

Anterior insular cortex plays a critical role in interoceptive attention

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Abstract Accumulating evidence indicates that the anterior insular cortex (AIC) mediates interoceptive attention which refers to attention towards physiological signals arising from the body. However, the necessity of the AIC in this process has not been demonstrated. Using a novel task that directs attention toward breathing rhythm, we assessed the involvement of the AIC in interoceptive attention in healthy participants using functional magnetic resonance imaging and examined the necessity of the AIC in interoceptive attention in patients with AIC lesions. Results showed that interoceptive attention was associated with increased AIC activation, as well as enhanced coupling between the AIC and somatosensory areas along with reduced coupling between the AIC and visual sensory areas. In addition, AIC activation was predictive of individual differences in interoceptive accuracy. Importantly, AIC lesion patients showed disrupted interoceptive discrimination accuracy and sensitivity. These results provide compelling evidence that the AIC plays a critical role in interoceptive attention.

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Introduction

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Competing interests:_ə uteors yrl ≰ te t no yr on ng tinfring ∉ sts⊱ ist.

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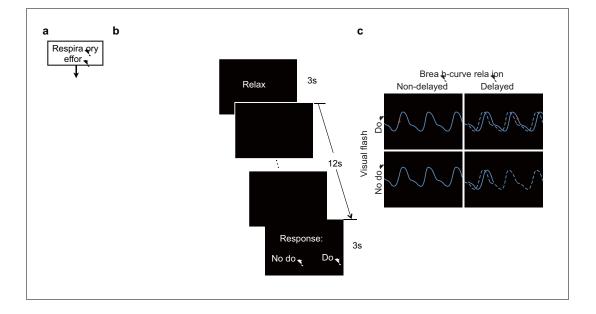
Results

Behavioral results of the fMRI studies

Imaging results of the whole brain analysis of the first fMRI study

ain effects of interocepti e attention and feedback delay, and their interaction

 $\begin{array}{c} & \stackrel{n}{\longrightarrow} & \text{in}_{F} & \not = \text{to in}_{F} & ee_{F} & \text{ptiv} & \text{t}_{F} & \text{ntion} & \text{SD} & \text{vs. } \text{DD} & \not = \text{sso i}_{F} & \text{vite}_{F} & \text{ne}_{F} & \text{ptiv} & \text{t}_{F} & \text{ntion} & \text{SD} & \text{vs. } \text{DD} & \not = \text{sso i}_{F} & \text{vite}_{F} & \text{ne}_{F} & \text{ntion} & \text{vor}_{V} & \sqrt{Fan, 2014} & Wu & et al., 2015 \\ \hline & Xuan & et al., & 2016 & \not = \text{nl} & \text{if}_{F} & \text{te} & \text{AlC} & \text{te} & \text{ors } I & \text{nt}_{F} & \text{rion}_{F} & \text{if}_{F} & \text{ul}_{F} & \text{ers} & \sqrt{ACC} & \text{n} \\ \hline & \text{te} & \text{supp} & \mathcal{R} & \text{nt} & r & \mathcal{m} & \text{ors} & v & \text{supp} & \text{rion}_{F} & \text{if}_{F} & \text{ort}_{F} & \sqrt{AC} & \text{n} \\ \hline & \text{te} & \text{supp} & \mathcal{R} & \text{nt} & r & \mathcal{m} & \text{otor} & F & \sqrt{A} & \text{n} & \text{te} & \text{supp} & \text{rion}_{F} & \text{rion}_{F} & \text{if}_{F} & \text{ote}_{F} & \text{supp} & \text{rion}_{F} & \text{rio$



ŢŢijİ FEF'n tġŢ sış r lon⁴ tġ intr pışit lawelus *Figure 2a Table 3*. In ition teis ➡ ontr st şų ↓ si²ninii ntl ↓ ss ➡ tiv tion or ç➡ tiv tion in tg ➡ op; ş²ions o tġŢ ult ^moŢ pitwor, **Raichle et al., 2001** in lu ini⁴ tġ tġ ų ntr l R; i l p; ront ➡ or‡ tġ Mi ↓ ‡ ^mpor ¹/₂ rus (_G4 n tġ post; rione ini⁴ ul ➡ or‡ . ➡ tiv tion in tġ AIC tġ Mi ↓ ront ¹/₂ rus tġ A n tġ ‡ ^mpor l pışit łum tion w s

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Table 1. t tinti s o 🚓 vior 🖙 sults o ta 👘 Istu 🕫 s.

