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学 位 論 文 題 目	Distribution of colour-selective activity in the monkey inferior temporal cortex revealed by functional magnetic resonance imaging
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論文内容の要旨

In monkey visual cortex, colour information is primarily processed in the ventral pathway through areas V1, V2, and V4 into the inferior temporal (IT) cortex. Recent studies have shown that the IT cortex, which is situated at the final processing stage of the ventral visual pathway, plays an important role in colour processing. Single cell recording studies have shown that there are numerous colour-selective neurons in the IT cortex, some of which are narrowly tuned to hues and/or saturations and exhibit task-related responses during colour discrimination. In addition, lesion studies have shown that bilateral ablation of the IT cortex disrupts colour discrimination, though ablation of V4 does not. Although many colour-selective neurons have been found in the IT cortex, their distribution in this cortical region remains not fully clear, especially in the anterior part of the IT cortex. In the present study, the author explored the distribution of colour-selective activity in the IT cortex using functional magnetic resonance imaging (fMRI) in alert macaque monkeys.

As exploratory examinations, he has measured retinotopic organization, motion-selective activity and shape-selective activity of visual cortex. The retinotopic organization was obtained by comparing responses to the horizontal meridian and vertical meridian stimuli and was helpful in determining the boundaries of visual areas. The motion-selective activity was obtained by contrasting responses to moving and static random-dot stimuli and used to determine the physiological isoluminance point of colour grating. The shape-selective activity was obtained by contrasting responses to object image stimuli and scrambled image stimuli. The distribution of the shape-selective activity was later compared with that of the colour-selective activity. These exploratory experiments were required for analyzing the results in the main experiment.

In the main experiments, he examined colour-selective activity in the IT cortex with two types of stimuli: an isoluminant colour grating and a multicoloured ('Mondrian') pattern that have been commonly employed in human fMRI and have identified colour-selective areas/regions in the fusiform gyrus, which is suggested to correspond to monkey IT cortex. The paradigm using gratings is to compare responses to an isoluminant, colour-varying grating (e.g. a red-blue grating) with responses to a luminance-varying grating. This paradigm identified colour-selective regions in the posterior part of human fusiform gyrus that is called V8/VO. The paradigm using Mondrian is to compare responses to a multicoloured ('Mondrian') pattern with responses to its achromatic counterpart. This paradigm identified colour-selective regions in the more anterior part of the fusiform gyrus, in addition to the posterior part. Earlier imaging studies of the monkey IT cortex used only the first paradigm, but the second paradigm may elicit more effectively the colour-selective activity in the anterior IT according to the findings in human fMRI. Moreover, Mondrian stimuli may be more suitable for activating higher areas, since the stimuli containing various hues could elicit responses from many neurons, each tuned to a specific hue. For that reason, he has used both grating and Mondrian stimuli to examine colour-selective activity in the IT cortex. As a result, he found that colour-selectivity is not uniformly distributed in the IT cortex, but is clustered in discrete subregions that are located in the posterior and the anterior part of the IT cortex. The colour-selective activity in the posterior IT was obtained both with the grating and Mondrian stimuli, but the positions of the activity were different dependent on the stimuli. On the other hand, the colour-selective activity in the anterior IT was obtained only with the Mondrian stimuli.

He has examined whether these topographical differences of colour-selective activity depending on the stimuli were attributable to the difference in the luminance contrast between the chromatic Mondrian stimuli and colour grating stimuli: although the luminance contrast in the chromatic Mondrian stimulus matched that in the achromatic Mondrian, the colour grating stimulus contained much smaller amount of luminance contrast than the luminance grating. To examine the possible influence of the luminance contrast in the chromatic Mondrian stimuli, he employed isoluminant Mondrian stimuli that contained much less luminance contrast than the achromatic ones, and compared the distributions of colour-selective activity obtained with this isolumiant Mondrian, the Mondrian containing matched luminance contrast and the isoluminant grating. The results have shown that the topography of the colour-selective activity obtained with the isoluminant Mondrian was very similar to that obtained with the Mondrian containing matched luminance contrast whereas it was very different from that obtained with the isoluminant grating. This indicates that the difference in the distribution of the responses to the Mondrian and grating stimuli in the IT cortex cannot be attributed solely to the difference in luminance contrast.

