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The Functional Brain Networks that Underlie Early Stone

Age Tool Manufacture

Supplementary Information

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Supplementary Discussion

Behavioural Results

Every participant was successful at removing flakes from a cobble by the final neuroimaging session. The statistical analysis of the debitage-related variables did not reveal a clear pattern of higher skill among one group over the other (Supplementary Table 1). Both groups produced a similar proportion of flakes to shatter on both low quality and high quality material, though the verbal group made significantly more whole flakes relative to flake fragments. The verbal group, on average, produced more flake mass than the nonverbal group, though this difference was not significant. Otherwise, both groups reduced a similar amount of shatter mass from the original cobble during the Oldowan task, leaving a similar amount of material unexploited on the core. The verbal group had fewer missed strikes than the nonverbal group, which could signify increased skill, but this difference was not significant. Some significant differences between the groups occurred among the measures of flake shape. The flakes produced by the nonverbal group had a shape that was significantly thinner and longer than those produced by the verbal group, which replicates the results of a previous study that looked at differences in knapping skill between verbally- and nonverbally-instructed novices in an interactive teaching environment¹⁸. The flakes made by the nonverbal group also had significantly smaller platforms relative to flake size than the verbal group, though platform shape on its own did not significantly differ between groups.

There is no evidence from the statistical analysis of the core tools that one group excelled over the other (Supplementary Table 1). Both groups had an almost identical proportion of successful bifaces (verbal = 0.652, nonverbal = 0.650). The verbal group's bifaces had a larger average breadth to thickness ratio than the nonverbal group, but this difference was not significant. These results imply that the two groups reached similar levels of skill, and any differences in localized neural activation reflect the type of tool constructed (Oldowan, Acheulian) and the training context (verbal, nonverbal).

		Nonverbal			Verbal			
Variable	Ν	Mean	S.D.	Ν	Mean	S.D.	Statistic	Sig.
Platform shape (width/thickness)	1719	3.68	2.42	1609	3.50	2.07	1.22^{D}	0.103
Flake shape (size/mass)	3157	2.96	4.16	2711	2.34	3.85	4.78^{D}	< 0.001*
Relative platform area	1710	27.54	33.1	1604	33.41	36.78	2.81^{D}	<0.001*
Proportion of flakes to shatter	35	0.89	0.10	36	0.89	0.11	612.00^{U}	0.836
Proportion of flakes on low quality material	32	0.84	0.15	35	0.85	0.16	589.00^{U}	0.715
Proportion of flakes on high quality material	31	0.93	0.09	30	0.91	0.12	422.50^{U}	0.535
Proportion of flakes to flake fragments	35	0.57	0.18	36	0.66	0.17	2.35^{t}	0.021*
Proportion of flake mass removed	35	0.48	0.20	36	0.56	0.22	771.00^{U}	0.105
Proportion of shatter mass removed	35	0.11	0.12	36	0.12	0.18	693.00^{U}	0.469
Proportion of remaining core mass	35	0.32	0.20	36	0.28	0.22	490.00^{U}	0.107
Relative number of missed strikes	35	0.15	0.22	36	0.12	0.10	671.00^{U}	0.637
Biface ratio (breadth/thickness)	13	1.89	0.34	15	2.00	0.54	0.62^{t}	0.538

Supplementary Table 1. Group differences in knapping skill using debitage and core variables

*Significant at p < 0.05

^DA Kolmogorov-Smirnov test was applied to cases with non-normal distributions and unequal variances. Statistic here refers to a D statistic.

^UA Mann-Whitney U test was applied to cases with non-normal distributions and equal variances. Statistic here refers to a U statistic.

'Student's t-test was applied to cases with normal distributions and equal variances. Statistic here refers to a t statistic.

