.

The following two experiments are designed to test this possibility. In this experiment, perceptual cursor adjustment was tested with and without the white background being present during the response. A main prediction from the reference-frame hypothesis is that more forward shifts should be observed even with maintained fixation when the background was removed and the reference frame is obscured. Forward shifts with fixation may not be as large as those found with eye tracking, because the field did not become totally dark, but substantial increase of the forward shift should be found to support the reference-frame hypothesis.

5.1. Method

The method was the same as the cursor adjustment in experiment 1 except as follows. Responses were delayed for 200 ms. After this short delay, the white background area turned black or remained unchanged. To minimise the afterimage, the outer area of the CRT monitor was painted in grey whose luminance was half of the white area, which turned black together with the white area. The remaining weak afterimage, which was not very obvious, should not have worked as effectively as the remaining background. Pursuit and fixation conditions were tested. The two trained observers were instructed more explicitly than in experiment 1 to track the target with their eyes, although the eye movement was not measured. The shutter goggle was worn to equate the viewing conditions, but it was always open. Three speeds were tested (10, 19, or 28°/s).

5.2. Results and discussion

Fig. 4 shows the results of the two observers. The error bars that represent 95% confidence intervals clearly show that there was no effect of background removal. Observer

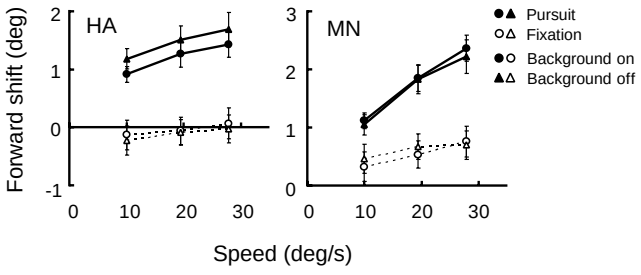

Fig. 4. The results of experiment 3 for the two participants. Mean horizontal shift of the cursor responses in the motion direction is plotted as a function of the target speed with (triangles) or without (circles) the white background during the response. Filled symbols with solid lines represent the pursuit condition, and open symbols with dashed lines represent the fixation condition. Error bars show 95% confidence intervals.

HA showed an increase of forward shifts without fixation, but not with fixation. It is therefore unlikely that the unavailability of a reference frame was the main cause of the open-loop-specific responses with fixation in experiments 1 and 2.

Observer MN showed some forward shifts even with fixation, but this is not crucial here because the overall amount of shift was much lower than that with fixation. It is not important for the current discussion whether the shifts are totally eliminated by fixation. Fixation might have been inaccurate, but this was not very likely for this trained observer. Perceptual forward shift could probably happen even with fixation in some cases (Kerzel, 2003).

The average response times were 1.32 s (HA) and 2.36 s (MN). HA was much faster probably because he became experienced in cursor control through experiment 1. Note that there was still no forward shift with fixation, which is not consistent with the results using a mouse (Kerzel, 2003). It is suggested that the control of a trackball with a finger is far less direct as an action than that of a mouse.

6. Experiment 4

In this experiment, the effect of visible frames was tested the other way round, that is, by testing open-loop pointing with a visible screen background. The observers viewed the screen through a mirror and pointed behind the it without seeing their hands (Yamagishi et al., 2001).

6.1. Method

A mirror was placed in front of the touchscreen at an angle of 45° so that the observers viewed the stimuli on the left through the mirror and pointed to the touchscreen behind the mirror. A black panel behind the mirror prevented the observers from seeing their hand and arm. The shutter goggle was used to control the viewing during the responses. The response was delayed for 200 ms as in experiments 2 and 3. Fixation was always maintained during the target motion. Three speeds were tested (10, 19, or 35°/s). Trained observers (HA, NY) who had participated in experiment 1 were tested.

