Neuropsychologia 83 (2016) 1–4

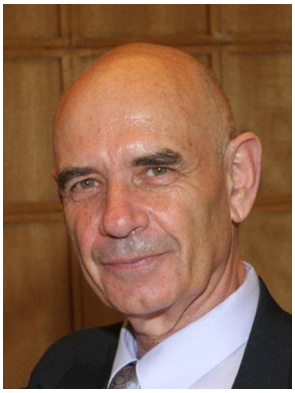
Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Editorial

Introduction to the special issue on functional selectivity in perceptual and cognitive systems - a tribute to Shlomo Bentin (1946-2012)



Shlomo Bentin, PhD, 1946–2012

This should have been the time for a festschrift for Shlomo Bentin, at the occasion of his "retirement" from the Hebrew University of Jerusalem where he had been a professor for many years at the Department of Psychology and at the Interdisciplinary Center for Neural Computation. We write "retirement" with double quotes, because no one who knew Shlomo Bentin could have conceived of him actually stopping to do what he was so passionate about—science. It is sad that instead of a festival, this special issue has to be in memory of Shlomo, who was tragically killed riding his bicycle while on sabbatical with Lynn Robertson in UC Berkeley in July 2012, at his prime, only weeks after receiving Israel's most distinguished honor for his ongoing scientific achievements, the Israel Prize in Psychology.

Shlomo's career paralleled the inception and evolution of the field of cognitive neuroscience, and his work exemplifies the bonuses of combining the 'neuro' with the 'psychology' to gain true insights about the human mind. The hallmark of cognitive neuroscience is converging evidence, and Shlomo and his numerous students combined sophisticated methods of experimental psychology, data from normal participants and from patients, and clever use of neuroimaging including EEG, MEG and fMRI—but always in the service of answering a theoretical question about cognition and the brain. In his early work, he investigated reading processes (e.g. Bentin, 1987; Frost et al., 1987). Based on his findings, among others using the special cases of Hebrew and Arabic, he argued (strongly, as always) for the critical importance of phonological processing in reading (e.g. Bentin and Ibrahim, 1996; Bentin and Leshem, 1993). This work did not stay within the ivory tower of the academia but, through Shlomo's efforts, actually changed how reading is taught in Israel's elementary schools to date. In the early 1990s, following a sabbatical at Yale, and inspired by human intracranial findings of Truett Allison, Gregory McCarthy and colleagues, which showed exquisite selectivity to faces and other objects at nearby sites in the inferior temporal cortex, he described for the first time an event related potential (ERP) recorded on the scalp that was selective for faces—famously known as the N170 (Bentin et al., 1996). This highly cited study (> 1000 citations to date) provided a new framework within which psychologists could non-invasively study high-level perceptual and cognitive processing in the human brain. In his following work he used this ERP as a precision tool to dissect face processing, including part-based vs. holistic processing (e.g., Sagiv and Bentin, 2001), detection vs. identification (e.g., Bentin and Deouell, 2000), domain-specificity vs. expertise (e.g., Carmel and Bentin, 2002; Harel et al., 2007), high-level vs. low-level effects (e.g., Bentin et al., 2002), mechanisms of congenital prosopagnosia (e.g., Bentin et al., 2007, 1999), rehabilitation of prosopagnosia (e.g., DeGutis et al., 2007), and more. While numerous studies came out of his lab, he treated every one of his studies as if it was his first, with the same endless enthusiasm and energy that characterized him to his last day.

Shlomo was equally dedicated to mentoring students and postdocs. He has mentored dozens of students, many of whom went on to become internationally-renown professors. His mentorship empowered students' academic freedom and at the same time he was always available for discussions—literally around the clock, 7 days a week (when he slept remains a mystery). He knew how to focus his students not by asking them 'what is the next experiment?' but rather 'what is the next question?'.

In this spirit, this special issue is devoted to questions about functional selectivity—the extent to which perceptual and cognitive systems, and their neural implementations, are specialized for specific tasks and domains. Following Shlomo's approach to cognitive neuroscience, the papers included in this special issue make use of diverse methods, including psychophysics, EEG, MEG, fMRI, TMS, single-unit recordings in humans and animals, and studies in patients.

We start off with questions regarding face processing vs. the processing of other visual objects, which were the center of Shlomo's work for many years. Functional selectivity for faces in the human brain was initially supported by lesion studies and the evidence of prosopagnosia (an impairment in face recognition). It

http://dx.doi.org/10.1016/j.neuropsychologia.2016.01.032

received a major thrust by the more or less concomitant reports in the mid-1990s of intracranial recordings (electrocorticography, ECoG) of a face-selective ERP named the N200 over the fusiform gyrus (Allison et al., 1994), from EEG recordings of the face-selective N170 over the occipito-temporal scalp (Bentin et al., 1996), and from PET and fMRI measurements of face-selective activations in the fusiform gyrus (Kanwisher et al., 1997; McCarthy et al., 1997; Sergent et al., 1992). These findings evolved over the years into a more elaborate complex of spatio-temporal category-selective responses in the ventral temporal cortex. Galit Yovel reviews in this special issue the EEG and fMRI markers that support the uniqueness of face processing and argues that they are correlated not only with one another, but importantly with the behavioral signatures of selective processing of faces (e.g. the famous inversion effect; Yin, 1969). Corentin Jacques and colleagues make use of the opportunity that fMRI and ECoG data are obtained from the same subjects (cf. Puce et al., 1997) and in a detailed investigation of 6 individual patients show good correspondence between the high frequency band of the ECoG signal and the BOLD response in mapping the category-selectivity in the ventral temporal cortex.

