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Enhancing the ecological validity of tests of lateralization and hemispheric interaction: Evidence from fixated displays of letters or symbols of varying complexity

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ABSTRACT

Two experiments expand upon behavioural evidence of interactions among lateralization, hemispheric interaction, and task complexity with findings from an ecologically valid procedure. Target displays of letters or symbols were presented at fixation in go/no-go matching tasks of physical or categorical identity. Simultaneously with the target, a distractor appeared in the left visual field or right visual field to weight processing of the target to the hemisphere ipsilateral to the distractor, or the distractor did not appear at all. Comparison of the respective distractor-present trials with distractor-absent trials measures the relative costs or benefits of hemispheric interaction.

Both experiments found that 3-item displays were processed faster and more accurately than displays of 5 items, suggesting they are relatively simple. Accuracy to the simple tasks showed left-hemisphere lateralization in the lexical task, right-hemisphere lateralization in the spatial task, a cost of hemispheric interaction compared to the advantaged hemisphere, and a benefit of hemispheric interaction compared to the less-advantaged hemisphere, suggesting that the contributions of the less-advantaged hemisphere interfere with processing, and that the advantaged hemisphere controls the lion's share. In contrast, 5-item displays for physical match in both experiments showed a significant benefit to accuracy of hemispheric interaction compared to the left hemisphere, an insignificant benefit compared to the right hemisphere, no lateralization, no cost of hemispheric interaction, and a consequence to performance that was more costly to the hemisphere that had been advantaged in simple tasks, suggesting that the advantaged hemisphere relinquishes control as tasks become more complex and complementary processing results from both increased collaboration and decreased lateralization between the hemispheres. The findings expand upon behavioural evidence, converge with imaging evidence, and suggest future directions for brain mapping.

1. Introduction

Lateralization of performance of the brain's hemispheres is commonly cited. Less well explored are the dynamics of interaction between the hemispheres. Early investigation into hemispheric specialization suggested some well-defined differences in processing, with left hemisphere (LH) dominance for language tasks (Broca, 1861; Dax, 1865; Wernicke, 1874) and right hemisphere (RH) dominance for spatial processing (Jackson, 1876). More recent research has indicated that in addition to these intrahemispheric advantages, the brain may dynamically switch between single hemisphere processing and combined hemisphere interaction, depending on the task (Banich & Belger, 1990; Belger & Banich, 1998; Lassen, Ingvar, & Skinhoj, 1978; Ringo, Doty, Demeter, & Simard, 1994).

Interaction between the hemispheres allows for greater access to neural space, and therefore more computational power (Ringo et al., 1994). However, as the human brain grew throughout evolution, the resulting increased transfer distances may have led to a slowing of communication across the larger hemispheres (Aboitiz, López, & Montiel, 2003; Varela, Lachaux, Rodriguez, & Martinerie, 2001). It is theorized that this decrease in transfer efficiency led to the development of specialized intrahemispheric networks, which increased processing speed and decreased excess cross talk from the contralateral hemisphere (Doron, Bassett, & Gazzaniga, 2012). Structural investigations of the brain have supported this theory by finding large, highly myelinated fibers

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facilitating hemispheric interaction, as well as smaller, less myelinated fibers allowing for fast local processing within each hemisphere (Aboitiz et al., 2003; Doron et al., 2012). These structural adaptations provide physical support for a dynamic system of lateralization in which tasks requiring minimal processing would be most efficiently processed by a single hemisphere (Adam & Güntürkün, 2009), and tasks requiring more complex processing would be better processed with both hemispheres together (Banich, 1998). It is difficult to determine whether the structural adaptations are the result of an evolutionary direction favoring improved within-hemisphere processing, or are the byproduct of the evolution of a larger human brain. In either case, these specialized networks appear to exist, providing a physical basis for modern patterns of lateralization.

If a dynamic system of lateralization and hemispheric interaction developed to increase processing efficiency, then such patterns should be measurable by comparing the processing efficiencies of each hemisphere separately and both hemispheres together. Banich and Belger (1990) designed a novel paradigm to test this theory in which participants were presented with sets of three letters arranged in the shape of an inverted triangle on a computer screen. In each trial, participants were asked to indicate whether any two of the letters matched. Two probe letters appeared simultaneously, one in the left visual field (LVF) and one in the right visual field (RVF), while a third target letter appeared below the probes and closer to the vertical midline in either the LVF or RVF. Within-hemisphere performance was measured from trials that presented matching letters to the same visual field, while hemispheric interaction was measured from trials that presented matching letters to opposite visual fields. To investigate whether task difficulty influenced performance, letter matches could either be a simple, physical match (e.g. A and A) or a more complex, categorical match (e.g. A and a). Simple tasks were found to be processed more efficiently when presented to a single hemisphere, while the more complex tasks were found to be processed more efficiently when matching stimuli were presented across hemispheres. The authors concluded that hemispheric interaction is beneficial for processing complex tasks, while intrahemispheric processing is beneficial for simpler tasks.

