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REPORT

Superior episodic memory in inconsistent-handers: a replication and extension using fNIRS

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ABSTRACT

A large body of evidence supports the existence of a robust handedness difference in episodic memory retrieval, with inconsistent-handedness being associated with superior memory across a wide variety of paradigms, including superior retrieval of lab-based and real world memories. Despite superior episidoc memory in inconsistent-handers, and despite neuroanatomical and neurophysiological differences in cortical regions between inconsistent- and consistent-handers, we are aware of no studies to date that have examined physiological activity in the brains of inconsistent- versus consistent-handers while engaged in memory tasks. The purpose of this paper, therefore, is to present a first look at this issue, using functional near-infrared spectroscopy (fNIRS) as a simple, non-invasive measure of frontal lobe activity during encoding and recall of list words in inconsistent- and consistent-handers. Behaviourally, we replicated prior studies, finding a significant inconsistent-handed advantage in free recall. Using fNIRS-derived oxygenated haemoglobin (O_2Hb) as a measure of frontal lobe activity, we found the first evidence for handedness differences in brain activity that are associated with the handedness differences in episodic retrieval. Specifically, the primary finding was that increased O_2Hb in the right hemisphere during recall was associated with better retrieval, but for consistent-handers only.

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Handedness; episodic memory; recall; fNIRS

A large body of evidence supports the existence of a robust handedness difference in episodic memory retrieval, with inconsistent-handedness being associated with superior memory across a wide variety of paradigms, including superior retrieval of lab-based (Chu, Abeare, & Bondy, 2012; Lyle, Hanaver-Torrez, Hackländer, & Edlin, 2012) and real world memories (Propper, Christman, & Phaneuf, 2005), better source memory (Lyle, McCabe, & Roediger, 2008), fewer false memories in the Deese-Roediger-McDermott paradigm (Christman, Propper, & Dion, 2004), a greater proportion of "remember" relative to "know" responses in recognition memory (Propper & Christman, 2004), more vivid autobiographical memories (Parker & Dagnall, 2010), more resistance to memory distorting information about slide shows depicting the scenes of crimes (Lyle & Jacobs, 2010), an earlier offset of childhood amnesia (Christman, Propper, & Brown, 2006), and better memory for prior hand usage (Edlin, Carris, & Lyle, 2013).

Relative to consistent-handedness, inconsistent-handedness is associated with (i) a larger corpus callosum (Luders et al., 2010), (ii) greater right, compared with left, hemisphere activation, and (iii) right hemispheric bias in interhemispheric asymmetry (Propper, Pierce, Geisler, Christman, & Bellorado, 2012). It has thus been hypothesised that inconsistent-handers have greater functional access to right hemisphere processes, which include the retrieval of episodic memories (e.g., Babiloni et al., 2006; Habib, Nyberg, & Tulving, 2003; Okamoto et al., 2011).

Although there has been much behavioural work on the topic of handedness and memory, we are aware of no studies to date that have examined physiological activity in the brains of consistent- versus inconsistent-handers while engaged in memory tasks. The purpose of this paper, therefore, is to present a first look at this issue, using functional near-infrared spectroscopy (fNIRS) as a simple, non-invasive measure of frontal lobe activity.

Method

Participants

Participants were 65 women, undergraduate, students at a mid-sized university, who participated for research credit for their Psychology course. Participants had normal or corrected-to-normal vision and hearing, had not been diagnosed with a mental illness or brain injury, were free from psychotropic medications, and completed both the memory task and had fNIRS recorded. The research was approved by the Montclair State University IRB and the US Army Human Research Protection Office. Participants

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provided their written informed consent to participate in the study. Two individuals were excluded from analyses due to 8 or more fNIRS channels (50% of the channels in the 16 channel system) failing to be maintained in the correct raw recording range for the duration of the experiment. One additional individual was excluded from analyses due to falling more than two standard deviations below the mean on the recall task, recalling only one of the 36 presented words (see Analyses and Results).