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		First sa	First sample			Second sample			
		Df	т	Cohen's d	Df	т	Cohen's d		
acc racy	intero s. 0.5	43	4.5 ***	2. 8	27	3.77***	2.59		
	intero s. extero	43	-2.36*	0.35	27	83	0.35		
ď	intero s. 0	43	3.09***	2.0	27	2.89***	2.67		
	intero s. extero	43	-2.3 *	0.35	27	-2.83**	0.50		
β	intero s. extero	43	-2.3 *	0.35	27	-2.83**	0.50		
RT	intero s. extero	43	2.89**	0.44	27	0.6	0. 2		

* p<0.05; **p<0.0 ; ***p<0.00 .

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Table 2. *; rsomer one Itioner op weinig nts√n Brys For torsel ngettery ntor the non-the vior Ine, sup ne nts or to inst to ger on n we ross to two s non-table s.

		Relative accuracy	Subjective difficulty	BPQ	Positive PANAS	HAMA	BDI
	Relati e acc racy	-					
st sample	S bjecti e diffic Ity	-0.43** (0.38)	-				
	BPQ	0.27 (0. 7)	-0. 5 (0.29)	-			
	Positi e PA AS	0.3 (.38)	-0.04 (0. 9)	-0.006 (0.9)	-		
	HA A	-0.006 (0.9)	-0. 4 (0.28)	0.25 (0.69)	-0.2 (0.25)	-	
	BD	-0.002 (0.9)	-0.004 (0. 9)	0.6 (0.32)	—0.06 (0.20)	0.70 ^{***} (> 00)	-
	Relati e acc racy	-					
2 nd sample	S bjecti e diffic Ity	-	-				
	BPQ	—0.7 (0.33)	-	-			
	Positi e PA AS	0. 2 (0.27)	-	0.07 (0.25)	-		
	HĄ A	0.29 (0.69)	-	0.40 (.90)	-0.034 (0.24)	-	
	BD	0.034 (0.24)	-	0.075 (0.25)	-0.43 (2.84)	0.47 [*] (4.96)	-
	Relati e acc racy	-					
st + 2 nd samples	S bjecti e diffic Ity	-	-				
	BPQ	0.06 (0.7)	-	-			
	Positi e PA AS	0.25 (. 6)	-	0.03 (0.5)	-		
	HĄ A	0. 2 (0.25)	-	0.3 * (4.9)	-0.09 (0.20)	-	
	BD	0.008 (0. 5)	-	0.4 (0.28)	-0.20 (0.56)	0.60 ^{***} (> 00)	-

* corrected p<0.05; ** corrected p<0.0 ; *** corrected p<0.00 ; al e in brackets represents Bayes factor. BPQ, body perception q estionnaire; PA AS, positi e and negati e affecti e sched le; HA A, Hamilton anxiety scale; BD , Beck depression in entory. DO : https://doi.org/ 0.7554/e ife.42265.009 Correlation bet een interocepti e acc racy and A C acti ation

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Table 3. At tiv tion n vertiv tion o to to involve in int wer ptive to ntion int wer ption - to the ption.

