Neuronal and behavioral mechanisms of Gestalt perception

Dissertation

zur Erlangung des Grades eines
Doktors der Naturwissenschaften

der Mathematisch-Naturwissenschaftlichen Fakultät
und
der Medizinischen Fakultät
der Eberhard-Karls-Universität Tübingen

vorgelegt
von

Johannes Rennig
aus Augsburg, Deutschland

September – 2014

Tag der mündlichen Prüfung: 11.12.2014

Dekan der Math.-Nat. Fakultät: Prof. Dr. W. Rosenstiel
Dekan der Medizinischen Fakultät: Prof. Dr. I. B. Autenrieth

1. Berichterstatter: Prof. Dr. / PD Dr. / Dr. Hans-Otto Karnath
2. Berichterstatter: Prof. Dr. / PD Dr. / Dr. Uwe Ilg

Prüfungskommission: Prof. Dr. / PD Dr. / Dr. Hans-Otto Karnath
Prof. Dr. / PD Dr. / Dr. Uwe Ilg
Prof. Dr. / PD Dr. / Dr. Hans-Christoph Nürk
Prof. Dr. / PD Dr. / Dr. Marc Himmelbach

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Acknowledgements

At first, I want to thank my thesis supervisor, Hans-Otto Karnath, who guided me throughout this work. With patience and confidence, he gave me the opportunity and freedom to grow professionally to the level where I am now. I also want to thank Marc Himmelbach for his support as a (co-)supervisor in two of my projects. With his professional attitude and practical guidance, he influenced my development as a scientist significantly. Furthermore, I am very thankful to Elisabeth Huberle and Bianca deHaan for bringing me into the Division of Neuropsychology and giving me the opportunity for my first scientific steps. Further, I am grateful to Merim Bilalić for an excellent cooperation and fruitful exchanges.

A big thank s goes out to my (former) lab colleagues: Ida Zündorf, for endless but never boring fMRI sessions, Walter Linzenbold and Jason Martin, for valuable help about neuroimaging, coffee breaks and sauna sessions, and Urszula Mihulowicz, for good and cordial conversations about science and beyond.

I am also very thankful to the members of my thesis committee, Uwe Ilg and Hans-Christoph Nürk. I thank you for your expertise feedback about my work, interesting discussions and valuable information. I further want to thank Tina Lampe and the whole staff of the Graduate Training Center Tübingen for financial and general support.

Of course, I want to thank my parents, Elisabeth and Frank, for their unconditional support throughout everything I did and do. Last but not least, I want to thank Silvana – you know how important you are.

Abstract

Principles of Gestalt perception have fundamentally influenced our understanding of visual cognition. In the past century, Gestalt psychologists postulated that the human brain determines single elements with common features as a single entity rather than a sum of separate parts. The importance of Gestalt perception is emphasized by the neuropsychological syndrome simultanagnosia. Patients suffering from this condition have lost the ability to integrate single elements into a superior entity. Simultanagnosia is usually associated with bilateral posterior temporo-parietal brain lesions but the exact neuroanatomy of global Gestalt perception and functions of areas already associated with this perceptual quality are still a matter of lively debates. Further, not much is known about behavioral characteristics of well-explored perceptual processes, like visual constancy, in the context of Gestalt perception.

The present work aimed at investigating neuronal and behavioral properties of Gestalt perception applying psychophysical methods and functional magnetic resonance imaging (fMRI). In previous neuroimaging studies the temporo-parietal junction (TPJ) was identified as a crucial brain structure involved in Gestalt perception. However, its specific role in Gestalt perception is still unclear. The functions attributed to this brain region range from attentional selection between the local and the global level of hierarchically organized stimuli to mere perceptual mechanisms of global processing. The neuroimaging studies included into this work explore mainly TPJ related perceptual functions.

In the first study, neuronal properties of TPJ in Gestalt perception were investigated. Based on observations in simultanagnosia patients that are able to perceive familiar complex stimulus arrangements but fail in recognition of novel stimulus configurations, it was hypothesized that TPJ areas mainly contribute to processing of novel object arrangements. A training study was conducted where subjects had to learn the perception of complex stimulus arrangements in order to examine this hypothesis. Neuronal processes of Gestalt perception in bilateral TPJ regions were assessed pre- and post-

training. It was demonstrated that an anterior right hemispheric TPJ region responded to perceptual training with global stimuli. The results indicated fundamentally changed TPJ contributions with increasing familiarity suggesting a different strategy of the brain for processing of highly familiar object arrangements.

In the second study, involvements of bilateral TPJ areas in global processing were investigated with an approach taking advantage of visual expertise. During presentation of specific chess arrangements TPJ signals of chess experts and novices were examined. As a consequence, it was possible to compare neuronal TPJ correlates for holistic perception in experts and serial perceptual strategies in novices. The result showed higher signals in bilateral TPJ areas for chess experts compared to novices while inspecting specific chess configurations. With this method a lot of the typical stimulus confounds in research about Gestalt perception, like size differences or differences in spatial frequencies between global/local stimulus levels, were avoided. Moreover, the nature of the stimuli and experimental tasks argues for a TPJ involvement during perception rather than for functions of attentional selection.

In the third study perceptual properties of visual size constancy were investigated in the context of Gestalt perception. While size constancy is a well-known phenomenon for regular objects this visual mechanism has not been investigated for stimuli forming a global Gestalt. Therefore, the perceptual performance for a global stimulus arrangement placed on different locations of a visual scene containing a 3D perspective was tested. For the first time, influences of size constancy were demonstrated also for global stimuli. Effects of size constancy on Gestalt perception suggest a perceptual hierarchy of global scenes even on stimuli that have to be integrated themselves.

Taken together the results show that the TPJ is involved in mere perceptual processes of Gestalt perception and that an anterior section of this structure has a specific role in processing of novel object arrangements. It was also demonstrated that Gestalt perception itself underlies visual top-down processes of visual constancy suggesting a superior role of global scene processing influencing even local grouping processes.

Contents

1 Introduction

1.1 Gestalt perception – global processing

1.1.1 Principles of global processing and Gestalt psychology

“I stand here at the window and see a house, trees, the sky. Theoretically I may try counting and say: there are 327 levels of brightness and color. Do I have “327”? No. Sky, house, trees; and the ‘327’ are impossible.”

Max Wertheimer, translated from ‚Untersuchungen zur Lehre von der Gestalt II‘, 1923.

Until the beginning of the 20th century research about human perception was dominated by an approach in psychology called structuralism. The basic principle of structuralism was that every percept is created from a linear combination of single sensations. This view was challenged by Gestalt psychology, which was initiated by the German psychologist Max Wertheimer with the beginning of the 20th century. In 1911, Max Wertheimer made an observation that can be considered as the beginning of this new direction in perception research: watching two distinct lights that were arranged close to each other alternating on and off he perceived an illusory motion that was not explainable by the simple combination of independent sensations. Perceiving this ‘apparent motion’ Wertheimer realized that perception is more than just a linear analysis of physical inputs. Together with his colleagues Kurt Koffka and Wolfgang Köhler he set up a psychological laboratory and developed the Gestalt laws of perceptual organization. These principles of visual perception are a series of rules that describe how the human mind integrates single elements into superior structures. The Gestalt laws, for example, state that every stimulus pattern is perceived in such way that the resulting structure is as simple as possible (law of "Prägnanz"/simplicity) or that similar elements (law of similarity, see Figure 1a) and those in close vicinity to each other (law of proximity, see Figure 1b) are grouped together. Another important Gestalt law is the law of good continuation stating that points, when connected, result in straight or smoothly curved lines are seen as belonging together (see Figure 1c, d). According to the law of good continuation, the first structure in Figure 1c is assumed being derived from the second illustration and not from the three other possible, but unlikely solutions. The general principle of this law is depicted in Figure 1d, where single elements are automatically connected to form a superior entity or so called 'Gestalt' (Goldstein, 2007; Koffka, 1935; Wertheimer, 1923).

Besides the descriptions of Max Wertheimer about the apparent movement perception and the Gestalt laws there are a lot of examples of (stable) visual stimuli providing evidence for the exceptional capacities of human visual perception. Typical perceptual phenomena that are explainable with mechanisms of Gestalt perception are illusory contours (e.g. in the Kanizsa triangle; Kanizsa, 1955), bistable images (like the illusory Necker cube; Kornmeier and Bach, 2005) or various other complex element configurations forming a global percept (see Figure 2). The essence of Gestalt perception is that the human mind is able to create sensations beyond the basic physical input. Especially the Gestalt based visual imagery leading to percepts with certain meaning, e.g. the perception of faces from randomly arranged elements, like trees or leafs, has been exploited by artists – even without any explicit knowledge about mechanisms of higher human vision.

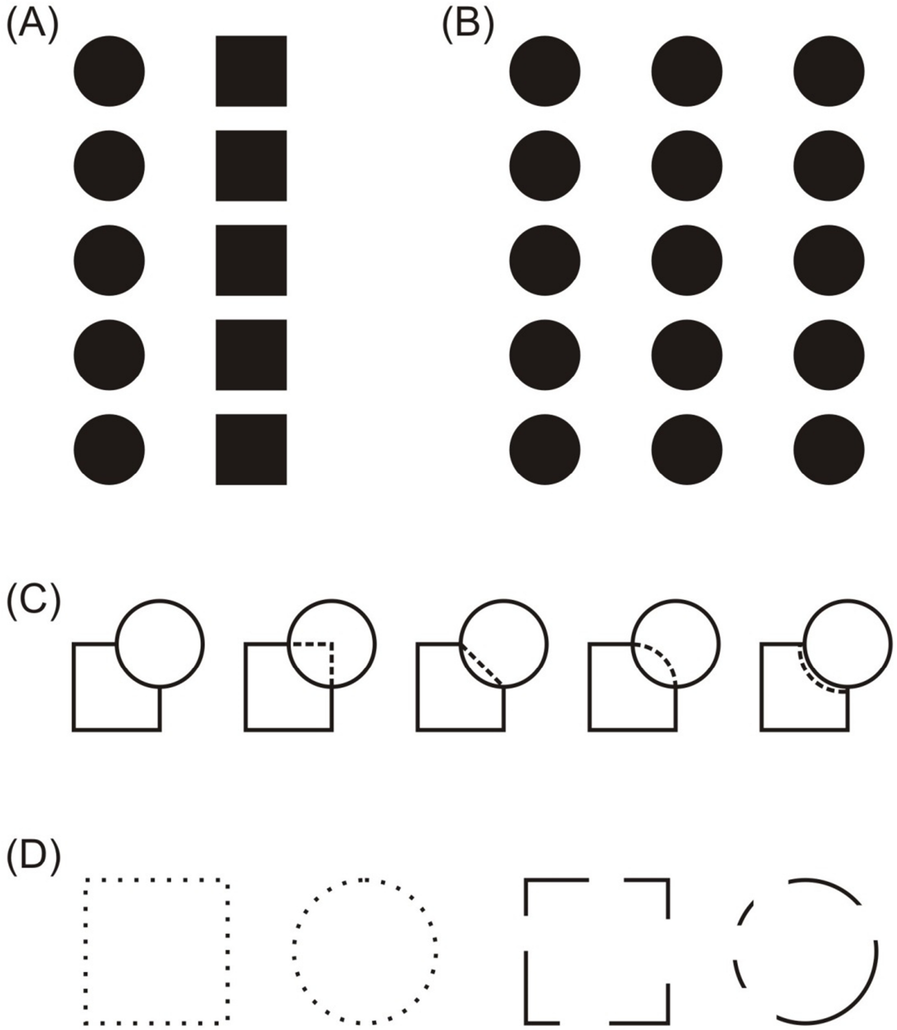

Figure 1

(A) Law of similarity, (B) Law of proximity, (C) + (D) Law of good continuation

From a psychological perspective the ability of the human mind to perceive a Gestalt – or to preattentively organize independent visual inputs into wholes – has the function of a perceptual heuristic (Goldstein, 2007). A heuristic can be defined as a cognitive rule of thumb that, in most cases, brings up a successful outcome based on relatively little effort. In the case of Gestalt perception a preattentive visual organization of the environment is a useful cognitive skill but can also bring up errors in the sense of illusionary percepts, like faces in trees or shapes of animals built from shades on the wall. To summarize these descriptions, the essence of Gestalt psychology is that *the* *whole is more than the sum of its parts* and the human mind has extraordinary perceptual abilities to automatically organize the visual world (Goldstein, 2007).

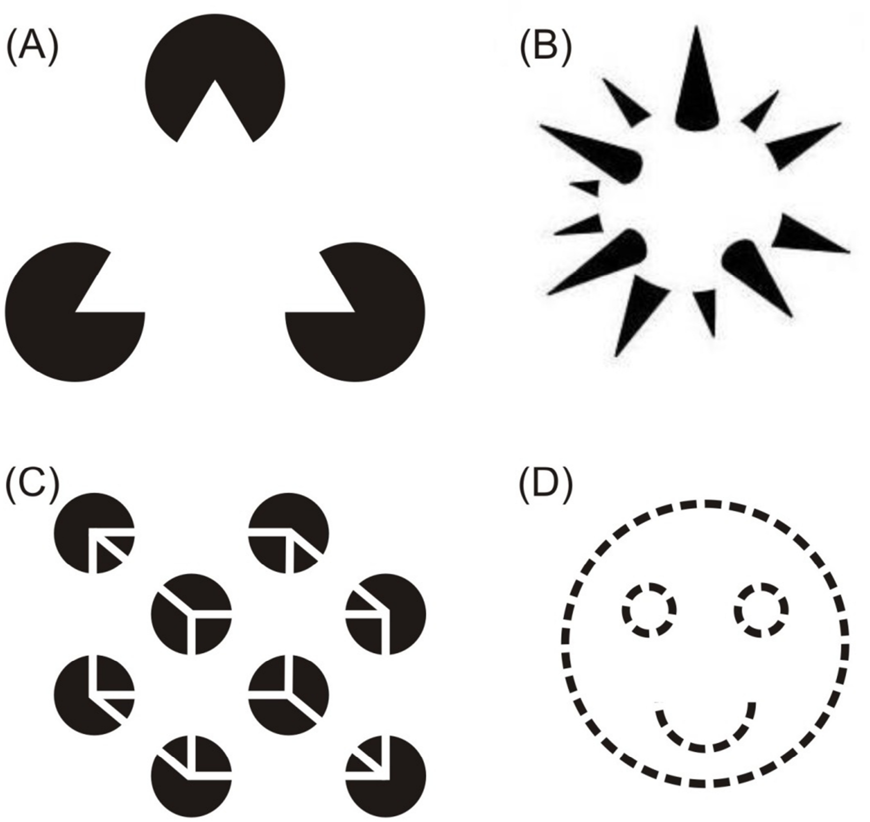

Figure 2

(A) Kanizsa Triangle, (B) Illusory ball with spikes, (C) Illusory Necker cube, (D) Illusory smiley

The first controlled empirical experiments about characteristics of Gestalt perception were conducted by David Navon (Navon, 1977, 1981; Navon and Norman, 1983). The stimulus Navon created for his research was a hierarchically organized letter where several local letters form a global structure depict a superordinate letter (see Figure 3; Navon, 1977). This so called 'Navon letter' was used to demonstrate the global precedence effect which states that global information of a visual scene precedes the analysis of local features. For incongruent stimuli (those with different global/local features), Navon showed that local elements did not interfere with the processing of global content while a significant influence was observable vice versa (Navon, 1977). Participants showed longer reaction times and higher error rates for incongruent letters when they had to report the local elements compared to the response behavior in congruent stimuli. No influence of congruency was observable for the global aspect of the stimuli. He further demonstrated shorter reaction times for global compared to local elements (Navon, 1981) and size invariance of the global precedence effect (Navon and Norman, 1983).

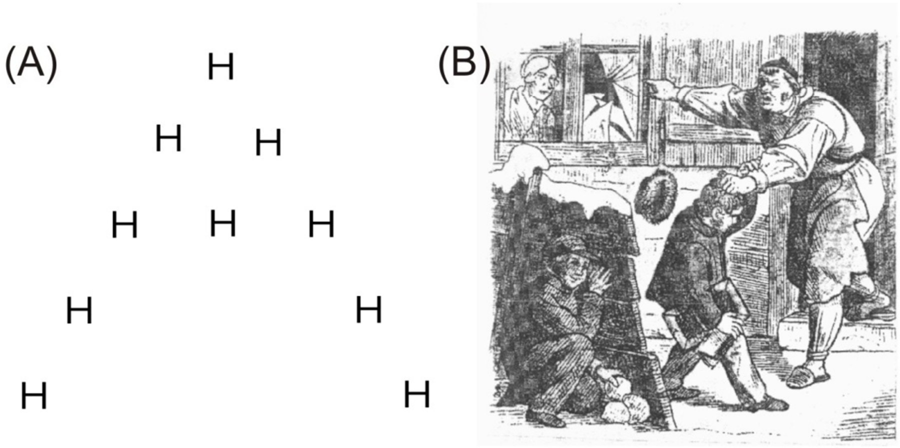

Figure 3

(A) Navon Letter (B) Broken Window Picture

1.1.2 Simultanagnosia

The importance of Gestalt perception in everyday life gets emphasized by the neuropsychological disorder simultanagnosia (Bálint, 1909; Wolpert, 1924). This condition is part of the Balint syndrome (Bálint, 1909) and often described as the inability to perceive multiple objects at the same time. However, the crucial impairment in simultanagnosia is the deficit in perceiving the superior meaning in a configuration of single elements. While simultanagnosia patients can easily report the local elements of a hierarchical stimulus, like the Navon letter (see Figure 3; Navon, 1977), they cannot perceive the superior letter, its global Gestalt. This effect is not only present for artificial stimuli but also in pictures of visual scenes: patients with simultanagnosia report single objects of, for example, a kitchen and conclude from this information that they see a kitchen, but are unable to capture the visual input as a whole. A typical tool used to diagnose simultanagnosia is the so called Broken Window picture from the Stanford-Binet Intelligence Scales (see Figure 3; Roid, 2003): in this picture patients usually report single objects ("a boy", "broken window", "a man", etc.) or locally restricted scenes ("boy is hiding", "man grabbing a boy"), but are not able to visually grasp the overall gist of the picture. In real life, patients suffering from simultanagnosia report severe impairments in a lot of activities of daily living like spatial orienting or reading.

There have been a lot of attempts trying to disentangle this complex syndrome. The most common explanation for the typical symptoms of simultanagnosia is based on deficits in spatial attention. It was demonstrated that patients suffering from simultanagnosia seem to have a narrowed field of attention responsible for local capture (Dalrymple et al., 2010a, 2011; Luria, 1959) or have severe deficits in generally shifting their attention from one location in space to another (Farah, 1990). Recent results indicated a diffusely distributed allocation of attention around the visual focus (Balslev et al., 2014). Further, a generally reduced visual processing speed inhibiting the formation of a global percept has been discussed (Duncan et al., 2003; Worthington and Young, 1996). A theoretical explanation for perceptual deficits in simultanagnosia can be derived from the Feature Integration Theory by Anne Treisman (Treisman and Gelade, 1980; Treisman, 1998). This approach suggests that attentional mechanisms responsible for perceptual binding of object features like shape, color or texture, are impaired in patients with simultanagnosia. In Treismans experiments (Treisman, 1998) deficits in visual binding were associated with erroneously combined object features of different visual targets. In conclusion, also object arrangements forming a superior Gestalt are not perceivable due to impaired attentional mechanisms of visual binding. Another cognitive ability that was connected to simultanagnosia is visual working memory (Berryhill and Olson, 2008a, 2008b; Coslett and Saffran, 1991). It was assumed that due to reduced capacities in visual working memory in simultanagnosia local elements vanish from conscious processing preventing the generation of a global percept. This view, however, is challenged by studies showing a perceptual advantage in simultanagnosia with an increasing number of local elements (Huberle and Karnath, 2010, 2006). These studies demonstrated that close element spacing increasing their overall number and, in conclusion, demanding more working memory capacities supported global processing in simultanagnosia.

After one decade of research an overall convincing explanation for the typical symptoms in simultanagnosia has not been found. Several other aspects of visual processing like primarily sensory qualities, e.g. the processing of spatial frequencies, or mechanisms of object processing, like figure ground segmentation or object invariance, have not been investigated in the context of simultanagnosia. Considering the typical deficits, the knowledge about mainly attentional impairments and perspectives regarding unresolved questions, simultanagnosia seems to emerge from a complex interaction of impaired attentional and sensory mechanisms as well as dysfunctional processes of object recognition. In conclusion, the same complex interaction can be claimed for mechanisms of Gestalt perception in the healthy brain.

1.1.3 Principles of object perception

Before introducing the neuronal foundations of Gestalt perception principles and neuronal correlates of object perception will be discussed. There are remarkable neuronal and theoretical differences, similarities and interactions that need to be emphasized to understand particular characteristics of these two perceptual qualities.

In contrast to Gestalt perception, object recognition is mainly characterized through mechanisms of edge detection, shape encoding or texture segmentation (Bergen and Adelson, 1988; Malik and Perona, 1990). These processing steps are meant to precede global perception to analyze a global form and detect its local elements. On the other hand, Gestalt perception is often designated as an essential element of holistic object recognition (Goldstein, 2007). This includes for example mechanisms of figure-ground-segmentation, i.e. grouping of similar elements together to define a figure from its background, or edge detection where occluded/separated contours have to be completed perceptually (Field et al., 1993; Hess et al., 2003; Hess and Field, 1999). In accordance with current definitions of visual object and Gestalt perception these two perceptual qualities differ mainly in conditions where object perception is not impaired, i.e. a visual object display is directly accessible. In general, the borders between object and Gestalt perception are fluent and complementary, why both perceptual qualities can hardly be distinguished on a merely theoretical level. Adding clinical and neuroanatomical perspectives to this question a distinction between object and Gestalt perception becomes more clearly defined. Simultanagnosia (see above) is defined by the inability to see two objects at the same time or to perceive meaningful arrangements of elements, while single objects can be identified. Visual or object agnosia is primarily defined by the inability to identify shapes that do not require mechanisms of visual integration or Gestalt perception (Goodale and Milner, 1992; Goodale et al., 1994). Further, both perceptual qualities and their corresponding impairments have characteristic neuronal correlates enabling a distinction on a neuroanatomical basis. The neuronal basis of object perception will be briefly discussed in a following paragraph, neuronal correlates of Gestalt perception that are a key aspect of the present work will be outlined in more detail.

1.1.4 Visual constancy

There are several perceptual principles describing top-down mechanisms in object recognition. One of the most important ones is the phenomenon of visual constancy. The mechanism of visual constancy is responsible for the perception of familiar objects at a standardized shape, size, or color and is also critical for the invariant identification of objects regardless of changes in perspective, distance, lighting or the size of the retinal image (Brunswik, 1934; Emmert, 1881; Fitzpatrick et al., 1982; Foster, 2011; Hebb, 1958; Leibowitz and Dato, 1966).

The present section will specifically consider size constancy, a visual mechanism responsible for invariant size perception (Emmert, 1881; Fitzpatrick et al., 1982). In general, size constancy is highly dependent on the visual context an object is placed in and cannot be triggered without applying a visual perspective. Within a visual scene objects of the same size will look bigger placed in the back of the scene than objects of the same physical size localized in the front. On the other hand, mechanisms of visual constancy enable perception of smaller objects placed in the back of a visual scene in an invariant size to physically bigger objects in the front. Also several well-known perceptual illusions, like the Ponzo or the Müller-Lyer illusion (Müller-Lyer, 1889; Ponzo, 1911), can be explained by mechanisms of size constancy (see Figure 4). These perceptual illusions occur when visual elements (e.g. vertical lines) are placed in a characteristic fashion within a visual environment containing a 3D perspective. Although size constancy is a well-known phenomenon for regular objects (Emmert, 1881; Fitzpatrick et al., 1982), few studies investigated interactions of size constancy and Gestalt perception. A study by Moore and Egeth (1997) revealed pre-attentional influences of visual constancy for grouping mechanisms. The length estimation of solid lines presented within a dot array was affected by the configuration of the dots in the background. When these dots formed a Ponzo or Müller-Lyer illusion, the length estimation changed depending on the arrangement of the surrounding dots. A study with simultanagnosia patients indicated a key role of the visual angle together with the retinal image for global object recognition (Huberle et al., 2010). Various Navon letters in different global sizes and viewing distances were presented. It was demonstrated that rather the retinal image than the physical size of an object has a major impact on global perception. These results showed that complex interactions of retinal influences and size constancy influence global Gestalt perception. Until now, there is no study investigating direct influences of visual constancy on hierarchically organized visual stimuli requiring visual top-down processes in the sense of Gestalt perception.

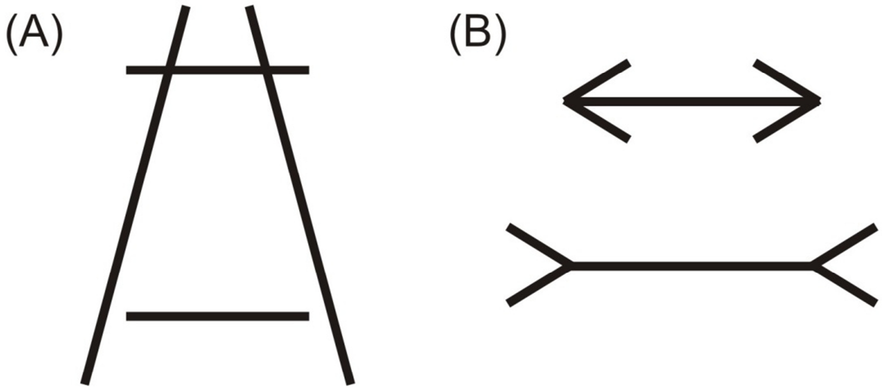

Figure 4
(A) Ponzo illusion, (B) Müller-Lyer illusion

1.2 Neuroanatomy of Gestalt perception

1.2.1 Neuroanatomy of object perception

A few decades ago Ungerleider and Mishkin (1982) proposed their model of a ventral occipito-temporal visual stream associated with object recognition and a dorsal occipito-parietal system responsible for object localization. Milner and Goodale (Goodale and Milner, 1992; Goodale et al., 1994) modified this model suggesting a connection of the ventral pathway to object recognition and an association of the dorsal stream with action related processing. From early visual areas of V1 to V3 analyzing basic components of visual input like line orientation or length (Dougherty et al., 2003; Hubel and Wiesel, 1965), object information propagates into the ventral visual stream, while action related information is analyzed in the dorsal stream (Goodale and Milner, 1992; Goodale et al., 1994). It is assumed that basic object information is processed in the lateral occipital complex (LOC), responsible for the encoding of shape and form (Grill-Spector et al., 1999; Grill-Spector, Kourtzi, & Kanwisher, 2001; Grill-Spector & Malach, 2004; Kourtzi & Kanwisher, 2001). Higher level processing of complex objects is meant to take place in more lateral and medial parts of the ventral stream. The (right) fusiform gyrus (fusiform face area, FFA) was associated with face recognition (Gauthier et al., 2000b; Kanwisher et al., 1997), a visual word form area was discovered within the left inferior temporal gyrus (Cohen et al., 2000), places and houses were connected to inferior/medial parts of the temporal gyrus, the so called parahippocampal place area (Epstein and Kanwisher, 1998). These findings led to the conclusion of a hierarchically organized axis for object perception starting in early visual areas encoding basic components to global representations in anterior areas of the ventral visual stream (Lerner et al., 2001). This traditional view is challenged by findings suggesting significant contributions of various top-down processes (Bar et al., 2006; Bar, 2003; Gilbert et al., 2001; Harel et al., 2010; Sigman et al., 2005) (see below) or mechanisms addressed to Gestalt perception (see above) in object recognition.