Materials

Instructions

All instructions and stimuli were presented on a 23 inch Dell Inspiron computer screen via SuperLab 5.0 (Cedrus Corporation). Cognitive Optical Brain Imaging Studio (COBI; fNIR Devices, LLC, 2013) for fNIRS recording, and fNIRSoft (Ayaz, 2010) and Matlab 9.0 (Mathworks, 2016), for fNIRS data extraction, software were run on a 17 inch Dell Inspiron.

Memory task

The memory stimuli were identical to that described in Propper et al. (2005). Per participant, one of two randomly created lists of 36 words each (two lists were created in order to eliminate any effects being attributable to the particular word list used), taken from Tulving, Schacter, and Stark (1982), were presented on the computer screen for 5 seconds each in upper case, Courier New font (see Propper et al., 2005).

Handedness

The Edinburgh Handedness Inventory (EHI; Oldfield, 1971), consists of 10 items on which participants are asked to indicate whether they perform "usually" or "always" with either their left or right hands, or if they have no hand preference. Choices of "always" are scored −10/+10 for left or right hand, respectively, while choice of "usually" is scored −5/+5 following the same orientation. Choice of "no preference" is scored as a "0".

Functional near-infrared spectroscopy

fNIRS is a non-invasive imaging method that measures changes in blood oxygenation subserving cortical areas. fNIRS systems use configurations of light-emitting optodes and detectors to infuse at least two different frequencies of light with near-infrared wavelengths into the superficial layers of the cortex. The "scatter back" of the light that is received by the detectors enables determination of the relative change in oxygenated haemoglobin and de-oxygenated haemoglobin (O_2Hb and dHb, respectively).

The fNIR400 system (Biopac Systems, inc.) is a continuous-wave system consisting of 16 channels made from a combination of 10 detectors and 4 optodes, with an optode-detector separation of 2.5 cm. Light from optodes is emitted at the two frequencies of 850 nm and 730 nm, for detection of O_2Hb and dHb, respectively, and data were recorded via a 2 Hz sampling rate. Using localisation of head measurements in accord with the 10–20 System, the centre of the bottom of the sensor pad was placed at Fpz, allowing for recording from the left and right dorsolateral prefrontal cortex (Broadman's areas 10, 46, 9, and 45). To be included in subsequent analyses, raw signal levels must have been maintained at greater than 400 mV and less than 4000 mV during the experiment, with Light Emitting Diode (LED) current and gains adjusted via COBI (fNIR Devices, LLC, 2013). COBI-derived O_2Hb and dHb, were calculated using the modified Beer-Lambert law.

Others (e.g., Matsuda & Hiraki, 2006; Schaeffer et al., 2014; Shimoda, Takeda, Imai, Kaneko, & Kato, 2008) have argued that O_2Hb demonstrates greater sensitivity to changes in cerebral blood flow (e.g., Hoshi, Kobayashi, & Tamura, 2001) and yields higher signal-to-noise ratio, than does dHb (Tian et al., 2012). Thus, we focus on O_2Hb here.

Note that continuous-wave FNIRS systems, such as that used here, do not measure absolute levels of O_2Hb, but rather measure change in oxygenated haemoglobin relative to a baseline. Thus, raw data consist of change, relative to baseline, with baseline defined here as the second set of 10 seconds occurring during the 40 seconds of baseline recorded (see below). This time period was chosen as baseline to ensure that the hemodynamic response examined would reflect true "baseline" rather than instruction processing or anticipation of baseline completion.

Procedure

Participants were tested individually. After reading and signing the consent form, participants' head measurements were taken and the fNIRS sensor pad placed such that the bottom of the pad was located at Fpz. If necessary, a wrap was placed around the head and sensor pad as well, to ensure the stability of the sensor and to reduce ambient light. Lights were off for the duration of fNIRS recording, and fNIRS was recorded continuously during all parts of the experiment.