6.2. Results and discussion

Fig. 5 shows the results. There was a technical problem in that the mirror setting restricted horizontal arm movement, and the results were a little less reliable than in the other experiments, as the larger error bars indicate. It is nevertheless clear that the forward shift was not substantially reduced when the shutter was open, that is, when the screen was visible during the responses. The amount of shifts was nearly the same as in experiment 2 with the same delay. The average response times were 1.03 s (HA) and 1.51 s (NY).

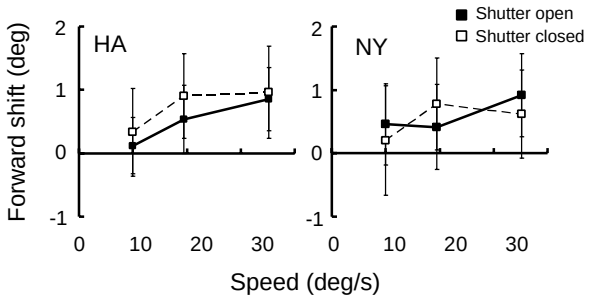

Fig. 5. The results of experiment 4 for the two participants. Mean horizontal shift of the pointing response in the motion direction is plotted as a function of the target speed with the shutter open (filled squares with solid lines) or closed (open squares with dashed lines). Error bars show 95% confidence intervals.

7. General discussion

7.1. Separate visual processing for perception and action

The forward shift in the perceived final position of a moving target was more pronounced in an open-loop reaching action than in a perceptual judgement. This result is consistent with a recent report of Kerzel and Gegenfurtner (2003), but now a qualitative as well as quantitative difference has been confirmed by the selective effect of eye fixation; it greatly reduced the forward shift in a perceptual judgement but not in an open-loop action. This is not explained by any possible difference in the output gain. The results therefore support the idea of separate visual processing for perception and action (Milner & Goodale, 1995). Evidence has accumulated for the functional difference in the ventral and dorsal brain pathways in monkey physiology and in human patient studies. The present results add another piece of evidence, showing a psychophysical double dissociation when taken together with earlier findings. For example, the result of Burr et al. (2001) is noteworthy because they also tested manual reaching action while many others tested grasping. They found that open-loop pointing was accurate during saccadic eye movements while perceptual judgement was compressed toward the saccadic target. In other words, they showed an example where manual reaching resists perceptual errors. Interestingly, they found that manual pointing was prone to compression when the reaching target was visible (i.e. closed-loop pointing), as found in this study. It is therefore the underlying representation, not the response mode itself, that must be considered when we discuss dissociation between perception and action.

Recently, Dyde and Milner (2002) demonstrated a psychophysical double dissociation in the effect of simultaneous orientation contrast. They found that a far frame induced a perceptual orientation contrast but did not affect the posting action, while an adjacent grating affected both perception and action. When the far and the adjacent inducers were oppositely slanted, the effect of the adjacent grating was nulled by the far frame in perception but not in posting action, re-

sulting in larger illusion in action than in perception. They argued that the adjacent grating affects both perception and action because the orientation contrast occurs at an early cortical site before the two pathways are separated, while the far frame affects only perception somewhere deeper in the ventral stream. While further investigation would be necessary to confirm the neural correlates, their claim that "we need to ask first where the likely locus of the illusion is going to be within the brain" (Milner & Dyde, 2003, p. 11) seems to give the right direction to sort out the controversy on the psychophysical results so far.

With their view, however, we should note that their results did not complete double dissociation in terms of the two pathways because they did not include a case where a dorsal pathway plays a major role. We have previously demonstrated such a case where action is more prone to the illusion of motion-related positional shifts (Yamagishi et al., 2001). There remained, however, the possibility that an automatic gain enhancement for immediate reaching action might explain the quantitative difference in the positional shifts without the need for separate visual representations. The current result of qualitative difference adds strong support for separate representations, suggesting that the positional illusion occurs within the dorsal pathway supporting direct visuomotor behaviour.

7.2. Action-specific visual extrapolation

The forward shift is considered to reflect visual extrapolation in our brain to anticipate the position of a moving target, which is particularly important for motor responses towards a moving target, given the large delay associated with physical action. Generally, larger and more robust forward shifts in action support this idea, suggesting that the extrapolation occurs within the visuomotor pathway.

