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Aurel Wannig[1*], Liviu Stanisor[1*], Pieter R. Roelfsema[1,2]

[1]Dept. of Vision and Cognition, Netherlands Institute for Neuroscience, an institute of the Royal Netherlands Academy of Arts and Sciences (KNAW), Meibergdreef 47, 1105 BA Amsterdam, The Netherlands

[2]Department of Integrative Neurophysiology, Center for Neurogenomics and Cognitive Research, VU University, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

* These authors contributed equally to this work.

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Correspondence should be addressed to P.R.R. (e-mail: p.roelfsema@nin.knaw.nl).

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. Here we recorded neuronal activity in area V1 of macaque monkeys and observed an automatic spread of attention to image elements outside the attentional focus, if they are 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 (RFs) tuned to simple features, like colours 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 at 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 in each other's good continuation, move in the same direction and have the same colour than parts of different objects. Treisman & Gelade[2] proposed 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 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 if 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**). **Figure 1a** illustrates an experiment that tested the influence of collinearity. The animals saw two bars near the fixation point (FP) that were potential targets for a saccade and, in addition, two more eccentric bars that could be ignored. We identified the target bar after 500ms by presenting a small dot on top of it, thus guiding attention towards this stimulus[11]. After an additional 500ms, the fixation dot disappeared cuing the animal to make a saccade to the target bar. In this example session, we recorded from a recording site with a RF on one of the relevant bars (site 1) and at the same time from site 2 with a RF on an irrelevant bar.

As expected, the appearance of the dot in the RF of site 1 triggered an increase in activity with a latency of 44ms (red response in **Fig. 1b**) that was absent if the dot appeared on the other bar (blue response). This effect appeared to spread to site 2 where activity was stronger if the dot appeared on the target bar collinear to RF-bar than if it appeared on the other bar ($p<0.01$, Wilcoxon test; **Fig. 1c**) and the latency of this indirect effect was 328ms (**Supplementary Fig. 1a**). To investigate whether the response modulation at the eccentric bar was due to perceptual grouping, we also included a control condition where the same eye movements were made, but the orientation of the central bars was orthogonal so that neither central bar grouped with the RF-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 where attention was directed towards and away from the stimulus grouped to the RF-bar ($\Delta_{grouped}$). Because the distance between the focus of attention and the RF-bar might influence activity in the absence of grouping[12] (**Supplementary Fig. 2**), we also computed response differences in the control condition where both central bars were orthogonal so that there was no collinearity grouping in either cuing 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.

The next experiment measured the influence of colour similarity on the spread of attentional modulation in an array of coloured dots (**Supplementary Methods**). The spread of the attentional modulation was stronger if the dot that was the target of the eye movement had the same colour as the dot in the RF than if these dots had different colours (**Fig. 2b**; $p<0.0001$, paired t-test), which suggests a spread of activity from attended stimuli to irrelevant stimuli with the same colour. The third experiment tested the conjoined influence of collinearity and colour similarity. We found that the spread of attentional modulation was strongest if the target bar and RF-bar were related to each other by both grouping cues, and weaker in 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 colour as the RF-bar, causing a negative grouping index (right bar in **Fig. 2c**). A two-way ANOVA revealed a main effect of colour ($F_{1,220}$=40.2, $p<10^{-4}$) and collinearity ($F_{1,220}$=5.4, $p<0.05$) but no significant interaction ($F_{1,220}<1$). Our final experiment tested the influence of common fate with an oscillatory movement of the bars, so that the RF-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 (**Fig. 2d;** $p<0.0001$, paired t-test).

These results show 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**). The attentional co-selection of irrelevant objects with a similar colour or motion as the target object may reflect feature-based attention as has been observed in area MT[13]. However, in the collinear configurations of Fig. 1c, the two relevant central bars had the same orientation and the effect of cueing on the representation of the irrelevant bars cannot be explained by feature-based attention. A previous study[14] showed that a chain of task-relevant collinear bars induces attentional modulation in V1 whereas the present results show that attention spreads from attended bars to nearby irrelevant bars, but only if they are collinear[15]. The present and previous 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**).

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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.

Reference List

1. Wertheimer,M. Untersuchungen zur Lehre von der Gestalt II. *Psycholog. Forschung* **4**, 301-350 (1923).

2. Treisman,A.M. & Gelade,G. A feature-integration theory of attention. *Cogn Psychol.* **12**, 97-136 (1980).

3. Duncan,J. Selective attention and the organization of visual information. *J. Exp. Psychol. Gen.* **113**, 501-517 (1984).

4. Egly,R., Driver,J., & Rafal,R.D. Shifting visual attention between objects and locations: evidence from normal and parietal lesion subjects. *J. Exp. Psychol. Gen.* **123**, 161-177 (1994).