Region	L/R	BA	Х	Y	Z	Т	Z	К
Positi e		271			-		-	
Cerebel m cr s			-30	-70	-24	3.02	nf.	7383
	R	9	32	-68	22	.99	nf.	7.000
v iddle occipital gyr s Cerebel m cr s	IX	7	-20	-78			7.80	
	D	4.4				.72		
nferior frontal gyr s	R	44	52	4	24	.24	7.63	
nferior parietal lob le	R	40	36	-48	44	. 9	7.62	
nferior parietal lob le		40	-38	-46	42	0.4	7.32	
Postcentral gyr s	R	2	46	-40	54	0.29	7.27	
S pramarginal gyr s	R	40	48	-34	42	0.00	7.5	
S perior occipital gyr s	R	7	22	-72	46	9.99	7.5	
Cerebel m V B			-32	-70	-52	9.78	7.06	
S perior parietal lob le (ntraparietal s lc s)	R	7	6	-78	52	9.69	7.02	
Cerebel m V	R		22	-74	-50	9.6	6.99	
v iddle frontal gyr s		46	-44	50	2	9.20	6.80	
v iddle frontal gyr s	R	46	42	42	24	9.6	6.78	
S pplementary motor area	R	6	8	4	76	8.92	6.68	
nferior occipital gyr s	R	37	52	-66	- 2	8.68	6.56	
Cerebel m cr s	R		2	-76	-36	8.66	6.56	
v iddle occipital gyr s (ntraparietal s lc s)	R	9	32	-76	34	8.58	6.52	
Thalam s	R		8	-20	2 Û	8.55	6.50	
nferior temporal gyr s	R	20	56	-38	-2 0	8.4	6.43	
nferior frontal gyr s	R	45	44	38	2	8.3	6.38	
S perior parietal lob le (ntraparietal s lc s)		7	-20	-72	46	8.2	6.33	
S pplementary motor area		6	-2	-4	74	8.08	6.27	
nferior frontal gyr s		44	-54	2	26	8.07	6.26	
Ca date	R		6	-8	24	7.89	6. 7	
Anterior cing late cortex	R	32	2	8	44	7.78	6. 2	
Vermis			-2	-74	- 2	7.76	6. 0	
iddle frontal gyr s	R	46	50	4	40	7.75	6. 0	
iddle frontal gyr s		46	-40	34	34	7.72	6.08	
S pramarginal gyr s		40	-60	-36	28	7.47	5.95	
iddle frontal gyr s	R	6	28	2	48	7.0	5.69	
Anterior ins lar cortex	R		34	20	4	6.98	5.68	
Postcentral gyr s		2	-62	-26	36	6.87	5.62	
nferior frontal gyr s		6	-52	8	2	6.84	5.59	
S perior frontal gyr s		6	-26	4	66	6.73	5.53	
iddle occipital gyr s (ntraparietal s lc s)		7	-24	-66	36	6.66	5.49	
ing al gyr s		8	- 8	-90	- 8	6.6	5.46	
S perior parietal lob le		0	-24	-44	72	6.55	5.42	
Ca date			-24	22	4	6.45	5.37	
		6	-o _40	22	56		5.23	
Precentral gyr s						6.23		
S perior occipital gyr s		8	-22	-92	28	6.20	5.2	

Table 3 continued on next page

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Table 3 continued

			MNI					
Region	L/R	BA	Х	Y	Z	Т	Z	К
v ^{iddle} occipital gyr s	R	8	30	-86	6	6.09	5.4	
F siform gyr s		37	-46	-46	-22	5.82	4.97	
Anterior ins lar cortex			-30	20	8	5.50	4.76	
C ne s		9	0	-88	34	5.22	4.57	
S perior parietal lob le		5	- 8	-60	66	5.8	4.54	
F siform gyr s	R	37	44	-32	-20	4.96	4.39	
egati e								
Anterior cing late cortex	R	32	4	38	-4	7.47	5.95	3232
Anterior cing late cortex		32	-6	38	-4	7.0	5.94	
S perior frontal gyr s		9	- 6	38	54	5.97	5.07	
v edial s perior frontal gyr s	R	32	0	52	20	5.33	4.65	
edial s perior frontal gyr s		32	-8	50	26	5.32	4.63	
iddle frontal gyr s		8	-24	30	56	5. 2	4.50	
S perior frontal gyr s		9	-20	32	48	4.54	4.08	
Prec ne s		23	- 0	-44	40	6.45	5.37	89
Prec ne s	R	23	6	-60	24	4.24	3.85	
v iddle temporal gyr s		2	-60	- 0	- 4	5.89	5.02	787

t≢ ntion √Figure 4b[#]. in il r≱≱l∉ sults y∉ ∉ o to ing we n terel t AIC w s us s tere er √Figure 4—figure supplement 1^{*}.