Once the experimenter determined, via COBI (fNIR Devices, LLC, 2013) signal verification, that raw signals were being appropriately recorded, a baseline condition was conducted, consisting of 40 seconds wherein participants focused on an "X" on the centre of the computer screen and were asked to refrain from moving, with their hands resting in their lap. A 2-second tone presented concurrently with a blank white screen immediately preceded and followed this baseline. Participants were then given information regarding list word presentation, and were instructed to "study the words, as you may be tested on them later". Immediately preceding and following list word presentation (Encoding Condition), participants heard a 2-second tone while viewing a blank screen.

Following list word presentation, participants completed the EHI as a distractor task, after which they were asked to recall out loud, as many words as they could from the list they saw earlier, while the experimenter recorded their answers (Recall Condition). Participants viewed an "X" on a white background while being given 3 minutes to recall as many words as they could remember. Participants were given notice at the 2 minute and 30 second point that they had 30 more seconds to complete this part of the task. See Figure 1 for graphic depiction of Procedure.

Analyses

Handedness

Participants' handedness was defined via a median split on the EHI such that individuals scoring +80 and above were categorised as Consistent-Right-Handers (CRH), and those scoring between −80 and +80 were Inconsistent-Handers (ICH) (see Pritchard, Christman, & Propper, 2013). Three individuals scoring −80 or below were excluded from analyses, given potential differences between these individuals and those scoring as CRH or ICH (see Pritchard, Christman, & Propper, 2013). Final $N = 59$, CRH $n = 34$, ICH $n = 25$.

Memory task

Hits (number of words recalled that had been presented previously), false alarms (words "recalled" but not presented on the list), and corrected scores (Hits minus false alarms), were examined as a function of Handedness Group.

FNIRS data

Using Matlab and/or fNIRSoft (Ayaz, 2010), O_2Hb (measured in micromolars, μM) from optodes in the left (optodes 1–8) versus right (optodes 9–16) hemispheres (LH and RH, respectively) were averaged as a function of the three minutes recorded during Encoding and the three minutes recorded during Recall (note that in order to account for the hemodynamic response lag, all times were examined beginning 6 seconds post-instruction completion to 6 seconds post-task completion). A 2 (Time: Encoding versus Recall) × 2 (Hemisphere: Left versus Right) × 2 (Handedness: CRH versus ICH) mixed-ANOVA, and appropriate post hoc tests, were performed on O_2Hb. Additionally, in order to examine relationships between memory and O_2Hb, correlations between Hits and measures of O_2Hb as a function of Time, Hemisphere, and Handedness, were also conducted.

Because of high within and between subject variability, and to therefore reduce such variability, in addition to analyses of raw O_2Hb, this measure was also converted into change (Δ) scores, wherein O_2Hb during encoding was subtracted from O_2Hb during recall for each hemisphere (ΔO_2Hb LH and ΔO_2Hb RH), thereby removing the variability found in raw scores that can obscure fNIRS results. Positive scores indicate increasing O_2Hb during Recall relative to during Encoding. ΔO_2Hb was examined via a 2 (Hemisphere) × 2 (Handedness) mixed-ANOVA. Additionally, Δ O_2Hb was examined via correlation with Hits as a function of Hemisphere and Handedness.