1.2.2 Aspects of top-down organization in object perception

The view of a top-down processing in object perception corresponding to mechanisms of Gestalt perception became the focus of increasing interest (Shulman et al., 1997; Sigman et al., 2005; Bar et al., 2006; Bar, 2003). This approach stands in contrast to the traditional view of a mainly bottom-up organization of visual perception with analysis of basic features in early visual areas being assembled to global representations in higher visual regions along the ventral pathway (Lerner et al., 2001) (see above). There are several theories addressing functions of attention and memory as crucial top-down mechanisms of holistic visual perception (Bullier and Nowak, 1995; Desimone, 1998; Kosslyn et al., 1993; Ullman, 1995). An early model by Ullman (1995) proposes a bidirectional process searching for correspondence between an input pattern and a stored representation. This model combines bottom-up and top-down processes of visual perception explaining automatic holistic processing of objects without mere serial assembling of global representations from local features. A distinct model of top-down object recognition including predictions about the perceptual course and neuroanatomy of object processing was proposed by Bar (Bar et al., 2006; Bar, 2003). This model postulates that a rough sketch of an object based on its low spatial frequency information is rapidly projected to the prefrontal cortex (PFC). This anatomical shortcut is realized through fast magnocellular processing along the dorsal stream (Maunsell et al., 1990; Shapley, 1990). The low-spatial frequency information activates possible interpretations about the visual input while high-spatial frequency components containing local details get analyzed along the ventral visual stream. These top-down heuristics get then back-projected to the ventral stream and together with the bottom-up analysis are integrated to a comprehensive object representation (Bar et al., 2006; Bar, 2003).

This model is compatible with established knowledge about mechanisms of global processing. According to the global precedence effect (Navon, 1977, 1981), global information gets extracted faster and is processed superior to local information. Moreover, the global content of any meaningful visual structure is generally coded in low spatial frequency bands while local details are represented in high spatial frequencies (Boeschoten et al., 2005; Hughes et al., 1990, 1996; Shulman et al., 1986; Shulman and Wilson, 1987). Bar's model of object recognition (Bar et al., 2006; Bar, 2003) gives further evidence about how global processing might work in the human brain. Interestingly, the neuroanatomy of Gestalt perception that will be discussed in detail in the next section suggests a dominant involvement of posterior temporo-parietal regions in Gestalt perception (see below).

1.2.3 Neuronal basis and functions of Gestalt perception

Regarding the neuronal basis of global processing and simultanagnosia a lot of diverse results have been reported. According to the mechanisms underlying bottom-up processes in object recognition with hierarchical assembling of elements to global structures (see above), similar procedures were assumed for Gestalt perception. Early neuroimaging studies investigating mechanisms of visual grouping proposed a hierarchical axis from local to global processing along the ventral visual stream (Lerner et al., 2001; Malach et al., 1995). This assumption was based on the knowledge about functions of the early visual areas coding basic visual features like line orientation, length or location (Dougherty et al., 2003; Hubel and Wiesel, 1965) and the propagation of object information through the LOC (Grill-Spector et al., 1999; Grill-Spector, Kourtzi, & Kanwisher, 2001; Grill-Spector & Malach, 2004; Kourtzi & Kanwisher, 2001) into the ventral visual pathway (Goodale and Milner, 1992; Goodale et al., 1994). Work of Fink and colleagues (Fink et al., 1997a, 1996, 1997b) supported this explanation also for the assembling of global percepts from local elements applying positron emission tomography (PET) or regional cerebral blood flow (rCBF) functional imaging. Although no directionality was investigated across these studies it was demonstrated that global information was processed in anterior regions of the ventral stream while local processing took place in more posterior ventral areas.

This directional view has been challenged by functional magnetic resonance imaging (fMRI) studies investigating the assembling of global forms in early and higher visual areas along the ventral visual pathway (Altmann et al., 2003; Kourtzi et al., 2003). Here, it was demonstrated that early visual areas showed neuronal signals comparable with those from higher object-sensitive areas (bilateral LOCs) while processing meaningful or random arrays built from local elements. It was concluded that within a recurrent process of connecting local elements with the same colinearity and feedback from higher object sensitive regions, also early visual areas contribute directly to the formation of a global percept. These studies were restricted to processing along the ventral visual pathway but demonstrate top-down processing during global perception for early visual processes. Moreover, there are several neuroimaging studies that localized functions of global processing in areas along the ventral visual pathway (Ferber et al., 2003; Han et al., 2002; Heinze et al., 1998; Ostwald et al., 2008). Further evidence for a ventral involvement in Gestalt perception comes from monkey studies suggesting local and global processing along the ventral stream (Sripati and Olson, 2009; Tanaka and Fujita, 2000; Tanaka et al., 2001). These studies showed that several neuron populations in the infero-temporal (IT) cortex responded selectively to global or local features of hierarchical visual stimuli. Differences were detected for neuronal localization (Tanaka et al., 2001) and timing (Sripati and Olson, 2009) of global and local processing.

The association of mechanisms of Gestalt formation with regions along the ventral visual stream stands in contrast to evidence from a wide range of neuroimaging and patient studies. Investigations with simultanagnosia patients showed that mainly bilateral (Clavagnier et al., 2006; Dalrymple et al., 2009; Friedman-Hill et al., 1995; Himmelbach et al., 2009; Huberle et al., 2010; Karnath et al., 2000; Robertson and Treisman, 1995) or only right hemispheric (Delis et al., 1986; Robertson and Lamb, 1991; Robertson et al., 1988) posterior temporo-parietal brain areas are involved in processing of global shapes. In a group study investigating lesion patterns of 7 simultanagnosia patients, lesions to bilateral subcortical fibre tracts were associated with deficits in global processing (Chechlacz et al., 2012). At this point it should be noted that there is no comprehensive lesion study investigating the neuronal underpinnings of simultanagnosia in a homogeneous patient sample allowing valid conclusions about the precise neuroanatomy of this deficit. An fMRI study with a simultanagnosia patient also revealed bilateral temporo-parietal brain regions as neuronal correlates of Gestalt perception (Himmelbach et al., 2009).

Functional neuroimaging studies with healthy human subjects identified a various number of posterior temporo-parietal brain regions as crucial loci of global processing. In a study measuring event-related brain potentials (ERPs) right-hemispheric temporo-parietal brain areas were associated with the perception of global aspects of Navon letters (Proverbio et al., 1998; Yamaguchi et al., 2000). In fMRI studies, bilateral (Huberle and Karnath, 2012) and right hemispheric (Weissman and Woldorff, 2005) posterior temporo-parietal junction (TPJ) regions and right-hemispheric IPS (intraparietal sulcus) areas (Zaretskaya et al., 2013) were identified as crucial region of Gestalt perception applying various kinds of global/local stimuli. Using neuromodulatory methods like TMS (transcranial magnetic stimulation) or tDCS (transcranial direct current stimulation) a stimulation of temporo-parietal brain areas was able to influence aspects of global perception (Bardi et al., 2013; Mevorach et al., 2005; Ritzinger et al., 2012; Romei et al., 2011, 2012; Zaretskaya et al., 2013).

In several studies applying various methods, a right hemispheric dominance for global perception has been found while the left hemisphere was associated with local processing. Behavioral studies showed that global stimuli presented in the left hemifield were identified faster and more precisely than in the right hemifield. For local elements an opposite pattern was found (Hübner, 1997, 1998; Kimchi and Merhav, 1991; Martin, 1979; Robertson et al., 1993; Van Kleeck, 1989; Yovel et al., 2001). In several neuroimaging studies this double dissociation between global/local and right/left hemispheric dominance was reported (Fink et al., 1997a, 1996, 1999; Han et al., 2002; Martens and Hübner, 2013; Proverbio et al., 1998; Yamaguchi et al., 2000). Other studies associated mainly right hemispheric brain signals with global processing without explicitly testing for local perception or hemispheric differences (Ferber et al., 2003; Zaretskaya et al., 2013). Further, there are patient reports describing symptoms of simultanagnosia after right but not left hemispheric brain lesions (Delis et al., 1986; Robertson and Lamb, 1991; Robertson et al., 1988). Additionally neuromodulatory studies applying TMS or tDCS found mainly effects on global processing after/during stimulation of right hemispheric brain regions (Bardi et al., 2013; Romei et al., 2011; Zaretskaya et al., 2013). The view about a global/local double dissociation being processed in the right/left hemisphere is challenged by a large quantity of reports from simultanagnosia patients that mainly demonstrated bilateral temporo-parietal lesion patterns (Balslev et al., 2014; Clavagnier et al., 2006; Dalrymple et al., 2010a, 2007; Huberle et al., 2010; Huberle and Karnath, 2006, 2010; Shalev et al., 2004; Thomas et al., 2012; Valenza et al., 2004). These bilateral lesion patterns in temporo-parietal brain areas seem to be the crucial reason for the emergence of simultanagnosia and, in conclusion, also in the healthy brain responsible for mechanisms of Gestalt perception. In addition, there are behavioral studies that did not find differences in global/local processing in the right/left hemifield (Blanca and Alarcón, 2002; Boles and Karner, 1996; Boles, 1984) and neuroimaging studies demonstrating bilateral temporo-parietal activation during global processing (Himmelbach et al., 2009; Huberle and Karnath, 2012) or stimulus depending effects for hemispheric dominance in local/global processing (Fink et al., 1997b). In general, these results can be summarized as a relative right hemispheric dominance for the assembling of local elements to a global Gestalt, but argue against a double dissociation in global/local processing in the right/left hemisphere. An additional theoretical argument for the latter view is the absence of the hypothetical deficit "*local*agnosia" after left hemispheric brain lesions.

In the referred studies investigating mechanisms of global processing a lot of different brain regions have been reported as crucial modules of Gestalt perception. The areas reported range mainly from object sensitive areas along the ventral visual stream (Altmann et al., 2003; Ferber et al., 2003; Fink et al., 1996, 1997b; Kourtzi et al., 2003) to posterior temporo-parietal areas usually associated with mechanisms of visual attention (Chechlacz et al., 2012; Clavagnier et al., 2006; Dalrymple et al., 2007; Friedman-Hill et al., 1995; Himmelbach et al., 2009; Huberle et al., 2010; Huberle and Karnath, 2006, 2010; Karnath et al., 2000; Thomas et al., 2012; Valenza et al., 2004; Weissman and Woldorff, 2005; Yamaguchi et al., 2000; Zaretskaya et al., 2013). This wide distribution of areas associated with Gestalt perception suggests a complex interaction of mechanisms of object perception, active and automatic attentional processes and primary sensory factors. Especially results gained from neuroimaging studies with healthy subjects applying various visual stimulations for global perception showed that there are several brain areas (ventral pathway, temporo-parietal/parietal regions) responding to global aspects of the respective stimuli. Yet, there are no studies investigating these complex interactions sufficiently. Although Gestalt perception is obviously part of the object recognition system direct interactions between these two perceptual qualities have not been investigated. There are few studies investigating object processing in simultanagnosia whereas no specific object recognition functions, like visual constancy or view point invariance, or anatomical connections were tested explicitly (Cooper and Humphreys, 2000; Demeyere et al., 2008). However, the influence of primary sensory processes on Gestalt perception has already been examined extensively. Several behavioral and neuroimaging studies already demonstrated influences of spatial frequency processing on global and local perception (Badcock et al., 1990; Fink et al., 1999; Han et al., 2002, 2003; Hübner, 1997; Lamb and Yund, 1996, 1993; Hughes et al., 1990, 1996; Shulman et al., 1986; Shulman and Wilson, 1987).

1.3 The temporo-parietal junction (TPJ)

1.3.1 Neuronal functions of the TPJ

The TPJ is a brain area located in the region between the temporal and parietal lobes, right at the posterior end of the sylvian fissure. Basically, it consists of the inferior parietal lobule, the supramarginal gyrus, the angular gyrus and the posterior parts of the superior temporal gyrus and is bounded on the posterior end by the occipital lobe. It is surrounded by important brain structures (temporal, parietal and occipital lobes) with a variety of cognitive functions. Therefore, TPJ itself has also been addressed with a wide range of features of human cognition.

On the right hemisphere the TPJ has mainly been associated with functions of visual attention. It has been shown that damage to the right hemispheric TPJ (rTPJ) is responsible for the emergence of ego- and allocentric neglect (Mort et al., 2003; Karnath and Rorden, 2012; Chechlacz et al., 2010, 2013) and, consequently, is a crucial region for the representation of space. In addition, lesions to the rTPJ were identified as the neuronal correlate for visual (and tactile) extinction (Chechlacz et al., 2013; de Haan et al., 2012). Studies applying functional imaging demonstrated that several functions of visual attention like visual search or detection of targets are linked to the rTPJ (de Haan et al., 2012; Himmelbach et al., 2006). A recent study investigating TPJ involvement in the perception of gratings (Beauchamp et al., 2012) showed the crucial role of the TPJ in target detection. Applying electrical stimulation to TPJ areas enhanced detection rates for low-salience stimuli while perception in undisturbed viewing conditions was unaffected. On the left hemisphere, TPJ (lTPJ) comprises on its posterior section in close vicinity of the angular gyrus Wernicke’s area, a brain region known to be responsible for language production and comprehension or the storage of verbal meaning (Friederici, 2006; Weniger, 2006). Further, (bilateral) TPJ areas were associated with social behavior (Decety and Lamm, 2007; Santiesteban et al., 2012), the Theory of Mind and empathy (Abu-Akel and Shamay-Tsoory, 2011; Gallagher et al., 2000; Samson et al., 2004; Saxe and Kanwisher, 2003; Young et al., 2007), temporal order judgments (Davis et al., 2009) or memory functions (Buckner et al., 2008; Sehm et al., 2011). Besides the referred cognitive functions mainly addressing spatial perception the TPJ has been associated with processes of Gestalt perception (Himmelbach et al., 2009; Huberle and Karnath, 2012; Robertson et al., 1988; Robertson and Treisman, 1995).

Further, there is evidence for an anatomical and functional subdivision of the TPJ. Several studies showed an involvement of the (right hemispheric) anterior TPJ region, mainly comprising the supramarginal gyrus, in memory functions or target detection (Bzdok et al., 2013; Kubit and Jack, 2013). Beyond, several other functions attributed to the TPJ (like Theory of Mind, perception of social interactions, attentional functions) were localized in anterior and posterior sections of this brain structure (Bzdok et al., 2013; Jakobs et al., 2012; Krall et al., 2014; Kubit and Jack, 2013; Seghier, 2013). Within in this framework, it is not clear if posterior and anterior parts of area TPJ are differently involved in mechanisms of Gestalt perception.

1.3.2 The TPJ in Gestalt perception

In several studies investigating neuronal mechanisms of Gestalt perception with functional neuroimaging bilateral or right hemispheric TPJ areas have been identified as crucial correlates of functions of global/local processing (Fink et al., 1996, 1997a; Himmelbach et al., 2009; Huberle and Karnath, 2012; Weissman and Woldorff, 2005; Yamaguchi et al., 2000). In addition, several case reports are known where bilateral posterior lesions comprising TPJ areas caused symptoms of simultanagnosia (Clavagnier et al., 2006; Huberle and Karnath, 2010; Robertson et al., 1988; Robertson and Treisman, 1995; Thomas et al., 2012; Valenza et al., 2004). It should be mentioned that in these patient studies no specific TPJ functions were able to be addressed, while mere perceptual functions/deficits of global perception were explored. Consequently, in this section only functional neuroimaging studies will be discussed in detail.

In studies by Fink and colleagues (Fink et al., 1996, 1997a) bilateral TPJ areas were identified as crucial areas for attentional shifts between global and local aspects of Navon letters. It was shown that bilateral TPJ areas were active in the cueing phase before a global/local stimulus was presented. During the perception phase mainly ventral areas were identified as neuronal correlates of global/local processing. An ERP study by Yamaguchi and colleagues (2000) supported this view. Here, the right hemispheric TPJ showed significant activation during the cuing phase for global cues but not for local ones. A different function was addressed to the right hemispheric TPJ area by a study of Weissmann and Woldroff (2005): TPJ was identified as a region responsible for maintaining a global percept while attentional control about local or global perception in Navon letters was controlled by the intraparietal sulcus (IPS). Moreover, this specific function of the IPS is supported by other neuroimaging (Weissman et al., 2002) or TMS studies (Romei et al., 2011). The results about a crucial involvement of TPJ areas for mere perception of global structures by Weissmann and Woldroff (2005) are in line with further studies investigating neuronal mechanisms of global processing. Himmelbach and colleagues (2009) revealed posterior bilateral

TPJ regions as crucial structures of Gestalt perception. In a simultanagnosia patient they compared trails with successful identification of a global Navon letter with those trails where identification failed. This study represented a unique opportunity to compare neuronal conditions of global perception and those situations where global perception was (pathologically) prevented with exactly the same stimulus properties against each other. Another study investigated neuronal mechanism of Gestalt perception in healthy subjects and identified bilateral TPJ areas as neuronal correlates of global processing (Huberle and Karnath, 2012). Here, neuronal mechanisms of intact global perception were compared to perception of scrambled global geometrical forms where local elements were interchanged. The results revealed a significant involvement of bilateral TPJ areas in global Gestalt perception. In both studies (Himmelbach et al., 2009; Huberle and Karnath, 2012) no local perception was necessary as both tasks only required global perception. An attentional shift from local to global or vice versa was not performed by the subjects. This emphasizes an involvement of bilateral TPJ regions in mere perception of global structures than attentional shifts between perceptual levels.

Assuming TPJ involvement in perceptual processes, the specific contributions of (bilateral) TPJ areas to global Gestalt perception are fairly unknown. A possible function could be the processing of novel stimulus configurations. This assumption is derived from observations in simultanagnosia patients with lesions to bilateral temporo-parietal brain areas that are able to identify familiar complex objects but fail in the recognition of unfamiliar stimulus arrangements or alienated illustrations of regular objects (Dalrymple et al., 2010a, 2009; Pavese et al., 2002; Robertson et al., 1997). In conclusion, familiar objects and object arrangements are processed without significant TPJ contribution while TPJ regions are active whenever novel visual scenes or arrangements of distributed visual information is processed. However, explanations for these behavioral observations could be a shift of neuronal processing for extensively trained global stimuli from visual integration in TPJ areas to mechanisms of object processing in infero-temporal regions along the ventral visual pathway. This hypothesis is in line with a previous study investigating neuronal training effects for a visual search task. The results showed that perceptual training can decrease parietal and lateral occipital signals in favor of a signal increase in early visual areas (Sigman et al., 2005). This activation change was interpreted as a redistribution of the functionality of different cortical areas involved in object identification. Moreover, processing of novel global structures may be restricted to more anterior parts of the TPJ as it was already demonstrated that this region can be anatomically and functionally be separated in an anterior and a posterior section (Bzdok et al., 2013; Jakobs et al., 2012; Krall et al., 2014; Kubit and Jack, 2013; Seghier, 2013).

2 Goals of this work

The present work aims at understanding neuronal and behavioral mechanisms of Gestalt perception. Applying functional imaging and behavioral methods the characteristics of global processing were investigated within three studies. In particular, two neuroimaging studies examined the role of bilateral TPJ areas in Gestalt perception. Perceptual influences of visual constancy on Gestalt perception, a perceptual quality known to be crucially involved in object processing, were investigated in a behavioral study.

In previous neuroimaging studies (Fink et al., 1996, 1997a; Himmelbach et al., 2009; Huberle and Karnath, 2012; Weissman and Woldorff, 2005; Yamaguchi et al., 2000) TPJ was identified as a region crucially involved in Gestalt perception. Some studies addressed attentional selection between global and local elements to the TPJ (Fink et al., 1996, 1997a; Yamaguchi et al., 2000), while others suggested TPJ involvement for mere perceptual mechanisms of Gestalt processing (Himmelbach et al., 2009; Huberle and Karnath, 2012; Weissman and Woldorff, 2005).

Assuming a perceptual involvement of TPJ in global processing, the first study aimed at investigating the specific role of TPJ within this perceptual process. Based on observations in simultanagnosia patients that are able to perceive familiar complex stimulus arrangements but fail in recognition of novel complex stimulus configurations, it was hypothesized that (bilateral) TPJ areas mainly contribute to processing of novel object arrangements.

In the second study, involvements of bilateral TPJ areas in global processing were investigated applying substantial different stimulus material. Here, neuronal TPJ signals of chess experts and novices while inspecting specific chess arrangements were examined. In this way it was possible to compare neuronal TPJ correlates for holistic perception in experts and serial perceptual strategies in novices. A lot of the typical methodological stimulus confounds in research about Gestalt perception like size differences or differences in spatial frequencies between global/local stimulus levels could be avoided with this approach.

In the third study, mechanisms of size constancy for global stimuli were investigated. While size constancy is a well-known phenomenon for regular objects (Emmert, 1881; Fitzpatrick et al., 1982) this visual mechanism has not been investigated for stimuli forming a global Gestalt. Placing a global stimulus arrangement in a visual scene containing a 3D perspective, also global stimuli should be influenced by size constancy. Effects of size constancy on Gestalt perception would also shed light on dominance or hierarchy of neuronal processes in visual perception.

3 Involvement of the temporo-parietal junction (TPJ) area in processing of novel global forms

Involvement of the temporo-parietal junction (TPJ) area in processing of novel global forms

Johannes Rennig[1], Marc Himmelbach[1], Elisabeth Huberle[1,3], Hans-Otto Karnath[1,2]

[1]Division of Neuropsychology, Center of Neurology, Hertie-Institute for Clinical Brain Research, University of Tübingen, Tübingen, Germany
[2]Department of Psychology, University of South Carolina, Columbia, USA
[3]Neurology and Neurorehabilitation Center, Luzerner Kantonsspital, Luzern, Switzerland

Corresponding author:
Johannes Rennig
Division of Neuropsychology
Center of Neurology
Hertie-Institute for Clinical Brain Research
University of Tübingen
D-72076 Tübingen
Phone: ++49 - 7071 - 29 80463
e-mail: johannes.rennig@uni-tuebingen.de

Author contributions

This chapter is an unpublished manuscript. Hans-Otto Karnath, Elisabeth Huberle, Marc Himmelbach and Johannes Rennig designed the experiments. Johannes Rennig acquired and analyzed all the data. Johannes Rennig wrote the paper with the help of Hans-Otto Karnath and Marc Himmelbach.

Abstract

The neuropsychological syndrome 'simultanagnosia' is characterized by the inability to integrate local elements into a global entity. This deficit in Gestalt perception is mainly apparent for *novel* global structures administered in clinical tests or when unfamiliar visual scenes have to be processed. Recognition of complex but familiar objects or well-known visual scenes is often unaffected. Recent neuroimaging studies and reports from simultanagnosia patients suggest a crucial involvement of temporo-parietal brain areas in processing of hierarchically organized visual material. In the present study we investigated the specific role of posterior temporo-parietal brain areas, namely the temporo-parietal junction (TPJ), in Gestalt perception. Based on perceptual characteristics known from simultanagnosia we hypothesized that TPJ is dominantly involved in processing of *novel* object arrangements.

To answer this question we performed a learning study with complex hierarchical stimuli and tested behavioral and neuronal characteristics of Gestalt perception pre- and post-training. The study included 16 psychophysical training sessions and two neuroimaging sessions (pre- and post-training). Subjects improved their behavioral performance for trained global stimuli and showed limited transfer to untrained global material. We found significant training dependent neuronal signal modulations in *anterior* right hemispheric TPJ regions derived from a previous neuroimaging study (Huberle and Karnath, 2012; Rennig et al., 2013a). These activation changes in *anterior* TPJ regions associated with Gestalt perception were specific to trained global stimuli while no systematic neuronal response changes were observed for recognition of untrained global stimuli, local elements and regular objects that served as control stimuli. In line with perceptual characteristics in simultanagnosia the results argue for an involvement of TPJ in processing of *novel* global structures. We discuss the training-induced signal modulations in the context of a more efficient or generally different strategy of the brain to process familiar global stimuli.

Introduction

A basic feature of visual perception and spatial orienting is the grouping of single elements into a superior global entity or so-called ‘Gestalt’ (Koffka, 1935; Wertheimer, 1923). The relevance of such visual top-down organization is emphasized through a neuropsychological deficit termed ‘simultanagnosia’ (Bálint, 1909; Wolpert, 1924), i.e. the inability to specifically recognize a global stimulus arrangement. Patients suffering from this impairment are able to perceive single objects while meaningful configurations of several elements or objects cannot be recognized. Evidence from lesion patterns in neurological patients with simultanagnosia as well as functional neuroimaging studies in healthy subjects suggest a crucial role of bilateral temporo-parietal junction (TPJ) areas in Gestalt perception (Clavagnier et al., 2006; Dalrymple et al., 2010; Friedman-Hill et al., 1995; Himmelbach et al., 2009; Huberle et al., 2010; Huberle and Karnath, 2006; Huberle and Karnath, 2012; Rennig et al., 2013; Weissman and Woldorff, 2005; Yamaguchi et al., 2000). These findings about neuronal correlates of visual Gestalt perception require an extension of our established knowledge about neuronal processing of visual information along the ventral visual stream (Goodale and Milner, 1992; Grill-Spector et al., 1999). Various studies have suggested a hierarchical axis of object processing along the ventral visual stream from local features encoded in early visual to global representations emerging in higher object sensitive areas (Lerner et al., 2001; Malach et al., 1995; Fink et al., 1997a; Altmann et al., 2003; Kourtzi et al., 2003). From this perspective it is striking that the hierarchical processing of complex arrangements and objects – the Gestalt of a rich visual scene – is not just another function of inferior temporal cortex but obviously driven by a distinct, much more dorsally located area, namely area TPJ.

While we know about its general involvement, the specific contribution of (bilateral) TPJ areas to global Gestalt perception is fairly unknown. A possible function could be the assembling of *novel* stimulus configurations. While familiar objects and object arrangements are processed without significant TPJ contribution, TPJ regions are active whenever we are exposed to a new visual scene or a new arrangement of distributed visual information in our environment. This assumption is in line with results from studies with simultanagnosia patients that are able to identify even complex objects but fail in the recognition of unfamiliar stimulus arrangements or alienated illustrations of regular objects (Dalrymple et al., 2010a, 2009; Pavese et al., 2002; Robertson et al., 1997). Indeed, various aspects of higher vision underlie continuous learning mechanisms. Human neuroimaging studies demonstrated that response behavior and neuronal activity in regions associated with object perception – like the lateral occipital complex (LOC) or fusiform face area (FFA) – changed significantly for extensively trained object stimuli (Dolan et al., 1997; Gauthier et al., 1999; Kourtzi et al., 2005; Kourtzi and DiCarlo, 2006; Op de Beeck and Baker, 2010). Other neuroimaging studies that investigated neuronal signal changes during learning of complex stimulus arrangements observed that perceptual training changes response characteristics in early visual (Zhang et al., 2010) and higher occipito-temporal/parietal regions (Mayhew et al., 2012). These observations suggest complex neuronal dynamics underlying mechanisms of object and form perception.

