nature neuroscience

Automatic spread of attentional response modulation along Gestalt criteria in primary visual cortex

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Visual attention can select spatial locations, features and objects. Theories of object-based attention claim that attention enhances the representation of all parts of an object, even parts that are not task relevant. We recorded neuronal activity in area V1 of macaque monkeys and observed an automatic spread of attention to image elements outside of the attentional focus when they were bound to an attended stimulus by Gestalt criteria.

The visual scene is initially represented in a distributed manner by neurons in early visual areas with small receptive fields tuned to simple features, such as colors and orientations. A single visual object typically activates a large number of neurons representing its various parts and features. However, we normally perceive objects that are composed of multiple parts, each with many features, implying that there are powerful grouping mechanisms that work to reconstruct objects from the individual features. These grouping mechanisms can take advantage of Gestalt grouping cues[1]; parts of the same object are more likely to be well aligned, move in the same direction and have the same color than parts of different objects. It was proposed[2] that selective attention integrates features into objects, and object-based attention theories suggest that attention spreads according to the Gestalt grouping cues so that image elements that belong to the same object are co-selected[3–5]. Previous studies have presented neurophysiological evidence for object-based attention[6,7], but there is a debate about whether attention spreads automatically according to Gestalt grouping cues[8–10].

To investigate whether attention spreads according to Gestalt cues, we trained three macaque monkeys in an eye movement task and recorded neuronal activity in the primary visual cortex (area V1) with implanted electrode arrays (**Supplementary Methods**). First, we examined the influence of collinearity (**Fig. 1a**). The monkeys saw two bars near the fixation point that were potential targets for a saccade and two more eccentric bars that could be ignored. We identified the target bar after 500 ms by presenting a small dot on top of it, thus guiding attention toward this stimulus[11]. After an additional 500 ms, the fixation dot disappeared, cueing the animal to make a saccade to the target bar. In this session (**Fig. 1a**), we simultaneously recorded from a recording site with a receptive field on one of the relevant bars (site 1) and from site 2 with a receptive field on an irrelevant bar.

As expected, the appearance of the dot in the receptive field of site 1 triggered an increase in activity with a latency of 44 ms (**Fig. 1b**) that was absent if the dot appeared on the other bar. This effect appeared to spread to site 2, where activity was stronger if the dot appeared on the target bar collinear to the receptive field bar than if it appeared on the other bar ($P < 0.01$, Wilcoxon test; **Fig. 1c** and **Supplementary Fig. 1**); the latency of this indirect effect was 328 ms (**Supplementary Figs. 2a** and **3**). To investigate whether the response modulation at the

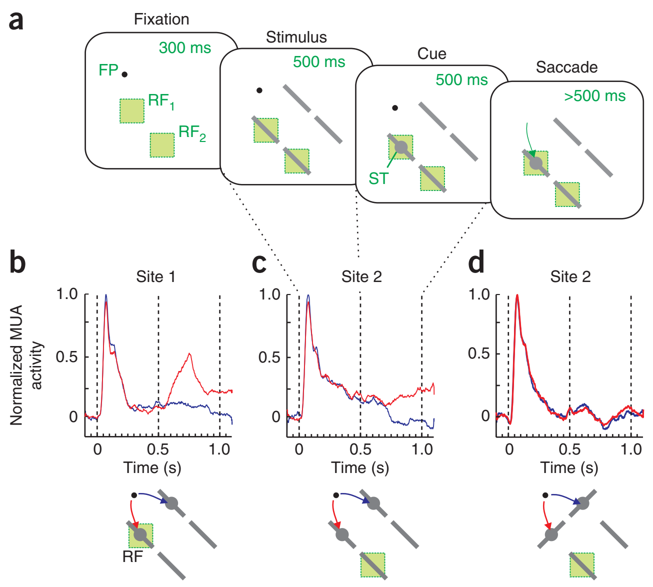

Figure 1 The effect of collinearity on the spread of attention. (**a**) Schematic sequence of stimulus and behavioral events during a trial. The monkey foveated a fixation point (FP). After 300 ms, an array of four bars appeared, and after 500 ms, a saccade target (ST) dot appeared over one of the more central bars. The fixation point disappeared after an additional 500 ms and the monkey made an eye movement toward the saccade target (green arrow). Neuronal responses were simultaneously recorded from two recording sites; receptive fields (RF_1 and RF_2) are shown as squares. (**b**) The multi-unit activity (MUA) of neurons at site 1 increased when the saccade target appeared in the receptive field, at a latency of 44 ms (red curve), but not if it appeared on the other bar (blue). (**c**) Neuronal responses at recording site 2. Cueing of the lower target bar, which is grouped to the receptive field bar, caused a stronger response than cueing of the upper target bar, at a latency of 328 ms. (**d**) Cueing of the central bars had little influence when they were orthogonal to the receptive field bar. Ethical permission was obtained from the institutional animal care and use committee of the Royal Netherlands Academy of Arts and Sciences.