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			MNI					
Region	L/R	BA	Х	Y	Z	т	Z	К
Positi e								
Anterior ins lar cortex	R		30	26	-4	5.26	4.60	68
nferior frontal gyr s	R	45	42	22	8	4.40	3.98	
Ca date	R		8	24	4	4.29	3.90	
nferior parietal lob le		40	-38	-54	42	5.23	4.58	598
Ang lar gyr s	R	39	44	-44	30	4.99	4.4	37
nferior parietal lob le	R	40	56	-54	44	4. 7	3.80	
v iddle frontal gyr s	R	6	34	8	46	4.78	4.26	780
iddle frontal gyr s	R	9	34	8	34	4.74	4.23	
v iddle frontal gyr s	R	46	34	28	32	4.32	3.92	
egati e								
ing al gyr s		7	- 0	-78	-4	6.2	5.22	443

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Table 5. A tiv tion o**b** in \not \not in \not \not \not in \not in \not in \not in in in

			MNI					
Region	L/R	BA	Х	Y	Z	т	Z	К
Positi e								
Anterior ins lar cortex	R		28	28	0	5.52	4.77	56
nferior frontal gyr s	R	47	40	26	- 0	4.66	4. 7	
v iddle frontal gyr s	R	9	40	4	40	5.36	4.67	2330
S pplementary motor area	R	8	4	22	54	5. 9	4.55	
Anterior cing late cortex	R	32	6	36	38	5. 2	4.5	
S perior frontal gyr s	R	8	6	30	44	4.7	4.2	
nferior frontal gyr s	R	45	46	22	6	4.50	4.05	
v iddle frontal gyr s	R	6	34	4	52	4.27	3.88	
S pplementary motor area		6	- 2	8	52	3.64	3.38	
Anterior cing late cortex	R	32	0	30	28	3.49	3.25	
S pramarginal gyr s	R	40	54	-46	26	4.9	4.35	748
iddle temporal gyr s	R	2	66	-32	- 0	4.70	4.20	
nferior parietal lob le	R	9	60	-48	42	4.56	4. 0	
S perior temporal gyr s	R	42	58	-40	6	4.49	4.04	

DO : https://doi.org/ 0.7554/e ife.42265.0 4

r \$ eer ptive to nton vBD_n DD * r rtim on to nom to AIC to to voCG n rom to AIC to vox Figure 4c n Figure 4-figure supplement 2. p B in to to to to to rem to the remove ptive nr for ptive to nto vox for the ntime remove ptive nr for to a nom to the ntime remove on the remove of the area of the second to
 $\mathbf{v} = \mathbf{p} \cdot \mathbf{ron} + \mathbf{p} \cdot \mathbf{n} + \mathbf{ron} + \mathbf{ron} + \mathbf{n} + \mathbf$

