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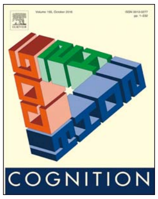

Original Articles

Small numbers are sensed directly, high numbers constructed from size and density

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ABSTRACT

Two theories compete to explain how we estimate the numerosity of visual object sets. The first suggests that the apparent numerosity is derived from an analysis of more low-level features like size and density of the set. The second theory suggests that numbers are sensed directly. Consistent with the latter claim is the existence of neurons in parietal cortex which are specialized for processing the numerosity of elements in the visual scene. However, recent evidence suggests that only low numbers can be sensed directly whereas the perception of high numbers is supported by the analysis of low-level features. Processing of low and high numbers, being located at different levels of the neural hierarchy should involve different receptive field sizes. Here, I tested this idea with visual adaptation. I measured the spatial spread of number adaptation for low and high numerosities. A focused adaptation spread of high numerosities suggested the involvement of early neural levels where receptive fields are comparably small and the broad spread for low numerosities was consistent with processing of number neurons which have larger receptive fields. These results provide evidence for the claim that different mechanism exist generating the perception of visual numerosity. Whereas low numbers are sensed directly as a primary visual attribute, the estimation of high numbers however likely depends on the area size over which the objects are spread.

1. Introduction

Research suggests the existence of a system specialized for the perception of numerosity in the brain (Burr & Ross, 2008; Harvey, Klein, Petridou, & Dumoulin, 2013; Nieder, 2005). Various species are capable to discriminate perceptual quantities (Dehaene, Dehaene-Lambertz, & Cohen, 1998; Nieder, 2005) and human neonates generalize across numbers within the first 3 days after birth (Izard, Sann, Spelke, & Streri, 2009). Studies in human and non-human primates led to the suggestion of the parietal area as the 'primary magnitude cortex': Electrophysiological work in monkeys revealed a magnitude network, comprising the intraparietal and the prefrontal cortex (Nieder & Miller, 2003). The analysis of neuronal response latencies suggested that parietal neurons first extract the numerosity information and then project it to the prefrontal cortex (Viswanathan & Nieder, 2013). Neurons in these areas show a selectivity for numerosity indicating that numerical quantity is a primary perceptual feature rather than a category abstracted from lower-level features (Nieder & Miller, 2003). This neuronal tuning profile for numerosity was confirmed in humans by brain imaging, revealing number specificity independent of other parameters as shape, density or spatial arrangement (Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). These representations are strongly influenced by topological invariants, such as connectivity and the inside/outside relationship (He, Zhou, Zhou, He, & Chen, 2015). A recent imaging study demonstrated overlapping representations of object size and numerosity in parietal cortex, suggesting that both might be processed by a mechanism analyzing general quantity (Harvey, Fracasso, Petridou, & Dumoulin, 2015).

How numerical magnitude is processed is still a matter of controversy in current psychophysical research: Burr and Ross (2008) were able to develop an adaptation method that induced a negative number aftereffect of visual numerosity. The interpretation of a primary number sense however has been challenged: Interdependencies between numerosity and object density and size suggest that number perception is constructed by integrating low-level features (Morgan, Raphael, Tibber, & Dakin, 2014; Dakin, Tibber, Greenwood, Kingdom, & Morgan, 2011; Tibber, Greenwood, & Dakin, 2012; Gebuis & Reynvoet, 2012a, 2012b). Studies suggest that which of these mechanisms is used for numerosity perception might depend on the actual number of dots that has to be estimated: Anobile, Cicchini, and Burr (2014) using a range of probe numerosities demonstrated that the perception of low but not high numerosities follows Weber's law. Allik, Tuulmets, and Vos (1991) had shown that changes in the physical size of numerous clouds leave number judgments invariant when the tested numerosity is low. These

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results are consistent with the existence of a number sense for low numerosities. We have recently shown that size adaptation affects numerosity judgments (Zimmermann & Fink, 2016). Changes in the number estimations depended on the numerosity in the probe patch in a logarithmic fashion: The higher the probe number, the bigger the amount of adaptation. Whereas for low numbers - which were comparably unaffected by changes in apparent size - a number sense might perceive numerosity directly, higher numbers might be derived from information of cloud size and dot density.

Direct numerosity perception and density estimation are processed at different levels of the neural hierarchy: Neurons whose activity is suited to construct a number sense have been found in the intraparietal cortex (Piazza et al., 2004; Viswanathan & Nieder, 2013). Density information however is processed within visual areas V1-TEO (Kastner, De Weerd, & Ungerleider, 2001). Receptive field sizes of neurons in areas V3 and V4, at the eccentricity of the number clouds of the current study (i.e., 7.8° in visual angle), are around 5° in visual angle (Gattass, Sousa, & Gross, 1988) and receptive field sizes of neurons in the intraparietal sulcus at that eccentricity are around 12° (Blatt, Andersen, & Stoner, 1990). Larger receptive field sizes predict that the adaptation aftereffect is distributed over a larger part of the visual field. The spatial spread of adaptation therefore allows inferences about the receptive field size of the adapted neurons. To investigate these separate mechanisms of number perception, I tested the adaptation spread of low and high numerosities. Numbers that are processed higher up in the visual hierarchy should show a larger spread of adaptation than those which are constructed from low-level visual features.