Intracranial electrodes also allow the disruption of specific regions via electrical stimulation. Previous studies showed that face perception is disrupted specifically by stimulating the right inferior occipital gyrus (Jonas et al., 2012) as well as stimulating the right but not the left fusiform gyrus (Jonas et al., 2015; Parvizi et al., 2012), corresponding to the well-known prevalence of right hemispheric posterior lesions in causing prosopagnosia (Bouvier and Engel, 2006) and of larger responses to faces in the right hemisphere. However, Vinitha Rangarajan and Josef Parvizi show evidence in this issue from two rare patients whose face perception was distorted by stimulating the left fusiform cortex, which they attribute to the patients' right hemispheric language dominance and left-handedness. While such observations suggest that hemispheric specialization for faces may be driven by language lateralization in humans, hemispheric specialization for visual processing is observed in other species as well, a topic reflected in the paper by Nadja Freund and colleagues in this issue. Using the asymmetrically organized visual system of pigeons as an animal model, these authors report that asymmetric top-down, experience-based effects on early visual processing shape the hemispheric specialization of visual responses in the avian brain, providing a mechanism by which hemispheric specialization of function can arise.

Quite surprisingly, recent studies in humans showed remarkable consistency in the distribution of functional selectivity in the ventral temporal cortex relative to macro-anatomical landmarks, such as sulci. Kevin Weiner and Karl Zilles provide a fascinating historical overview of one such forgotten and re-discovered landmark, the mid-fusiform sulcus, which demarcates the border between face-selectivity (laterally) and place-selectivity (medially), and also between different cytoarchitectonic zones. Different cytoarchitectonic zones presumably support different computations, and Weiner and Zilles discuss different ways in which functions may be distributed across such zones, leading to a new suggestion regarding the question of domain-specificity vs. visual expertise.

Domain-specificity vs. visual expertise was one of the major debates which Shlomo Bentin took part in—do faces represent a unique stimulus for which we have specialized, domain-specific processing mechanisms, or are the putative 'markers' of face-selectivity in fact markers of visual expertise, since we are all face experts. One way to address this question is by investigating neural mechanisms of faces and objects of expertise processing in individuals with prosopagnosia. Shlomo and his colleagues investigated subjects with a congenital form of prosopagnosia, who do not have atypical brain anatomy or brain lesions, and found that their N170 response to faces was normal, but not selective—in fact it was as large for objects as for faces (Bentin et al., 1999; DeGutis et al., 2007). These findings suggested that to be able to recognize (individuate) faces, faces need to be detected early on and streamed to specialized processing. Interestingly, they also found that with training, subjects could learn to better recognize faces, and this improvement was correlated with increased selectivity of the N170 response (DeGutis et al., 2007). In this issue, Nilly Weiss, Elite Mardo, and Galia Avidan argue against a generalized expertise deficit in prosopagnosia based on data from a unique case of a subject with severe congenital propoagnosia, who nonetheless developed high expertise in recognizing horses. Barton and Corrow, in contrast, show that the face processing deficit in a cohort of patients with acquired prosopagnosia (prosopagnosia associated with a brain lesion) extends also to other types of objects of expertise such as cars and fonts. As they note, because natural lesions are involved, it is not clear if this speaks for a common mechanism for processing faces, cars and fonts, or whether this is a 'neighborhood effect', with adjacent but distinct circuits damaged in the same patients. Assaf Harel, who worked as a graduate student with Shlomo on the question of perceptual expertise (Harel et al., 2010), delineates in this special issue how interactions between the visual input and top-down processes such as semantic knowledge and attention may affect the formation of visual expertise.

This special issue also examines methodological issues that are relevant to the techniques that Shlomo used throughout his career, including EEG. Liu-Shuang and colleagues describe a new technique inspired by the steady-state visual evoked potential approach (SSVEP), which offers much higher efficiency in the identification and definition of a functional response and signal to noise ratio. Using their fast periodic visual stimulation technique in EEG, they dissociate between face-selective (normal) and face individuation (impaired) responses in an acquired prosopagnosic patient in ultra-short (a few minutes) experiments. This new approach can be used to study neural mechanisms of face perception in infants, as suggested by Stefanie Hoehl in this issue in her review of the development of category selectivity. Developmental studies will offer a critical perspective on the question of how domain specificity and expertise arise.