Preliminary Meta-Analysis

Previous neuroarchaeological research suggests that stone knapping behaviours do not require working memory involvement but do overlap with language-processing areas^{1,14,15,17}. This interpretation was based mainly on the lack of activation in the dorsolateral prefrontal cortex, which is considered to be an important component of the working memory system. This claim may have been premature, however, as working memory is a distributed neural system with multiple integrated, cortical regions. Indeed, a recent ALE meta-analysis of neuroimaging studies focused on stone knapping reveals that working memory plays an essential role in stone knapping, especially during Acheulian tool replication⁶⁷. By plotting the coordinates of eight significant clusters from a recent neuroarchaeological study¹ in the same space as the coordinates from a visual working memory (VWM) meta-analysis¹⁹ and a language-processing meta-analysis that includes phonological, lexico-semantic, and sentence processing neuroimaging studies³⁴, we also found that stone knapping functional activation not only overlaps with language centres but also overlaps with the VWM network, a fact that has been overlooked in previous studies (Supplementary Fig. 1).

Neuroimaging Results

fNIRS is unique in that it simultaneously measures the changes in concentration of both oxygenated haemoglobin (oxy-Hb) and deoxygenated haemoglobin (deoxy-Hb). Here we present the results for both chromophores. Supplementary Table 2 shows the list of all significant ANOVA results related to the oxy-Hb signal. The results reported in the main text (highlighted in grey in Supplementary Table 2) reflect active clusters with the highest-order effect (an Interaction effect in the case of overlap between a Main Effect and an Interaction; a Main Effect otherwise) that were also significantly higher than the motor baseline task. Effects that were not

significantly greater than motor baseline but lie within the temporal cortex were also included because we did not control for sound production in the motor baseline task. In total, we focused on six clusters that showed a significant effect of Task and four clusters where Oldowan and Acheulian toolmaking were modulated by the linguistic context of training. Note that all of the Group main effects were subsumed by an overlapping Task x Group interaction.

Supplementary Table 3 shows the list of all significant ANOVA results related to concentrations of deoxy-Hb. The ANOVA revealed multiple clusters showing a significant main effect of Group and Task, as well as significant Group x Task interactions. Ten of these significant clusters overlapped spatially with significant oxy-Hb clusters. In nine of these clusters, there was an inverse relationship between deoxy-Hb and oxy-Hb (highlighted in grey in Supplementary Table 3). Oxy-Hb and deoxy-Hb signals tend to be negatively correlated with each other⁶⁸. Critically, six of these nine clusters overlapped with the oxy-Hb results reported in the main text, including the right temporal pole, left superior temporal gyrus, right postcentral gyrus, left middle frontal gyrus, and two areas in the left precentral gyrus (PrG; Supplementary Fig. 3). These deoxy-Hb results lend further support to the conclusions reached in the main text.

			MN	I Coordi	nates	Volume	M Aoyy-Hb
Localization		Sig. Effect ²	(mm)			(mm^3)	$(\mu M) \pm SEM$
			Х	у	Z	(11111)	(µ101) = 512101
Task n	nain effect						
Left	Superior temporal gyrus	A>O	-60.8	-31.9	17.7	3600	6.18 ± 0.06
Left	Precentral gyrus ^{*α}	O>A	-31.7	-4.3	59.7	3584	6.26 ± 0.07
Right	Postcentral gyrus ^{α}	A>O	46	-25.2	62	1688	5.07 ± 0.05
Right	Postcentral gyrus*	O>A	58.5	-14.7	32.3	1624	6.55 ± 0.12
Left	Precentral gyrus*	A>O	-50.2	5.8	33.5	1104	4.92 ± 0.05
Right	Middle temporal gyrus	A>O	67.7	-33.6	2.8	536	4.39 ± 0.02
Right	Precentral gyrus ^{α}	A>O	61.9	7	28.7	432	5.81 ± 0.20
Left	Supplementary motor area*	A>O	-9.9	1.4	75.7	352	4.73 ± 0.07
Left	Postcentral gyrus*	O>A	-50.7	-14.2	32.8	320	5.18 ± 0.11
Group main effect							
Right	Rolandic operculum ^{α}	NV>V	63.4	-12.3	11.6	6904	7.03 ± 0.10
Left	Inferior parietal lobule ^{*α}	NV>V	-55.2	-31.4	38.9	6312	7.38 ± 0.08
Left	Superior frontal gyrus ^{*α}	NV>V	-22.5	-0.7	65.8	5688	6.48 ± 0.06
Right	Postcentral gyrus ^{α}	NV>V	36.3	-33.1	71	328	5.30 ± 0.13
Group x Task interaction							
Dight	Tomporal polo	V: O>A; A:	57.2	0.6	5 0	1069	6.92 ± 0.09
Kight	remporar pole	NV>V	57.5	9.0	-3.0	4908	0.83 ± 0.08
Left	Middle frontal ourus*	NV: O>A;	27.0	1 /	64.0	1028	8.40 ± 0.13
Len	Wildle Homai gyrus	O: NV>V	-21.9	-1.4	04.9	4920	0.40 ± 0.13
Right	Supramarginal gyrus	O: NV>V	63.7	-26	19.9	4008	6.39 ± 0.07
Left	Supramarginal gyrus	V: A>O; O:	-55 5	-42.6	33	2456	5 13 + 0.04
Lon	Supramarginar gyrus	NV>V	55.5	12.0	55	2150	5.15 ± 0.01
Right	Postcentral gyrus	V: A>O; O: NV>V	46.7	-32	62.8	1864	6.88 ± 0.13
Right	Postcentral gyrus	NV: A>O	60.3	-2	30.2	1192	5.78 ± 0.11
Right	Inferior frontal gyrus*	A: V>NV	51.4	37.2	13.5	776	4.79 ± 0.05
Left	Precentral gyrus*	NS	-40.3	6.5	46.2	624	5.00 ± 0.06