The present experiment was designed to test the hypothesis that (bilateral) TPJ areas are involved in processing of *novel* stimulus arrangements requiring mechanisms of Gestalt perception, while complex but familiar stimuli are processed with less or no TPJ contribution. We conducted a learning experiment in which subjects were repetitively exposed over one week to hierarchical stimuli in which a global Gestalt is perceived by the integration of local elements. Before and after the training period the effects of stimulus characteristics were tested behaviorally and with functional magnetic resonance imaging (fMRI). A measureable neuronal response to Gestalt perception training in area TPJ together with significant behavioral training effects would provide evidence for the specific role of this structure in the perception of *novel* stimulus configurations. In a previous study (Rennig et al., 2013a) it was demonstrated that the left *anterior* TPJ area responded stronger to global stimulus arrangements than an independent *posterior* TPJ section. Further, there exists evidence for an involvement of the (right hemispheric) *anterior* TPJ region, mainly comprising the supramarginal gyrus, in memory functions or target detection (Bzdok et al., 2013; Kubit and Jack, 2013). Within in this framework we investigated *posterior* and *anterior* parts of area TPJ separately and hypothesized significant signal changes due to Gestalt perception learning in (bilateral) *anterior* TPJ regions.

Material and Methods

Participants

24 right-handed subjects (mean age: 26.1, SD: 2.7, 11 male) participated in the present study. All had normal or corrected to normal vision, reported no history of neurological or psychiatric impairment and gave their written informed consent. The study was approved by the local ethics committee.

Stimuli & Procedure

The whole investigation consisted of two fMRI sessions, two psychophysical test sessions and 16 behavioural training sessions. The study started with the first (pre-training) fMRI measurement that was followed by a pre-training psychophysics session on the next day. One week after the first fMRI measurement a second (post-training) fMRI measurement was performed, again followed by a psychophysical test on the next day. Between the pre- and post-measurements 16 training sessions were performed on four days (always four sessions/day).

Pre- and post-training fMRI investigation

During the fMRI measurements and the psychophysical tests sessions subjects were presented with three different kinds of stimuli (Fig. 1). Two stimulus classes consisted of hierarchically organized stimuli where a global geometrical shape was built from local geometrical elements by integration (Fig. 1a, b). A third stimulus class consisted of black and white images of everyday objects (Fig. 1c). From the *three* stimulus classes we derived *four* experimental tasks: global perception of circles/squares (GCS; Fig 1a), global perception of triangles/stars (GTS; Fig. 1b), local perception of circles/squares (LCS; Fig. 1a) and object perception (OBJ; Fig. 1c). From the two hierarchically organized stimulus classes only one was used in the forthcoming training period (GCS; Fig. 1a). The other hierarchically organized stimulus task (GTS; Fig. 1b) as well as the local (LCS; Fig 1a) and object recognition task (OBJ; Fig. 1c) served as controls.

The two sets of global/local stimuli were constructed as follows (see Fig. 1): A) global circles/squares constructed from local circles/squares or B) triangles/stars that were created from small images of triangles/stars. Both sets consisted from four different combinations local and global features (two congruent and two incongruent combinations). Each stimulus consisted of 900 small elements organized in 30 columns and 30 rows covering an area of 21.0° x 18.0° (width x height). The local elements had a size of 0.7° x 0.6°. In order to minimize spatial certainty and local learning effects, all global objects were presented at one of four different positions within an individual stimulus image (left top, right top, left bottom, right bottom; see Fig. 1a, b). Further, luminance and contrast were varied between the objects and their background (e.g., dark objects presented in light background and vice versa, see Fig. 1a, b). In order to modulate global Gestalt perception the global shapes were parametrically degraded by exchanging a proportion of 20-, 40-, 60- or 80 % of the small, local images across the respective global object images (GCS/LCS, GTS; see Fig. 2). In correspondence to the procedure and findings by Huberle and Karnath (2012), the 20%-scrambled condition represented ‘intact’ perception of the global Gestalt and the 80%-scrambled condition represented ‘disturbed’ perception. For the object recognition task (OBJ; Fig. 1c) we used 20 black and white images of everyday artificial (manmade) or natural objects derived from the Bank of Standardized Stimuli (BOSS; Brodeur et al., 2010). Object stimuli were gradually superimposed with visual noise patterns to degrade perceptibility in correspondence with the scrambling of the global shapes (see Fig. 2; OBJ). The average size of the depicted objects matched the average size of the global stimuli from the two sets of global/local stimuli.

All fMRI measurements consisted of six sessions with a duration of 9 min 16 sec each. In all four tasks (GCS, GTS, LCS, OBJ) subjects had to perform a dichotomous decision. Via button presses on a single device with two buttons they indicated whether they saw a global circle or square (GCS), a global triangle or star (GTS), a local circle or square (LCS) or an artificial or natural object (OBJ). In the GCS and GTS tasks subjects thus had to do a global perception task of a hierarchical form. In the LCS task, with the same stimuli as in GCS, local perception was required. In the OBJ task, they had to perform an object recognition task.

To integrate all four tasks in a feasible way we used an event-related mini-block design (see Fig. 3). For every fMRI session and every participant the block sequence was identical. After an initial fixation period of 10 sec the sequence of consecutive mini-blocks began (see Fig. 3). It started with the mini-block for GCS, followed by those for GTS, LCS and OBJ. This series was repeated in same order four times per fMRI session. Every mini-block started with a cue that was presented for 1500 ms and contained information about the following task. Additionally, it instructed the correct button responses for the presented stimuli, e.g. left button press for a global square, right button press for a global circle in the GCS block shown in figure 3. The left-right assignment of the responses for the respective stimuli and the hand used for the responses were kept constant throughout all behavioral and fMRI measurements for an individual participant and fully balanced across the participants. After a short fixation period of 1000 ms following the cue the actual task started. Every mini-block contained eight stimulus trials and two interleaved null trials. Every experimental stimulus appeared for 300 ms followed by a fixation period of 2700 ms. No stimuli were shown in the null trials, which therefore consisted of a fixation period of 3000 ms. During the fixation period following stimulus presentation, subjects were required to give a response by pressing one of the two buttons. We used interleaved null trials to make the experiment less predictable for the subjects, provide a BOLD baseline measurement and to jitter the time between successive stimuli and responses. With several limitations (no null trails in direct succession, no null trails at the beginning or end of a mini-block, no trials with same scrambling rate in direct succession) all four scrambling rates per task and the two blank periods were distributed in a pseudo-randomized order in the respective mini-blocks. Hence, every mini-block contained both target stimuli (e.g. global circles and squares) in all four scrambling rates. Furthermore, factors like congruency of global and local elements, global target stimulus position on the stimulus image and luminance were distributed equally over all stimuli of one fMRI session. Every participant completed 128 trials of experimental stimuli within one fMRI session.

Eye Tracking

To ensure that eye movement patterns did not differ between the four stimulus classes and the two fMRI measurements we recorded eye movements during all fMRI sessions with an MR compatible tracking device (MR-LR Sensomotoric Instruments). Preprocessing of the eye tracking data included blink interpolation applying spline fitting algorithms, saccade detection and smoothing of x and y positions. Afterwards, the absolute distance of gaze from the fixation dot was calculated for every sampled data point. These distances were sorted by task (GCS, GTS, LCS, OBJ). Gaze data of the whole mini-blocks went into later data analysis; fixation periods (before and after the actual experiment) and cue events were discarded from the analysis.

Behavioral testing & learning procedure

The same stimuli and tasks as in the scanner were used in the behavioral test sessions conducted on the day after the corresponding pre- and post-training fMRI measurements. Stimuli were shown with the same size as in the scanner on a CRT monitor, the behavioral tasks were identical. Responses were collected with a standard keyboard where subjects had to press arrow buttons for left or right. The left-right assignment for the respective stimuli was the same as in the scanner. The distance between the observant and the screen was kept constant with a chin rest. The four tasks (GCS, GTS, LCS, OBJ) were administered block-wise in four consecutive blocks of 12 min 32 sec. Each block comprised 288 experimental stimuli of one task. In this test also interleaved null trials were used to make the experiment less predictable. The number of null trials was reduced by half as no specific neuronal imaging parameters had to be taken into account. Similar design limitations as in the scanner (no null trails in direct succession, no trails with same scrambling rate in direct succession) were applied to get a feasible pseudo-randomized test design. Within every test block (e.g. GCS) factors like congruency, target position and luminance were equally distributed over all stimuli that were presented in the respective block.

The learning sessions were conducted without a chin rest to provide more comfortable conditions for the subjects. In total, 16 learning sessions that lasted for 16 min 20 sec were conducted. Four sessions were done consecutively within one day resulting in four training days. The training days were randomly distributed over five possible days between the pre-training behavioral test and the post-training fMRI measurement. In these learning sessions subjects were presented only with stimuli from the GCS task (global perception of circles/squares) using an adaptive staircase scenario. The behavioral task in these sessions was the same as described above. Via button presses subjects had to indicate if they saw a global circle or square; key mapping was kept constant. In contrast to the test sessions, subjects were provided with a feedback about their performance after each trial. Every learning session started with the easily perceivable 20 %-scrambling condition and the difficulty of the task (i.e. scrambling rate of the stimuli) increased depending on the subject's performance. As soon as ten consecutive trials reached a percent correct value of 70 %, task difficulty was increased by 10 % scrambling between scrambling levels of 20 % to 50 %. In order to measure behavioral improvements in perceptually demanding conditions more precisely, scrambling increased by only 2 % as soon as a subject exceeded the 50 % scrambling threshold. If subjects performed in 10 consecutive trials worse than 30 % correct the task difficulty was reduced by 2 %. Every training session lasted for a fixed number of 320 trials.

Four variables were analyzed as dependent variables for perceptual learning per training session: accuracy (ACC), reaction times (RT), maximum scrambling rate and mean scrambling rate. 'Maximum scrambling rate' is the maximum scrambling rate achieved in the respective training session; 'mean scrambling rate' is the average scrambling rate from the same training session. ACC and RT were averaged per subject and training session for scrambling rates that were achieved on the first training day. We only analyzed scrambling rates where the respective subject was able to perceive significantly above chance level (ACC ≥ 70 %) at the end of the last training sessions of the first training day. For the analysis trials of 20 % scrambling were excluded since no behavioral learning effects for ACC were expected. For every subject we thus had an individual profile of scrambling rates (e.g. 9 scrambling levels from 40 - 62 %) and corresponding ACC and RT values that were extracted from each training session. This resulted in a 16 (training sessions) x N (= number of scrambling levels that went into the analysis) matrix for ACC and RT. As ACC rates and RTs differed systematically regarding their absolute values between the different scrambling levels (lower ACC values, longer RTs for stimuli with higher scrambling rate) we normalized these variables. For every column of our ACC and RT matrices (representing a certain scrambling level) we subtracted the value of the first training session from the values of all 16 sessions. Therefore, these normalized values represent a comparable measure of learning for ACC and RT from the 16 training sessions over all scrambling rates. Finally, these normalized values were averaged for each subject over the respective columns (scrambling rates) resulting in two learning indices per training session representing learning effects for ACC and RT. In the end, we had four values quantifying behavioral learning (maximum and mean scrambling rate, ACC and RT indices) for each of our 16 training sessions for every subject. For an analysis of training days, we simply averaged the indices of the four training sessions conducted on the same day.

Functional MRI data acquisition & analysis

We acquired EPI images with the following parameters: TR = 2000 ms; TE = 35 ms; FOV = 192 × 192 mm; flip angle: 90°; 30 axial slices with a thickness of 3 mm, interleaved acquisition; matrix size = 64 x 64. In both fMRI measurements a high-resolution T1-weighted anatomical images (1 x 1 x 1 mm^3) was acquired from each subject. For all analyses of the fMRI data we used the Statistical Parametric Mapping software package (SPM8; Wellcome Department of Imaging Neuroscience, London, UK; http://www.fil.ion.ucl.ac.uk/spm). At first, images recorded during pre- and post-measurement fixation were discarded. Preprocessing of neuroimaging data involved spatial realignment to the mean image including unwarping. The mean EPI resulting from motion-correction was co-registered to the anatomical image for every participant and the respective transformations were applied to all functional images. The individual T1 anatomical images were segmented and normalized to the standard SPM T1 template. All EPI images were then normalized using parameters derived from the T1 unified segmentation and smoothed with a FWHM of 8 mm.

In the first level analysis of each participant we implemented a general linear model comprising 16 separate predictors for each experimental condition (20-, 40-, 60- and 80% scrambling; four tasks) convolved with the hemodynamic response function as originally implemented in SPM8. Cue events were modeled as regressor of no interest, whereas fixation periods and null trials were not modeled explicitly. This resulted in 23 regressors including seven regressors of no interest comprising movement parameters from realignment and cue events. A high-pass filter with a cut-off period of 128 s was applied to eliminate low-frequency noise components. A correction for temporal autocorrelation in the data was applied using an autoregressive AR (1) process.

We defined regions of interest (ROIs) for analyses of neuronal effects of global perception learning. For a functional localization of global processing we used results from two previous studies investigating neuronal correlates of Gestalt perception (Huberle and Karnath, 2012; Rennig et al., 2013a). The functional ROIs from the study by Huberle and Karnath (2012) emerged from the same contrast with the same stimuli (GCS20% vs. GCS80%) and the same experimental task as in the present work and were successfully used for a functional re-analysis (Rennig et al., 2013a) (see Fig. 4). Therefore, our ROIs derived from a previous study provide an independent localization of Gestalt perception in the human brain. The bilateral TPJ ROIs, originally from Huberle and Karnath (2012), come from a re-analysis of their data using SPM8 (Rennig et al., 2013a). This re-analysis included the same steps as in the present fMRI analysis; this ensured maximum comparability between the two functional localizations of Gestalt perception. The bilateral TPJ ROIs (Huberle and Karnath, 2012; Rennig et al., 2013a) were thresholded at $p < .001$ (uncorrected for multiple comparisons), further details about the re-analysis can be taken from Rennig et al. (2013). In the left hemisphere two distinct functional ROIs, an *anterior* and a *posterior* cluster, emerged from the re-analysis. According to structural labeling of the AAL atlas (Tzourio-Mazoyer et al., 2002) the *anterior* ROI overlapped anatomically with the supramarginal gyrus (SMG) and the superior temporal lobe (STL). The *posterior* ROI comprised mainly the angular gyrus (AG), the middle temporal lobe (MTL), the middle occipital gyrus (MOG) and reached at its *anterior* borders marginally into the SMG. On the right hemisphere, a single cluster comprising *anterior* and *posterior* TPJ sections survived the statistical threshold of $p < 0.001$. This larger cluster comprised two local maxima that could be separated, comparable to the TPJ clusters in the left hemisphere, at a slightly higher threshold of $p < .0008$ (Fig. 4). The two sections were easily separable according to the AAL atlas into an *anterior* and *posterior* section. Here, the *anterior* ROI comprised SMG and a small part of the STL, the *posterior* ROI included the AG, MTL, STL and MOG. Based on reported functional differences between *anterior* and *posterior* TPJ sections (Bzdok et al., 2013; Kubit and Jack, 2013), clear anatomical allocations, the similarities between *anterior* and *posterior* clusters on the left and the fact that a slightly higher statistical threshold neatly separated two identifiable local minima in the anterior, respectively posterior part of the right TPJ, we decided to analyze four ROIs that circumscribed the anterior and posterior TPJ in each hemisphere. MNI coordinates of the center of mass and size of the four ROIs were: (R) anterior: x: 61.0, y: -38.8, z: 30.7; 2357 mm^3; posterior: x: 45.8, y: -55.4, z: 25.6; 10605 mm^3 (L) anterior: x: -58.0, y: -30.5, z: 26.5; 3060.0 mm^3; posterior: x: -44.6, y: -58.8, z: 26.9; 9495 mm^3 (see Fig 4). Once we specified conditions of interest, the ROI analysis was performed on the mean percent signal change (PSC) which was extracted using Marsbar SPM Toolbox from all voxels within the selected regions.

For a complementary exploration of the available data, we used individual contrast images obtained from the first-level analysis from each participant and each condition for a subsequent whole brain analysis. Areas significantly involved in the perception of a global Gestalt were identified as those voxels showing significantly higher signals for 20%-scrambled global shapes ('intact' global perception) compared to 80%-scrambled shapes ('disturbed' global perception). Therefore, for the whole brain analysis we calculated three different contrasts from the pre-training fMRI measurement: GCS20% vs. GCS80%, GTS20% vs. GTS80%, GCS20% + GTS20% vs. GCS80% + GTS80%.

Results

Behavioral testing & learning procedure

The behavioral test results outside the scanner were consistent with those collected in the scanner. We thus present the behavioral data from the fMRI sessions as these are more relevant for the interpretation of our neuroimaging results. We calculated separate 2 x 4 x 4 repeated measures ANOVAs with the factors 'measurement' (pre- vs. post-training), 'task' (GCS, GTS, LCS, and OBJ), and 'stimulus' (20-, 40-, 60-, 80 %) for RT and ACC values. We observed a significant three way interaction of all factors for ACC ($F_{(9,15)} = 4.59$, $p = .005$) and RT ($F_{(9,15)} = 2.94$, $p = .032$). All other main effects and two way interactions were also significant (p-values $< .05$). We thus tested each experimental factor level of our 4 x 4 (task, scrambling) design pre- against post-training. Thus, we performed 16 *t*-tests per dependent variable that were corrected for multiple comparisons, applying Bonferroni correction. For ACC, three comparisons from the GCS (20, 40, 60 % scrambling; $T_{(23)} = 4.11$, $p < .001$; $T_{(23)} = 4.27$, $p < .001$, $T_{(23)} = 5.92$, $p < .001$), one for the GTS (60 %; $T_{(23)} = 3.53$, $p = .002$) and two from the OBJ task (20, 60 % scrambling; $T_{(23)} = 3.95$, $p = .001$; $T_{(23)} = 6.11$, $p < .001$) showed significant differences between pre- and post-training measurements. All other tests did not reach significance even without Bonferroni correction. For RT, all comparisons but those for GTS 80 %-scrambling and all LCS levels showed significant results. However, without a Bonferroni correction all individual comparisons showed significant results ($p < .05$). As RTs decreased for virtually all tasks, only the behavioral data for ACC are illustrated in figure 5. The results illustrate a perceptual improvement that was most prominent in the trained global perception task.

The results during the behavioral training are illustrated in figure 6. They indicate strong behavioral improvements over several variables measuring perceptual abilities of global Gestalt processing. We analyzed maximum scrambling rate, mean scrambling rate, ACC, and RT for training sessions and days. To analyze learning effects over sessions we calculated linear regressions for every participant and each of the four dependent variables over the 16 training sessions. We used individual *beta* and R^2 values to calculate one-sample *t*-tests to demonstrate significant deviations of the regression line from zero. For all four variables these tests showed significant results for *beta* and R^2 (maximum scrambling rate: *beta*: mean = .24, $T_{(23)}$ = 5.05, $p < .001$, R^2: mean = .21, $T_{(23)}$ = 5.31, $p < .001$; mean scrambling rate: *beta*: mean = .20, $T_{(23)}$ = 5.63, $p < .001$, R^2: mean = .27, $T_{(23)}$ = 6.04, $p < .001$; ACC: *beta*: mean = .004, $T_{(23)}$ = 5.31, $p < .001$, R^2: mean = .23, $T_{(23)}$ = 5.37, $p < .001$; RT: *beta*: mean = 2.66, $T_{(23)}$ = 3.61, $p = .002$, R^2: mean = .25, $T_{(23)}$ = 5.38, $p < .001$). To further analyze the general effects across training days, neglecting within-day variability, we averaged the results of the 4 training sessions held on one day and conducted the same analysis over training days as we did over sessions. Also in this analysis, one-sample *t*-tests for the four variables showed significant results for *beta* and R^2 (maximum scrambling rate: *beta*: mean = .95, $T_{(23)}$ = 5.22, $p < .001$, R^2: mean = .49, $T_{(23)}$ = 7.86, $p < .001$; mean scrambling rate: *beta*: mean = .77, $T_{(23)}$ = 5.68, $p < .001$, R^2: mean = .56, $T_{(23)}$ = 8.80, $p < .001$; ACC: *beta*: mean = .014, $T_{(23)}$ = 4.95, $p < .001$, R^2: mean = .52, $T_{(23)}$ = 7.21, $p < .001$; RT: *beta*: mean = 8.97, $T_{(23)}$ = 3.31, $p = .003$, R^2: mean = .46, $T_{(23)}$ = 6.32, $p < .001$).

We further tested our behavioral data in terms of ‘stimulus type’ (e.g. global circle vs. square) and ‘congruency’ looking for possible effects evoked by the nature of the applied task or stimulus construction. These analyses showed no effects possibly biasing our main analyses of behavioral or neuronal data. Further, these analyses demonstrated that our hierarchical stimuli (GCR, GTS, LCR) had the expected characteristics of typical global/local stimuli and evoked the global precedence effect (Navon, 1977). The analyses and results can be inspected in the supplementary methods section.

Eye tracking

During all stimulation periods subjects were able to fixate properly and did not exceed the central fixation area (± 3° visual angle in x and y direction) during stimulus presentation. To inspect the data for systematic differences between the tasks or measurements, we calculated the mean distance between gaze position and the fixation cross across all mini-blocks for each task, separately for the two measurements and every subject. With this variable we calculated a 2 x 4 repeated measures ANOVA with the following factors and levels: ‘measurement’ (pre- vs. post-training) and ‘task’ (GCS, GTS, LCS, and OBJ).

This ANOVA showed no significant interaction ($F_{(3,20)} = 0.70$, $p = .56$) or main effects (‘measurement’: $F_{(1,22)} = 0.04$, $p = .38$; ‘task’: $F_{(3,20)} = 0.35$, $p = .79$).

fMRI

ROI analysis

We performed ROI analyses with mean PSC extracted from our four TPJ regions associated with global processing (see Fig. 4; see above ‘Functional Data Analysis’). For each ROI, we performed a 2 x 2 x 4 repeated measures ANOVAs with the following factors and levels: ‘measurement’ (‘pre-’ vs. ‘post-training’), ‘stimulus’ (‘intact’ vs. ‘disturbed’) and ‘task’ (GCS, GTS, LCS, OBJ). For the *anterior* right hemispheric TPJ ROI we observed a significant three-way interaction effect of ‘measurement’, ‘stimulus’ and ‘task’ ($F_{(3,21)} = 3.51$, $p = .033$), a significant two-way interaction of ‘measurement’ and ‘stimulus’ ($F_{(3,21)} = 10.87$, $p = .003$) and a significant main effect for ‘task’ ($F_{(1,23)} = 18.21$, $p < .0001$). Based on the significant three-way interaction we performed four two-way ANOVAs separately for every task with the factors ‘measurement’ (‘pre-’ vs. ‘post-training’) and ‘stimulus’ (‘intact’ vs. ‘disturbed’). For the trained task (GCS), we observed a significant interaction of ‘measurement’ and ‘stimulus’ ($F_{(3,21)} = 14.33$, $p = .001$). For the GDS task a nearly significant interaction of ‘measurement’ and ‘stimulus’ ($F_{(3,21)} = 3.62$, $p = .070$) was evident. For LCS and OBJ no main effects or interactions came close to a significant result ($p > .10$). Even with a Bonferroni correction for all four ANOVAs resulting in a *p*-threshold of .0125 the interaction for the trained GCS task can still be considered as significant. The PSC results of the four tasks and the two measurements are illustrated in figure 7. Based on the significant two-way interaction for GCS we performed 4 paired *t*-tests comparing PSC values for ‘intact’ and ‘disturbed’ (20 and 80 % scrambling) and ‘pre-‘ and ‘post-training’ measurements. At first, we compared the two scrambling rates per measurement. We observed a significant difference comparing PSC values for ‘intact’ and ‘disturbed’ (20 vs. 80 % scrambling) for the ‘pre-‘ ($T_{(23)} = 4.89$, $p < .001$), but not for the ‘post-training’ measurement ($T_{(23)} = -1.50$, $p = .15$) (see Fig. 7, GCS). Comparing PSC values for the two scrambling rates between the two measurements revealed a significant result for ‘intact’ (20 % scrambling; $T_{(23)} = 2.96$, $p = .007$) and a marginally significant result for ‘disturbed’ global perception (80 % scrambling; $T_{(23)}$ = -2.13, p = .044) (see Fig. 8). These results clearly illustrate learning dependent changes that were specific for the trained global perception task (GCS). We demonstrate a significant decrease for ‘intact’ and a significant increase for ‘disturbed’ global perception task (see Fig. 8). Further, the significant difference in the *anterior* TPJ in the pre-training measurement indicating a significant involvement of this structure in Gestalt perception disappeared (verified by 2- and 3-way interactions, see also Fig. 7). In the *posterior* right hemispheric TPJ ROI we observed significant main effects for ‘task’ ($F_{(3,21)}$ = 5.63, p = .005) and ‘stimulus’ ($F_{(1,23)}$ = 13.15, p = .001). The 2 x 2 x 4 ANOVA for the *anterior* left hemispheric TPJ ROI revealed no significant results. In the left *posterior* TPJ ROI, we observed significant main effects for ‘measurement’ ($F_{(1,23)}$ = 9.83, p = .005) and ‘stimulus’ ($F_{(1,23)}$ = 19.51, $p < .001$). These results indicate that the learning dependent changes can exclusively be attributed to the *anterior* right hemispheric TPJ ROI, while the other ROIs did not respond significantly to perceptual training.

To ensure that the results are specific for our distinct ROI we performed the same analysis in four bilateral brain regions associated with visual attention or expertise. The localization of these ROIs was defined from literature. We took the peak voxels from the result tables, built spheres of the average size of our functional ROIs (radius: 8 mm) around these voxels and extracted PSC. We chose two regions associated with visual attention: bilateral medial (Neggers et al., 2007; coordinates: R: x: 32, y: -4, z: 48; L: x: -28, y: -4, z: 56) and lateral (Neggers et al., 2007; R: x: 48, y: 4, z: 32; L: x: -44, y: 0, z: 48) frontal eye fields (FEF). We further took two definitions of the fusiform face area (FFA) as an area associated with visual expertise (Gauthier et al., 1999, 2000a): FFA_1 (Kanwisher et al., 1997; R: x: 40, y: -55, z: -10; L: x: -35, y: -63, z: -10), FFA_2 (Gauthier et al., 1999; R: x: 41, y: -55, z: -10; L: x: -40, y: -46, z: -12). We then conducted the same ANOVAs as with our functionally defined TPJ ROIs for each of the described control ROIs. For both lateral FEF ROIs no significant main or interaction effects were observable ($p > .05$). Both medial FEF ROIs showed a significant main effect for ‘task’ (R: $F_{(3,21)}$ = 8.80, p = .001; L: $F_{(3,21)}$ = 5.64, p = .005). In the right FFA_1 we observed a significant main effect for ‘task’ ($F_{(3,21)}$ = 25.54, $p < .001$), in the left FFA_1 the analysis revealed main effects for ‘measurement’ ($F_{(1,23)}$ = 4.43, p = .046), ‘task’ ($F_{(3,21)}$ = 40.77, p < .001) and ‘stimulus’ ($F_{(1,23)}$ = 5.03, p = .035). The right FFA_2 showed significant main effects for ‘task’ ($F_{(3,21)}$ = 26.99, p < .001) and ‘stimulus’ ($F_{(1,23)}$ = 7.40, p = .012) and a significant interaction for these factors ($F_{(3,21)}$ = 3.85, p = .024). In the left FFA_2 ROI we observed significant main effects for ‘task’ ($F_{(3,21)}$ = 34.61, p < .001) and ‘stimulus’ ($F_{(1,23)}$ = 17.56, p < .001). Summarizing, no significant interactions between the factor ‘measurement’ and factors ‘task’ and/or ‘stimulus’ were evident in the analyses of the control ROIs. These results indicate that the significant three-way interaction observed for our right hemispheric TPJ ROI reflects specific neuronal changes induced through global perception training.