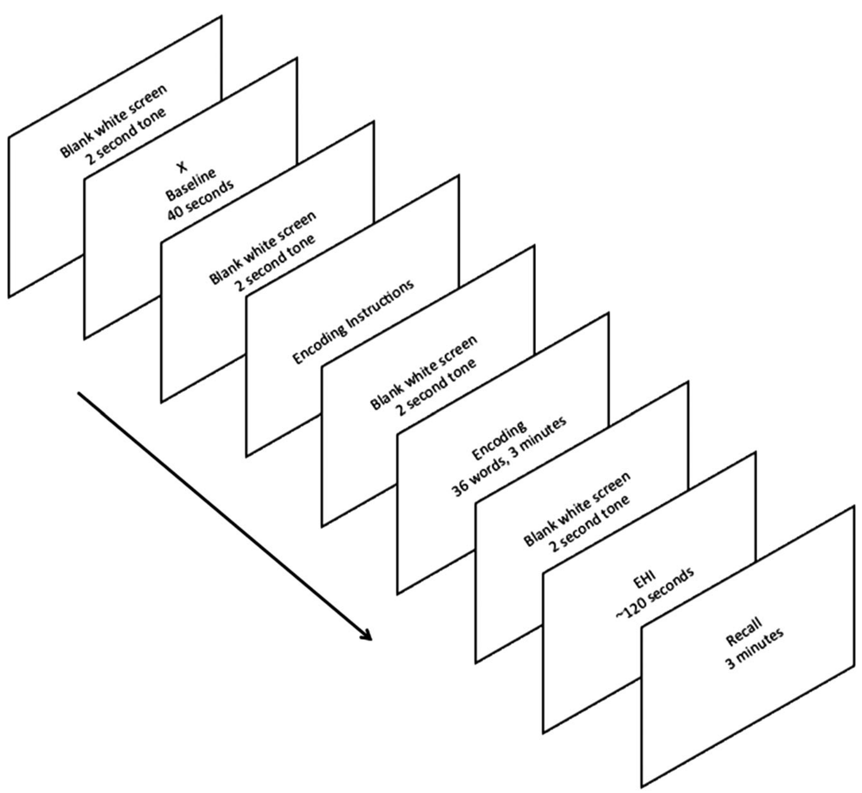

Figure 1. Procedure for baseline, encoding, and recall.

Results

Memory task

Replicating previous work, ICH significantly outperformed CRH on memory measures, including Hits (CRH $\bar{x} = 7.53$, sd = 2.63, ICH = 8.84, sd = 2.01; unpaired *t*-test (57) = 2.08, $p < .05$; Cohen's $d = 0.55$) and Corrected Scores (CRH $\bar{x} = 7.15$, sd = 2.89, ICH $\bar{x} = 8.64$, sd = 2.10; unpaired *t*-test (57) = 2.10, $p < .05$; $d = 0.55$). Handedness differences in False Alarms were not significant, but were in the predicted direction (CRH $\bar{x} = .38$, sd = .65, ICH $\bar{x} = .20$, sd = .50, $p > .2$). Note that further examination of False Alarms was not possible due to the low variability ($\bar{x} = .30$, sd = .60; Median and Mode both = 0) and restricted range (Minimum = 0, Maximum-2) of this measure). Similarly, we focus below on Hits, and not on Corrected Scores, for that same reason.

FNIRS

O_2Hb

The 2 (Time: Encoding versus Recall) × 2 (Hemisphere: Left versus Right) × 2 (Handedness: CRH versus ICH) mixed-ANOVA revealed a main effect of Time ($F(1, 57) = 78.56$, $p < .01$, $d = 2.32$), with Recall resulting in significantly greater O_2Hb ($\bar{x} = 1.09$, sd = 1.06) compared with Encoding ($\bar{x} = .01$, sd = .55), regardless of Hemisphere or Handedness (see Figure 2). No other comparisons approached significance ($p > .1$).

Correlations between LH O_2Hb, RH O_2Hb, and Hits as a function of Encoding, Recall, and Handedness revealed a positive correlation between Hits and RH O_2Hb during Recall in CRH only ($r = .44$, $p < .01$; see Figure 3). No other correlations were significant.

Δ O_2Hb

Main effects and interactions in the 2 (Hemisphere) × 2 (Handedness) mixed-ANOVA examining Δ O_2Hb were not significant ($p > .1$ for all comparisons). Nevertheless, paired *t*-tests comparing LH Δ O_2Hb versus RH Δ O_2Hb as a function of handedness revealed a strong trend toward increased LH Δ O_2Hb versus RH Δ O_2Hb in ICH (LH ΔO_2Hb $\bar{x} = 1.07$, sd = .86; RH Δ O_2Hb $\bar{x} = .84$, sd = .86, t (24) = 1.92, $p = .067$). Differences between LH ΔO_2Hb ($\bar{x} = 1.14$, sd = .91), and RH Δ O_2Hb ($\bar{x} = 1.18$, sd = 1.15) in CRH did not approach significance ($p > .7$; see Figure 4).