5. Driver,J., Davis,G., Russell,C., Turatto,M., & Freeman,E. Segmentation, attention and phenomenal visual objects. *Cognition* **80**, 61-95 (2001).

6. Roelfsema,P.R., Lamme,V.A., & Spekreijse,H. Object-based attention in the primary visual cortex of the macaque monkey. *Nature* **395**, 376-381 (1998).

7. Wannig,A., Rodriguez,V., & Freiwald,W.A. Attention to surfaces modulates motion processing in extrastriate area MT. *Neuron* **54**, 639-651 (2007).

8. Shomstein,S. & Yantis,S. Object-based attention: sensory modulation or priority setting? *Percept. Psychophys.* **64**, 41-51 (2002).

9. Lamy,D. & Egeth,H. Object-based selection: the role of attentional shifts. *Percept. Psychophys.* **64**, 52-66 (2002).

10. Richard,A.M., Lee,H., & Vecera,S.P. Attentional spreading in object-based attention. *J. Exp. Psychol. Hum. Percept. Perform.* **34**, 842-853 (2008).

11. Hoffman,J.E. & Subramaniam,B. The role of visual attention in saccadic eye movements. *Percept. Psychophys.* **57**, 787-795 (1995).

12. Connor,C.E., Preddie,D.C., Gallant,J.L., & Van Essen,D.C. Spatial attention effects in macaque area V4. *J. Neurosci.* **17**, 3201-3214 (1997).

13. Martinez-Trujillo,J.C. & Treue,S. Feature-based attention increases the selectivity of population responses in primate visual cortex. *Curr. Biol.* **14**, 744-751 (2004).

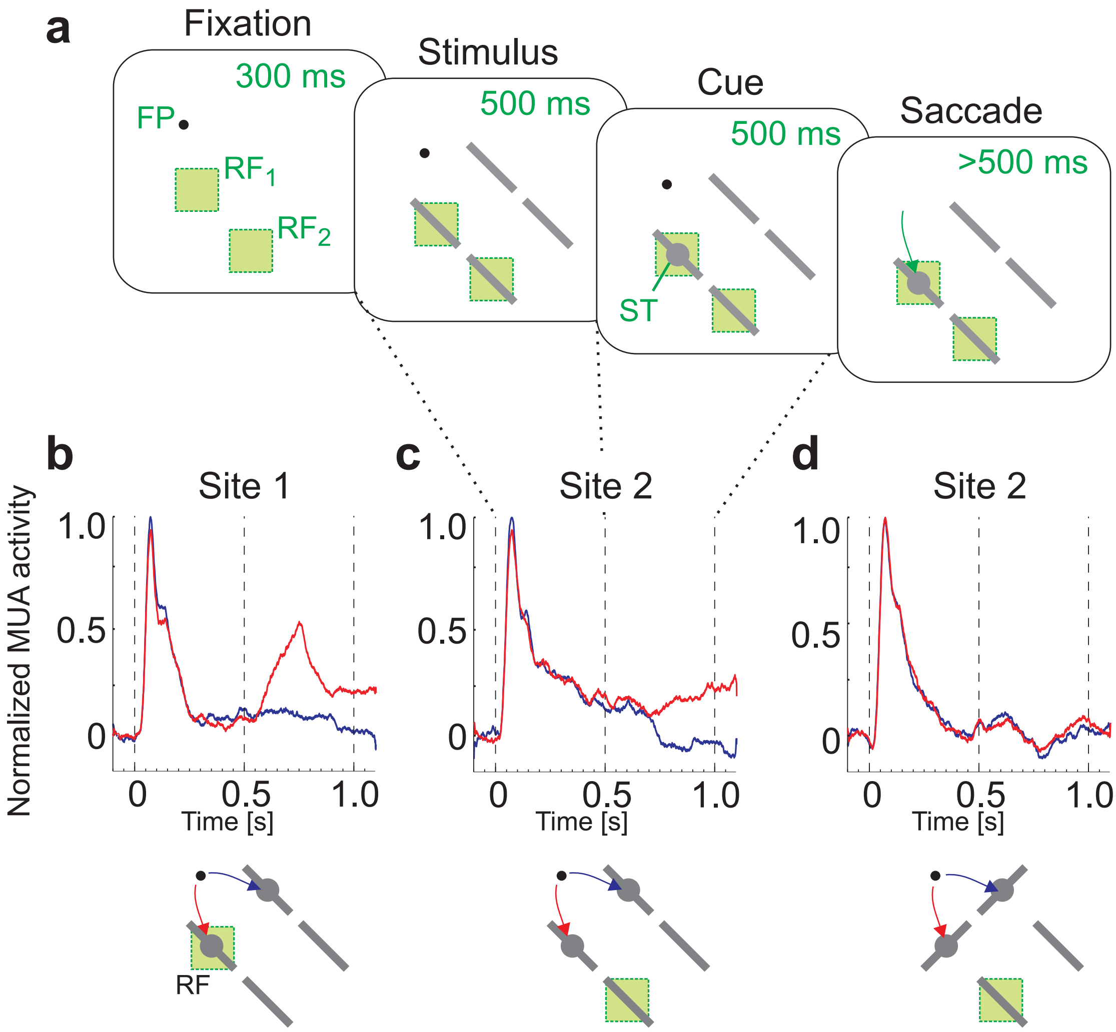
14. Li,W., Piech,V., & Gilbert,C.D. Contour saliency in primary visual cortex. *Neuron* **50**, 951-962 (2006).