Region-of-interest (ROI) analysis results of the second fMRI study

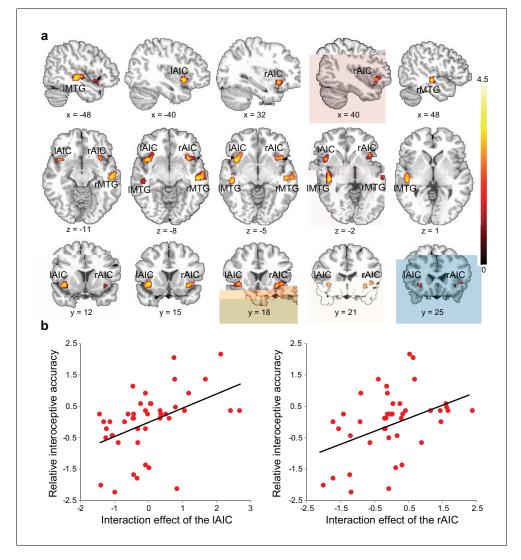


Figure 3. Relationship bet een brain acti ation and beha ioral performance across participants. (a) This as re ealed in a regression analysis of contrast images for the interaction bet een interocepti e attention deployment (BDT s. DDT) and breath c r e feedback condition (delayed s. no-delayed), ith performance acc racy on interocepti e and exterocepti e tasks as regressor-of-interest and co ariate, respecti ely. A C, anterior ins lar cortex; TG, middle temporal gyr s. (b) Correlational patterns bet een the interaction effect of bilateral A C acti ation and relati e interocepti e acc racy. Data ere normalized as z-scores. DO: https://doi.org/ 0.7554/e ife.42265.0 5

The follo ing so rce data is a ailable for fig re 3:

Source data 1. CSV file containing data for *Figure 3b*. DO : https://doi.org/ 0.7554/e ife.42265.0 6

Lesion study results: the necessity of the AIC in interoceptive attention

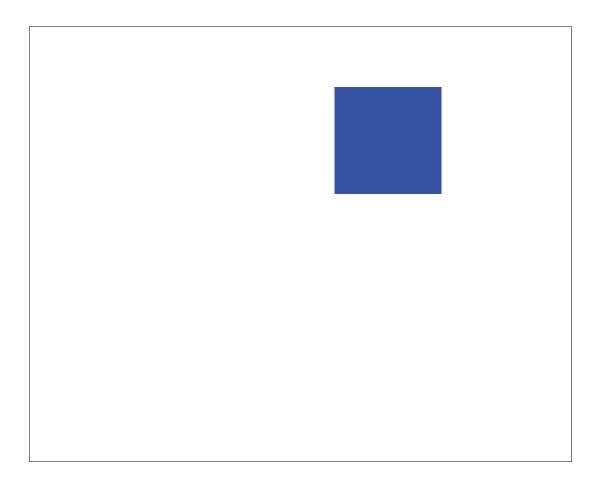
Figure 6 shows the insult relation of religing the AIC prime rate of the most of religing the signal relation of the relati

Discussion

sint I be show that the AIC is involve in interest pity the ntion tow rote spectrum rote in with the unter rote interest of the active rote and the active rote active ro

The necessity of the AIC in interoceptive attention

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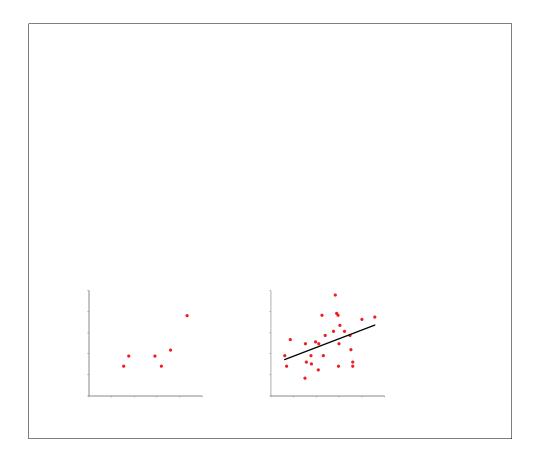
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Table 7. & ositive n 🕫 tive per sope sicle i lint 🖝 tion, 🛩 ts with te nor start AIC s te er .