We repeated the same fMRI analysis applying a linear parametric modulation taking into account reaction times for each individual trial. With this method every stimulus presentation is modeled individually depending on the respective reaction time. This approach ensures that differences in neuronal activation (e.g. between pre- and post-training measurements) are not driven by mere differences in cognitive processing speed (Büchel et al., 1998; Wood et al., 2008). This analysis brought up comparable results to the ones presented above. As the independent ROIs from our previous studies (Huberle and Karnath, 2012; Rennig et al., 2013a) were created without parametric modulations we adhered to the present approach (see above) to keep data analyses comparable between the different studies.

Whole brain analysis

With the data from the pre-training fMRI measurement we performed three contrasts to compare ‘intact’ to ‘disturbed’ global perception before training: GCS20% vs. GCS80%, GTS20% vs. GTS80%, GCS20% + GTS20% vs. GCS80% + GTS80%. Two of these contrasts (GCS20% vs. GCS80%, GCS20% + GTS20% vs. GCS80% + GTS80%) clearly revealed posterior temporo-parietal brain areas as crucial regions of Gestalt perception (Fig. 9). The comparison of ‘intact’ versus ‘disturbed’ Gestalt perception over both global perception tasks (GCS, GTS) showed a significant involvement of the right TPJ (temporo-parietal junction) for ‘intact’ global perception (p < .05, FWE corrected; Fig. 9a). The same comparison with a more liberal statistical threshold ($p < .001$, uncorrected; Fig. 9a) revealed bilateral TPJ activations as well as activity in bilateral precuneal regions and right hemispheric orbitofrontal cortex, superior parietal lobe and basal ganglia (not visible in Fig. 9a). A comparison of ‘intact’ versus ‘disturbed’ perception restricted to the GCS task revealed bilateral TPJ areas as the neuronal correlate of Gestalt perception only for an uncorrected statistical threshold of $p < .001$ (Fig. 9b). Applying the same contrast separately for the GTS task the same bilateral TPJ regions (besides several other activation clusters) were observable only for a very liberal statistical threshold ($p < .01$; results not shown). The results are in good agreement with evidence from previous studies showing a significant involvement of (bilateral) TPJ areas in global Gestalt processing (Himmelbach et al., 2009; Huberle and Karnath, 2012; Rennig et al., 2013a).

Discussion

The present study investigated the role of bilateral *anterior* and *posterior* TPJ regions in global Gestalt perception. In particular, we asked if *anterior* TPJ areas are mainly involved in the processing of *novel* complex stimuli. A behavioral training over one week familiarized subjects with complex global stimulus material. We hypothesized that increasing familiarity with the test stimuli would change response characteristics of *anterior* TPJ areas pre- and post-training. On the behavioral level, we observed clear improvements in the trained global perception task (GCS) while for the untrained global perception task (GTS) only slight training effects were evident. Over the 16 training sessions and four training days subjects showed a continuous decrease of reactions times and increasing accuracy values, indicating enhanced ability to integrate global visual arrangements. No significant behavioral changes were observed for the untrained local perception task (LCS), whereas in the untrained object perception task (OBJ) moderate behavioral changes were evident. It is possible that the slight improvement in the latter condition is due to simple memory effects evoked by repeated standardized testing with identical stimuli from a limited stimulus set. The behavioral results are in good agreement with studies showing a partial specificity of learning for trained (object) stimuli (Baeck and Op de Beeck, 2010; Furmanski and Engel, 2000; Grill-Spector et al., 2000; Sigman and Gilbert, 2000). In these studies, subjects showed clear training effects on the trained stimulus class while learning effects were less pronounced for untrained but similar stimuli.

The comparison of pre- and post-training BOLD signals in the delineated regions of interest demonstrated for the first time training effects in area TPJ. Significant changes were observed in our *anterior* right hemispheric TPJ ROI for the trained global perception tasks (GCS). In the control tasks requiring untrained global perception (GTS), local processing (LCS) and object recognition (OBJ), no systematic signal modulations were observed. In our *posterior* right hemispheric, and both left hemispheric TPJ ROIs no statistically significant effects were evident. In conclusion, the signal changes argue for an involvement of the *anterior* right hemispheric TPJ region in processing of mainly *novel* complex stimulus configurations. With increasing familiarity for the tested stimuli this TPJ section showed fundamentally different response characteristics. The results are in good agreement with observations in patients with simultanagnosia. While even complex familiar objects can be recognized, these patients fail in the identification of *novel* stimulus arrangements or alienated (unfamiliar) illustrations of regular objects (Dalrymple et al., 2010a, 2009; Pavese et al., 2002; Robertson et al., 1997). The present findings suggest that this observation occurs due to learning dependent signal modulations. Further, the results are in line with evidence dividing TPJ anatomically and functionally into an *anterior* (SMG) and *posterior* (AG) section (Bzdok et al., 2013; Kubit and Jack, 2013). The present results fit well with a previous neuroimaging study (Rennig et al., 2013a) where it was demonstrated that the left *anterior* TPJ area responded stronger to global stimulus arrangements than an independent *posterior* TPJ section. Further, there exists evidence for an involvement of the (right hemispheric) *anterior* TPJ region in memory functions or target detection (Bzdok et al., 2013; Kubit and Jack, 2013). Beyond, several other functions attributed to the TPJ (like Theory of Mind, perception of social interactions, attentional functions) were localized specifically in *anterior* and *posterior* sections of this brain structure. Whereas the *anterior* right hemispheric TPJ has been associated with attention, spatial cognition, target detection or memory functions, the posterior TPJ showed mainly associations with social reasoning (Bzdok et al., 2013; Jakobs et al., 2012; Krall et al., 2014; Kubit and Jack, 2013; Seghier, 2013).

In the pre-training fMRI measurement, we were able to replicate the results from the study of Huberle and Karnath (2012) using identical (GCS) or similar (GTS) stimulus material but applying a fundamentally different fMRI procedure (event-related mini block design, see Methods section; Fig. 9). This further strengthens the assumption that area TPJ represents a crucial region for global Gestalt processing (Himmelbach et al., 2009; Huberle and Karnath, 2012; Rennig et al., 2013a).

We assume that the observed neuronal signal changes in area TPJ correspond to a more efficient processing of ‘intact’ global stimuli and a higher sensitivity for degraded but potential global targets (Kourtzi et al., 2005). In any case, the training induced enhancements of neuronal responses for ‘disturbed’ global perception observed in the present study are in line with neuroimaging studies indicating that visual learning of degraded (Dolan et al., 1997; George et al., 1999), masked (Grill-Spector et al., 2000; James et al., 2000) or noise embedded (Kourtzi et al., 2005; Schwartz et al., 2002) targets increases neuronal signals. Likewise, neurophysiological studies have suggested that training with low-salience targets or objects in cluttered scenes leads to stronger neuronal signals indicating a higher sensitivity to target features and facilitation for the detection and integration of a (potential) global form (Kobatake et al., 1998; Logothetis et al., 1995; Rainer et al., 2004; Sakai and Miyashita, 1991; Tovee et al., 1996). This enhanced neuronal sensitivity can be explained as an increased internal signal-to-noise ratio for trained stimuli supporting the selection of a global shape (Dosher and Lu, 2006). In contrast, lower neuronal responses observable for ‘intact’ global processing after training indicates more efficient neuronal processing for high-salience, unambiguous targets. This effect is known from previous neuroimaging studies investigating perceptual learning effects on pop-out targets (Chao et al., 2002; Henson et al., 2000; Jiang et al., 2000; Kourtzi et al., 2005; Koutstaal et al., 2001; van Turennout et al., 2000). These effects were confirmed by similar results from neurophysiological studies in monkeys (Schoups et al., 2001). Especially a study by Kourtzi and colleagues (Kourtzi et al., 2005) that investigated perceptual learning with shapes arranged from Gabor elements showed interactions between stimulus saliency and learning induced neuronal activation changes. It was demonstrated that trained shapes that were difficult to perceive due to a fuzzy background produced higher neuronal responses than untrained versions of these stimuli in early and higher visual areas. In contrast, trained shapes that were easy to perceive showed a lower neuronal signal compared to untrained ones in higher visual areas. A recent study investigating TPJ involvement in the perception of gratings (Beauchamp et al., 2012) confirmed these observations as well as our present results. It was demonstrated that electrical stimulation of human TPJ areas enhanced detection rates for low-salience stimuli while perception in undisturbed viewing conditions was unaffected. In general, our results are in good agreement with existing evidence on neuronal effects of visual learning. Further, we do not attribute the observed signal modulations in the area TPJ to mere changes in visual attention, because no systematic activation changes were observable in bilateral frontal eye fields. Moreover, the nature of our stimuli that varied in contrast, position and coloring suggests that local processing of single elements or object parts was not trained but actually visual top-down processing in the sense of Gestalt perception.

However, alternative explanations such as a shift of neuronal processing for extensively trained global stimuli from visual integration in area TPJ to other regions – of course – are also plausible. For example, a previous study investigating neuronal training effects for a visual search task demonstrated training dependent parietal and lateral occipital signal decreases in favor of an increase in early visual areas (Sigman et al., 2005). This activation change was interpreted as a redistribution of the functionality of different cortical areas involved in object identification. In the present study, a possible shift in neuronal activation may have occurred from integration related processes in area TPJ in favor of a stronger ventral involvement and mechanisms of object processing.

We conclude that (*anterior* right hemispheric) TPJ regions are involved in processing of mainly *novel* global stimuli. For the first time we showed that fMRI signals in TPJ regions are modulated through extensive perceptual training with complex global configurations. With increasing familiarity these areas changed sensitivity and selectivity for complex stimulus arrangements. The findings thus strengthen the view about the (right hemispheric) TPJ as a crucial module for Gestalt perception (Himmelbach et al., 2009; Huberle and Karnath, 2012; Rennig et al., 2013a).

Acknowledgements

This work was supported by the DFG (Ka 1258/10-1) and the European Union (ERC StG 211078).

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Captions

Figure 1: Stimuli applied in the experiment. Examples for the two stimulus categories requiring Gestalt perception: (A) global/local circles and squares (GCS/LCS), (B) global/local triangles and stars (GTS). Examples from the object recognition task (OBJ) (C). The hierarchically organized stimuli (A, B) showed a circle/square or a triangle/star (global level) that were constructed from 900 (30 x 30) elements (circles/squares, triangles/stars). Stimuli consisted of four different possible combinations of objects at the local and global level and varied in contrast and luminance. The object stimuli were images of natural or artificial (manmade) objects (C). All targets were displayed at four different positions and similar in perimeter and size.

Figure 2: Example stimuli for the different degradation levels for the two global tasks (GCS, GTS), the local task (LCS) and the object perception task (OBJ). The configurations at the global level (GCS, GTS) were parametrically degraded by exchanging the objects at the local level with each other. The object stimuli (OBJ) were parametrically superimposed with visual noise. Illustrated are stimuli with scrambling rates of 20-, 40-, 60-, and 80%.

Figure 3: Event-related mini block design. All fMRI sessions followed the same procedure: GCS, GTS, LCS and OBJ. This sequence was repeated four times per fMRI session. Every mini block was introduced by a cue indicating the respective task and key mapping. This was followed by two iterations of four stimuli and an interleaved blank period. Every mini block contained a 20 %, 40 %, 60 % and 80 % version of the two possible stimuli (e.g. circle or square).

Figure 4: ROIs in bilateral TPJ regions. ROIs were identified based on the data from the study of Huberle and Karnath (2012) as those voxels showing significantly higher BOLD signals for 20%-scrambled objects (‘intact’ global perception) compared to 80%-scrambled objects (‘disturbed’ global perception) based on a voxel-level threshold of $p < 0.001$ (uncorr.). The

results are presented on a 3D rendered surface for the left and right hemisphere and axial slices. The four ROIs are depicted in the lower panel on the same axial slices. MNI coordinates of the center of mass and size of the ROIs: (R) anterior: x: 61.0, y: -38.8, z: 30.7; 2357 mm^3; posterior: x: 45.8, y: -55.4, z: 25.6; 10605 mm^3 (L) anterior: x: -58.0, y: -30.5, z: 26.5; 3060.0 mm^3; posterior: x: -44.6, y: -58.8, z: 26.9; 9495 mm^3.

Figure 5: Behavioral results from the two fMRI measurements. (A) Accuracy (ACC, in percent correct) for all four tasks (GCS, GTS, LCS, OBJ), both fMRI measurements (M1, M2) and scrambling rates (20- , 40- , 60- , 80 %). (B) For every task, we calculated the difference between pre- and post-training measurement for accuracy (ΔACC, in percent correct). Results are illustrated for all four tasks (GCS, GTS, LCS, OBJ) and scrambling rates (20- , 40- , 60- , 80 %). The asterisk indicates significant differences between the particular conditions. Two asterisks represent highly significant results.

Figure 6: Results from the behavioral training sessions. Maximum and mean scrambling rate in percent scrambling and normalized accuracy (ΔACC, in percent correct) and reaction times (ΔRT, in ms) for every training sessions and days averaged over all participants. The four training sessions constituting a training day (e.g. 1- 4) are grouped in the 'Sessions' column.

Figure 7: ROI analysis. Percent signal change for the four tasks and two fMRI measurements are illustrated for 'intact' (20 % scrambled) and 'disturbed' global perception (80 % scrambled). Results are presented for right *anterior* TPJ ROI. Error bars indicate standard error of the mean. The asterisk indicates significant differences between the particular conditions.

Figure 8: ROI analysis. Percent signal change comparing 'intact' (20 % scrambled) and 'disturbed' global perception (80 % scrambled) directly between the two fMRI measurements. Results are presented for right *anterior* TPJ ROI. Error bars indicate standard error of the mean. The asterisk indicates significant differences between the particular conditions.

Figure 9: fMRI results, whole brain analysis. Displayed are the results of two analyses contrasting 'intact' global Gestalt perception (20 %-scrambled stimuli) versus 'disturbed' perception (80 %- scrambled stimuli). The results are presented on a 3D rendered surface for the left and right hemisphere and axial slices. (A) Contrast of 'intact' (20%-scrambled stimuli) and 'disturbed' (80 %-scrambled stimuli) over both global perception tasks (GCS, GTS) corrected for multiple comparisons (FWE, $p < .05$, depicted in blue). This comparison revealed an area in the right hemispheric TPJ region as the neuronal correlate of Gestalt perception. The same contrast over both global perception tasks (GCS, GTS) *un*corrected for multiple comparisons ($p < .001$, depicted in red) revealed bilateral TPJ regions, bilateral precuneal areas and right hemispheric orbito-frontal cortex, superior parietal lobe and basal ganglia (not visible in the figure) as neuronal correlates of global Gestalt perception. (B) Contrast of 'intact' (20 %-scrambled stimuli) and 'disturbed' (80 %-scrambled stimuli) for the GCS task *un*corrected for multiple comparisons ($p < .001$). This comparison revealed bilateral TPJ regions as the neuronal correlate of Gestalt perception.

Figures

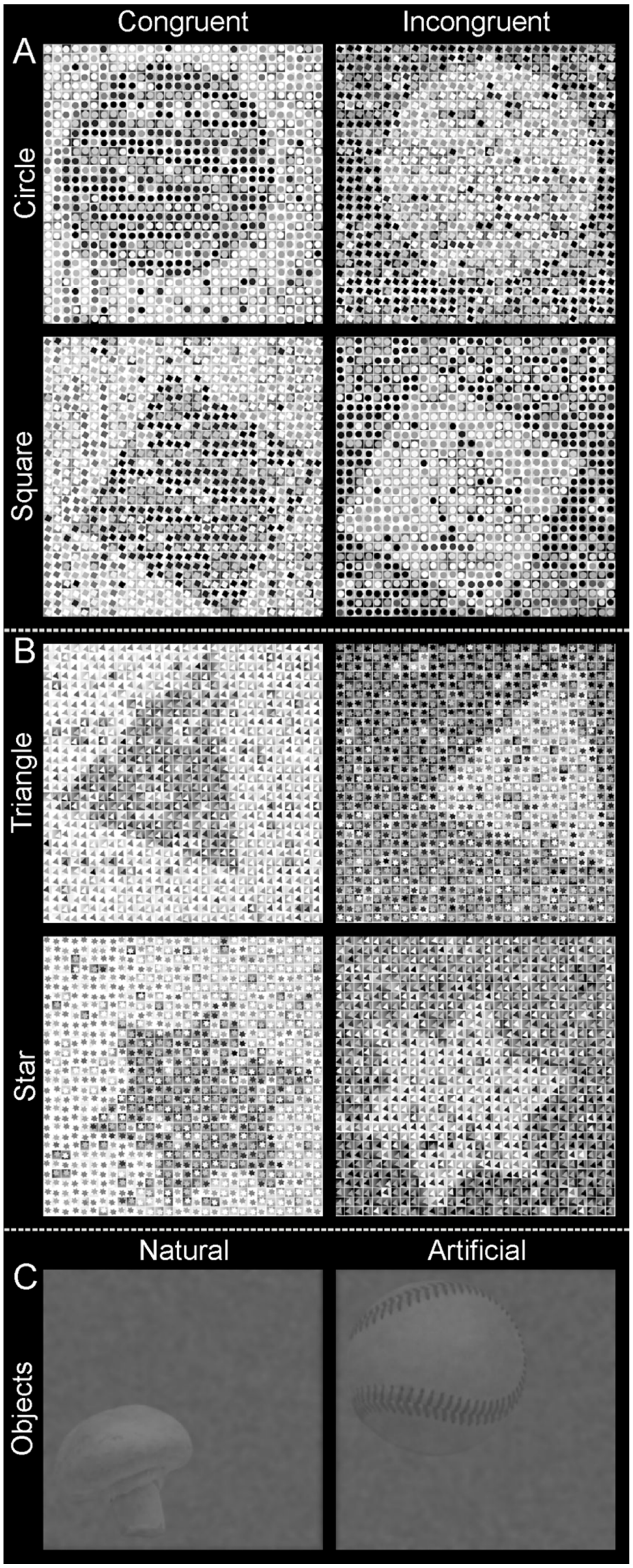


Figure 1

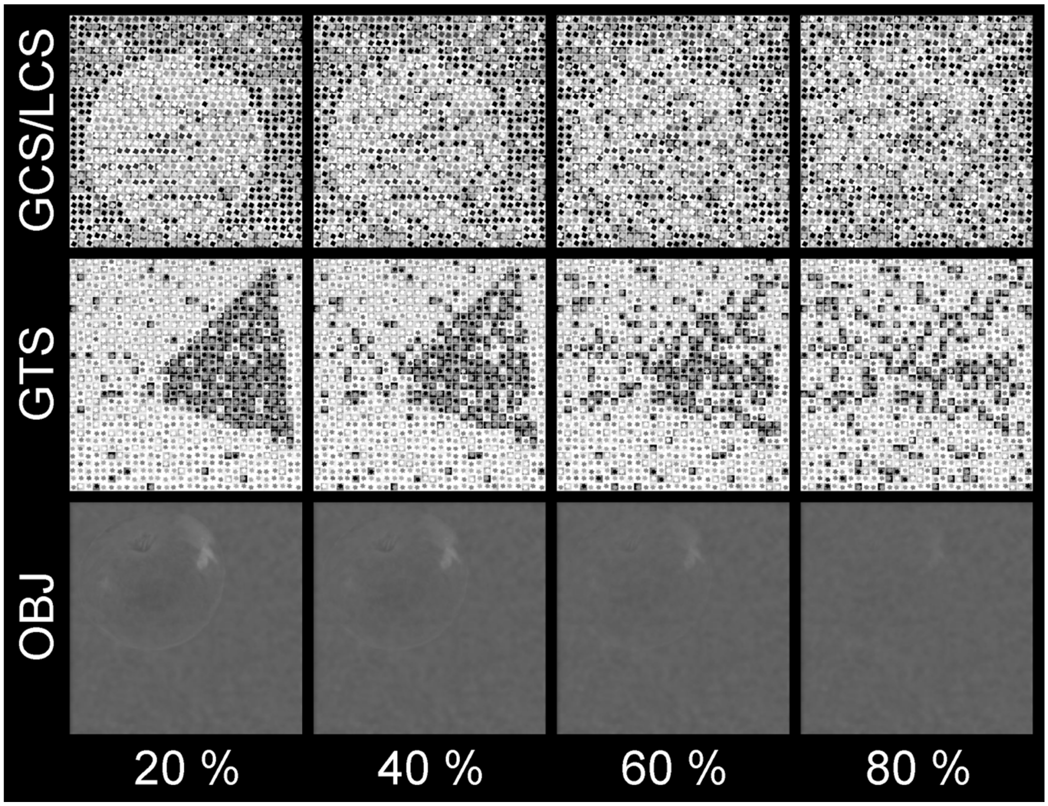


Figure 2

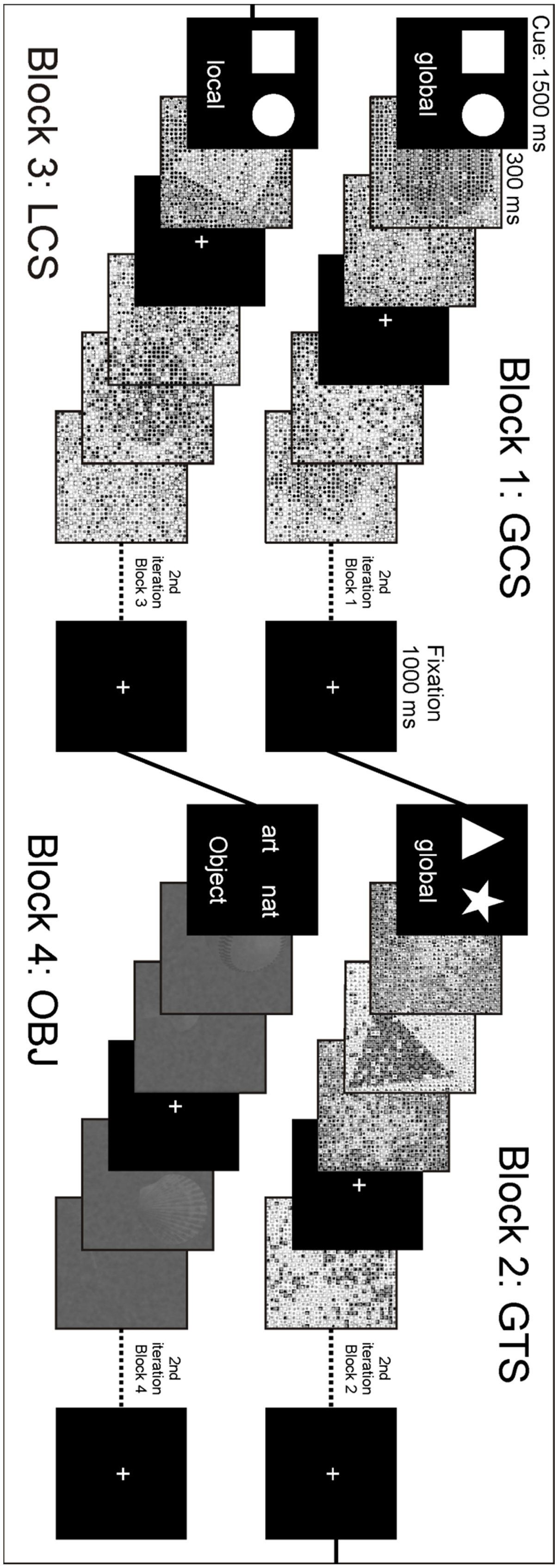

Cue: 1500 ms
global
300 ms
Block 1: GCS
2nd iteration Block 1
Fixation 1000 ms
global
Block 2: GTS
2nd iteration Block 2
local
Block 3: LCS
2nd iteration Block 3
art nat
Object
Block 4: OBJ
2nd iteration Block 4

