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論文内容の要旨

Visual grouping is an essential component of the visual perception of objects. It is the process by which multiple discrete elements are bound into a single object. Visual grouping is caused by bottom-up factors such as similarity and continuity of the dots. It is also known that visual grouping is affected by top-down factors such as prior knowledge and past experience with the objects. Neurological observations made in human patients and in fMRI studies of healthy human subjects suggest that the posterior parietal cortex plays a key role in visual grouping. It remains unknown, however, how parietal cortex are involved in visual grouping.

To investigate the neuronal mechanisms underlying visual grouping, the author designed a grouping detection task controlled by top-down attention, and performed extra-cellular single unit recording from lateral bank of intra-parietal sulcus (L-IPS) while the task was being performed by monkeys. The visual stimuli consisted of multiple discrete dots, and the monkeys were required to detect the target defined by specific arrangements of the dots. In addition, he manipulated the monkeys' attention to the grouping of the elements, and examined the effect of attention on the neuronal responses. The visual stimuli were composed of 5 square black or white dots (1.2 deg at the edge) arranged in a cross. A total of 20 types of visual stimuli composed of different arrangements of dots were prepared. In four of the 20 stimuli, three dots with the same contrast (either black or white) were aligned either horizontally or vertically and these four stimuli served as the target. The remaining 16 stimuli were non-targets. The target stimuli were characterized by two visual features: the orientation of the three dots with the same contrast that was either horizontal or vertical (target orientation) and the contrast of three-aligned dots, which was either white or black (target contrast). The monkeys performed the detection task while their attention was directed towards a particular target orientation.

He recorded the activities of 107 single neurons in the L-IPS while two monkeys performed a grouping detection task. He found that L-IPS neurons selectively responded to the visual stimulus, and a majority of neurons exhibited stronger selectivity for the target orientation than the target contrast. This orientation selectivity was enhanced when the target orientation matched the attended orientation. Moreover, the orientation-selective responses correlated with the monkeys' behavior. These results suggest that L-IPS neurons play important roles in the visual grouping and detection of objects comprised of discrete elements.

Although it is known that there are two functional classes of cortical neurons, excitatory pyramidal neurons and inhibitory interneurons, it remains largely unknown how these two classes contribute to visual perception and cognition. Recently, several attempts have been made to classify extracellularly recorded neurons according to known differences in the waveforms of their action potentials (e.g., Mitchell et al., 2007, Neuron). These studies suggest that classification of neuron type will provide valuable new information that could be crucial to understanding neural processing within local circuits in the cerebral cortex.

In order to examine how different classes of neurons are involved in visual grouping, he classified recorded neurons according to the waveforms of their action potentials, and compared the response properties of classified neurons. He found that putative pyramidal neurons, which had broader action potentials, exhibited selectivity for the target orientation, and the selectivity was enhanced by attention. By contrast, putative inhibitory neurons, which had narrower action potentials, did not exhibit such selectivity or enhancement. Instead interneurons responded more strongly to the target stimuli than to the non-targets, regardless of the orientation of the target. These results suggest that different classes of parietal neurons contribute differently to the visual grouping of discrete elements.

Classification of L-IPS neurons showed that pyramidal neurons exhibited selectivity for the target stimulus, and clearly indicates that L-IPS neurons signal information about the grouped stimulus to other cortical areas. Neurons in L-IPS may provide feedback signals and affect the activity related to visual grouping in the early visual area. However, no study has explored in detail the feedback projection related to the visual grouping. In an attempt to study the contribution of feedback projection on visual grouping, he examined whether there is an anatomical basis for integration of visual signals from both sides of blind spot (BS) by cortico-geniculate feedback neurons in V1. The blind spot is the region in the visual field that corresponds to the optic disk in the retina. No visual information exists in the blind spot because there is no photoreceptor within the optic disk. Nonetheless, we perceive color and/or patterns there that are the same as in the surrounding visual field. This phenomenon is known as perceptual filling-in, and closely related to the visual grouping. Neural mechanisms under perceptual filling-in at the blind spot has been examined in detail, and this provides a good physiological model to investigate the anatomical basis for integration of visual signals related to visual grouping.

He recorded neuronal activity from V1 of a cat and mapped the receptive fields of V1 neurons. After identifying the blind spot region in V1, he inserted a glass micropipette filled with biotinylated dextran amine (BDA) into a location adjacent to the blind spot region in V1, and injected BDA by iontophoresis. BDA labeled axons were traced around the neuron-free gap in layer A of LGN. He observed that numerous axons traverse the neuron-free gap that retinotopically corresponds to BS within LGN. This indicates that visual signals from one side of BS are conveyed to the opposite side via a feedback connection. Cortico-geniculate feedback projection may integrate visual signals from around BS and contribute to perceptual filling-in at BS.

