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Bilateral parietal activations for complex visual-spatial functions: Evidence from a visual-spatial construction task

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ABSTRACT

In this paper, we examine brain lateralization patterns for a complex visual-spatial task commonly used to assess general spatial abilities. Although spatial abilities have classically been ascribed to the right hemisphere, evidence suggests that at least some tasks may be strongly bilateral. For example, while functional neuroimaging studies show right-lateralized activations for some spatial tasks (e.g., line bisection), bilateral activations are often reported for others, including classic spatial tasks such as mental rotation. Moreover, constructive apraxia has been reported following left- as well as right-hemisphere damage in adults, suggesting a role for the left hemisphere in spatial function. Here, we use functional neuroimaging to probe lateralization while healthy adults carry out a simplified visual-spatial construction task, in which they judge whether two geometric puzzle pieces can be combined to form a square. The task evokes strong bilateral activations, predominantly in parietal and lateral occipital cortex. Bilaterality was observed at the single-subject as well as at the group level, and regardless of whether specific items required mental rotation. We speculate that complex visual-spatial tasks may generally engage more bilateral activation of the brain than previously thought, and we discuss implications for understanding hemispheric specialization for spatial functions.

1. Introduction

Hemispheric specialization, i.e., the notion that the brain's two hemispheres differ with regards to the functions they subserve, the types of stimuli they prefer, and their computational makeup, has long been a topic of interest for those studying the brain, its cognitive functions, and its behavioral output. The topic has found its way into conventional wisdom (albeit often in distorted form) and continues to be a matter of lively discussion (e.g., Efron, 1990; Hugdahl and Westerhausen, 2010). Some of the earliest indicators that the two hemispheres are not created equal were the observations by Broca (1861) and Wernicke (1874) of "language areas" in the left hemisphere. It has also long been known that basic sensory and motor function cross over on their way from the body periphery to the cerebral cortex: The primary motor cortices of the two hemispheres control movement of the contralateral extremities and the somatosensory cortices receive tactile input from the contralateral side of the body (Penfield and Boldrey, 1937). Similarly, the visual cortices receive visual input from the contralateral side of the visual field (Holmes, 1918).

These known lateralizations enabled Sperry et al. (1969)'s crucial research on "split-brain" patients. In these patients, the fibers of the corpus callosum (and often also the anterior commissure) were cut to treat intractable epilepsy. As a result, direct inter-hemispheric communication was impossible, so that sensory information from one side of the body and the visual field was only available to the contralateral hemisphere. This provided a unique opportunity for investigating what one hemisphere can do on its own with the available information. For example, Sperry and colleagues found that the patients could not produce the names of objects presented visually to solely the right hemisphere. This is consistent with the idea that language is largely left-lateralized, at least in adults, for which there is converging evidence from countless studies using different methodologies (e.g., Broca, 1861; Lenneberg, 1967; Binder et al., 1996; Stromswold et al., 1996; Bookheimer et al., 1997).

In 1965, Bogen and Gazzaniga introduced another paper on split-brain cognition and hemispheric specialization by stating that "*an increasing accumulation of clinical data suggests that complementary functions in man may be verbal v. visuospatial*" (p. 394), thus attributing

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visual-spatial function to the right hemisphere. In further support of this notion, they reported that two split-brain patients could perform visual-spatial construction tasks with the left hand (steered by the right hemisphere), but not with the right hand (steered by the left hemisphere). This notion of a verbal left and a spatial right hemisphere is also reflected in the "Hemispheric Crowding" hypothesis (Teuber, 1974), according to which early left-hemisphere lesions result in visual-spatial impairments because verbal skills are assumed by the right hemisphere and thus "crowd out" the visual-spatial abilities it normally supports.

Much research has followed these initial findings and resulted in more detailed articulations of hemispheric lateralization. With respect to language, it is now known that while certain aspects, such as syntax and semantics, indeed rely predominantly on the left hemisphere, others, such as prosody, involve the right hemisphere (Weintraub et al., 1981; George et al., 1996). With respect to visual-spatial functions, two theoretical frameworks have embraced the idea that they may be differentially localized to the right vs. left hemisphere as a consequence of the nature of information-processing preferences in the two hemispheres. Kosslyn (1987) proposed that the left hemisphere has a processing preference for categorical spatial information (e.g., the difference between categories 'above' and 'below'), while the right hemisphere tends to process coordinate spatial information (i.e., the detailed information required for reaching and navigation). Ivry and Robertson (1998) proposed that visual and auditory information undergo differential filtering by the two hemispheres, resulting in processing biases such that the left hemisphere tends to achieve representations with more 'local' detail while the right hemisphere achieves representations that are more 'global' in nature. Empirical studies have lent support to both views (e.g., Kosslyn et al., 1989, 1998; Laeng, 1994; Ivry and Robertson, 1998), and the two frameworks and their predictions are compatible with each other (Okubo and Michimata, 2004; Borst and Kosslyn, 2010). Notably, both frameworks emphasize that these hemispheric processing preferences are relative, not absolute. Despite these more detailed articulations of hemispheric lateralization, the general idea articulated by Bogen and Gazzaniga − that language and space are preferentially represented by the left vs. right hemispheres − has permeated the literature.