Figure 3

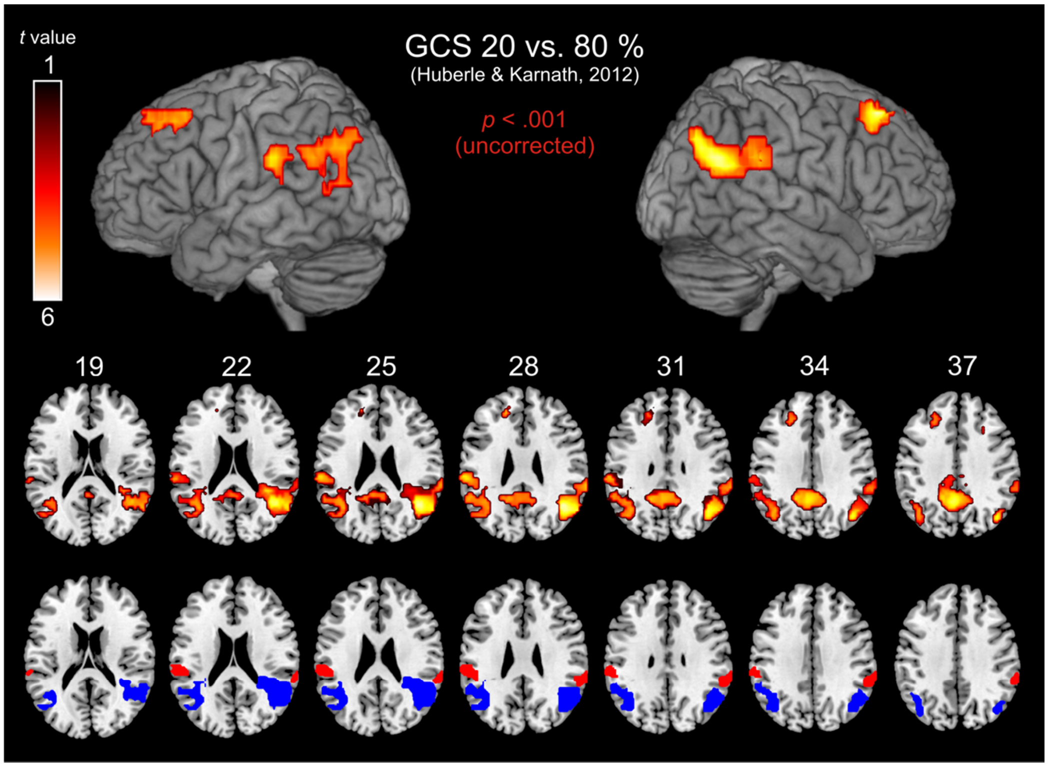
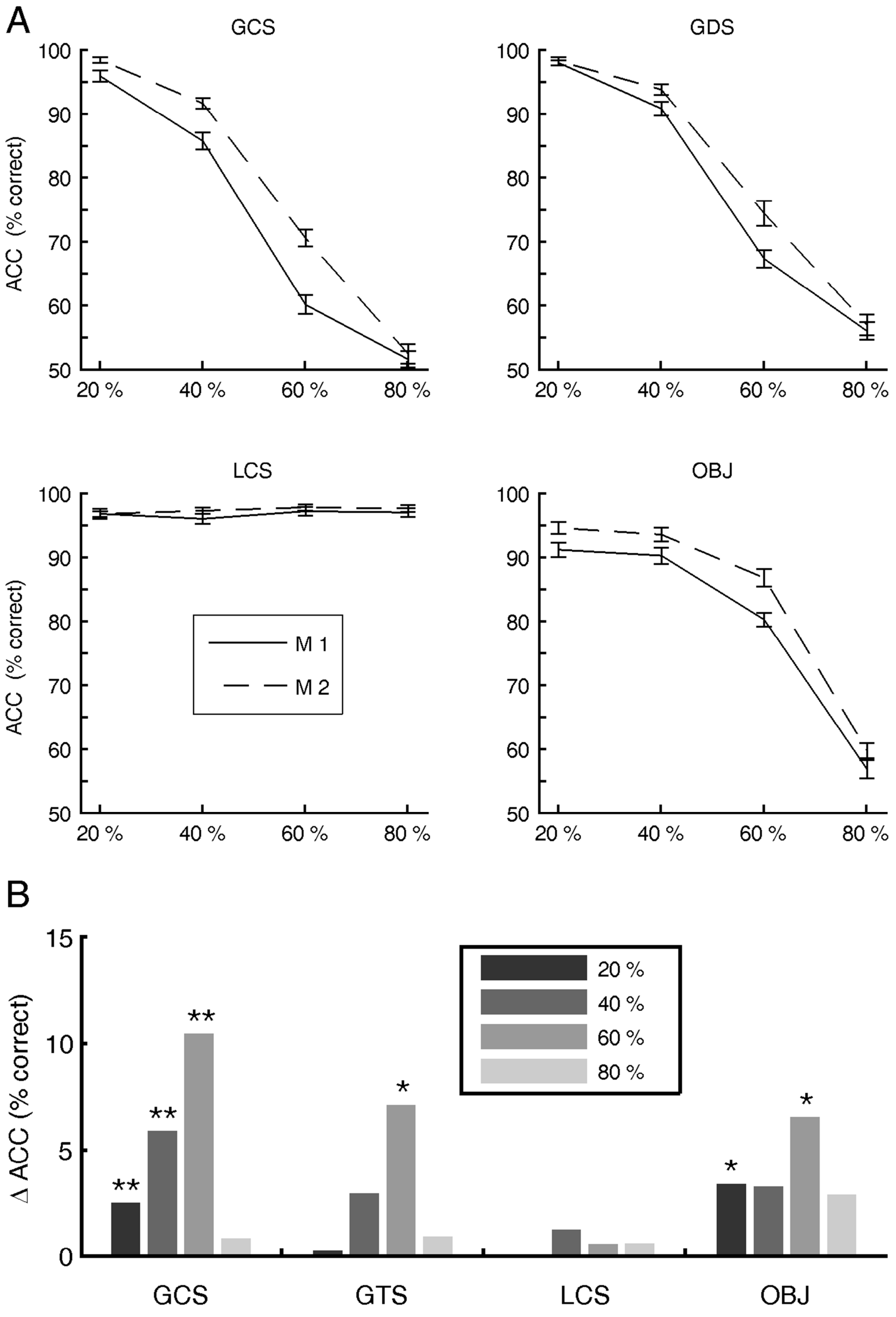

t value
1
6
GCS 20 vs. 80 %
(Huberle & Karnath, 2012)
p < .001
(uncorrected)
19
22
25
28
31
34
37

Figure 4


A
GCS
GDS
LCS
OBJ
ACC (% correct)
100
90
80
70
60
50
20 %
40 %
60 %
80 %
M 1
M 2
B
Δ ACC (% correct)
15
10
5
0
20 %
40 %
60 %
80 %
**
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*
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GCS
GTS
LCS
OBJ

Figure 5

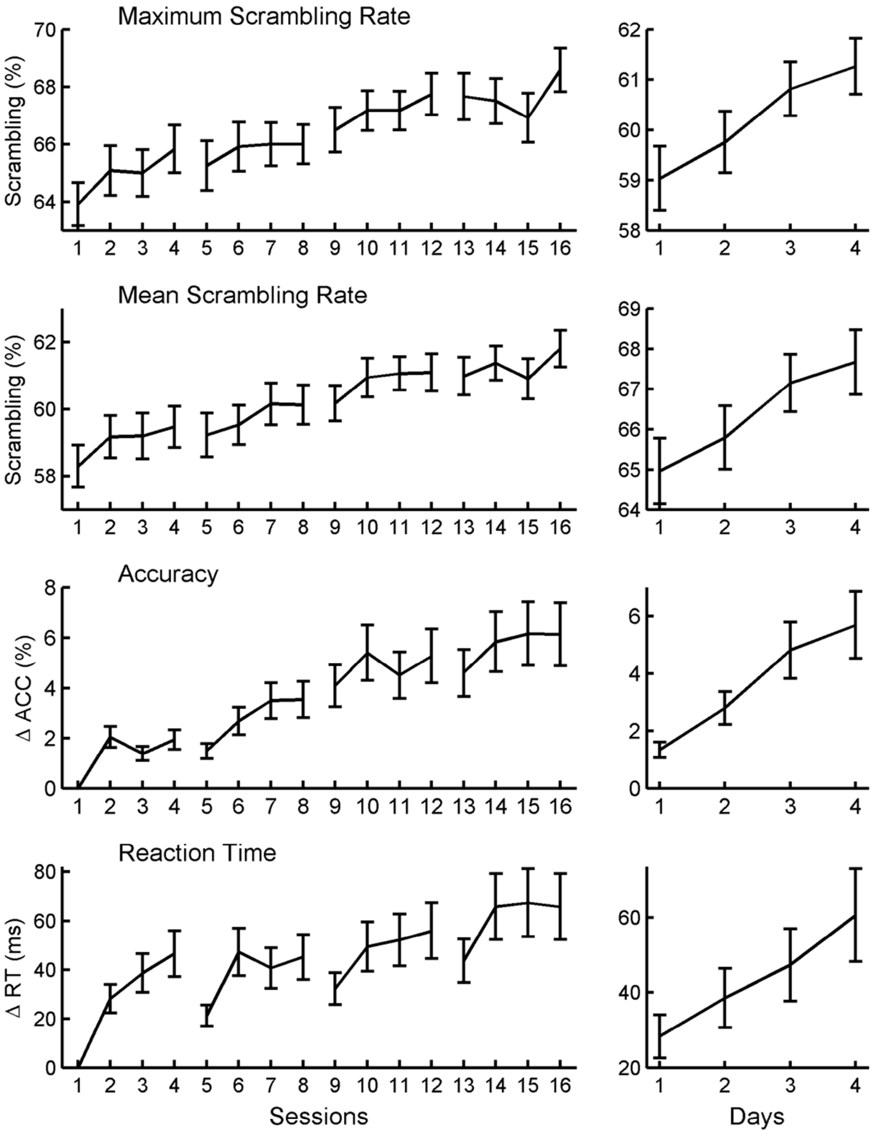

Maximum Scrambling Rate
Scrambling (%)
70
68
66
64
62
61
60
59
58
Mean Scrambling Rate
Scrambling (%)
62
60
58
69
68
67
66
65
64
Accuracy
Δ ACC (%)
8
6
4
2
0
Reaction Time
Δ RT (ms)
80
60
40
20
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Sessions
1 2 3 4
Days

Figure 6

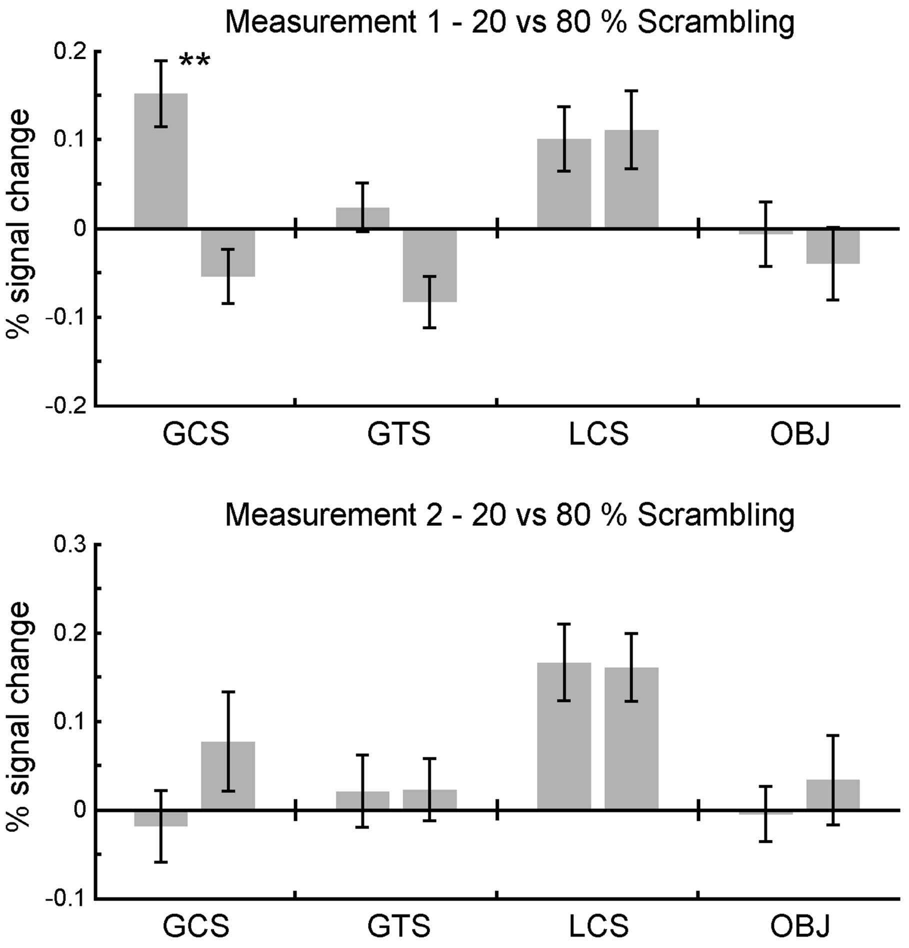

Measurement 1 - 20 vs 80 % Scrambling
% signal change
0.2
0.1
0
-0.1
-0.2
**
GCS
GTS
LCS
OBJ
Measurement 2 - 20 vs 80 % Scrambling
% signal change
0.3
0.2
0.1
0
-0.1
GCS
GTS
LCS
OBJ

Figure 7

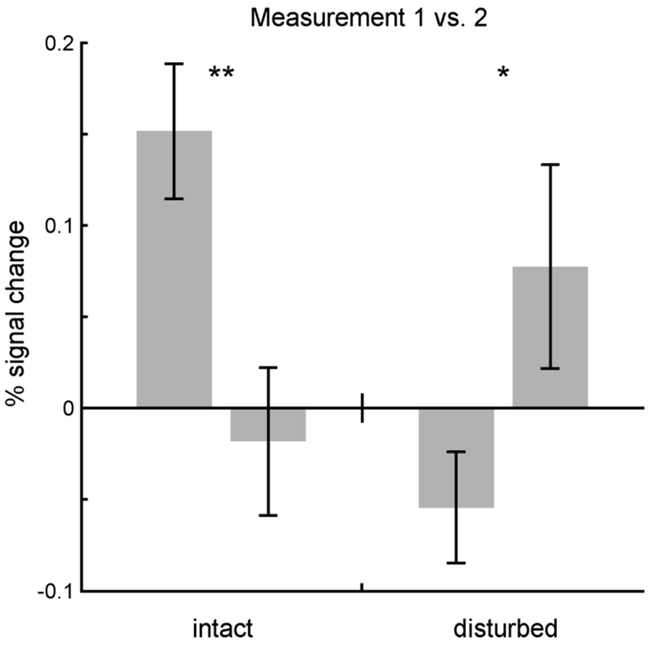
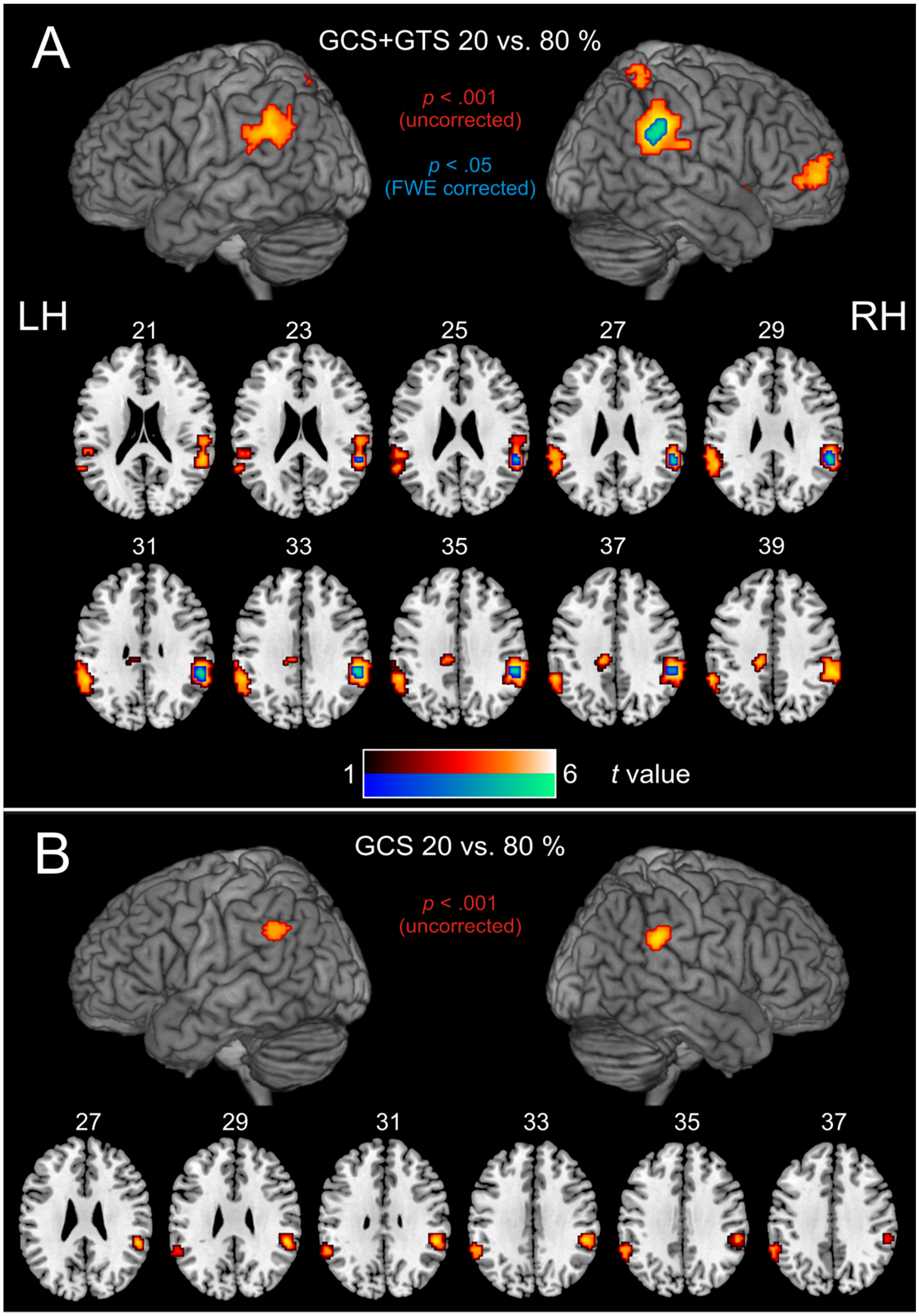


Figure 8


A
GCS+GTS 20 vs. 80 %
p < .001
(uncorrected)
p < .05
(FWE corrected)
LH
RH
21
23
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27
29
31
33
35
37
39
1
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t value
B
GCS 20 vs. 80 %
p < .001
(uncorrected)
27
29
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Figure 9

Supplementary Methods & Results

All tasks were dichotomously organized, i.e. subjects always had to discriminate between two stimulus types within each task (e.g. global circles vs. squares). To ensure that stimuli did not differ systematically regarding 'type' we further tested for possible differences within each task (e.g. global circles vs. squares). Therefore, we conducted a 2 x 4 x 2 repeated measures ANOVA with the following factors and levels: 'measurement' (pre- vs. post-training), 'task' (GCS, GTS, LCS, OBJ) and 'type' (type 1 vs. 2; e.g. global circles vs. squares). For ACC, the analysis showed significant main effects for 'measurement' ($F_{(1,22)} = 12.89$, $p = .002$) and 'task' ($F_{(3,20)} = 12.41$, $p < .001$) as well as a significant interaction for 'measurement' x 'task' ($F_{(3,20)} = 21.47$, $p = .030$). For RT the same result pattern was observable: main effects for 'measurement' ($F_{(1,22)} = 24.17$, $p < .001$) and 'task' ($F_{(3,20)} = 57.46$, $p < .001$), significant interaction for 'measurement' x 'task' ($F_{(1,23)} = 5.63$, $p = .006$). The results showed behavioral differences between the different tasks and measurements but no effects between the two stimulus types administered within each task. Due to these results we were able to treat both conditions of each stimulus class in the same fashion over all behavioral and neuroimaging analyses.

To ensure that congruency effects that are typical for hierarchically organized stimuli (Navon, 1977) were also evoked by our stimulus material, we analyzed our behavioral data in terms of the factor 'congruency'. We restricted the analysis to the 'intact' global perception conditions (20 % scrambling) and analyzed ACC values and RTs. To test for 'congruency' we contrasted congruent and incongruent targets from our global and local recognition tasks (GCT, GTS, LCS). Here, we pooled the data for global perception by averaging values from GCS and GTS. As we were not interested in any learning dependent effects in terms of congruency we pooled the data from both behavioral measurements and conducted 2 x 2 ANOVAs and paired *t*-tests (Bonferroni corrected) for ACC and RT. The descriptive results showed comparable ACC values for global and local perception for congruent but not incongruent trials. We further observed shorter RTs for congruent trials for both perceptual qualities. The descriptive results are summarized in Table 1. Concerning ACC there was a significant main effects for 'congruency' ($F_{(1,23)}$ = 20.01, p < .001) but not for 'task' ($F_{(1,23)}$ = 2.51, p < .13) and a significant interaction between 'task' and 'congruency' ($F_{(1,23)}$ = 6.10, p = .021). With two following *t*-tests we compared ACC values of global and local perception for congruent and incongruent trials. There was a significant difference between global and local perception for incongruent ($T_{(23)}$ = 2.46, p = .022), but not for congruent trials ($T_{(23)}$ = 0.67, p = .51). For RT the results showed significant main effects for 'congruency' ($F_{(1,23)}$ = 21.47, p < .001) and 'task' ($F_{(1,23)}$ = 8.67, p < .007) and a significant interaction between 'task' and 'congruency' ($F_{(1,23)}$ = 15.06, p = .001). Following *t*-tests showed a significant difference for incongruent ($T_{(23)}$ = 3.84, p = .001), but not for congruent trials ($T_{(23)}$ = 1.32, p = .20). Here, we showed that global perception is less influenced by incongruent local elements than local perception is influenced by an incongruent global aspect in a hierarchical structure. These results are in line with the global precedence effect (Navon, 1977) stating a dominance of global over local perception. Regardless of significant differences between congruent and incongruent stimuli both versions can be processed conjointly as they do not differ regarding their basic perceptual properties.

Table 1.

Descriptive ACC and RT values for congruent and incongruent, global and local stimulus conditions.

	congruent		incongruent	
ACC	mean	SD	mean	SD
global	98.11 %	1.81 %	97.00 %	2.78 %
local	98.52 %	2.78 %	94.86 %	4.28 %
RT				
global	466.96 ms	106.27 ms	475.23 ms	108.14 ms
local	476.61 ms	117.04 ms	510.45 ms	113.83 ms

4 The temporo-parietal junction contributes to global Gestalt perception – evidence from studies in chess experts

The temporo-parietal junction contributes to global Gestalt perception – evidence from studies in chess experts

Johannes Rennig[1a], Merim Bilalić[2a], Elisabeth Huberle[1,3], Hans-Otto Karnath[1,4], Marc Himmelbach[1]
[a]shared first authorship

[1]Division of Neuropsychology, Center of Neurology, Hertie-Institute for Clinical Brain Research, University of Tübingen, Tübingen, Germany
[2]Department of Neuroradiology, University of Tübingen, Tübingen, Germany
[3]Neurology and Neurorehabilitation Center, Luzerner Kantonsspital, Luzern, Switzerland
[4]Department of Psychology, University of South Carolina, Columbia, SC 29208, USA

Corresponding author:
Johannes Rennig
Division of Neuropsychology
Center of Neurology
Hertie-Institute for Clinical Brain Research
University of Tübingen
D-72076 Tübingen
Phone: ++49 - 7071 - 29 80463
e-mail: johannes.rennig@uni-tuebingen.de

Author contributions

This chapter was published in *Frontiers in Human Neuroscience* (Rennig et al., 2013). Merim Bilalić and Johannes Rennig contributed equally to this work. Marc Himmelbach, Merim Bilalić and Johannes Rennig designed the present approach. Elisabeth Huberle and Merim Bilalić acquired the data. Johannes Rennig and Merim Bilalić analyzed the data. Johannes Rennig wrote the paper with the help of Marc Himmelbach and Hans-Otto Karnath.

frontiers in
HUMAN NEUROSCIENCE

ORIGINAL RESEARCH ARTICLE
published: 28 August 2013
doi: 10.3389/fnhum.2013.00513

The temporo-parietal junction contributes to global gestalt perception—evidence from studies in chess experts

Johannes Rennig[1]*†, Merim Bilalić[2]†, Elisabeth Huberle[1,3], Hans-Otto Karnath[1,4] and Marc Himmelbach[1]

[1] Division of Neuropsychology, Center of Neurology, Hertie-Institute for Clinical Brain Research, University of Tübingen, Tübingen, Germany
[2] Department of Neuroradiology, University of Tübingen, Tübingen, Germany
[3] Neurology and Neurorehabilitation Center, Luzerner Kantonsspital, Luzern, Switzerland
[4] Department of Psychology, University of South Carolina, Columbia, SC, USA

Edited by:
Magdalena Chechlacz, University of Oxford, UK

Reviewed by:
Harriet A. Allen, University of Birmingham, UK
Dario Cazzoli, University of Oxford, UK

***Correspondence:**
Johannes Rennig, Division of Neuropsychology, Center of Neurology, Hertie-Institute for Clinical Brain Research, University of Tübingen, Hoppe-Seyler-Str. 3, D-72076, Tübingen, Germany
e-mail: johannes.rennig@uni-tuebingen.de

† These authors have contributed equally to this work.

In a recent neuroimaging study the comparison of intact vs. disturbed perception of global gestalt indicated a significant role of the temporo-parietal junction (TPJ) in the intact perception of global gestalt (Huberle and Karnath, 2012). This location corresponded well with the areas known to be damaged or impaired in patients with simultanagnosia after stroke or due to neurodegenerative diseases. It was concluded that the TPJ plays an important role in the integration of individual items to a holistic percept. Thus, increased BOLD signals should be found in this region whenever a task calls for the integration of multiple visual items. Behavioral experiments in chess experts suggested that their superior skills in comparison to chess novices are partly based on fast holistic processing of chess positions with multiple pieces. We thus analyzed BOLD data from four fMRI studies that compared chess experts with chess novices during the presentation of complex chess-related visual stimuli (Bilalić et al., 2010, 2011a,b, 2012). Three regions of interests were defined by significant TPJ clusters in the abovementioned study of global gestalt perception (Huberle and Karnath, 2012) and BOLD signal amplitudes in these regions were compared between chess experts and novices. These cross-paradigm ROI analyses revealed higher signals at the TPJ in chess experts in comparison to novices during presentations of complex chess positions. This difference was consistent across the different tasks in five independent experiments. Our results confirm the assumption that the TPJ region identified in previous work on global gestalt perception plays an important role in the processing of complex visual stimulus configurations.

Keywords: gestalt perception, visual grouping, temporo-parietal junction, object perception, expertise, fMRI, simultanagnosia, chess

INTRODUCTION

A crucial aspect of visual object recognition is the grouping of single elements to a global entity or so-called gestalt (Wertheimer, 1923; Koffka, 1935). The neuronal correlates of global processing or visual integration are still a matter of lively debates. Patients suffering from simultanagnosia, the inability to perceive a global gestalt first described as part of the Bálint syndrome (Bálint, 1909), typically show bilateral lesions in posterior parieto-temporal brain areas, whereas a remarkable variability concerning the exact localization is still prevalent (Rizzo and Hurtig, 1987; Friedman-Hill et al., 1995; Rafal, 1997; Karnath et al., 2000; Tang-Wai et al., 2004; Valenza et al., 2004; Huberle and Karnath, 2006, 2010; Thomas et al., 2012). Moreover, there is an inconsistency between functional imaging studies that attributed global perception to unilateral regions along the ventral visual pathway (Fink et al., 1996, 1997a,b) and other studies that found an association with posterior parietal and/or parieto-temporal areas (Yamaguchi et al., 2000; Himmelbach et al., 2009; Huberle and Karnath, 2012; Zaretskaya et al., 2013).

Research in chess experts provided a large body of data addressing neuronal correlates of visual skills (Bilalić et al., 2010, 2011a,b, 2012; Krawczyk et al., 2011). For research on object recognition and visual integration chess appears to be particularly suitable as it features various, clearly distinguishable individual objects that allow the composition of complex stimulus configurations with graded complexity. Furthermore, chess provides the opportunity to compare highly trained experts with novices based on a standardized rating system (Elo, 1978). Behavioral studies demonstrate that domain-specific knowledge, acquired through prolonged and focused training (Ericsson et al., 1993), enables experts to quickly grasp the essence of complex chess positions (DeGroot, 1978; Bilalić et al., 2008a). Instead of perceiving individual chess objects serially like novices, experts perceive meaningful units of several objects, called chunks (Chase and Simon, 1973) or templates (Gobet and Simon, 1996), which are linked with typical actions through pattern recognition mechanisms (Bilalić et al., 2008a,b, 2009, 2010). A typical chess position featuring numerous individual objects represents a single meaningful unit to chess experts. In a recent series of fMRI studies, Bilalić et al. (2010, 2011a,b, 2012) demonstrated that chess experts also showed different neuronal response patterns in the ventral visual system compared to novices. Typically, chess experts showed higher signal increases mostly in the temporal lobe compared to novices during the observation of chess stimuli. A study by Krawczyk et al. (2011) using comparable stimulus material revealed a similar result pattern with higher signals in temporal and frontal brain areas for experts compared to novices.