Selectivity in the visual system goes beyond face recognition. Faces frequently disclose emotions through facial expressions. In a study by Elizabeth B DaSilva, Kirsten Crager, and Aina Puce in this issue, they reveal late ERPs (i.e. >200 ms) that are sensitive to the expressed emotion of the face. Although both faces and other body parts may help person recognition, neural regions selective to non-face body parts largely do not overlap with regions selective to faces. Paul E. Downing and Marius V. Peelen review studies that used TMS to disrupt the occipito-temporal extra-striate body area (EBA) or the nearby occipital face area (OFA), showing a double dissociation between these sites of stimulation and the effects on processing of faces and body parts. They further discuss the specific body dimensions to which this region is sensitive.

Another domain of selectivity, which has been extensively studied in the visual domain, is reading words. The visual word form area (VWFA) has been identified within the left occipito-temporal cortex (Dehaene et al., 2002). Nadin Sigalov, Shachar Maidenbaum and Amir Amedi describe fMRI investigations of congenitally blind subjects using a visual-to-auditory sensory-substitution device (SSD). They show that the VWFA in congenital blind participants responds selectively to reading words via the SSD and not to scrambled versions of the stimuli or to heard versions of the words. The implication is that the VWFA is a word form area, but not exclusively visual. This view is extended further in a review of multisensory processes by Murray and colleagues. Based on evidence from EEG, TMS, and fMRI, they contend that the primary visual cortex is a locus of multisensory interactions that

directly impact a range of behaviors in healthy individuals from stimulus detection to object discrimination. The effects of cross-modal attention are also reviewed by Steven Hillyard and his colleagues, focusing on their results from EEG studies. Specifically, they show that auditory stimuli can attract visual attention towards the location of the sounds automatically, and induce a contralateral positivity and reduced alpha power contralateral to the side at which the sound was presented.

Category selectivity likely builds upon both low-level and high-level features. A unique window was opened by Shlomo in his studies of patient LG, a rare patient suffering from congenital agnosia (inability to recognize objects and faces; Gilaie-Dotan et al., 2005). An extensive investigation of LG done with Sharon Gilaie-Dotan and others showed that LG's intermediate regions V2 and V3 were functionally abnormal. Gilaie-Dotan summarizes eight years of studying LG, which allows her to chart the visual functions for which these intermediate areas are essential. Ani Flevaris and Lynn Robertson review their work with Shlomo Bentin on how attentional selection of low and high spatial frequency channels, in the right and left hemispheres, mediate the processing of local and global aspects of a visual display. From a different perspective, Kamila M. Jozwik, Nikolaus Kriegeskorte, and Marieke Mur examined distributed responses across the ventral temporal cortex to determine whether local visual features or semantic category membership drive the distributed representation of objects and perception. Their results and model suggest that semantic categories build upon feature sensitivity in the ventral temporal cortex, but behaviorally categorical judgments are also based on feature-independent semantic category membership. Downstream from the ventral temporal cortex, perhaps the most exquisite functional selectivity of neuronal responses has been found in single-unit recordings from the human hippocampus, which revealed neurons that respond selectivity to a particular person or landmark (e.g. the “Jennifer Anniston” neuron), regardless of how they are presented (e.g., by name or picture). Rodrigo Quian-Quiroga reviews these findings and suggests that these ‘concept cells’ provide an invariant, explicit, and sparse representation of the meaning of consciously perceived stimuli. Further he suggests that such neurons may serve as a basis for forming associations in episodic, declarative memory.

Several additional papers in this issue discuss functions that are not strictly perceptual. Memory is traditionally divided into semantic (general) memory and episodic (personal, contextual) memory. Louis Renault and colleagues make a functional distinction of ‘personal semantics’, that is, autobiographical facts. Using late ERP components, which played a central role in Shlomo's early studies of language and memory (N400 and LPP), they show a distinction between such autobiographical memories and both general semantic and unique episodic events. Piazza and Eger review the functional specificity of number representation, making the distinction between the perception of cardinality, or numerosity, and the more abstract manipulation of numbers as in math. Finally, within the domain of language, Xiao, Friederichi, and colleagues use fMRI to show that understanding complex syntax depends on a left hemisphere fronto-temporal network, which develops in early (pre-school) childhood.

We believe Shlomo would have been happy to see this collection of articles about functional selectivity in perceptual and cognitive systems; a topic that was at the center of his work to his last day. He would have been happy because as much as Shlomo was utterly devoted to the work of science, he was also devoted to the scientific conversation as a human endeavor. Whether it involved his scrupulous editorial work as editor-in-chief of *Neuropsychologia* from 2005 to 2007 (he read word-for-word every version of every article he edited and provided editorial guidance), his numerous collaborations across the globe (USA, Canada, China, France, Germany to name a few), or heartfelt scientific skirmishes, he believed that opinions should be fearlessly expressed and discussed. All of us who knew Shlomo know that he did not shy away from debates. He was willing to fight for a cause whether as a field-commander leading his troops in real battlefields, as an activist fighting for peace between Israelis and Palestinians, or fighting over theories in science. This was not because he liked to argue, but rather because he deeply and emotionally cared about science and about people (as well as the academic world, politics, good food, good wine, and art). Most importantly, he believed in the power of open discussions. He is deeply missed.

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