Supplementary Table 2. Regions of significant activation (oxy-Hb) as determined by a twoway ANOVA between Group (verbal and nonverbal) and Task (Oldowan and Acheulian)¹.

¹Grey highlighted areas reflect active clusters with the highest-order effect (an Interaction effect in the case of overlap between a Main Effect and an Interaction; a Main Effect otherwise) that were also significantly higher than the motor baseline task.

²A=Acheulian, O=Oldowan, V=Verbal, NV=Nonverbal, NS=Not significant

*Indicates cluster where knapping activation is significantly higher than motor baseline activation

 $^{\alpha}$ Main effect subsumed by an Interaction effect. Note that localization labels reflect the centre of mass of each cluster using MNI labelling conventions; thus, labels used for overlapping main effects and interactions might differ because the centres of mass differed.

Supplementary Table 3. Regions of significant activation (deoxy-Hb) as	determined by a two-
way ANOVA between Group (verbal and nonverbal) and Task (Oldowan	and Acheulian). ¹

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Localization		Sig. Effect ²	MNI Coordinates (mm)		Volume	$M \Delta \text{deoxy-Hb}$	
			х	У	Z	(mm^3)	$(\mu M) \pm SEM$
	Task main effect						
Right	Precentral gyrus ^{α}	O>A	43.1	-16.2	59.5	2728	5.24 ± 0.04
Left	Precentral gyrus	O>A	-49.2	-2.6	33.9	944	5.18 ± 0.08
Right	Postcentral gyrus ^{α}	A>O	58.9	-12.7	29.6	920	5.27 ± 0.08
Left	Superior temporal gyrus	O>A	-62.1	-37.6	14.7	744	4.91 ± 0.06
Right	Inferior frontal gyrus	A>O	53.0	29.1	15.7	704	5.02 ± 0.08
Left	Middle frontal gyrus	O>A	-39.3	30.0	41.0	600	4.94 ± 0.07
Left	Inferior frontal gyrus	O>A	-53.4	15.7	34.5	400	4.57 ± 0.05
Right	Superior parietal lobule ^{α}	A>O	36.0	-59.8	60.4	384	4.46 ± 0.04
T 0	Group main effect		7 0 (10 5	1000	
Left	Superior temporal gyrus	NV > V	-59.6	-17.4	10.7	1920	5.74 ± 0.07
Right	Postcentral gyrus	V > N V	55.9	-24.0	45.8	1120	$5./4 \pm 0.11$
Left	Precentral gyrus ^a	NV > V	-41.9	0./	50.0	648	4.83 ± 0.05
Left	Middle frontal gyrus	V > N V	-46.4	28.2	34.0	640	5.00 ± 0.06
Cr	oun y Task interaction						
UI UI	oup x rask interaction	NV· A>O·					
Right	Precentral gyrus	$V \cdot O > A \cdot O$	523	-4.6	49 9	2704	625 ± 0.09
itigin	i iccontiur gyrus	V>NV	02.0	1.0	17.7	2701	0.25 = 0.07
	- ·						6 0 0 0 0 0
Left	Precentral gyrus	O: NV>V	-40.4	7.9	46.9	2384	6.33 ± 0.09
Left	Precentral gyrus	NS	-26.7	-0.6	58.8	2016	5.38 ± 0.06
Right	Superior parietal lobule	NS	40.8	-50.0	62.4	1120	$5.52\ \pm 0.08$
Right	Superior temporal ovrus	NV: O>A;	59.2	-21.6	69	1000	4.80 ± 0.04
Kigin	Superior temporar gyrus	A: V>NV	57.2	-21.0	0.7	1000	4.00 ± 0.04
Left	Superior temporal gyrus	V: A>O; A: V>NV	-64.4	-9.6	0.4	928	4.66 ± 0.04