2. Experiment 1

In order to test whether spatial spread of adaptation varies for low and high numerosities, I tested the effect of number adaptation on number clouds when both, adapter and probe were presented spatially offset (see Fig. 1B). Neurons with small receptive fields should be insensitive to adapters presented far from their receptive field. Neurons with large receptive field however should respond invariantly to the spatial offset between adapter and probe. Although the latter prediction is not clear-cut since the visual field is covered with a population of partially overlapping receptive fields, adaptation on average should still be stronger in that case.

2.1. Methods

2.1.1. Participants

Six subjects (3 female, 3 male, mean age 35 years) participated in Experiment 1 for the adaptation experiment and 6 different subjects (2 female, 4 male, mean age 32 years) for the baseline measurement. Seven different subjects (5 female, 2 male, mean age 29 years) participated in the main Experiment 2 and seven different subjects (4 female, 3 male, mean age 30 years) in the control experiment. All had normal or corrected to normal vision and were naive to the purpose of the experiment. Experiments were carried out in accordance with the Declaration of Helsinki. All experiments were approved by the local ethics committee of the psychological department of the Heinrich-Heine University Düsseldorf. Data sets for each study can be found on the Open Science Framework here.

2.1.2. Apparatus

Subjects were seated 70 cm from a Eizo FlexScan T57S. The visible screen diagonal was 20 in., resulting in a visual field of 40° × 30°. Stimuli were presented on the monitor with a vertical frequency of 120 Hz on a homogeneously gray background.

Experiment 1 consisted of a baseline measurement and an adaptation experiment. Subjects were required to keep gaze directed at the fixation point that was presented in screen center (black rectangle, size: 0.5° × 0.5°). The baseline measurement started with the presentation of a blank screen for 1000 ms. Two rectangular number clouds (probe and reference) were shown for 600 ms at an horizontal eccentricity of ± 7.8° and 1.5° below the horizontal meridian (see Fig. 1A). Numerosity patches used for probes and adapters where bunches of red[1] dots (radius: 3 pixels) presented on a homogeneously gray background. The probe cloud contained either 4, 7, 12, 15, 20, 50 or 100 dots and was shown always on the right and the reference cloud always on the left side. For each of these seven probe numbers, one of the two adapters contained twice and the other adapter half of the dot number (these numbers were brought down to a round number). Presentation of these dot numbers was randomized across trials. For each of the seven probe numbers a full psychometric function was measured. To this end, the numerosity in the reference cloud was systematically varied between −90% to +90% of the dot number in the probe cloud. For probe numbers 4 and 7, the reference numerosity was varied in 7 equiprobable steps and for numbers 12–100, the reference numerosity was varied in 11 equiprobable steps. Subjects were instructed to report which cloud contained the higher dot number by pressing the left or right arrow key. Each psychometric function contained 55 trials, except functions for probe numbers 4 and 7, which contained 35 trials.

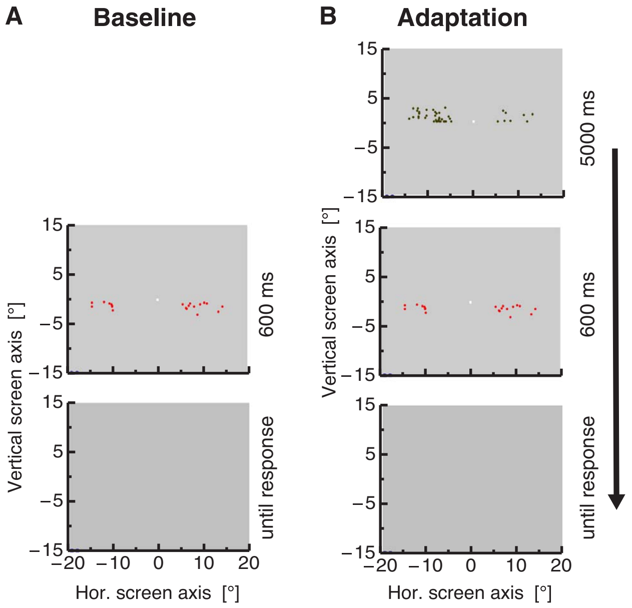

Fig. 1. Experimental 1 - setup. **A** Experimental setup of the baseline measurement. Numerosity clouds consisted of a specific number of dots randomly placed within a rectangular area size of 8° × 2.4°. Two numerosity clouds were presented for 600 ms. The probe numerosity cloud was shown always on the right side and the reference cloud on the left. Subjects were asked to report which cloud contains the higher number of dots. **B** Experimental setup of the adaptation experiment. The adapters were presented for 5000 ms. The spatial position of the adapters was switched in separate sessions. After the adapters disappeared two numerosity clouds were presented for 600 ms. The probe numerosity cloud was shown always on the right side and the reference cloud on the left. Subjects were asked to report which cloud contains the higher number of dots.

In the adaptation experiment two adapters were shown before presentation of the probes. The adapters were centered ± 7.8° to the left and right of the fixation point and 1.5° above the horizontal meridian. The adapters consisted of a specific number of dots randomly placed within a rectangular area size of 8° × 2.4°. The adapters were presented for 5000 ms. After offset of the adapter stimuli two rectangular number clouds (probe and reference) were shown for 600 ms. The remaining procedure was identical to the baseline measurement.

Data from each subject were measured in two separate sessions: Either the adapter with twice the amount of dots as the probe was on

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[1] For interpretation of color in Figs. 1–6, the reader is referred to the web version of this article.