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Received 31 January; accepted 21 June; published online 18 September 2011; doi:10.1038/nn.2910

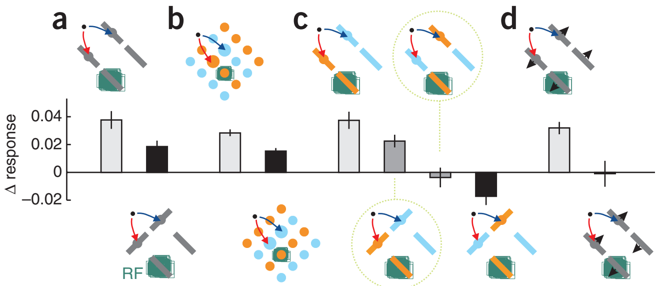

Figure 2 Effects of Gestalt cues on the spread of enhanced activity at the population level. (**a**) The influence of collinearity. (**b**) Effect of color similarity. (**c**) Combined effect of collinearity and color similarity. (**d**) Effect of common fate. Histograms depict the average differences in activity between cueing conditions (see insets) for grouped (light gray bars) and nongrouped configurations (black bars). Error bars denote s.e.m. Green rectangles illustrate the superimposed (and scaled) locations of the receptive fields of all recording sites relative to the stimuli, indicating that the neurons were not directly activated by the surrounding stimuli.

eccentric bar was a result of perceptual grouping, we also included a control condition in which the same eye movements were made, but the orientation of the central bars was orthogonal, so that neither central bar grouped with the receptive field bar. In this situation, cueing of the central bars had little influence over activity evoked at site 2 ($P = 0.32$, Wilcoxon test; **Fig. 1d** and **Supplementary Fig. 1b**). Thus, the cueing effect only occurred in case of grouping, as if attention spread according to the Gestalt rule of good continuation.

To quantify these effects at the population level, we determined the difference in activity between conditions in which attention was directed toward and away from the stimulus grouped to the receptive field bar ($\Delta_{grouped}$). Because the distance between the focus of attention and the receptive field bar might influence activity in the absence of grouping[12] (**Supplementary Fig. 4**), we also computed response differences in the control condition in which both central bars were orthogonal so that there was no collinearity grouping in either cueing condition ($\Delta_{ungrouped}$). We found that $\Delta_{grouped}$ was significantly larger than $\Delta_{ungrouped}$ ($P < 0.0001$, paired *t* test; **Fig. 2a**), indicating that there is an increased spread of enhanced activity along collinear line elements (**Supplementary Fig. 5** illustrates the effects of grouping on V1 activity before cue appearance).

We next measured the influence of color similarity on the spread of attentional modulation in an array of colored dots (**Supplementary Methods**). The spread of the attentional modulation was stronger if the dot that was the target of the eye movement was the same color as the dot in the receptive field than if these dots were different colors ($P < 0.0001$, paired *t* test; **Fig. 2b**), which suggests a spread of activity from attended stimuli to irrelevant stimuli with the same color. We also tested the conjoined influence of collinearity and color similarity and found that the spread of attentional modulation was strongest if the target bar and receptive field bar were related to each other by both grouping cues, and weaker in the case of one grouping cue only, suggesting an additive effect of Gestalt principles (**Fig. 2c**). In the absence of collinearity, cueing of the upper central bar even induced a stronger response if it had the same color as the receptive field bar, causing a negative grouping index (**Fig. 2c**). A two-way ANOVA revealed a main effect of color similarity ($F_{1,220} = 40.2$, $P < 10^{-4}$) and collinearity ($F_{1,220} = 5.4$, $P < 0.05$), but no significant interaction ($F_{1,220} < 1$). Finally, we tested the influence of common fate with an oscillatory movement of the bars, so that the receptive field bar and the adjacent target bar either moved in or out of phase. The spread of attentional modulation was most pronounced for bars moving in phase ($P < 0.0001$, paired *t* test; **Fig. 2d**).

These results indicate that enhanced neuronal activity spreads from attended stimuli to irrelevant stimuli that are bound by Gestalt grouping cues. In a control experiment, we presented the same bars, but directed the monkey's attention to a stimulus in the other hemifield. In this task, the effects of grouping on V1 activity were attenuated, confirming that they reflect the spread of attention from the central bars onto the peripheral bars (**Supplementary Results** and **Supplementary Fig. 6**). The attentional co-selection of irrelevant objects with a similar color or motion as the target object may reflect feature-based attention, as has been observed in area MT[13]. However, in the collinear configurations shown in **Figure 1c**, the two relevant central bars had the same orientation and the effect of cueing on the representation of the irrelevant bars could not be explained by feature-based attention. A previous study[14] found that a chain of task-relevant collinear bars induces attentional modulation in V1, whereas our results indicate that attention spreads from attended bars to nearby irrelevant bars, but only if they are collinear[15]. These results, taken together, suggest a common framework for the effects of collinearity and feature similarity. These Gestalt grouping cues may promote the spread of selective attention to all parts of the same object, thereby facilitating the reconstruction of coherent objects from their initially fragmented representations in early visual cortex (see **Supplementary Discussion**).

Note: Supplementary information is available on the Nature Neuroscience website.

ACKNOWLEDGMENTS
We thank J. Poort, B. Dagnino, B. van Vugt and J. Fecteau for additional data collection, and K. Brandsma and D. Vleesenbeek for biotechnical support. This work was supported by NWO-ALW grant 816.02.018 and by an NWO-VICI grant 016.075.608 awarded to P.R.R.

AUTHOR CONTRIBUTIONS
A.W. designed the stimuli, performed recordings, analyzed data and wrote the paper. L.S. designed the stimuli and performed recordings. P.R.R. conceived the project, supervised the data acquisition and analysis, and wrote the paper.

COMPETING FINANCIAL INTERESTS
The authors declare no competing financial interests.

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