Right	Postcentral gyrus	$0 \cdot NV > V$	597	-12.0	297	856	530 + 0.09
Right	Supramarginal gyrus	NS	593	-45.6	35.5	856	472 ± 0.04
Right	Middle frontal gyrus	NV· O>A	41.6	13 3	55.5	784	5.17 ± 0.09
Left	Paracentral lobule	O: V>NV	-7.9	-32.2	78.2	632	4.83 ± 0.06
Right	Inferior frontal gyrus	O: NV>V	60.0	17.5	3.2	504	5.27 ± 0.09
Right	Postcentral gyrus	NS	33.2	-37.5	66.2	440	4.65 ± 0.05
Diaht	Middle termorel arms	V: A>O; A:	60.0	20.6	76	424	1 66 - 0 04
Right	whome temporal gyrus	V>NV	00.9	-20.0	-/.0	424	4.00 ± 0.04
Right	Inferior frontal gyrus	NV: O>A	63.3	-12.6	29.3	224	4.65 ± 0.08

¹Grey highlighted rows represent clusters that overlap and share an inverse relationship with significant oxy-Hb clusters (see Supplementary Table 1).

²A=Acheulian, O=Oldowan, V=Verbal, NV=Nonverbal, NS=Not significant

^{α}Main effect subsumed by an Interaction effect. Note that localization labels reflect the centre of mass of each cluster using MNI labelling conventions; thus, labels used for overlapping main effects and interactions might differ because the centres of mass differed.

Supplementary Figures



Supplementary Figure 1. Areas of functional overlap between a prior study of early stone age knapping¹ (red), language-processing³⁴ (light green), and/or VWM¹⁹ (purple), including (a) right inferior frontal gyrus (*pars triangularis*), (b) bilateral ventral PrG, (c) left inferior parietal lobule, and (d) bilateral dorsal PrG. Overlap between spheres is represented by turquois, mauve, and yellow colours. This figure demonstrates that stone knapping overlaps with the VWM network to an even greater extent than it overlaps with language centres.



Supplementary Figure 2. Post-experiment interview subject responses by group (nonverbal = red; n = 14, verbal = blue; n = 14) to the question, "Did you think with language while knapping?" Subjects' responses were coded as one of three categories. A completely negative response to the question was coded as 'Spatial Thinking.' Responses that indicated minimal involvement of inner speech while thinking about the task were coded as 'Spatial Thinking with Some Words,' and participants who emphasized inner speech as their main mode of thinking or mentioned recalling entire phrases from the instruction videos were coded as 'Inner Speech.' Error bars represent standard error.

SUPPLEMENTARY INFORMATION



Supplementary Figure 3. Relationship between significant, overlapping oxy-Hb (purple) and deoxy-Hb (red) clusters (N = 31). Overlap between clusters is represented by turquoise. Bar plots compare relative oxy-Hb (blue) and deoxy-Hb (orange) concentrations across tasks. % Signal Change is in μ M units.

Supplementary References

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