cortex xxx (2017) 1–10

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research report

Decoding early and late cortical contributions to individuation of attended and unattended objects

Claire K. Naughtin [a,**], Jason B. Mattingley [a,b], Angela D. Bender [a] and Paul E. Dux [a,*]

[a] School of Psychology, The University of Queensland, Australia
[b] Queensland Brain Institute, The University of Queensland, Australia

ARTICLE INFO

Article history:
Received 20 April 2017
Reviewed 20 May 2017
Revised 29 May 2017
Accepted 19 October 2017
Action editor Gereon Fink
Published online xxx

Keywords:
Individuation
Subitizing
fMRI
Illusory contours

ABSTRACT

To isolate a visual stimulus as a unique object with a specific spatial location and time of occurrence, it is necessary to first register (*individuate*) the stimulus as a distinct perceptual entity. Recent investigations into the neural substrates of object individuation have suggested it is subserved by a distributed neural network, but previous manipulations of individuation load have introduced extraneous visual confounds, which might have yielded ambiguous findings, particularly in early cortical areas. Furthermore, while it has been assumed that selective attention is required for object individuation, there is no definitive evidence on the brain regions recruited for attended and ignored objects. Here we addressed these issues by combining functional magnetic resonance imaging (fMRI) with a novel object-enumeration paradigm in which to-be-individuated objects were defined by illusory contours, such that the physical elements of the display remained constant across individuation conditions. Multi-voxel pattern analyses revealed that attended objects modulated patterns of activity in early visual cortex, as well as frontal and parietal brain areas, as a function of object-individuation load. These findings suggest that object individuation recruits both early and later cortical areas, consistent with theoretical accounts proposing that this operation acts at the junction of feed-forward and feedback processing stages in visual analysis. We also found dissociations between brain regions involved in individuation of attended and unattended objects, suggesting that voluntary spatial attention influences the brain regions recruited for this process.

1. Introduction

Object individuation – the process of segmenting an object in a visual scene, isolating its boundaries, and registering it as a distinct perceptual entity – is fundamental to how vision is used to guide behaviour. This process provides a link between bottom-up feature detection and the identification of stable and coherent objects (Wutz & Melcher, 2014), and without it,

* *Corresponding author*. School of Psychology, McElwain Building, The University of Queensland, St Lucia, Queensland 4072, Australia.
** *Corresponding author*. School of Psychology, McElwain Building, The University of Queensland, St Lucia, Queensland 4072, Australia.
E-mail addresses: claire.naughtin@gmail.com (C.K. Naughtin), paul.e.dux@gmail.com (P.E. Dux).
https://doi.org/10.1016/j.cortex.2017.10.013
0010-9452/

individuals show deficits in their ability to locate an object in space and make the appropriate motor movement towards it (Perenin & Vighetto, 1988). Object individuation processes are typically measured in tasks that require participants to report on the number of distinct items in a visual display (e.g., the number of simple shapes, or the identity of simple shapes; Xu & Chun, 2006; Ester, Drew, Klee, Vogel, & Awh, 2012; Mazza, Pagano, & Caramazza, 2013; Naughtin, Mattingley, & Dux, 2016a). Individuation processes are argued to play a key role in a range of different cognitive abilities including enumeration, multiple object tracking and visual short-term memory. For example, in "enumeration" or "subitizing" paradigms, in which the number of briefly presented shapes must be responded to, fast and accurate responding is commonly observed for up to three to four target items, suggesting participants individuate multiple objects simultaneously (Trick and Pylyshyn, 1994). In contrast, participants' reaction times (RTs) and error rates increase for set sizes beyond the ~four item range. Here, we use enumeration as our measure of individuation, which extends upon our previous work where we employed working memory tasks to assess this operation (see Naughtin et al., 2016a; Naughtin, Mattingley, & Dux, 2016b).