Extrapolation would be also necessary for perception to compensate for neural transmission and processing delays, but it should not be as urgent as for motor responses. Perceptual forward shift is therefore likely supported by a cognitive, or post-perceptual, mechanism that is sensitive to various parameters such as gravity or friction, as the term 'representational momentum' implies (Hubbard, 1995a,b). Perceptual forward shift has been found to be more prominent when the motion signal is weak, such as in a sampled motion display (Kerzel, 2003). In the case of smooth motion, as in the present experiments, the effect may not be a result of cognitive or perceptual extrapolation. Judging from the crucial effect of eye fixation, it is suggested that the forward shift is mostly caused by the tracking eye movement. It is possible that the overshoot of eye, after sudden disappearance of the target, leads to a shift of the persisting image (Kerzel, 2000), but there is the alternative possibility that the visuomotor signal to control the eyes somehow affects perception. The latter seems interesting, suggesting substantial interaction between the two pathways, but more investigation is required before any conclusions can be drawn. Also, inconclusive is the question as to whether the purely perceptual or cognitive extrapolation was totally excluded in the present setting. In some cases, small forward shifts remained in perceptual responses even with fixation, suggesting weak effects of perceptual or cognitive extrapolation, although imperfect fixation or partial action components of the responses may explain it.

7.3. Frame of reference for perception and action

It has been argued that differences between relative and absolute judgements (Vishton, Rea, Cutting, & Nunez, 1999) or in the reference frames (Bruno, 2001) are important in perception and action tasks. The present results cannot be explained solely by an artefact of available frames of reference, because external control of frames of reference did not change the pattern of results (experiments 3 and 4). But we can nevertheless interpret the results in terms of the frames of reference, providing further insights into the underlying mechanism of visual extrapolation.

The results are consistent with the idea that the visuomotor system innately uses an egocentric frame of reference (Milner & Goodale, 1995). In this case, the egocentric frame can be either head-centred or body-centred, but it must be independent of the eye position. The specific pattern of forward shifts in open-loop pointing is explained if we assume that visual extrapolation is facilitated in the egocentric representation. The results of the other conditions are explained if perceptual judgement depends on both egocentric and allocentric representations. When the eyes track the target, the retinal slip obscures the screen frames, and the judgement would rely more on the egocentric representation. Smaller forward shifts in perception than in open-loop action could be a result of an interaction between the two representations. When the eyes are fixated, the background is more stabilised and the judgement would rely more on the allocentric representation. Moreover, if the egocentric representation is assumed to be available only for online processing, reduction of open-loop responses after a long delay is also explained. But note that a simple retinotopic representation, instead of a genuine allocentric one, can be used in the above discussion for the present results.

Physiological findings support the above idea, indicating that the posterior parietal cortex is involved in co-ordinate transformations from retinotopic into head-centred and body-centred representations for action control (Andersen, Snyder, Li, & Stricanne, 1993; Cohen & Andersen, 2002; Rizzolatti, Fogassi, & Gallese, 1997). It would be interesting to see whether a position of a moving target is extrapolated or not in the related parietal areas, compared to a stationary one. The egocentric representation could affect perceptual judgement as well, because the parietal lobe has been suggested to have a role for spatial perception (Rizzolatti et al., 1997). The site for the allocentric frame is less understood. While supplementary eye field in the frontal cortex has been suggested to represent an object-centred space (Olson,

2003), further studies are required to understand how such a representation is build up. The current results do not have direct implications for allocentric representations, anyway.

7.4. Concluding remarks

In summary, this study revealed that the distinct forward shift in the final position of a moving target for open-loop reaching action is a signature of target extrapolation specific to visual processing for the direct control of action. The underlying mechanism of extrapolation is not specified in this study. One possibility is that extrapolation is inherent in the front-end sensors. Fu, Shen, and Dan (2001) showed that filters that have bi-phasic temporal responses yield to a spatial shift of the response distribution, which is obvious for blurred stimuli but not for broadband stimuli with sharp edges. This idea is consistent with the conjecture that extrapolation occurs in the visuomotor system through the dorsal pathway, which receives dominant input from the magnocellular pathway and is considered to show a low-pass spatial frequency tuning that causes blurring of edges. Contrary to this idea, Nijhawan and Kirschfeld (2003) suggested a possible ventral origin of visual anticipation. More precise understanding of visual extrapolation is therefore open to further studies.