In CRH only, RH Δ O_2Hb during Recall was positively and significantly correlated with Hits ($r = .38$, $p < .05$); no other correlations were significant (see Figure 5).

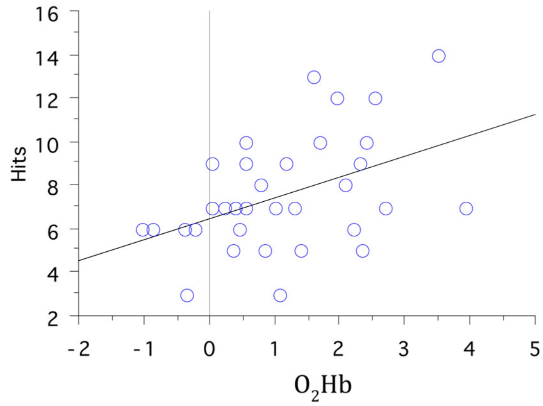

Figure 3. Significant positive correlation between RH O_2Hb during recall and hits in CRH.

Discussion

While a substantial body of evidence has demonstrated a robust and systematic advantage in episodic recall in inconsistent, relative to consistent, handers, to our knowledge no study to date has simultaneously looked at both behavioural and physiological measures. Behaviourally, we replicated prior studies, again finding a significant inconsistent-handed advantage in free recall. Using fNIRS

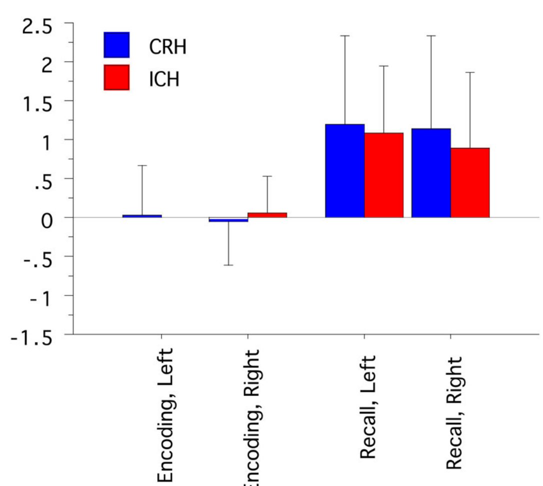

Figure 2. O_2Hb as a function of time, hemisphere and handedness. Only significant effect is that of time, with recall resulting in significantly greater O_2Hb than encoding.

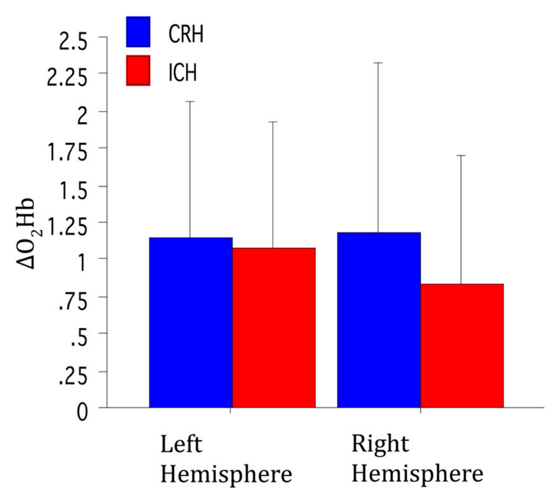

Figure 4. ΔO_2Hb as a function of time, hemisphere, and handedness. Note that only the difference between LH and RH Δ O_2Hb in ICH approached significance ($p = .067$, see text).