Based on the assumption that the behavioral advantage of chess experts is, at least partially, based on superior skills in the visual integration of multiple chess pieces we hypothesized that there should be a difference in the BOLD signal in regions that were functionally mapped in an independent study of global perception using substantially different stimulus material (Huberle and Karnath, 2012). In detail, the temporo-parietal junction (TPJ) was investigated by using an independent set of data from chess experts as well as novices. Several studies investigating neuronal processes of visual grouping used stimuli that may have evoked neuronal responses depending on low-level visual features like spatial frequencies of luminance changes (e.g. Fink et al., 1996; Huberle and Karnath, 2012). The stimuli examined in the ROI analyses of the present approach were substantially different from simple hierarchical Navon-like (Navon, 1977) stimulus material. The relationships between chess pieces that support the emergence of a global percept are not based on low-level visual features but on the knowledge about these pieces and their semantic relations. We compared signal levels in chess experts and novices in region of interest (ROI) analyses using four independent fMRI datasets taken from previously published studies on chess expertise (Bilalić et al., 2010, 2011a,b, 2012). We analyzed three ROIs defined by the data from Huberle and Karnath (2012). All three regions were located in the area of the right or left TPJ. While in three of these studies (Bilalić et al., 2010, 2011b, 2012) visual processing required an analysis of highly complex chess positions, one task (Bilalić et al., 2011a) focused on simple object perception.

MATERIALS AND METHODS

PARTICIPANTS

Eleven subjects (3 males/8 females; mean age 24.6 years, SD ± 0.7 years) participated in the study of Huberle and Karnath (2012). Subjects had normal or corrected to normal vision and reported no history of neurological impairment affecting their visual capacity. In all four studies of Bilalić et al. (2010, 2011a,b, 2012) expert as well as novice chess players participated (**Table 1**). Tournament players get rated based on their performance against other rated players. The international chess Elo scale is an interval scale with a theoretical mean of 1500 and standard deviation of 200 (Elo, 1978). Experts are players with a rating of 2000 Elo points or more. The experts included in the present studies were rated with an average around 2100 points. Novice players were hobby players who played chess occasionally. Their chess skills were clearly inferior to experts but they had no difficulties in identifying chess pieces and their functions. All players were male and right-handed. The Institutional Review Board of the Ethic Committee of Tübingen University approved both studies and written informed consent was obtained from all participants. All studies were performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Table 1 | Participants in the studies of Bilalić et al. (2010, 2011a,b, 2012): group, mean age, mean skill level as measured by the Elo rating (see Methods) with standard deviation (SD), number of standard deviations above the mean, and number of participants in each group in all four experiments.

Experiment	Group	Age ± SD	Elo ± SD	SDs above mean	*n*
1	Expert	30 ± 2	2117 ± 53	3	7
	Novice	28 ± 1	–	–	8
2	Expert	29 ± 7	2130 ± 147	3	8
	Novice	29 ± 5	–	–	8
3	Expert	30 ± 2	2117 ± 53	3	7
	Novice	29 ± 1	–	–	8
4	Expert	30 ± 5	2108 ± 148	3	8
	Novice	29 ± 4	–	–	15

PROCEDURE AND STIMULI

In the study of Huberle and Karnath (2012) a global circle or square was constructed from smaller local images of circles or squares. **Figure 1A** illustrates examples from this set of stimuli. Objects at the global level were scrambled by exchanging a certain percentage of the local images with each other, thereby producing a set of stimuli at scrambling levels of 20-, 40-, 60- and 80%. The behavioral results of a two-alternative forced choice (2AFC) task to report the category of the object at the global level ("global circle" vs. "global square") showed that in 20% scrambled stimuli the global gestalt was easily perceived (97% Correct) whereas 80%-scrambling almost completely prevented global perception (52% Correct).

The four studies of Bilalić et al. (2010, 2011a,b, 2012) comprised five analyses of complex chess related visual stimuli. We combined the data from two analyses, originally reported by Bilalić et al. (2010, 2012), because the data of these analyses came from the same imaging sessions with the same subjects. In the following we address this set of data as Experiment 4.

Experiment 1 (Bilalić et al., 2011b)

Participants indicated if the current stimulus was the same as the previous one. There were four classes of stimuli: chess and face stimuli, which were presented upright or upside-down (**Figure 1B**). The face stimuli were black-white pictures of students (Leube et al., 2001, 2003). The chess stimuli were full-board positions taken from a four-million-chess-game database (ChessBase Mega Base 2007, ChessBase GmbH, Hamburg, Germany; www.chessbase.com). Stimuli from four categories (faces upright, chess upright, faces inverted, chess inverted) were presented in blocks of five stimuli. A single stimulus lasted for 2.75 s and was followed by a random noise mask for 0.25 s. A baseline (gray screen with a central fixation cross) was presented at the beginning, after each block, and at the end of the experiment for

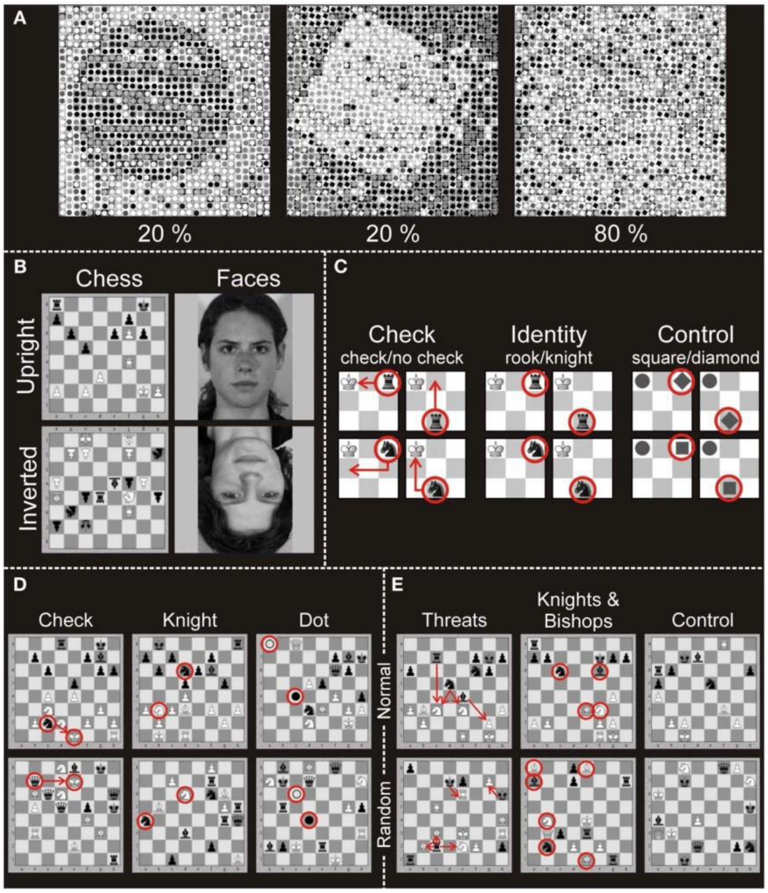

FIGURE 1 | Stimuli applied in the different experiments. (A) Illustration of the global stimuli used in the experiment of Huberle and Karnath (2012). The pictures show two 20% scrambled global objects (circle, square; intact global perception) and one 80% scrambled global object (disturbed global perception). **(B)** Stimuli used in Experiment 1 (Bilalić et al., 2011b). Pictures of full-board chess positions or faces were presented upright or inverted. Participants had to indicate whether the currently presented stimulus matched the previously presented stimulus. **(C)** Stimuli of Experiment 2 (Bilalić et al., 2011a). The stimuli were presented on a 3 × 3 miniature chess board. In the check task participants indicated whether the black piece (knight or rook) gives the white king check. In the identity task participants indicated whether the presented black piece is a rook or a knight. In the control task participants identified geometrical shapes (square or diamond). **(D)** Stimuli of Experiment 3 (Bilalić et al., 2011b). Pictures of full-board chess positions were presented. Participants had to indicate whether the white king was in check in the check task, whether there were knights of both colors presented in the knight task, or whether two dots (black and white) were present in the control (dot) task. **(E)** Stimuli of Experiment 4 (Bilalić et al., 2010, 2012). Pictures of full-board chess positions were presented. Participants had to indicate whether the number of black threats (how many times black can take white) was four in the threat condition, whether the number of knights and bishops was four in the knights and bishops task and whether the number of all pieces on the board was 15 in the control task. In all three tasks of Experiments 3 and 4, there were two types of positions: normal (taken from chess games of masters) and random (pieces were randomly distributed on the board).

14 s. All four conditions were presented four times in each of three runs (12 blocks of each condition in all runs).

Experiment 2 (Bilalić et al., 2011a)

This experiment featured three tasks. In the check task, participants indicated if the white king was attacked (i.e., given check) by the only present black piece. There were four different stimuli with two pieces on a 3 × 3 miniature chess board (**Figure 1C**). The white king was always on the first square of the upper left corner, while the identity of the other piece (knight or rook) and its location (middle of the lower row or the end of the upper row) varied. In the Identity task, participants were presented with the same stimuli as in the check task, but this time they identified the black piece presented. In the non-chess control task, chess pieces had been exchanged by gray-colored geometrical shapes (a circle for the king; a diamond and square for knight and rook, respectively). In parallel to the two chess tasks, the identity (diamond or square) and position (middle of the lower row or the end of the upper row) of the target stimulus were varied, and participants indicated its shape. Stimuli were presented in a block design. There were four runs and 12 blocks in each of them (four blocks for each condition in a single run). The runs were block-randomized and counterbalanced across participants. The experiment started with an empty 3 × 3 board (baseline) for 13.5 s and was followed by a written instruction for 3 s indicating the task type (check, identity, or control). After the instruction an empty 3 × 3 board was presented for 1.5 s. After 1 s a black center cross appeared and was presented for 0.5 s to warn participants about the upcoming stimulus. The following stimulus lasted for 2 s. There were four trials (stimuli) in a block, and after each block the baseline was presented.

Experiment 3 (Bilalić et al., 2011b)

These tasks were similar to the previous experiment—recognizing if the white king was in check (check task), recognizing if knights of either color were present (knight task), and recognizing if a dot of either color was presented (dot task—see **Figure 1D**). The stimuli, however, consisted of full chess positions (containing 15–18 pieces) presented on a full 8 × 8 square chess board. There were two types of positions—normal and random. The normal positions were taken from the same ChessBase database as in Experiment 1 and were typical middle-game positions of master games not previously known to the participants. The random positions were generated by distributing the pieces on the board randomly using the rule that any piece of either color can occur on any square (Vicente and Wang, 1998; Gobet and Waters, 2003). There were four runs with 12 blocks each, comprising two blocks per condition (3 tasks × 2 position types) in a single run. The runs were block-randomized and counterbalanced across participants. The experiment started with a gray screen with a black center cross, which lasted 5–10 s, immediately followed by the instruction for 2.5 s, after which the actual block started. The stimulus was presented for 4 s and was followed by a mask made of a scrambled chess position, which lasted for 0.5 s. There were four trials (stimuli) in each block, and baseline was always presented after each block.

Experiment 4: (Bilalić et al., 2010, 2012)

In this experiment full chess boards with 15–18 pieces were presented in normal and random positions. New middle-game positions were sampled from the ChessBase database. The tasks involved enumerations of chess pieces and their relations (**Figure 1E**). In the threats task, players indicated whether the number of threats (black to white) was four. In the knights and bishops condition, the task was to indicate whether the number of knights and bishops of both colors was four. Finally, in the non-chess control task, all pieces regardless of color or type were counted (indicate if the number is 15).

There were six runs, two for each task. There was only one task (e.g., threats task) in a single run. In one run, 10 meaningful and 10 meaningless stimuli were presented randomly. The runs were block-randomized and counterbalanced across participants. We first presented a starting board (all pieces at their initial location) with a fixation cross as a baseline with jittered duration (6–10 s). After a short gap (0.5 s), the target stimulus was presented until response, followed by the baseline of the next trial. Before the actual sessions, participants were given two practice trials for each task. The reaction time (i.e., the time to complete the task) was the time between stimulus onset until the participant pressed the button.

In all experiments, the stimuli were projected on a screen above the head of the participant via a video projector placed in the adjacent room. The setup resulted in a visual field of 14.6° for the whole scene. Participants saw the stimuli through a mirror mounted on the head coil and indicated their decision by pressing one of two buttons of an MRI-compatible response device held in their right hand.

MRI ACQUISITION

All fMRI data were acquired using a 3-T scanner (Siemens Trio) with a 12-channel head coil at the University Hospital of Tübingen. All measurements covered the whole brain using standard echo-planar-imaging (EPI) sequences. For the experiments of Bilalić et al. (2010, 2011a,b, 2012) the following parameters were used: TR = 2.5 s; FOV = 192 × 192 mm; TE = 35 ms; flip angle: 90°; matrix size = 64 × 64; 36 slices with thickness of 3.2 + 0.8 mm gap resulting in voxels with a resolution of 3 × 3 × 4 mm^3. The study of Huberle and Karnath (2012) used the following parameters: TR = 2 s; FOV = 192 × 192 mm; TE = 40 ms; flip angle: 90°; matrix size = 64 × 64; 24 axial slices with a thickness of 5 mm.

FUNCTIONAL MRI DATA ANALYSIS

The imaging data of Huberle and Karnath (2012) were originally processed using Brain Voyager®, whereas the data of Bilalić et al. (2010, 2011a,b, 2012) were analyzed using SPM5 (Wellcome Department of Imaging Neuroscience, London, UK; http://www.fil.ion.ucl.ac.uk/spm). Brain Voyager® and SPM differ from each other in some crucial aspects. For example, volume normalization in BrainVoyager® transforms the data to the Talairach space whereas normalization in SPM is based on templates in MNI space (Goebel et al., 2006; Lancaster et al., 2007). For the sake of a direct transfer between the studies we re-analyzed the dataset of Huberle and Karnath (2012) using SPM8 (Wellcome Department of Imaging Neuroscience, London, UK; http://www.fil.ion.ucl.ac.uk/spm). Only for the data of Huberle and Karnath (2012) temporal offsets of slice acquisition were accounted for by a temporal realignment. For both studies further preprocessing included spatial realignment of all images of a subject to the mean functional image for motion correction. Only in the studies by Bilalić et al. (2010, 2011a,b, 2012) residual motion artifacts induced by a susceptibility-by-movement interaction were additionally addressed using the unwarp function of SPM5. The mean EPI and all functional images were co-registered to the anatomical image for every participant. All images were normalized using the respective T1-weighted template and smoothed with a FWHM of 8 mm. Modeling of the time series of hemodynamic activation was based on the canonical response function as implemented in SPM5 and SPM8. A high-pass filter with a cutoff of 128 Hz eliminated low-frequency noise components and a correction for temporal autocorrelation in the data was applied using an autoregressive AR(1) process.

In the re-analysis of the Huberle and Karnath (2012) data, predictors for each experimental condition were constructed by a convolution of stimulus onsets for 20-, 40-, 60- and 80%-scrambled objects with the hemodynamic response function. The resulting design matrices comprised 4 experimental regressors, one for each scrambling level. Additionally, we included six covariates to capture residual movement-related artefacts. We used the individual participants' contrast images obtained from the first-level analysis for the second-level analysis. Areas involved in the intact perception of global gestalt were identified as those voxels that showed significantly higher signals for 20%-scrambled objects (intact global perception) compared to 80%-scrambled objects (disturbed global perception) based on a voxel-level threshold of $p < 0.001$ (uncorr.) with a cluster extent of at least 50 voxels in the area of the TPJ. We used a relatively liberal threshold to get bilateral ROIs and extend the analysis also to a left-sided TPJ area that was delineated using the same methods and thresholds that served for the right hemisphere. The results of this re-analysis were topographically consistent with the original results produced with Brain Voyager®. However, because of small differences in the statistical procedures between both analysis packages the extent of individual clusters based on individual thresholds were slightly different. The individual clusters that resulted from the re-analysis and which were used for the later ROI analyses are specified in **Figure 2**. In the further analyses we will label the three ROIs according to their localization as right, left anterior and left posterior TPJ ROI.

In the first two experiments of Bilalić and colleagues (Bilalić et al., 2011a,b), all trials were modeled with their full duration. In Experiment 3 (Bilalić et al., 2011b) the first second and in Experiment 4 (Bilalić et al., 2010, 2012) the first three seconds of each trial were used in order to keep the duration for each condition constant. The rest of the trial was also explicitly specified as a nuisance regressor, while the baseline was implicitly modeled. The mean percent signal changes (PSC) within each ROI were extracted for each participant and condition using MarsBar (http://marsbar.sourceforge.net). The PSC was calculated by dividing the maximum of the time course of the respective estimated event for this condition by the beta value for the constant session mean regressor. PSC values from experts and novices for the respective experiments and conditions were then analyzed with repeated measures ANOVAs.

RESULTS

In all experiments, chess experts showed a clear behavioral advantage compared to novices for chess related stimuli but not for the control stimuli (for details see: Bilalić et al., 2010, 2011a,b, 2012). To have an overview over all experiments and the respective results see **Table 2**.

EXPERIMENT 1

For Experiment 1 we calculated a 2 × 2 × 2 repeated measures ANOVA with the following factors and levels: expertise (expert vs. novice) × task (chess vs. face) × presentation (normal vs. inverted presentation).

Right TPJ

Experts showed stronger activation in the right TPJ area compared to novices depending on the stimulus category administered in the particular tasks (**Figure 3A**). Significantly stronger activations were evident for chess related stimuli in experts, while we found no significant difference between experts and

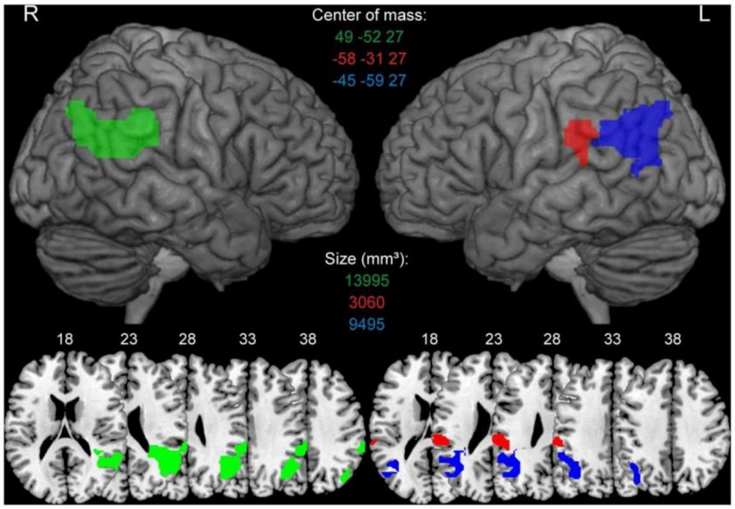

FIGURE 2 | Regions of interests (ROIs) derived from Huberle and Karnath (2012). ROIs were identified as those voxels that showed significantly higher BOLD signals for 20%-scrambled objects (intact global perception) compared to 80%-scrambled objects (disturbed global perception) based on a voxel-level threshold of $p < 0.001$ (uncorr.). The green color indicates the right TPJ ROI, red describes the left anterior TPJ ROI, blue indicates the left posterior TPJ ROI. ROIs are presented on a 3D rendered surface and axial slices for the left and right hemisphere. MNI coordinates of the center of mass and size of every ROI in mm^3 is denoted in the corresponding color.

Table 2 | Results of statistical comparisons between experts and novices are indicated by a '+' if a significant difference for the respective experiment and factor combination was observed and '0' if the difference was not significant.

Experiment task	1 N-Back		2 Detection (mini chess board)			3 Detection (full chess board)			4 Counting		
Conditions	**Chess**	**Faces**	**Check/ no check**	**Rook/ knight**	**Control**	**Check/ no check**	**Identity**	**Control**	**Threats**	**Knights & bishop**	**Control**
TPJ RIGHT											
Result	+	0	0	0	0	+	+	+	+	+	0
TPJ LEFT ANTERIOR											
Result	+	0	0	0	0	+*	0	0	+	+	0
TPJ LEFT POSTERIOR											
Result	+	0	0	0	0	+*	0	0	0	0	0

The asterisks mark significant results derived from preceding full factorial analyses with p-values slightly above 0.05 (please see results section for Experiment 3).

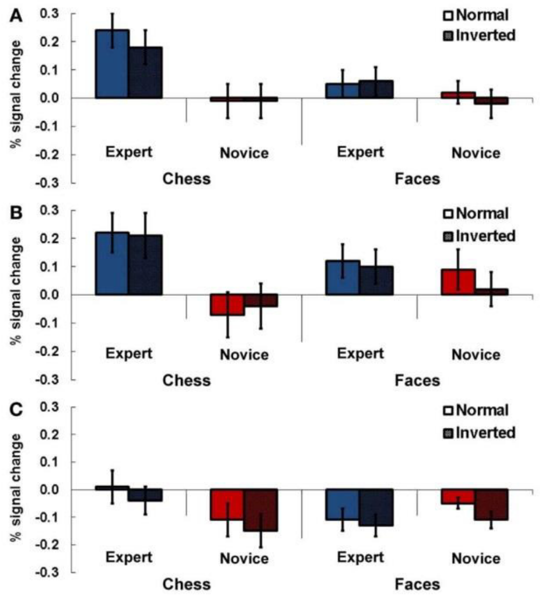

FIGURE 3 | Results Experiment 1. Percent signal change (PSC) for the two experimental conditions chess and faces (normal and inverted presentation) for experts and novices. Subjects had to indicate whether the currently presented stimulus matched the previously presented stimulus. Results are presented for TPJ ROI right **(A)**, left anterior **(B)** and left posterior TPJ **(C)**. Error bars indicate standard error of the mean.

novices for faces. The statistical analysis showed a significant main effect for task [$F_{(1,\,13)} = 6.74$, $p = 0.02$, $\eta_p^2 = 0.34$] and a significant interaction effect for the factors expertise and task [$F_{(1,\,13)} = 8.92$, $p = 0.01$, $\eta_p^2 = 0.41$]. Two separate Two-Way ANOVAs for the two tasks (chess/faces, with factors presentation and expertise) showed a significant main effect for expertise for chess related stimuli [$F_{(1,\,13)} = 7.14$, $p = 0.02$, $\eta_p^2 = 0.36$] while no effect was observed in the control condition [faces, main effect expertise: $F_{(1,\,13)} = 0.86$, $p = 0.37$, $\eta_p^2 = 0.06$]. In these analyses, there was no effect involving the factor presentation ($p > 0.12$).

Left anterior TPJ

In the anterior left TPJ ROI a similar result pattern emerged. There was a stronger activation in this region for experts than in novices depending on the stimulus material administered (**Figure 3B**). In this ROI experts also showed stronger activations for complex chess related stimuli, while no meaningful difference between experts and novices was observable for faces. This was approved by the statistical analysis: a Three-Way ANOVA showed a significant interaction effect for expertise and task [$F_{(1,\,13)} = 15.09$, $p = 0.002$, $\eta_p^2 = 0.54$]. The following separate ANOVAs for the two tasks revealed a significant main effect for expertise for chess stimuli [$F_{(1,\,13)} = 7.50$, $p = 0.017$, $\eta_p^2 = 0.37$], while a significant main effect in the faces condition was present for the factor presentation only [$F_{(1,\,13)} = 6.67$, $p = 0.02$, $\eta_p^2 = 0.34$].

Left posterior TPJ

For the posterior left TPJ ROI the previous result pattern was not observable (see **Figure 3C**). The Three-Way ANOVA showed a significant main effect for presentation [$F_{(1,\,13)} = 16.99$, $p = 0.001$, $\eta_p^2 = 0.57$] and a significant interaction effect for the factors task and expertise [$F_{(1,\,13)} = 8.68$, $p = 0.011$, $\eta_p^2 = 0.40$]. In the subsequent Two-Way ANOVAs for the two different tasks (chess/faces) a significant main effect for presentation was observable in the chess task [$F_{(1,\,13)} = 5.28$, $p = 0.039$, $\eta_p^2 = 0.29$] while no effect was present for faces [$F_{(1,\,13)} = 2.84$, $p = 0.12$, $\eta_p^2 = 0.18$].

EXPERIMENT 2

For Experiment 2 a 2 × 3 repeated measures ANOVAs with the factors expertise (expert vs. novice) and task (check vs. identity vs. control) were calculated for each ROI. These analyses did not reveal any differences between experts and novices (see **Figure 4**).

Right TPJ

For the right TPJ region we found a significant main effect for task [$F_{(2,\,28)} = 4.44$, $p = 0.021$, $\eta_p^2 = 0.24$].

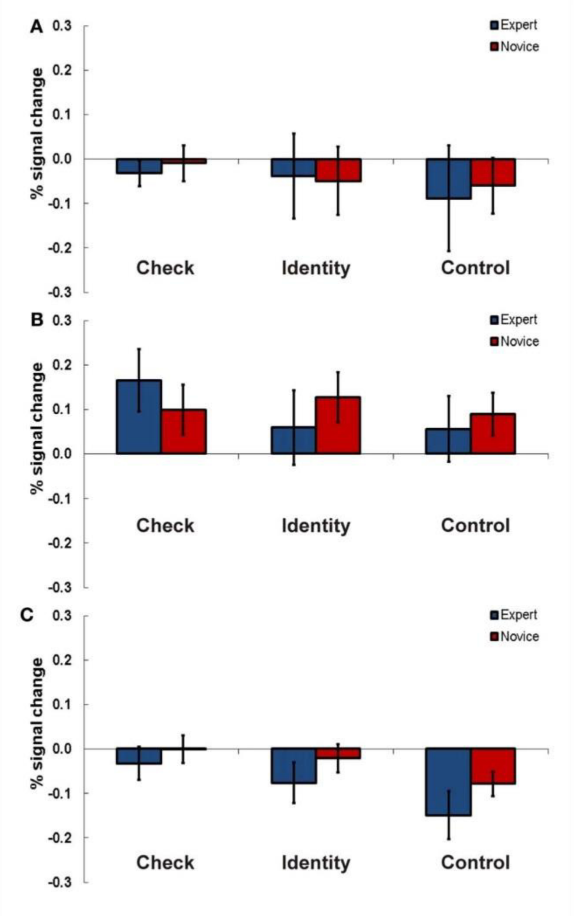

FIGURE 4 | Results Experiment 2. Percent signal change (PSC) for the three experimental conditions check (indicate if knight is in check), identity (recognition of a chess piece), and control (recognition of a geometrical shape) for experts and novices in TPJ ROI right **(A)**, left anterior **(B)**, and left posterior TPJ **(C)**. Error bars indicate standard error of the mean.

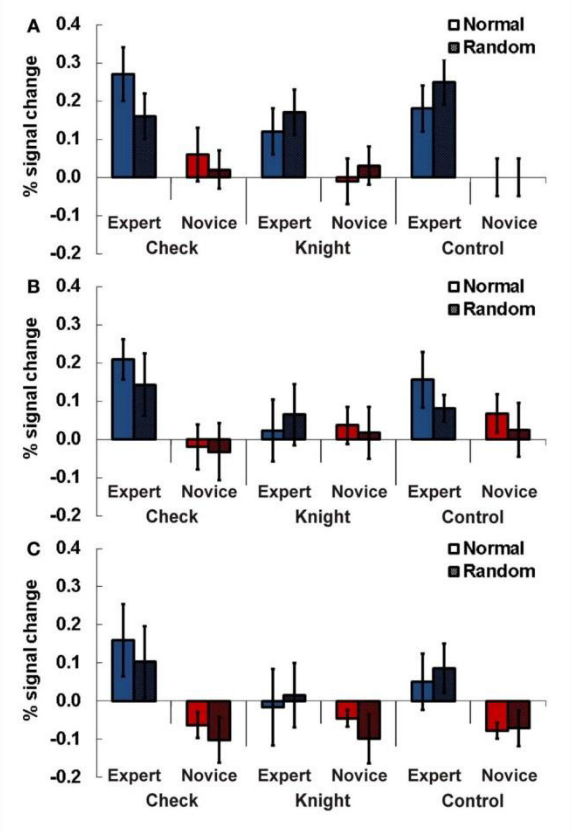

FIGURE 5 | Results Experiment 3. Percent signal change (PSC) for the three experimental conditions check (recognizing if the white king is in check), knight (recognizing if black/white knights are present), and control (recognizing if a black/white dot is presented) for experts and novices in normal (chess pieces arranged according to real chess matches) and random (chess pieces in randomized distribution) chess arrays. Results are presented for TPJ ROI right **(A)**, left anterior **(B)**, and left posterior TPJ **(C)**. Error bars indicate standard error of the mean.