Acknowledgements

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イリュージョンと色彩心理

Illusion and color perception

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キーワード: 錯視、色の対比、色の同化、ムンカー錯視、ネオン色拡散、色ファントム、色立体視

Keyword: illusion, color contrast, color assimilation, Munker illusion, neon color spreading, chromatic visual phantoms, chromostereopsis

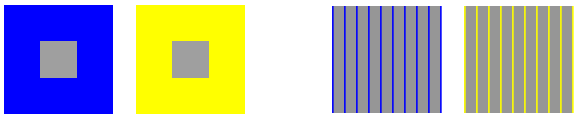
1. はじめに

錯視（visual illusion）というと、多くの場合、ミュラー・リヤー錯視やツェルナー錯視のような幾何学的錯視（geometrical illusion）すなわち形の錯視を指す[1]。しかし、錯視は形、明るさ、運動といった視覚のモダリティの数だけあると考えられる。すなわち、色の錯視も知られている。しかし、これまで知られていた色の錯視の種類は、他のモダリティに比べて少なく、その錯視量も多いとは言えなかった。

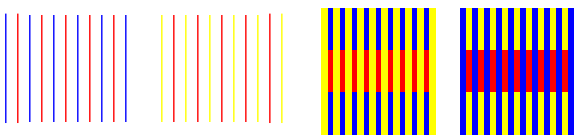
ところが、近年になって、錯視と呼ぶにふさわしい色の錯視が知られるようになってきた。ここでは、これらを分類してみたい。

2. 色相の錯視

色相の錯視としては、従来から、色の対比（color contrast）と色の同化（color assimilation）が知られていた。しかし、いずれも劇的な錯視というほどの効果はない。ところが、最近の研究によると、対比という点では遠隔色対比[2]が、同化という点ではムンカー錯視[3]が、錯視と呼ぶにふさわしい強度の色相の変化を与えることがわかった。

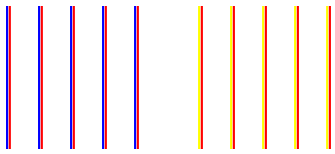


色の対比　　色の同化



遠隔色対比　　ムンカー錯視

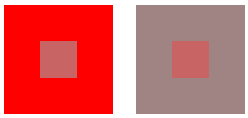
そのほか、近年発見された色の同化としては近接色同化がある[2]。もっとも、ゲーテやシュブルールの原著を調べれば、すでに記述があるのかもしれない。



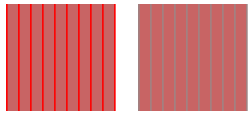
近接色同化

3. 彩度の錯視

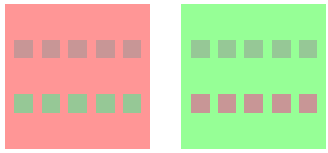
彩度の錯視としては、彩度対比（saturation contrast）が知られている。彩度同化というものには知られていないようであるが、筆者が自作してみたところ、十分効果はあるようであった。しかし、いずれも錯視量は多いとは言えない。しかし、最近立命館大学の学生が発見した彩度錯視（酒井の色対比）は、色が消えて無彩色に見えるという劇的な見え方をする[4]。この錯視は色の恒常性のメカニズムとも関係すると考えられる。