However, from our reading of the literature, the evidence is much less consistent regarding right-lateralization of visual-spatial functions than it is regarding left-lateralization of language. On one hand, there is evidence in favor of right-lateralization. Behavioral studies show that tasks tapping memory for spatial location are performed better for stimuli presented to the left hand (Witelson, 1976) or in the left visual field (Kimura, 1969; Durnford and Kimura, 1971; Tucker et al., 1999; Postma et al., 2006). Lesion studies indicate that injury to the right hemisphere, especially the parietal lobe, results in dramatic impairments in the spatial domain that are evident in drawing, construction, and orientation tasks as well as in left-right disorientation and apraxia for dressing (Brain, 1941; McFie et al., 1950; Hecaen et al., 1956; Vallar, 1998). Hemispatial neglect, in which patients have difficulty perceiving stimuli or parts of stimuli contralateral to their lesion site, is much more common after lesions to the right than lesions to the left hemisphere (Bisiach and Luzzatti, 1978; Vallar, 1998). A telltale sign is a rightward bias in the line bisection task: When asked to mark the center of a horizontal line, patients with right-parietal lesions place their mark too far to the right (Schenkenberg et al., 1980), whereas healthy adults are quite accurate and if anything tend to have a small leftward bias (Jewell and McCourt, 2000). The same rightward bias can be induced experimentally by temporarily disrupting right parietal cortex through repetitive transcranial magnetic stimulation (rTMS); left-sided rTMS has no spatially biasing effect (Fierro et al., 2000). Lastly, functional neuroimaging studies requiring line bisection judgments (Fink et al., 2001; Çiçek et al., 2009) reveal activations predominantly in right parietal and premotor cortex. All this points to significant right-hemisphere lateralization for certain spatial functions.

On the other hand, there is also ample evidence for left-hemisphere involvement in some visual-spatial tasks. Lesion studies have reported impairments in visual-spatial skills, especially visual-spatial constructive functions, following left-hemisphere lesions (McFie et al., 1960; Arrigoni and De Renzi, 1964; Gainotti et al., 1977). Returning to the evidence derived from split-brain patients mentioned above, Gazzaniga's (1995) review qualifies the initial report (Bogen and Gazzaniga, 1965) on two split-brain patients who could perform visual-spatial tasks with their left hand (right hemisphere) but not their right hand (left hemisphere) by noting that in other patients, neither hemisphere by itself could perform well on visual-spatial tasks, and in yet other patients, the left hemisphere performed better. Similarly, the occipito-parietal (dorsal) "where" pathway (Ungerleider and Mishkin, 1982) for localizing and/or interacting with objects in space is bilaterally represented (Haxby et al., 1991), although there is some evidence that the two hemispheres differ with respect to the way in which they represent object location, with the right hemisphere favoring a metric (coordinate) and the left hemisphere favoring a relative (categorical) approach (Kosslyn et al., 1989, 1998).

Most relevant to the present study is the functional neuroimaging literature on the most classic of all spatial tasks − mental rotation (Shepard and Metzler, 1971). In this task, participants are presented with pictures of two three-dimensional objects and asked to judge whether they are identical (true if one is a rotated view of the other) or not (false if one is a reflected version of the other). Various versions of this task have been widely used to gauge spatial abilities in children and adults (Vandenberg and Kuse, 1978; Kosslyn et al., 1990; Frick et al., 2013) and to evaluate gender differences in spatial abilities (Voyer et al., 1995; Peters, 2005). The related functional neuroimaging literature often reports bilateral, rather than right-lateralized, parietal activations (Cohen et al., 1996; Richter et al., 1997, 2000; Vingerhoets et al., 2002).[1] Support for the possibility that mental rotation often engages bilateral areas, and certainly is not unequivocally right-lateralized, also comes from two meta-analyses of mental rotation neuroimaging studies (Zacks, 2008; Tomasino and Gremese, 2016).

Notably, the latter meta-analysis (Tomasino and Gremese, 2016) also revealed that the degree of lateralization can be modulated by stimulus type and strategy: If the task involves bodily as opposed to non-bodily stimuli (e.g., hands vs. objects) and if participants used motor-based as opposed to visual imagery-based strategies (e.g., “imagine rotating the object” vs. “imagine the object rotating in space”), activation becomes more bilateral compared to the right-lateralized activations observed for non-bodily stimuli and non-motor strategies. This is consistent with dissociations observed in patients with unilateral brain lesions, where right-sided lesions are associated with mental rotation impairments for objects (but not hands) and non-motor (but not motor-based) rotation strategies, whereas the opposite holds for left-sided lesions (Tomasino et al., 2003; Tomasino and Rumiati, 2004). It is also consistent with similar findings on line bisection, where activation becomes more bilateral (due to increasing left-sided activations) if stimuli are presented in near vs. far space (i.e., within reach) and if the bisection task is active (i.e., involving a motor component) rather than purely perceptual (Weiss et al., 2003).

In sum, the mixed pattern of lateralization results for visual-spatial tasks contrasts with the relatively unequivocal evidence for language lateralization, highlighting that we do not yet have a full understanding of whether and how spatial functions are lateralized in the brain. In part, this may be due to the fact that there is no monolithic spatial

[1] While some studies indicate that lateralization may differ between sexes and at different points in the menstrual cycle (Gur et al., 2000; Hugdahl et al., 2006; Schöning et al., 2007; Zhu et al., 2015), the results are inconsistent across studies and may be due to small sample sizes. For example, some studies (Thomsen et al., 2000; Levin et al., 2005) found stronger right parietal activations for male than female participants, whereas other studies (Jordan et al., 2002; Clements et al., 2006) reported stronger right parietal activations in women.