15. Freeman,E., Sagi,D., & Driver,J. Lateral interactions between targets and flankers in low-level vision depend on attention to the flankers. *Nat. Neurosci.* **4**, 1032-1036 (2001).

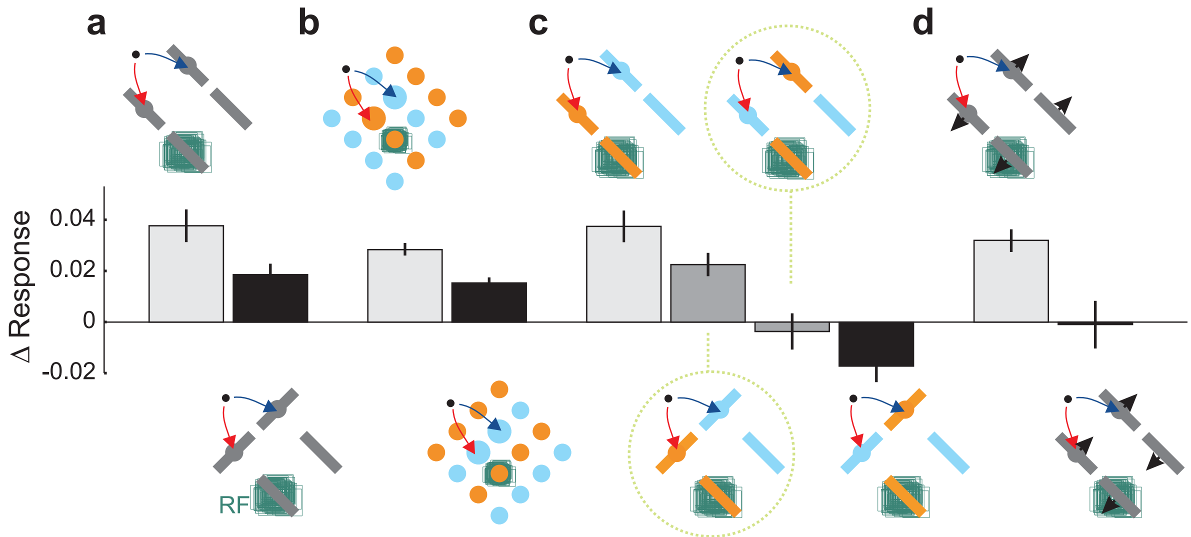
Figure legends

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 300ms, an array of 4 bars appeared and after 500ms a saccade target dot (ST) appeared over one of the more central bars. The FP disappeared after an additional 500ms and the monkey made an eye movement towards the ST (green arrow). Neuronal responses were simultaneously recorded from two recording sites; RFs are shown as squares. (**b**) The activity of neurons at site 1 increased when the ST appeared in the RF, at a latency of 44ms (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 RF-bar, caused a stronger response than cueing of the upper target bar, at a latency of 328ms. (**d**) Cueing of the central bars had little influence when they were orthogonal to the RF-bar. Ethical permission was obtained from the institutional animal care and use committee of the Royal Netherlands Academy of Arts and Sciences.

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 (bright bars) and non-grouped configurations (black bars). Error bars denote s.e.m. Light green rectangles illustrate the superimposed (and scaled) locations of the RFs of all recording sites relative to the stimuli, indicating that the neurons were not directly activated by the surrounding stimuli.



a
Fixation
300 ms
FP
RF1
RF2
Stimulus
500 ms
Cue
500 ms
ST
Saccade
>500 ms
b
Site 1
c
Site 2
d
Site 2
Normalized MUA activity
1.0
0.5
0
0
0.5
1.0
Time [s]
RF



a
b
c
d
Δ Response
0.04
0.02
0
-0.02
RF