彩度対比



彩度同化

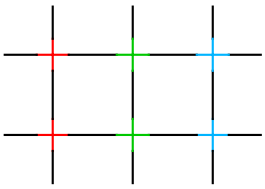


酒井の色対比

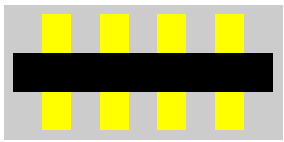
4. 色の補完

色の補完（completion）あるいは充填現象（filling-in）は色の同化と同じメカニズムであるとも考えられるが、主観的輪郭とセットになって現れたり、広い領域に渡って効果が見られる点が、色の同化とは異なる。ネオン色拡散（neon color spreading）[5]、色ファントム（chromatic visual

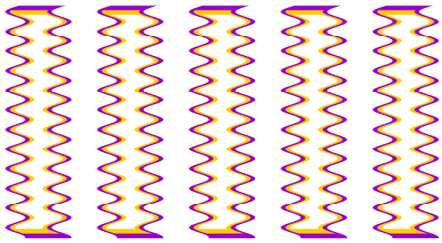
phantoms）[6]、ウォーターカラー錯視（watercolor illusion）[7]などが知られている。



ネオン色拡散



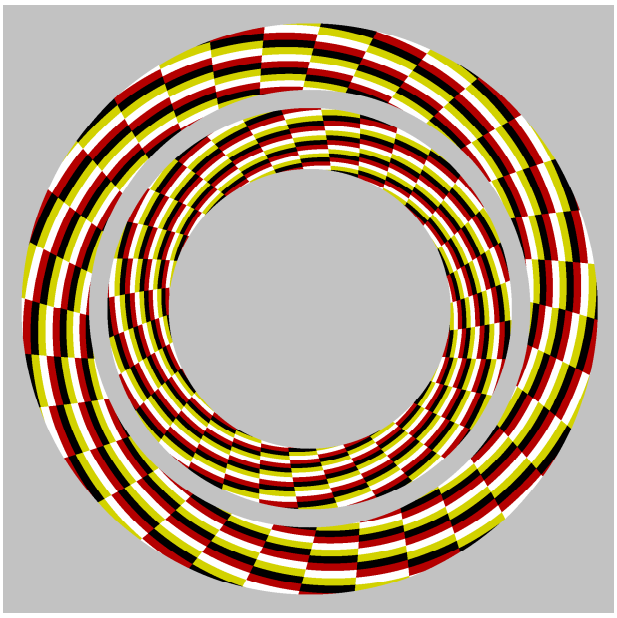
色ファントム



ウォーターカラー錯視

5. 運動による色の出現

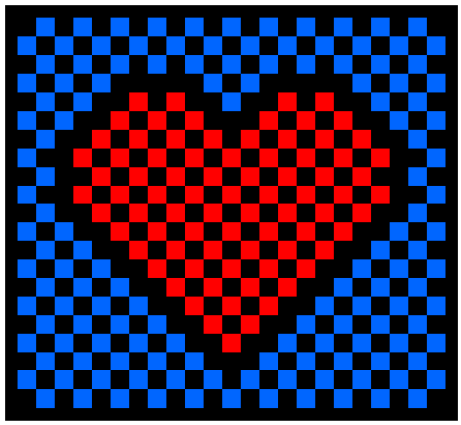
色の付いていない図形を動かすと、色が見えることがある。ベンハムのコマ（Benham's top）あるいはフェヒナー色（Fechner color）が有名である。最近、ベンハムのコマよりも遅い速度で発生する色誘導が発見された[8]。



図の中心に目を近づけると内側のリングの赤味が増し、目を遠ざけると外側のリングの赤味が増して見える錯視。

6. 色立体視（進出色・後退色）

赤が手前に、青が奥に見えると記述される色立体視（chromostereopsis）という現象がある。CRTや液晶モニターで見ると劇的である。近年色立体視の研究も進み、逆の見え方をする人も少なくないこと、どちらの見え方でも、視距離は大きい方が効果が大きいことなどがわかった[9]。



色立体視「浮かぶハート(floating heart)」

7. おわりに

「色の錯視」という研究カテゴリーは、これからさらなる発展が期待できると思われる。

文献

[1] 後藤倬男・田中平八（編）（2005）錯視の科学ハンドブック　東京大学出版会

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