In a follow up study, Belger and Banich (1998) expanded on the original paradigm to test the relationship between computational complexity and hemispheric interaction. In addition to manipulating complexity with simple physical and complex categorical matches, perceptual load was manipulated by increasing the number of letters presented per trial. Therefore, task complexity could range from the most simple 3-item physical identity task to the most complex 5-item categorical identity task. The 5-letter tasks were presented in a similar manner to the 3-letter tasks, with two probe letters stacked one above the other in each of the LVF and RVF, and a single target letter appearing below the probes and closer to the vertical midline in either the LVF or RVF. All target letters were uppercase in the physical match trials, and the target letter was lowercase in the categorical match trials. Consistent with the findings of the original experiment (Banich & Belger, 1990), there was a benefit of intrahemispheric processing to 3-item physical matches and benefit of interhemispheric processing to more complex displays, whether the complexity increase was due to computation alone (3-item categorical matches), perceptual load alone (5-item physical match), or both computation and perceptual loads (5-item categorical matches) (Belger & Banich, 1998).

Subsequent research has shown that these effects are not limited to the processing of letters. Koivisto (2000) presented participants with two pictures either in the LVF or RVF, or across the two visual fields, and asked them to make either a simple, physical match (e.g. Horse & Horse) or a more complex, semantic category match (e.g. Horse + Frog). A response time advantage was found for the more complex categorical match when stimuli were presented across the visual fields. In order to rule out that these results were impacted by an unequal perceptual load between the unilateral and bilateral trials (i.e. a single visual field containing all of the stimuli during unilateral trials), a second experiment presented two probes and a target in the inverted triangular arrangement utilized by Banich and Belger (1990) to equate the number of stimuli processed by a hemisphere for a match in bilateral and unilateral trials. Consistent with the first experiment, a response time advantage was found for the more complex categorical matches when presented across visual fields, and for the simpler physical match when presented to a single visual field, suggesting that there is a positive relationship between hemispheric interaction and task complexity.

The dynamics of hemispheric interaction have been further observed across multiple modalities. Passarotti, Banich, Sood, and Wang (2002) presented participants with a numerical dichotic listening task in which they made either a simple physical match (e.g. 4 + 4) or a more complex categorical match (e.g. is the second number less than the first). The two numbers were presented either to the same ear (within hemisphere trials) or to opposite ears (across hemisphere trials). A within-hemisphere advantage was found for the simple task regardless of ear of the target number, and this advantage decreased for the more complex categorical match. This positive relationship between task complexity and hemispheric interaction was also demonstrated with unilateral finger movements. While it would be expected that finger movements would be best performed with the dominant hand, Hausmann, Kirk, and Corballis (2004) found that by increasing the complexity of the movements from a single finger to multiple fingers in sequence, the preferred-hand advantage disappeared. The disappearance was due to a stronger decrease in tapping rate with the dominant than non-dominant hand, leading the authors to conclude that the more complex, multiple-finger task overtaxed the dominant hemisphere, leading to recruitment of the other hemisphere and resulting in equal performance across hands. These studies suggest that the dynamics of hemispheric interaction are not limited to visual processing, but may extend across multiple modalities.

Along with behavioural evidence, neuroimaging supports a positive relationship between hemispheric interaction and task complexity. Studies using functional magnetic imaging (fMRI) or Positron Emission Tomography (PET) have documented shifts to more bilateral activation as the difficulty of finger movements increased from simple to more complex (Rao et al., 1993), as verbal working memory "n-back tests" required the recall of a letter that was further back in the sequence (Jonides et al., 1997), as the rule for colour and pattern matching tasks became increasingly difficult (Klingberg, O'Sullivan, & Roland, 1997), and as semantic-processing tasks became more difficult from the inclusion of words that have more than one meaning (e.g. bank: river or financial institution) (Rodd, Davis, & Johnsrude, 2005; Zempleni, Renken, Hoeks, Hoogduin, & Stowe, 2007). However, recent imaging evidence (Davis & Cabeza, 2015) expands on the findings to suggest that the pattern varies depending on whether the brain region involved is task-specific or task-general. In a novel approach, they selected two tasks that were likely to involve different brain networks: semantic word matching and visual face matching. fMRI measured functional connectivity in pairs of homologous cortical regions that are activated by either or both of the tasks. During scanning, stimuli for the matches were lateralized, either with both to the same visual field (within-hemisphere condition) or one to each visual field (both-hemisphere condition), and task difficulty varied from easy to medium to hard. As expected, behavioural findings revealed the advantage to response time in the both-hemisphere condition generally increased with task difficulty: In