Left anterior TPJ

Also in the anterior left TPJ area we found a significant main effect for task [$F_{(2,\,28)} = 3.63$, $p = 0.04$, $\eta_p^2 = 0.21$]. Additionally, the interaction of task and expertise was significant [$F_{(2,\,28)} = 4.68$, $p = 0.015$, $\eta_p^2 = 0.26$]. *Post-hoc t*-tests looking for significant differences between experts and novices in the three tasks did not show any significant results.

Left posterior TPJ

In the posterior left TPJ region the Two-Way ANOVA showed a significant main effect for task as well [$F_{(2,\,28)} = 15.98$, $p = 0.001$, $\eta_p^2 = 0.53$].

EXPERIMENT 3

In this particular experiment a 2 × 3 × 2 design was used. It contained the following factors and levels: expertise (expert vs. novice) x task (check vs. knight vs. dot) x position (normal vs. random).

Right TPJ

In the right-hemispheric TPJ region experts showed stronger activations compared to novices across all three tasks (see **Figure 5A**). A Three-Way ANOVA including all factors confirmed this observation by a significant main effect for expertise [$F_{(1,\,13)} = 7.70$, $p = 0.016$, $\eta_p^2 = 0.24$]. We observed a slightly non-significant interaction effect for the factors task and position [$F_{(1,\,13)} = 3.82$, $p = 0.07$, $\eta_p^2 = 0.19$]. No other main effects or interactions were significant (all $p > 0.28$).

Left anterior TPJ

In the anterior left-hemispheric ROI the Three-Way ANOVA revealed an interaction effect for the factors expertise and task just above the adopted type-1 error probability threshold of 0.05

$[F_{(2,\ 26)} = 3.12, p = 0.06, \eta_p^2 = 0.20$, see **Figure 5B**]. Subsequent separate 2 × 2 ANOVAs for the different tasks showed a significant main effect for expertise in the check task $[F_{(1,\ 13)} = 5.12, p = 0.042, \eta_p^2 = 0.28]$.

Left posterior TPJ

The analysis for the posterior left-hemispheric ROI also revealed an interaction effect for the factors expertise and task slightly above the probability threshold $[F_{(2,\ 26)} = 3.23, p = 0.056, \eta_p^2 = 0.20$, see **Figure 5C**]. Separate 2 × 2 ANOVAs for the different tasks demonstrated a significant main effect for expertise in the check task $[F_{(1,\ 13)} = 4.78, p = 0.048, \eta_p^2 = 0.27]$.

EXPERIMENT 4

For Experiment 4 a 2 × 3 × 2 design was applied. It comprised the following factors and levels: expertise (expert vs. novice) × task (threat vs. knight & bishop vs. control) × position (normal vs. random).

Right TPJ

In the right-hemispheric TPJ region experts compared to novices showed higher signals for chess related stimuli than for control material (see **Figure 6A**). This result was confirmed by a Three-Way ANOVA showing a significant main effect for expertise $[F_{(1,\ 21)} = 13.19, p = 0.002, \eta_p^2 = 0.37]$ and an interaction effect for the factors expertise and task $[F_{(2,\ 42)} = 5.18, p = 0.01, \eta_p^2 = 0.20]$. In separate ANOVAs for every task (threat, knight & bishop, control) significantly higher activations for complex chess stimuli were confirmed for chess experts compared to novices. The main effect for expertise was significant for the threat $[F_{(1,\ 21)} = 29.24, p < 0.001, \eta_p^2 = 0.58]$ and the knight & bishop task $[F_{(1,\ 21)} = 8.68, p = 0.008, \eta_p^2 = 0.29]$, but slightly not for the control task $[F_{(1,\ 21)} = 3.65, p = 0.07, \eta_p^2 = 0.15]$.

Left anterior TPJ

For the anterior left-hemispheric TPJ region we observed a similar result pattern. Experts compared to novices showed stronger neuronal activations for chess related stimuli than for control material (see **Figure 6B**). A Three-Way ANOVA confirmed this observation with a significant main effect for expertise $[F_{(1,\ 21)} = 12.42, p = 0.002, \eta_p^2 = 0.40]$ and a significant interaction effect of expertise and task $[F_{(2,\ 42)} = 5.89, p = 0.006, \eta_p^2 = 0.24]$. The subsequent Two-Way ANOVAs for the three tasks revealed significant main effects for the factor expertise for the threat $[F_{(1,\ 21)} = 5.54, p = 0.029, \eta_p^2 = 0.23]$ and the knight & bishop task $[F_{(1,\ 21)} = 10.20, p = 0.005]$, while no effect was present for control material $[F_{(1,\ 21)} = 1.85, p = 0.19, \eta_p^2 = 0.35]$.

Left posterior TPJ

In the posterior left TPJ we found a significant three-way interaction for expertise x task x position $[F_{(2,\ 42)} = 4.12, p = 0.024, \eta_p^2 = 0.18$, see **Figure 6C**]. Subsequent ANOVAs for every task showed a significant interaction for position and expertise $[F_{(1,\ 21)} = 4.39, p = 0.05, \eta_p^2 = 0.19]$ in the knights & bishop task. The following *post-hoc* t-tests supported a difference between experts and novices for normal $[T_{(21)} = 2.32, p = 0.03$, Cohen's $d = 0.95]$ but not random presentations $[T_{(21)} = 1.29, p = 0.21, d = 0.59]$. However, the difference for normal presentations barely missed the priorily adopted significance threshold of $p = 0.05$ after Bonferroni correction.

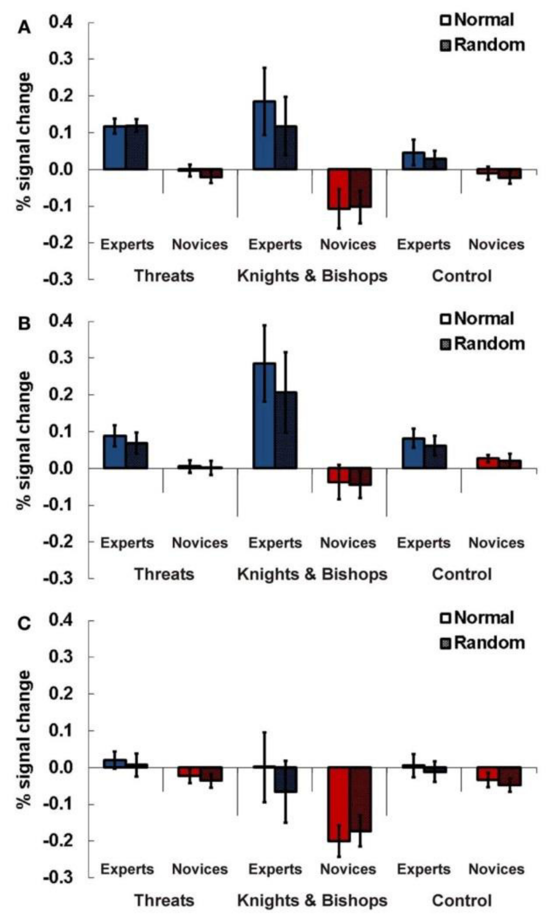

FIGURE 6 | Results Experiment 4. Percent signal change (PSC) for the three experimental conditions threats (indicated whether the number of threats of black to white was four), knights and bishops (indicate whether the number of knights and bishops of both colors was four), and control (non-chess control task, all pieces regardless of color or type were counted, indicate if the number is 15) for experts and novices in normal (chess pieces arranged according to real chess matches) and random (chess pieces in randomized distribution) chess arrays. Results are presented for TPJ ROI right **(A)**, left anterior **(B)**, and left posterior TPJ **(C)**. Error bars indicate standard error of the mean.

DISCUSSION

In a series of four independent ROI analyses the BOLD signal changes in bilateral TPJ areas during the perception of complex chess related visual stimuli were investigated. We examined possible neuronal differences between chess experts and novices in left and in right TPJ regions that were associated with localized signal increases in an independent experiment on global perception (Huberle and Karnath, 2012). We hypothesized that superior visual processing skills for highly familiar, complex material (expert view) are strongly associated with enhanced visual integration abilities: chess experts perceive chess situations rather at the global level (full chess board) whereas novices focus on the local level (individual chess pieces). Indeed, experts compared to novices showed higher signals in bilateral TPJ areas during the presentation of complex but highly familiar chess stimuli in three of four ROI analyses. These signal differences were consistent for all stimuli with meaningful, chess-related content. Furthermore, the absence of significant differences between experts and novices in experiment 2 is in good agreement with our hypothesis. The stimuli used in Experiment 2 (Bilalić et al., 2011a; see **Figure 1C**) displayed a simplified version of a checkerboard with three by three fields. In the other experiments stimuli consisted of full chess boards and multiple chess pieces in various configurations (Bilalić et al., 2010, 2011b, 2012; see **Figures 1B,D,E**).

Our observations strengthen previous data that suggested a significant role of the TPJ in the processing of complex object configurations (Huberle and Karnath, 2012). This assumption is in good agreement with our current knowledge about the typical bilateral area of damage or degeneration in patients with simultanagnosia (Rizzo and Hurtig, 1987; Friedman-Hill et al., 1995; Rafal, 1997; Karnath et al., 2000; Tang-Wai et al., 2004; Valenza et al., 2004; Huberle and Karnath, 2006; Huberle et al., 2010; Thomas et al., 2012). Against the assumption that TPJ plays a specific role for global perception it might be argued that it simply controls attentional switches between or the balancing of local and global visual inputs. Mosaic stimuli like the ones used by Huberle and Karnath (2012) would allow for a detection of global shapes by low scale visual feature detectors early in the visual system, balanced with information coming from high scale visual feature detectors by the TPJ. However, the observation of similar signal changes in a set of experiments using chess board stimuli argues against this interpretation. The relationships between the local items, i.e., chess pieces, are not created through physical features but through semantic relations between the local stimuli whereas the physical characteristics are substantially different from the typical stimuli used in studies on visual integration (e.g., Fink et al., 1996; Huberle and Karnath, 2012). Thus, we assume that our observation of consistent signal changes at the TPJ in two experimentally very different situations with substantially different stimulus material supports a role of TPJ in visual integration processes beyond attentional control.

The ROIs for the right and left hemisphere analyzed in the present study were different. Whereas a single ROI was analyzed for the right hemisphere, two separated ROIs were used for the left hemisphere. This was the consequence of the transfer of the functional definition of these ROIs from the preceding global perception experiment (Huberle and Karnath, 2012) to the chess expert datasets based on accepted voxel- and cluster-level thresholds. Thus, the definition of these regions was based on objective statistical criteria to allow reproducibility. Obviously, using other voxel- and cluster-level thresholds or slightly different first- and second-level statistics might have resulted in somewhat different delineations of the ROIs. However, the general pattern of the results would not differ. The signal patterns in the analyzed ROIs suggested a relative lateralization of visual integration to the right hemisphere. We found strong interaction effects including the factor expertise for the large right TPJ ROI, whereas only the anterior left TPJ ROI revealed consistent differences between experts and novices during the presentation of complex visual material across Experiments 1, 3, and 4. In contrast, the more posterior left TPJ region showed much less consistent results with a somewhat conclusive signal pattern only for Experiment 3. The idea of a relative lateralization that was not tested explicitly would be in agreement with several studies arguing for a right hemispheric specialization for global aspects in visual integration (Martin, 1979; Robertson et al., 1988; Fink et al., 1997b; Yamaguchi et al., 2000) and perception of complex chess configurations (Krawczyk et al., 2011). Nevertheless, one study reported a left hemispheric dominance for processing of global features of complex visual material (Fink et al., 1997b). This variability between fMRI studies depending on the particular task and samples may also indicate that global perception processes are bilaterally represented in the human left and right hemispheres. The fact that the vast majority of the patients showing simultanagnosia suffered bilateral brain damage (Rizzo and Hurtig, 1987; Friedman-Hill et al., 1995; Rafal, 1997; Karnath et al., 2000; Tang-Wai et al., 2004; Valenza et al., 2004; Huberle and Karnath, 2006, 2010; Thomas et al., 2012) supports this assumption.

The observed association of superior skills with an increased BOLD signal in a confined cortical structure is also in line with studies investigating the neuronal effects of visual perceptual training and expert view in other brain regions. However, in numerous functional imaging studies on perceptual learning it was demonstrated that training results in higher BOLD signals in task-related brain areas (Gauthier et al., 1999; Grill-Spector et al., 2000; Furmanski et al., 2004; Op de Beeck et al., 2006; Jastorff et al., 2009). Particularly in the context of global perception, an increase of BOLD signal amplitudes was associated with an improvement of complex stimulus processing through learning (Maertens and Pollmann, 2005; Zhang and Kourtzi, 2010; Zhang et al., 2010; Mayhew et al., 2012). Beyond, research on expert-novice differences showed higher BOLD signals in experts (Gauthier et al., 2000; Rhodes et al., 2004; Harley et al., 2009). Our observations may also be addressed to prolonged training effects causing modulation and fine-tuning of other non-visual areas (Moore et al., 2006; Guida et al., 2012). We therefore suggest that the increase of the BOLD signal in the TPJ represents an important contribution to the behavioral difference between experts and novices. Further, we did not observe any significant effects for inverted presentations or random chess positions, arguing for highly automatized global processing mechanisms for chess configurations in over-trained experts. Whereas other complex visual stimuli like faces become more or less incomprehensible by an inversion, chess boards are still interpretable. Therefore, we did not expect clear-cut inversion effects for global chess stimuli in the TPJ ROIs, similar to the well-established differences for faces in the respective brain areas (Epstein et al., 2006).

However, neuroimaging studies of learning and expertise in other cognitive domains, like visual working memory (WM), showed different or even opposite BOLD result patterns with behavioral changes (Landau et al., 2004; Kelly and Garavan, 2005; Jaeggi et al., 2007). Jaeggi et al. (2007) demonstrated higher BOLD signals in low-performers than in experts in a working memory task. Landau and colleagues (Landau et al., 2004) found that learning led to a decrease of BOLD signals in several cortical brain areas. Obviously, there may exist several other factors, like advantages in working memory or motivation driving neuronal signals in expert view. However, the present study highlights an important contribution of visual integration and the associated neuronal structures to superior visual skills in chess experts.

In conclusion, our data show that fMRI signals in the TPJ are increased during the observation of complex stimuli in experts who experienced an extensive training that most likely resulted in superior skills of visual integration. The results of our cross-paradigm ROI analyses shows that such signal increases are not only observed using highly selective global/local stimulus material in within-subject comparisons but can be detected in between-subject comparisons using stimulus material from a different field of research. In good agreement with previous fMRI studies (Himmelbach et al., 2009; Huberle and Karnath, 2012) and patient reports (Rizzo and Hurtig, 1987; Friedman-Hill et al., 1995; Rafal, 1997; Karnath et al., 2000; Tang-Wai et al., 2004; Valenza et al., 2004; Huberle and Karnath, 2006; Huberle et al., 2010; Thomas et al., 2012) the presented data supports the assumption of a crucial involvement of the left and the right TPJ in global gestalt perception.

ACKNOWLEDGMENTS

This work was supported by the European Union (ERC StG 211078), the DFG (Ka 1258/10-1; Bi 1450/1-2) and the Open Access Publishing Fund of the University of Tübingen.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 29 April 2013; accepted: 10 August 2013; published online: 28 August 2013.

Citation: Rennig J, Bilalić M, Huberle E, Karnath H-O and Himmelbach M (2013) The temporo-parietal junction contributes to global gestalt perception—evidence from studies in chess experts. Front. Hum. Neurosci. ***7****:513. doi: 10.3389/fnhum.2013.00513*

This article was submitted to the journal Frontiers in Human Neuroscience.

5 The role of size constancy for the integration of local elements into a global shape

The role of size constancy for the integration of local elements into a global shape

Johannes Rennig[1], Hans-Otto Karnath[1,2], Elisabeth Huberle[1,3]

[1]Center of Neurology, Division of Neuropsychology, Hertie-Institute for Clinical Brain Research, University of Tübingen, Tübingen, Germany
[2]Department of Psychology, University of South Carolina, Columbia, SC 29208, USA
[3]Neurology and Neurorehabilitation Center, Luzerner Kantonsspital, Luzern, Schweiz

Corresponding author:
Elisabeth Huberle
Neurology and Neurorehabilitation Center
Luzerner Kantonsspital
Spitalstrasse
CH-6000 Luzern 16, Switzerland
Phone: ++41 – 44 - 2 55 55 95
e-mail: elisabeth.huberle@luks.ch

Author contributions

This chapter was published in *Frontiers in Human Neuroscience* (Rennig et al., 2013). Elisabeth Huberle, Hans-Otto Karnath and Johannes Rennig designed the experiments. Johannes Rennig acquired and analyzed all the data. Johannes Rennig wrote the paper with the help of Elisabeth Huberle and Hans-Otto Karnath.

frontiers in
HUMAN NEUROSCIENCE

ORIGINAL RESEARCH ARTICLE
published: 03 July 2013
doi: 10.3389/fnhum.2013.00342

The role of size constancy for the integration of local elements into a global shape

Johannes Rennig[1], **Hans-Otto Karnath**[1,2] **and Elisabeth Huberle**[1,3]*

[1] Division of Neuropsychology, Center of Neurology, Hertie-Institute for Clinical Brain Research, University of Tübingen, Tübingen, Germany
[2] Department of Psychology, University of South Carolina, Columbia, SC, USA
[3] Neurology and Neurorehabilitation Center, Luzerner Kantonsspital, Luzern, Switzerland

Edited by:
Magdalena Chechlacz, University of Oxford, UK

Reviewed by:
Arnaud Saj, University Hospital of Geneva, Switzerland
Celine R. Gillebert, University of Oxford, UK

***Correspondence:**
Elisabeth Huberle, Neurology and Neurorehabilitation Center, Luzerner Kantonsspital, Spitalstrasse, CH-6000 Luzern 16, Switzerland
e-mail: elisabeth.huberle@luks.ch

Visual perception depends on the visual context and is likely to be influenced by size constancy, which predicts a size and distance invariant perception of objects. However, size constancy can also result in optical illusions that allow the manipulation of the perceived size. We thus asked whether the integration of local elements into a global object can be influenced by manipulations of the visual context and size constancy? A set of stimuli was applied in healthy individuals that took advantage of the "Kanizsa" illusion, in which three circles with open wedges oriented toward a center point are placed to form an illusionary perception of a triangle. In addition, a 3D-perspective view was implemented in which the global target ("Kanizsa" triangle) was placed in combination with several distractor circles either in a close or a distant position. Subjects were engaged in a global recognition task on the location of the "Kanizsa" triangle. Global recognition of "Kanizsa" triangles improved with a decreasing length of the illusory contour. Interestingly, recognition of "Kanizsa" triangles decreased when they were perceived as if they were located further away. We conclude that the integration of local elements into a global object is dependent on the visual context and dominated by size constancy.

Keywords: visual constancy, global perception, Gestalt, Kanizsa, visual context, perceptual grouping

INTRODUCTION

Principles of Gestalt perception have strongly influenced our understanding of visual cognition. In the past century, Gestalt psychologists like Koffka (1935) and Wertheimer (1923) postulated that the human brain determines single elements with common features as a single entity rather than a sum of separate parts. Stimuli used to investigate the integration of multiple elements into a complex object can be found in Navon letters (Navon, 1977), i.e., hierarchically organized visual stimuli where a global letter is constructed from an array of local letters, or the "Kanizsa" illusion (Kanizsa, 1955). This illusion consists of an arrangement of circles with a wedge like gap (so called "pac-man") that form an illusory angular figure. The "Kanizsa" illusion evokes neuronal responses similar to "real" geometrical figures in early and higher visual areas along the ventral stream (Hirsch et al., 1995; Ffytche and Zeki, 1996; Larsson et al., 1999; Halgren et al., 2003; Stanley and Rubin, 2003; Maertens and Pollmann, 2005, 2007; Maertens et al., 2008). Regarding the spatial characteristics of "Kanizsa" illusions it has been demonstrated that their global recognition performance decreases with an increasing length of the illusory contours (Kojo et al., 1993; Liinasuo et al., 1997). This observation is in line with a recent study showing that the spatial distance between local letters is crucial for recognition of Navon letters in neurological patients with simultanagnosia (Huberle and Karnath, 2006).

Besides physical properties of objects themselves, the visual environment plays an important role for efficient object recognition. In this context, the phenomenon of visual constancy is a crucial factor of human visual perception. Visual constancy is a key mechanism that allows the perception of familiar objects at a "standardized" shape, size, or color and is also critical for the invariant identification of objects regardless of changes in perspective, distance, lighting or the size of the retinal image (Emmert, 1881; Brunswik, 1934; Hebb, 1958; Fitzpatrick et al., 1982). Various perceptual illusions like the Ponzo or the Müller-Lyer illusion (Müller-Lyer, 1889; Ponzo, 1911) are explained by size constancy—a crucial aspect of visual constancy enabling invariant size perception. Moore and Egeth (1997) revealed a preattentional influence for grouping mechanisms in the way that the length estimation of simple lines presented within a dot array was affected by the configuration of the dots in the background. When these dots formed a Ponzo or Müller-Lyer illusion, the length estimation changed depending on the arrangement of the surrounding dots. Importantly, the effect was present although the participants were unaware of the dot configurations in the background.

A previous study (Beck, 1975) demonstrated a significant role of perspective on global recognition performance. Global perception improved if the global target was perceived further away by tilting the stimulus; global recognition was supported by this perspective change which produced a closer retinal spacing between local elements. We therefore asked whether global recognition performance is dependent on the perceived distance between the individual elements of hierarchically organized stimuli and hypothesized that a perspective manipulation inducing larger distances between local elements by means of size constancy might result in decreased global recognition. In contrast to the work by Beck (1975), the present study aimed to achieve a distance manipulation by mechanisms of size constancy preserving a constant retinal image. In detail, we presented healthy observers with a 3D perspective view of an edged wall, in which an illusory "Kanizsa" triangle in an array of distractors was placed either at the close (Front condition) or the distant (Back condition) part of the wall. We assumed that the distant section of the wall would be perceived subjectively larger compared to the close section although the physical and retinal image remained unchanged. If size constancy influences Gestalt perception, the illusory contours of the "Kanizsa" triangles presented in the Back condition should be more difficult to perceive (cf. Beck, 1975), resulting in a decrease in recognition performance.

METHODS

PARTICIPANTS

Twenty healthy individuals (5 males, 15 females; average age 24.0 years, $SD = 3.9$) participated in Experiments 1 and 2; another 20 observers (6 males, 14 females; average age 25.5 years, $SD = 4.4$) took part in Experiments 3 and 4; 22 subjects (2 males, 20 females; average age 23.4 years, $SD = 4.1$) were tested in Experiment 5. All participants had normal or corrected-to-normal vision, no history of brain damage, and gave their informed consent before the participation in the study, which has been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

In Experiments 2 and 4, one participant had to be excluded for the final analysis due to low performance. Even in the easiest stimulus conditions where all other subjects showed an accuracy between 80–100%, this subject's performance did not exceed the 50% chance rate. We attributed this behavior to a lack of motivation or comprehension. In Experiment 5, three participants had to be excluded due to the same reason.

STIMULI

Experiment 1

Stimuli displayed an edged stone wall with a perpendicular arrangement of the different parts of the wall (**Figure 2A**). The two main parts of the wall were oriented in parallel to the horizontal outline of the stimuli and appeared to be located close to the observer (Front) or further away (Back). In addition, the Front could be located to the left or the right from the center of the stimulus. All stimuli had a size of 19° × 19° visual angle, in which the Front covered an area of 19.0° × 9.5° with a size of the individual stones of 3.5° × 1.0°. The size of the Back was 7.0° × 5.0° with a size of individual stones of 1.4° × 0.4°. A fixation dot was placed at the center of the stimulus.

Finally, a 3-2-3 array of white circles composed of wedge-like gaps (also known as "pacman") was superimposed on the wall. The size of the array was 4.0° × 4.0°. The center of this array was placed in the center of the Front or the Back and thus located 6.5° to the right or the left from the central fixation dot. Three of the eight "pacmen" were oriented to enable the perception of an illusory triangle, while the remaining "pacmen" had a random orientation. The triangle was located at one of following positions within the array: (1) top/left, (2) top/right, (3) bottom/left, (4) bottom/right. The four possible positions were balanced for both presentation conditions (Front, Back) and sides (left, right) in all experiments. In order to facilitate the integration of the local "pacman" into a global triangle, we manipulated the size of the "pacmen." In detail, the following sizes of the "pacmen" were used: 0.4° (Size 1), 0.5° (Size 2), 0.6° (Size 3), 0.7° (Size 4), and 0.8° (Size 5). The distance of 1.8° (calculated from the center of the "pacmen") between the individual elements remained unchanged across conditions. Examples of the five sizes are shown in **Figure 1**.

Experiment 2

Experiment 2 aimed to test for differences in the integration of local elements into a global shape irrespective to the global perspective, but with respect to the local surround. The stimuli displayed a straight wall without the presence of edges (**Figure 2B**). The vertical extension of this wall was 11.0°, which was the average of the Front and Back in Experiment 1. In parallel to Experiment 1, the individual stones covered a size of 1.4° × 0.4° (Back) or 3.5° × 1.0° (Front). The stimulus parameters of the 3-2-3 array were identical to Experiment 1.

Experiment 3

Experiment 3 aimed to test for differences in the integration of local elements into a global shape irrespective of the local surround, but with respect to the global perspective. The stimuli for Experiment 3 were comparable to the stimuli used for Experiment 1 with the exception that individual stones were replaced by a uniform gray surface (average of all pixels belonging to the stone wall in Experiment 1; **Figure 3A**). The 3D-perspective was generated by a squared pattern on the bottom in front of the wall.

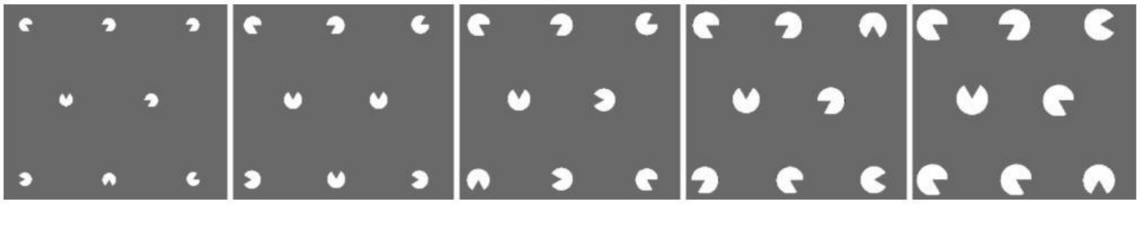

FIGURE 1 | Five 3-2-3 arrays with the five sizes of pacmen, with a Kanizsa triangle in the left upper corner; from left to right: Size 1–5.