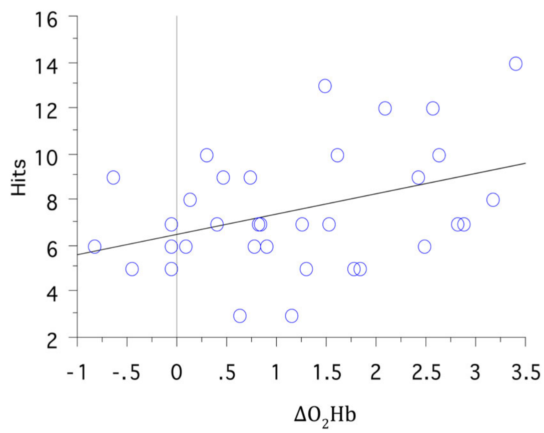

Figure 5. Significant positive correlation between RH Δ O_2Hb during recall and hits in CRH.

as a measure of frontal lobe activity, we found the first evidence for handedness differences in brain activity that are associated with the handedness differences in episodic retrieval. Specifically, the primary finding was that increased RH activity during recall was associated with better retrieval, but for consistent-handers only.

This result is consistent with past findings that right frontal activation is associated with episodic retrieval (e.g., Okamoto et al., 2011). The novel finding here is that this effect was obtained for consistent-handers only. Why did inconsistent-handers not show this expected pattern? One possibility is that inconsistent-handers' neuronal organisation for recall is different from that of consistent-handers. For example, it has been suggested that individual differences in handedness effects on cognitive task performance reflects, in part, increased access to right hemisphere processes in inconsistent-handers (e.g., Prichard, Propper, & Christman, 2013). Relatedly, it has been argued that inconsistent-handers rely on interhemispheric interaction to a greater degree than consistent-handers, for recall of episodic information (e.g., Propper et al., 2005) Other work indicates increased neuronal structural symmetry in inconsistent-, relative to consistent-handers (e.g., O'Donnell et al., 2010). It is possible that episodic memory retrieval in the inconsistent-handed reflects altered structural representation, with both the left and right hemispheres contributing to the task, in ways that might vary as a function of some unknown characteristic, for example, of recall difficulty, word frequency, or some other possible mediator. Such cortical arrangements may result in an obscuring of relationships between right hemisphere 02Hb and recall, or, a linear relationship between these two variables may simply not exist in this population. Future research should further investigate these possibilities.

The only physiological effect to approach significance for inconsistent-handers was a marginally significant effect in which activation levels increased from encoding to retrieval in the left hemisphere more than in the right. Although caution is needed in interpreting such a marginal effect, it raises an interesting possibility that perhaps inconsistent-handers, but not consistent-handers, are able to recruit left hemisphere regions to assist in the retrieval process. This possibility aligns with the potentially altered neuronal representation of episodic memory suggested above in this population. Interestingly a main effect of Time, such that O_2Hb was greater during Recall compared with Encoding, regardless of hemisphere or handedness, suggests perhaps greater effort during this condition relative to encoding. Future work can investigate this possibility by varying word list difficulty, perhaps.

Although tentative and preliminary, the current results represent the first examination of the neural substrates underlying the robust behavioural episodic retrieval advantage in inconsistent-handers. It should be pointed out that only women were included in this research; certainly exclusion of men limits generalisability generally. Given that women are generally superior than men at episodic memory tasks (e.g., Herlitz, Nilsson, & Backman, 1997; Rentz et al., 2016), given the differences in neuronal organisation between men and women that may influence memory performance (e.g., Ramirez-Carmona, Garcia-Lazaro, Dominguez-Corrales, Aguilar-Castaneda, & Roldan-Valadez, 2016), and the practical considerations involved in recruiting sufficient numbers of men participants in an increasingly female-dominated field of study, only women were included here. Future work should consider examining men to determine if the findings here are applicable to this gender. It is recommended that other researchers using functional brain imaging techniques to study memory processes include degree of handedness as a variable in their analyses, as our results suggest that different handedness groups exhibit different patterns of brain activation during episodic retrieval.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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