He recorded neuronal activities in L-IPS while monkeys performed a grouping detection task. He found that pyramidal neurons in L-IPS exhibited selectivity for the orientation of the target, and this selectivity was enhanced by attention to a particular target orientation. This result indicates that L-IPS neurons signal information about the grouped stimulus to other cortical areas. In the anatomical experiment, he found the feedback connection linking the visual fields surrounding the blind spot, which may be involved in the integration or interaction of visual information present at separate locations within the visual field. Neuronal activity in V1 is modulated by the presentation of visual stimuli in the receptive field surround, and it has been suggested that this contextual modulation is related to the visual grouping (Gilbert et al., 2000). Presumably, L-IPS neurons provide feedback signals to the early visual areas and facilitate visual grouping by way of the contextual modulation there.

These results provide the first physiological evidence that L-IPS neurons make an important contribution to visual grouping by combining visual and attentional signals to bind discrete visual elements. A recurrent circuit between the L-IPS and early visual areas may be critical for visual grouping through the interchange of feedforward and feedback signals.

博士論文の審査結果の要旨

本研究は頭頂連合野が「視覚グルーピング」にどのように関与するかをサルを用いた慢性電気性実験で調べたものである。視覚グルーピングとは視野上に存在する離散的要素をつなぎ合わせ単一の視覚対象としてとらえることである。グルーピングは要素間の関係に基づいて生じるが、トップダウンのメカニズムによっても影響されることが知られている。脳損傷患者を用いた研究では頭頂葉がグルーピングに関与していることが示唆されている。しかしながら、グルーピングがどのような神経メカニズムによって生じているかは明らかでない。そこで申請者はグルーピング検出課題を遂行中のサルの頭頂間溝皮質外側壁(L-IPS)から電気生理記録を行い、グルーピングの神経メカニズムについて調べた。

視覚刺激は十字に配置した５つの白または黒の正方形ドットによって構成される。サルは連続的に提示される視覚刺激から同じコントラストのドットが縦または横のいずれかの方位に一直線に並んだパターンをターゲット刺激として検出する。さらにどちらの方位のターゲットが提示されやすいかを予め手掛かりとして与え、サルが特定の方位に注意を向けるように操作した。

L-IPS から 107 個のニューロン活動を記録した。多くのニューロンがターゲット刺激の方位の特徴について強い選択性を示し、方位選択性は選択的注意を向けることによって強められた。さらに方位選択性の強さはサルのターゲット検出時間と相関を示した。これらの結果は L-IPS ニューロンがトップダウン的注意によって影響される視覚グルーピングに重要な役割を果していることを示唆する。

次に、グルーピング検出課題を遂行中のサルの L-IPS から記録した細胞をスパイク波形に基づいて錐体細胞と介在細胞に分類し、異なるクラスのニューロンがグルーピングにどのように関与しているか調べた。

錐体細胞に対応すると考えられる広いスパイク幅のニューロンはターゲット刺激の方位について選択的な反応を示し、方位選択性は選択的注意によって強められていた。一方介在細胞に対応すると考えられる狭いスパイク幅のニューロンは錐体細胞のような方位選択性または選択性の増強を示さなかった。これらの結果から L-IPS の錐体細胞と介在細胞は視覚グルーピング課題に異なった様式で寄与していることが明らかになった。

L-IPS のニューロンをクラス分けして解析を行った結果、L-IPS の錐体細胞はグルーピングされた視覚対象の情報を選択的に表現し、その情報を他の領域に伝達していることが示された。このことから L-IPS ニューロンの活動は初期の視覚野でのグルーピングに関連した活動に影響を与える可能性が考えられる。

以上の結果をまとめると、頭頂間溝皮質のニューロンは離散的要素によって構成される視覚対象を選択的に表現し、その選択性は注意によって強められた。このことは頭頂間溝皮質がトップダウンの影響を受ける視覚グルーピングに重要な働きをしているということを示唆する。またニューロンをクラス分けした解析と解剖学的手法を用いた実験の結果から、頭頂間溝皮質ニューロンの活動が他の領野でのグルーピングに関連した活動に影響を与えることが示唆された。

これらの内容は既に３編の論文として国際的学術誌に受理ないし発表されている。本研究の発見の重要性、論文の内容の明快さに鑑み、審査委員会全員一致で学位を授与するに値すると決定した。