Functional magnetic resonance imaging (fMRI) studies have shown that the individuation of multiple perceptual items across spatial locations influences activity in several brain areas, including parts of the frontal, parietal and occipital cortices (e.g., Naughtin et al., 2016b; Xu & Chun, 2009). However, while previous studies suggest that individuation processes recruit a distributed network in the brain, their manipulations of individuation load also introduced variations in other low-level visual properties (e.g., the total number of visual elements, overall contrast or luminance, or eccentricity) that could lead to changes in brain areas that are sensitive to these visual properties, as opposed to individuation per se. As a result, it remains unknown precisely which areas are uniquely involved in object individuation processes.

Although individuation of multiple objects was initially thought to be pre-attentive (Pylyshyn, 1989), several recent investigations into the neural bases of individuation have shown that this operation relies on selective attention to create a coarse representation of an object and to direct resources to it for further featural analysis (Burr, Turi, & Anobile, 2010; Kahneman, Treisman, & Gibbs, 1992; Xu & Chun, 2009; Mazza & Caramazza, 2015; but see, Bahrami et al., 2010; Vuilleumier & Rafal, 1999, for evidence of unconscious enumeration processes). For example, electroencephalography (EEG) studies on enumeration have shown that a lateralized, negative going event-related potential (ERP) – the attention-related N2pc component (Woodman & Luck, 1999) which typically emerges approximately 200–300 msec post-stimulus onset in parieto-occipital electrodes – is modulated by the overall number of targets presented in a visual display (Ester et al., 2012; Mazza & Caramazza, 2011). Specifically, N2pc amplitude increases with object numerosity and then reaches an asymptote at approximately three to four targets (Anderson, Vogel, & Awh, 2014; Ester et al., 2012; Pagano, Lombardi, & Mazza, 2014). The plateau corresponds with the observed subitizing limit at which participants are no longer able to correctly report the number of items presented in brief visual displays. On the basis of this numerosity-related modulation of the N2pc, Mazza and Caramazza (2015) proposed that the N2pc reflects the operation of an attention-based, capacity-limited individuation mechanism that emerges approximately 200–300 msec after stimulus onset. However, as these studies focused exclusively on task-relevant objects (but see, Jeong & Xu, 2013; Naughtin et al., 2016b), it is currently unclear whether ignored (unattended) items are also individuated, and whether patterns of neural activation are distinguishable for attended and unattended objects.

In a recent EEG study, we introduced a novel paradigm that addressed these two shortcomings of prior work by using multiple illusory squares as the objects to be individuated (Naughtin et al., 2016b). Participants were presented with groups of four circular place holders on either side of fixation. On each trial, quarter segments were removed briefly from each disk, such that some groups yielded a new illusory square and others did not (see Fig. 1). This approach meant that we could manipulate the number of objects participants had to individuate (or ignore), while holding other low-level physical stimuli constant. We found that the number of individuated target objects modulated P1 amplitude – a positive-going potential that peaked between 100–140 msec post-stimulus. This suggested that individuation for attended items arises early in the visual processing hierarchy, and challenged previous studies that had attributed this process to a later temporal locus (200–300 msec post-stimulus, N2pc; Ester et al., 2012; Mazza et al., 2013; Mazza & Caramazza, 2015). Conversely, individuation of unattended items was only evident at the N2pc (Naughtin et al., 2016b). These findings suggest distinct timecourses for individuation of objects within and outside the focus of attention.

In the present study, we again employed our novel illusory-object enumeration paradigm to explore the early and late cortical contributions to the individuation of attended and unattended objects in regions of the brain isolated in our previous study examining individuation operations in visual working memory (Naughtin et al., 2016a). A neural correlate of object individuation should be sensitive to the number of distinct visual items under conditions in which low-level visual properties are carefully matched. We had three main objectives. First, we aimed to assess whether object individuation is associated with unique activation patterns in early visual processing brain areas. Second, we aimed to determine the wider extent of the object individuation network beyond early visual cortical regions. Third, because object individuation of attended and unattended objects produces distinct neural timecourses (Naughtin et al., 2016b), we determined whether patterns of neural activation were distinguishable for attended and unattended objects.

2. Experimental procedures

2.1. *Participants*

We recruited 14 participants for this experiment (9 females, $M = 27.4$ years, $SD = 5.4$). This sample size was based on a power analyses conducted by Naughtin et al. (2016a) on the effect size reported in a similar study by Xu (2009). All had