He finally compared the distribution of colour-selective activity with that of shape-selective activity in the IT cortex. He found that the colour- and shape-selective activity tends to overlap little in the anterior IT whereas the colour-selective activity in the posterior IT and early visual areas overlapped with the shape-selective activity. This finding was consistent with the results of previous electrophysiological recording experiments comparing the responses of neurons to colour and shape stimuli and suggests that colour and shape information is clustered in different modules specifically tuned to each attribute.

The present study shows that colour-selective activity is clustered in discrete regions of the monkey IT cortex and that these colour-selective regions are distributed in both the anterior and posterior IT. The difference in the response properties and the retinotopy suggests that these regions may correspond to different spots of colour-selective activity reported in human fusiform gyrus: the colour-selective activity in the posterior IT may correspond to V8/VO which is in the posterior part of the fusiform gyrus, and colour-selective activity in the anterior IT may correspond to V4α and regions in the more anterior part of the fusiform gyrus.

博士論文の審査結果の要旨

色覚は日常生活で重要な意義を有する視覚機能であり、皮質損傷の症例から色覚の成立には大脳高次視覚野が極めて重要であることが知られている。色覚情報の処理については、網膜をはじめとする視覚系の初期段階では多くのことが調べられてきたが、高次領野での処理についてはまだ不明の点が多い。サルの大脳皮質における最近の研究から、高次視覚野である下側頭皮質が色知覚において非常に重要な役割を果たしていることが明らかになってきている。しかしながら、下側頭皮質内で色情報がどのように分布しており、部位によってどのように異なった性質の情報が表現されているかは、よく分かっていない。

そこで本申請者は、サル大脳皮質の色選択的活動を、機能的核磁気共鳴画像法(fMRI)を用いて測定し、下側頭皮質における色選択性の分布と特性について検討した。色選択的活動の同定には、これまでヒトのfMRI研究で用いられてきた２種類の方法を用いた。ひとつは正弦波状に色度のみが変化する色グレーティング（等輝度グレーティング）と輝度のみが変化する輝度グレーティング刺激を用いそれらに対する活動を比較するものであり、もうひとつの方法は、様々な色・輝度の小四角形で構成された色刺激（モンドリアン刺激）とそれと輝度コントラスト分布の等しい無彩色刺激を用い、それらに対する活動を比較するものである。

注視課題を訓練した２頭のサルについて覚醒下で実験を行なった結果、グレーティング刺激を用いた場合、下側頭皮質の後部に色選択的な活動を示す小領域があることが明らかになった。一方、モンドリアン刺激を用いた方法では、下側頭皮質後部領域の活動に加え、下側頭皮質の前部領域にも色選択的な小領域が見出された。後部領域の活動部位は、この２種類の刺激によって異なった位置に現れ、両者の間にはほとんど重なりがなかった。これらの結果により、下側頭皮質内において、色選択性は一様に分布しているわけでなく、特定の小領域に集中していることが明らかになった。また、色選択的小領域の位置が刺激に依存することから、刺激によっては異なった小領域が色知覚を行っていることが示唆された。また、モンドリアン刺激が下側頭皮質前部の小領域を賦活させるとの結果は、ヒトの高次領野で色覚に関わっていると考えられている紡錘状回前部がグレーティング刺激では賦活されないがモンドリアン刺激により賦活されるとの知見とも対応し、サル下側頭皮質前部領域とヒト紡錘状回前方部とが対応している可能性を示唆する。

本申請者は、さらに下側頭皮質における活動分布が刺激によって異なった要因について検討を行い、モンドリアン刺激に含まれる輝度コントラストでは説明できないことを明らかにした。モンドリアン刺激は様々な色相で構成されており、鋭い色相選択性を示す下側頭皮質前部内の色選択性ニューロンを活動させるのに適していた可能性が考えられた。

以上、本研究の結果は、色知覚が高次視覚野の性質の異なる複数の機能ドメインで担わ

れていることを強く示唆しており、今後の電気生理学的研究を行う上で重要な指針を与えるものであり、色覚のメカニズムの理解に重要な貢献をなすものである。実験方法は適切に考えられ、導かれている結論も妥当であり、それらは明快かつ平易な英語で記載されている。これらのことから本論文は、学位論文として十分にふさわしい内容であるものと結論された。