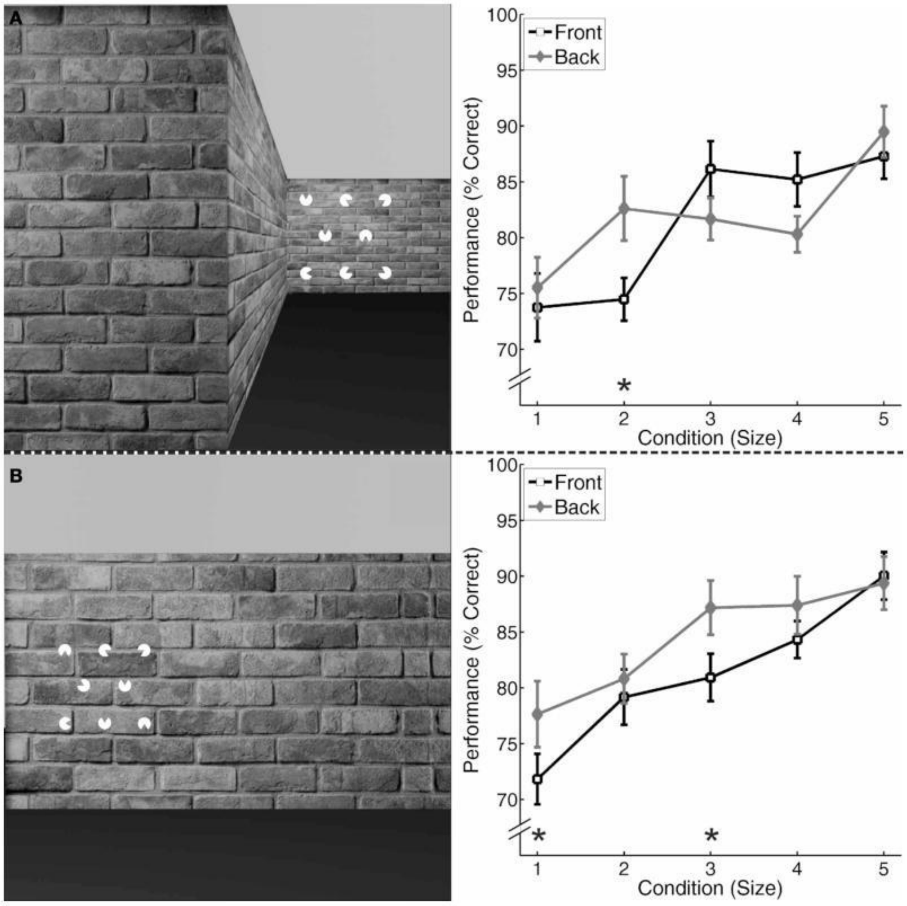

FIGURE 2 | Left: 3-2-3 array of white "pacmen" forming a "Kanizsa" triangle in one of four possible positions presented on one side of a shifted wall. (A) Stimulus for Experiment 1: 3-2-3 array presented on a naturalistic wall; **(B)** Stimulus for Experiment 2: 3-2-3 array presented on a wall appearing close (Front condition). The distant condition (Back) is not shown explicitly. **Right:** Results of Experiments 1 and 2 **(A,B)**: displayed is the average percentage and standard errors of correct identification of "Kanizsa" triangles for the five different conditions of the "pacman" (Size 1–5) and two locations (Front, Back). $^*p < 0.01$, Bonferroni corrected for five comparisons.

Experiment 4

In parallel to Experiment 3, Experiment 4 aimed to test for differences in the integration of local elements into a global shape irrespective of the local surround, but with respect to the global perspective. The 3-2-3 array was embedded in a gray square (average of all pixels belonging to the stone wall in Experiment 1; **Figure 3B**) with a size of 4.8° × 5.4°, while the remaining stimulus parameters were identical to Experiment 1.

Experiment 5

Experiment 5 should control the possibility of an influence of local perspective effects by the size of the gray square used in Experiment 4. It consisted of two different parts: a preliminary test and the main experiment. In the preliminary test, the stimulus set of Experiment 4 was used but the 3-2-3 array was removed and a second gray square was added. In addition, the size of the gray square in the Back remained constant (4.8° × 5.4°) while the size of the square in the Front was presented in ten different sizes (4.8° × 5.4°, 5.0° × 5.6°, 5.2° × 5.8°, 5.4° × 6.0°, 5.6° × 6.2°, 5.8° × 6.4°, 6.0° × 6.6°, 6.2° × 6.8°, 6.4° × 7.0°, 6.6° × 7.2°). **Figure 3C** shows a square of 6.4° × 7.0°, which was the size closest to the mean perceived size (see Results). We then determined the condition, in which the participant's perceived an equal size of the two gray squares. This condition was used for the main experiment, which was identical to Experiment 4.

PROCEDURE

All experiments were conducted in a room with dimmed light; stimuli were presented on a 19 inches CRT monitor with subjects located 57 cm in front of it. Stimulus presentation and data collection were controlled by a custom-made program using MatLab

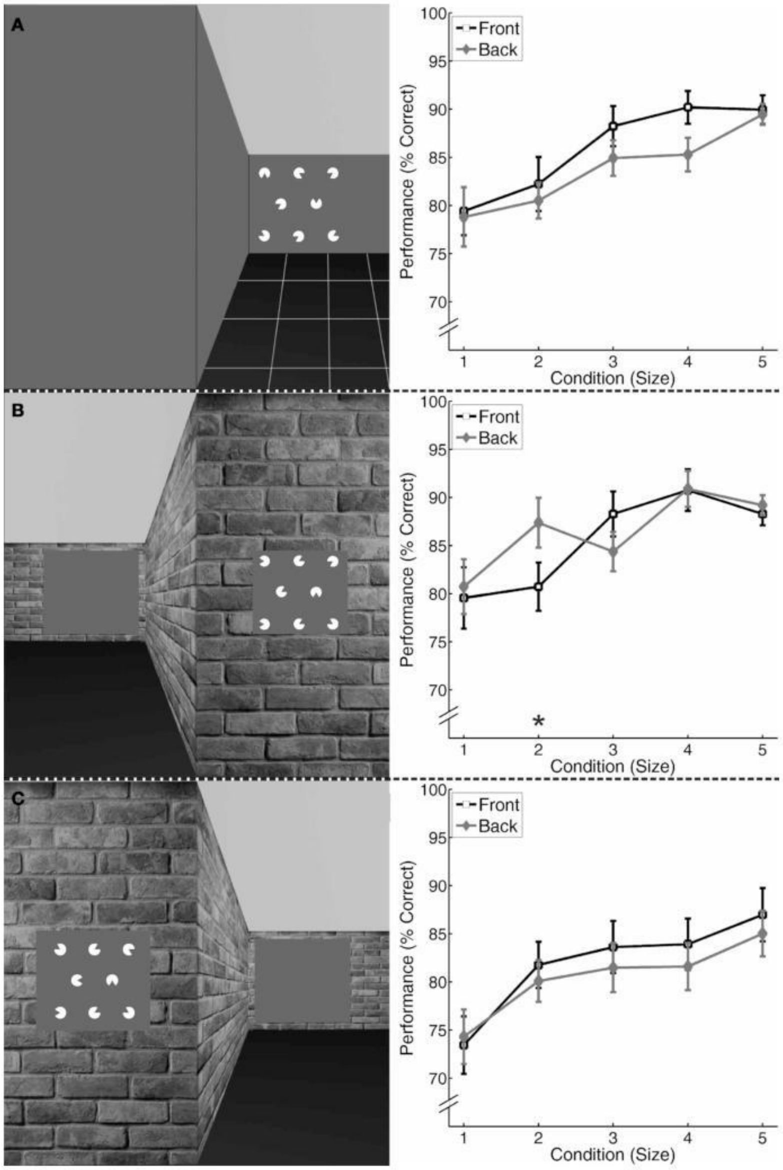

FIGURE 3 | Left: 3-2-3 array of white "pacmen" forming a "Kanizsa" triangle in one of four possible positions presented on one side of a shifted wall. (A) Stimulus for Experiment 3: 3-2-3 array presented on a uniform gray wall; **(B)** Stimulus for Experiment 4: 3-2-3 array presented on a gray box within a naturalistic wall. **(C)** Sample Stimulus for Experiment 5: 3-2-3 array presented on a size adjusted gray box within a naturalistic wall (6.4° × 7.0°, which was the size closest to the mean perceived size). **Right:** Results of Experiments 3–5 **(A–C)**: displayed is the average percentage and standard errors of correct identification of "Kanizsa" triangles for the five different conditions of the "pacman" (Size 1–5) and two locations (Front, Back). $^*p < 0.01$, Bonferroni corrected for five comparisons.

2003b (MathWorks) and the Psychophysics Toolbox (Version 2.54; Brainard, 1997).

Experiments 1–4

The same design and procedure were used for Experiments 1–4. Each experiment consisted of ten conditions (Front: Size 1–5, Back: Size 1–5) that were repeated 48 times, resulting in a total number of 480 trials. All trials were presented in a random order in three blocks of 160 trials each. Before the onset of the first trial, all observers were familiarized with the type of stimuli and task in a short practice session.

Each trial started with a stimulus presentation of 250 ms followed by a blank interval between 2250 and 3250 ms, in which the central fixation dot was presented in a gray background. This procedure resulted in a trial duration between 2500 and 3500 ms. During the blank interval, participants were engaged in a two alternative forced choice task on the position of the triangle. That is, they were instructed to indicate, if the location of the perceived triangle was at the top or the bottom of the 3-2-3 array by pressing a button in their right or left hand. The design was balanced for the position of the target triangle as well as the location of the array (left or right) with respect to its position (Front or Back). Further, the keymapping was counterbalanced across participants. Participants were instructed to maintain fixation throughout the study.

Experiment 5

The preliminary test consisted of ten conditions (Size 1–10) that were repeated 16 times each resulting in a total number of 160 trials. All trails were presented within one block. The participants were instructed to indicate which of the two squares was perceived larger. The condition of subjective equality was used for the main part of Experiment 5, which was identical to Experiments 1–4.

RESULTS

Experiment 1

Figure 2A shows that the percentage of correct responses tended to increase with an increasing size of the "pacman" for both Front and Back presentation conditions. We performed a repeated-measures ANOVA on the percentage of correct responses with Size (Size 1–5) and Position (Front, Back) as independent factors. The analysis revealed a significant interaction between the two factors [$F_{(4,\ 16)} = 4.50$, $p = 0.01$]. Simple main effects were investigated by comparing Front and Back positions for every size of the "pacman" by paired T-tests. Using a Bonferroni-correction to correct for multiple comparisons (resulting in an alpha level of.01) we observed significant differences for Size 2 [2: $T_{(19)} = 3.63$, $p = 0.002$], but not for Sizes 1 and 3–5 [1: $T_{(19)} < 1$, $p = 0.41$; 3: $T_{(19)} = -2.20$, $p = 0.041$; 4: $T_{(19)} = -2.48$, $p = 0.023$; 5: $T_{(19)} = 1.41$, $p = 0.18$]. Bonferroni-corrections regarding the post-hoc tests were applied for all conducted experiments.

Experiment 2

In parallel to Experiment 1, the percentage of correct responses showed a clear tendency to increase with an increasing size of the "pacman," again for both presentation conditions (see **Figure 2B**). In parallel to Experiment 1, we conducted a repeated-measures ANOVA with the same factors and observed a significant interaction between these factors [$F_{(4,\ 15)} = 27.85$, $p < 0.001$] as well as a significant difference between the two positions for Sizes 1 and 3 [1: $T_{(18)} = 5.59, p < 0.001$; 3: $T_{(18)} = 3.67$, $p = 0.002$], but not for 2, 4, and 5 [2: $T_{(18)} = 1.32$, $p = 0.21$; 4: $T_{(18)} = 1.76$, $p = 0.10$; 5: $T_{(18)} < 1$, $p = 0.61$].

Experiment 3

Performance was higher, if the 3-2-3 array was presented in the Front and tended to increase with an increasing size of the "pacman" for both presentation conditions (see **Figure 3A**). The repeated measures ANOVA with Size and Position as independent factors revealed a significant main effect for Size [$F_{(4,\ 13)} = 10.81$, $p < 0.001$] and Position [$F_{(1,\ 16)} = 9.81$, $p = 0.006$] but no significant interaction [$F_{(4,\ 13)} = 1.38, p = 0.30$].

Experiment 4

Performance tended to increase with an increasing size of the "pacman" (**Figure 3B**). The repeated-measures ANOVA revealed a significant interaction between the two factors [$F_{(4,\ 13)} = 4.58$, $p = 0.02$]. By comparing Front and Back positions with paired T-tests for each size, we revealed significant differences for Size 2 [$T_{(15)} = 3.34$, $p = 0.004$], but not for Sizes 1, 3–5 [1: $T_{(15)} < 1$, $p = 0.45$; 3: $T_{(15)} = -2.05$, $p = 0.60$; 4: $T_{(15)} < 1$, $p = 0.91$; 5: $T_{(15)} < 1, p = 0.48$].

Experiment 5

Also in this experiment, performance showed a clear tendency to increase with an increasing size of the "pacman" (see **Figure 3C**). Two squares were perceived equally large if the square in the Front condition was 41% larger than in the Back. With the adjusted square, performance again increased with an increasing size of the "pacman" (see **Figure 3C**). For the main experiment, the repeated measures ANOVA revealed a significant main effect for Size [$F_{(4,\ 14)} = 9.61$, $p = 0.001$], but not for Position [$F_{(1,\ 17)} = 2.97$, $p = 0.13$]. The interaction effect was also not significant [$F_{(4,\ 14)} < 1, p = 0.70$].

Comparison experiment 1 vs. 3

To directly test for effects of local details, we performed a three-way ANOVA with Size (1–5), Position (Front, Back) and Experiment (1 and 3) as independent factors. This ANOVA revealed a significant three-way interaction of Size, Position and Experiment: [$F_{(4,\ 34)} = 8.05, p < 0.001$] that strengthens the assumption for a crucial role of the visual context regarding effects of visual constancy in visual integration.

DISCUSSION

The present study aimed to investigate the role of size constancy for global recognition in a task requiring the integration of local elements into a global object. We took advantage of the "Kanizsa" illusion while size constancy was achieved by a 3D-perspective in which the "Kanizsa" illusion was placed. According to previous observations emphasizing the length of the illusory contours as a crucial factor for the perception of "Kanizsa" triangles (Kojo et al., 1993; Liinasuo et al., 1997), we assumed that global recognition performance was lower if the local elements were perceived to be further away from each other (Beck, 1975). A general decrease in recognition performance was thus assumed for the Back compared to the Front. In line with these predictions is the data of Experiment 3, demonstrating lower global recognition performance of the target object in the Back than in the Front condition. Noteworthy, in this experiment only global information of the visual background was available, while local information (individual stones, texture) was removed. A similar but not significant pattern was observed in Experiment 5 after the size of the gray square was adjusted and thus equally large perceived in the Front and Back.

In this context, data from patients with simultanagnosia, a rare neurological disorder describing the inability to perceive a global Gestalt (Bálint, 1909), should be noted: global recognition performance in simultanagnosics can be modulated by the spatial distance between local elements and improves with smaller distances between elements (Huberle and Karnath, 2006). Further work indicated a key role of the visual angle together with the retinal image for global object recognition (Huberle et al., 2010). It could be demonstrated that rather the retinal image than the physical size of an object has a major impact on global perception. In addition, saliency has been linked to global recognition performance in simultanagnosics (Huberle and Karnath, 2010). However, the current results extent previous work and indicated that the perceived size might be more important for the recognition of a global Gestalt than its physical size. Further, the present findings cannot simply be attributed to retinal images and saliency, which were identical between the Front and Back condition. The explanation might rather be found in a systematic effect of size constancy on global perception that is attributed to the limited amount of local context information immediately available to the observer. In case of the absence of local context information a pronounced effect of size constancy on global perception is evident. Size constancy underlies the observation that separate objects presented in an enriched visual context are rather perceived at a subjective size. A recent study investigating size constancy in a virtual reality environment demonstrated that despite of an identical physical and retinal image perceived object size was mainly determined by perspective manipulations (Kenyon et al., 2008).

The results of the remaining experiments indicated a more complex interaction between size constancy and the integration of local elements into a global object. First, the data of Experiment 1 suggested an influence of local context information, namely the stone-like surface used for the wall. If the "pacmen" were large, the results were similar to Experiments 3 and 5. However, for small sizes of the "pacmen" the reversed pattern—higher global recognition performance in the Back than in the Front—was observed. Similar results became evident for Experiment 4. The differences in the global recognition performance between Experiments 4 and 5 might also be explained by local context information. In Experiment 5, the gray square in the Front condition was more than 40% larger than in Experiment 4 and therefore covered more of the local surround. Moreover, the stimulus presentation of Experiment 3 is comparable to earlier work by Beck (1975), where global stimuli were also presented on a plane background. Further, local context information should also be regarded together with visual crowding, the interaction between nearby contours or "visual clutter" on visual discrimination and object recognition (Levi, 2008; Pelli and Tillman, 2008). "Visual clutter" surround global targets might disturb global recognition performance (Dakin and Baruch, 2009; Kingdom and Prins, 2009; Lau and Cheung, 2012; Robol et al., 2012). The idea of an interaction with local context information was further strengthened by the results of Experiment 2. Local context information with a minimized global surround (flat wall with small and large stones) showed a lower global recognition performance if large stones (equal to the Front) were used instead of smaller ones (similar to the Back). Moreover, the results of this experiment suggest that global recognition performance in the remaining experiments was mainly influenced by perspective manipulations and was independent from local context information. However, the present data cannot answer the question if local details changed the perceived size between local elements or influenced visual integration in general. Evidence about visual crowding and object perception (Levi, 2008; Pelli and Tillman, 2008), nevertheless, suggests a general influence of local details on integration processes. These observations reported here were mainly restricted to Sizes 2–4 while differences between Back and Front presentation for Sizes 1 and 5 were less pronounced over all experiments. We address this effect to a higher experimental sensitivity for the middle sizes of the stimulus spectrum. Moreover, missing variability for Size 5 can be attributed to a general ceiling effect for the 'easiest' condition, while Sizes 2–4 appeared to be more sensitive to reveal perspective differences between the Back and Front presentation.

Recent work observed a faster recognition of meaningful arrays creating illusory contours compared to random configurations of local elements in a noisy visual background indicating also an involvement of early visual areas in integration mechanisms (Wang et al., 2012). Further, neuroimaging studies have identified distinct neuronal networks of illusory contour processing (Hirsch et al., 1995; Ffytche and Zeki, 1996; Halgren et al., 2003; Maertens and Pollmann, 2005, 2007). However, the evidence of influences of size constancy on Gestalt perception supports the view of contributions of later visual areas to processes of visual integration. Various studies showed that functions of object perception get affected by size constancy (Emmert, 1881; Fitzpatrick et al., 1982; Kenyon et al., 2008) and localized object processing beyond early visual areas along the ventral visual pathway (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992; Grill-Spector, 2003). Therefore, the presented results demonstrating influences of size constancy on Gestalt perception are in line with various findings from patients with simultanagnosia and healthy subjects attributing global perception to posterior parietal brain areas (Rizzo and Hurtig, 1987; Friedman-Hill et al., 1995; Rafal, 1997; Karnath et al., 2000; Tang-Wai et al., 2004; Valenza et al., 2004; Himmelbach et al., 2009; Huberle and Karnath, 2012; Thomas et al., 2012).

The current results suggest an important role of size constancy on global perception of hierarchically organized visual stimuli. In accordance with previous findings, the distance between local elements in illusory global objects composed of local elements appears to be a crucial factor for global recognition. Emphasizing the importance of the perceived size of a global figure in visual integration, the data extend previous findings in patients with simultanagnosia that attributed global recognition performance to the retinal size rather than the physical. To our knowledge, the work shown here represents the first manipulation of global recognition with mechanisms of size constancy preserving a constant retinal image and, thus, highlights the role of the perceived size of a global object in the process of visual integration. Size constancy influences our perception and leads to an enlarged inter-element spacing in hierarchically organized global figures. Finally, local context information shows an interaction with size constancy.

ACKNOWLEDGMENTS

This work was supported by a grant of the Bundesministerium für Bildung und Forschung (BMBF-Verbund 01GW0654 "Visuospatial cognition") the Deutsche Forschungsgemeinschaft (DFG) and the Open Access Publishing Fund of the University of Tübingen. We thank Maren Prass for her helpful discussion.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 29 April 2013; accepted: 17 June 2013; published online: 03 July 2013.

Citation: Rennig J, Karnath H-O and Huberle E (2013) The role of size constancy for the integration of local elements into a global shape. Front. Hum. Neurosci. **7***:342. doi: 10.3389/fnhum.2013.00342*

6 Conclusions & future directions

The present work shows that TPJ areas are involved in mere perceptual mechanisms of Gestalt processing and have a specific role in recognizing novel object arrangements. Furthermore, it was demonstrated that Gestalt perception itself underlies visual top-down processes of visual constancy suggesting a superior role of global scene processing influencing even local grouping processes.

At first, learning dependent changes during Gestalt perception in bilateral TPJ regions were investigated. It was hypothesized that the area TPJ mainly contributes to processing of novel object arrangements. Anterior and posterior sections of this structure were examined separately. In a training study subjects had to learn the perception of complex stimulus arrangements. Neuronal processes of Gestalt perception in bilateral (anterior and posterior) TPJ regions were assessed pre- and post-training. It was demonstrated that an anterior right hemispheric TPJ region responded significantly to perceptual training with global stimuli. The results indicated fundamentally changed TPJ contributions with increasing familiarity suggesting a different strategy of the brain for processing of highly familiar object arrangements. In this study, the fate of global processing stayed mainly unclear. At the end of the present paragraph this issue and a model explaining interactions of visual integration and object processing will be discussed in more detail. The main message of this model is a switch in neuronal processing from temporo-parietal areas associated with global Gestalt perception to a more ventral representation of familiar global stimulus arrangements. From a methodological point of view, the investigation of such processes has to be realized applying functional localizers for object sensitive areas of the ventral visual pathway. Consequently, a less extensive study design for the pre- and post-training fMRI measurements would have been necessary. Therefore, it would have been possible to apply independent and individual functional localizers for areas like the LOC or FFA as typical regions of object processing or visual expertise (Gauthier et al., 1999; Grill-Spector et al., 2000) within one experimental measurement. The present approach using several control conditions in a very extensive experimental procedure prevented the execution of two or more additional localizer experiments. Moreover, with fewer conditions learning effects may have been detectable in other TPJ regions but the anterior right hemispheric ROI.

Further, involvements of bilateral TPJ areas in global processing were investigated with an approach taking advantage of visual expertise. During presentation of specific chess arrangements TPJ signals of chess experts and novices were examined. As a consequence, it was possible to compare neuronal TPJ correlates for holistic perception in experts and serial perceptual strategies in novices. The result showed higher signals in bilateral TPJ areas for chess experts compared to novices while inspecting specific chess configurations. With this method a lot of the typical stimulus confounds in research about Gestalt perception, like size differences or differences in spatial frequencies between global/local stimulus levels, were avoided. Moreover, the nature of the stimuli and experimental tasks argues for a TPJ involvement during perception rather than for functions of attentional selection. Unfortunately, in the present experiment separate analyses of the anterior and posterior right hemispheric TPJ cluster were not conducted. There were a clear functional distinction between the anterior and posterior TPJ cluster on the left hemisphere in the present study and different learning effects in the right hemisphere in the first study. These observations suggest generally different neuronal response characteristics for global stimuli also for right hemispheric anterior and posterior TPJ areas. Therefore, a separate investigation of anterior and posterior TPJ clusters in both hemispheres may be necessary to gain deeper understanding of global processing in the human brain. In the present study, it was not possible to control for several cognitive processes like rule processing, memory or attentional functions potentially biasing the reported results. It would be necessary to conduct separate experiments with chess experts for the purpose of investigating global processing. Only with feasible study designs and selected subject groups or stimuli the mentioned confounds would be avoided.

Finally, perceptual properties of visual size constancy were examined in the context of Gestalt perception. Size constancy is a well-known phenomenon for regular objects, but has not been investigated for hierarchical stimuli forming a global Gestalt. Therefore, the perceptual performance for a global stimulus arrangement placed on different locations of a visual scene containing a 3D perspective was tested. For the first time, influences of size constancy were demonstrated also for hierarchical stimuli. Effects of size constancy on Gestalt perception suggest a perceptual hierarchy of global scenes even on stimuli that have to be integrated themselves. This study may have brought up stronger results through all 5 experiments without applying the two extreme size conditions (1 and 5). The results clearly showed that in the extreme size conditions no significant differences were observable. In conclusion, an omission of these conditions would have increased statistical power. Further, a direct comparison of size constancy effects on coherent objects and hierarchical stimuli is an open question remaining from this study. It would be interesting to test if mechanisms of size constancy have different effects on regular object stimuli or global structures that need to be integrated. Moreover, it has not been investigated if mechanisms of size constancy for coherent objects are preserved in simultanagnosia. Size constancy represents a top-down mechanism requiring a holistic perception of a visual scene. Therefore, it is very likely that size constancy for regular objects is impaired in patients with simultanagnosia. Results demonstrating impaired as well as preserved mechanisms of size constancy in simultanagnosia would provide valuable evidence about processes of high level human vision.

The integration-to-object processing model

The most significant open question about the present results is the change in processing strategies of the brain for perception of highly familiar complex object arrangements. One explanation would be the reduction of efforts of visual integration in favor of processes of object perception. Within this model, complex visual input consisting from several independent elements is being perceived with help of mechanisms of Gestalt perception provided from bilateral TPJ areas. With increasing familiarity, less integration effort is needed reducing TPJ activity during the perceptual process. As a consequence of familiarity the object arrangement is being perceived as a coherent entity not requiring mechanisms of Gestalt perception through the ventral object recognition pathway. This hypothesis is in tradition of the Recognition-by-components theory of Irving Biederman (Biederman, 1987). Biederman's theory postulated that even coherent objects are being assembled from sub-components bound together according to rules resembling the general Gestalt laws. As neuronal activations for several complex attentional and object recognition tasks change depending on visual expertise (Gauthier et al., 1999; Grill-Spector et al., 2000) or are even re-distributed over the brain (Kourtzi et al., 2005; Sigman et al., 2005) an hypothesis about a directional changes of brain activity from Gestalt perception to object recognition could explain several unresolved questions. Combining elaborated methods of fMRI and psychophysics the integration-to-object processing model could be investigated in an appropriate manner. However, there is a lack of studies investigating interactions of global Gestalt perception and object recognition. In conclusion, not only learning studies but also connectivity analyses between areas associated with Gestalt (e.g. TPJ) and object perception (e.g. LOC, FFA) or patient studies applying several paradigms of Gestalt and object processing could still be realized. Further, behavioral and neuronal characteristics of Gestalt perception and typical properties of object perception, like visual constancy or object invariance, are largely unexplored. In the framework of Gestalt and object perception, applying various methods of behavioral investigations and neuroimaging techniques with healthy subjects and neurologic patients, many open questions can be addressed.

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