Region	L/R	BA	MNI	Y	Z	Т	Z	К
Positi e	L/ K	DA	Λ	1	4	1	4	K
nferior frontal operc m	R	44	52	8	26	7.49	5.96	5895
Precentral gyr s	R	6	58	0	36	6.7	5.52	3073
ns la cortex	R	0	38	0	4	6.35	5.30	
P tamen	R		20	8	0	6.33	5.29	
Rolandic operc m	R	48	48	4	0	6.0	5.09	
Ca date	R	40	8		4	5.86	5.00	
nferior frontal gyr s	R	45	42	36	0	4.35	3.94	
Postcentral gyr s	R	43	58	- 6	32	6.95	6.55	2078
S pramarginal gyr s	R	2	66	-22	34	6.04	5.	2070
S perior temporal gyr s	R	42	62	-32	20	5.28	4.6	
Precentral gyr s	K	6	-58	0	30	6.89	5.63	55
P tamen		0	-20	0	2	6.04	5.	5.
S pplementary motor area		6	-8	-4	64	5.90	5.02	
Ca date		0	-8	-4	2	5.4	4.70	
Triangle nferior fronal gyr s		48	-0 -38	32	24	5.2	4.70	
		40	-38	-42	24	5. 9	4.55	
S perior temporal gyr s ns la cortex		44	-46		8	5. 9		
	R	۷	4	-2	64	5. 9	4.55	
S pplementary motor area	Γ	6	-56	-28	40	5. 3	4.50	
S pramarginal gyr s S perior frontal gyr s		6	-38	-20	58	4.73	4.30	
		3	-56	-20	34	4.73	4.22	
Postcentral gyr s			-38					
v iddle frontal gyr s	D	6		-8	52	4.48	4.04	F(0
viddle temporal gyr s Cerebel mV b	R	37	48	-60	8	5.44	4.72	569
			- 6	-74	-48	4.95	4.38	427
Cerebel m V			-24	-66	-52	4.75	4.24	
egati e		7		<u> </u>	,	7.00	E 05	5004
C ne s		7	- 0	-96	6	7.30	5.85	5904
C ne s	R	8	4	-90	28	6.80	5.40	
ing al gyr s	R	8	4	-62	-2	6.05	5.	
ing al gyr s		8	- 8	-74	-8	5.26	4.60	
Calcarine		8	0	-76	8	5.	4.49	
F siform gyr s		8	-24	-80	- 6	4.95	4.38	
Calcarine	R	7	20	-54	6	4.72	4.22	
Cerebel m Cr s			-38	-78	- 8	4.37	3.95	
v iddle occipital gyr s		8	- 6	-86	-4	4.22	3.84	

DO: https://doi.org/ 0.7554/e ife.42265.022

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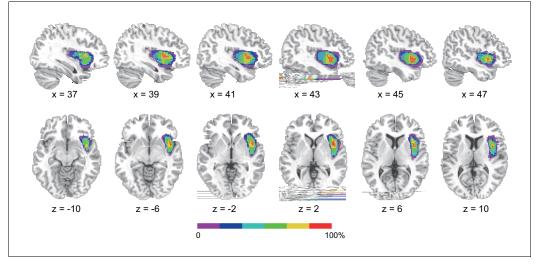
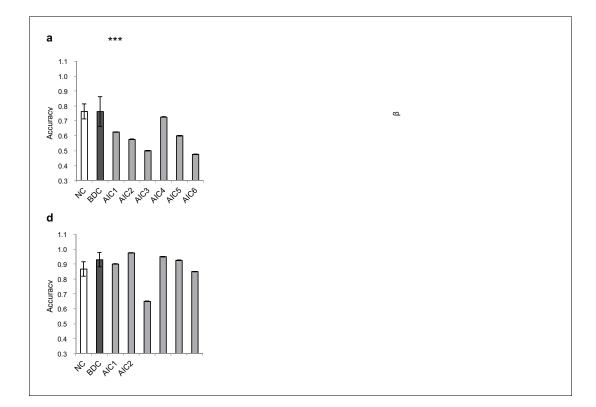


Figure 6. Reconstr ction of anterior ins lar cortex lesions of six patients. Red color indicates 00% o erlap. eft lesions ere flipped to the right side to map the lesion o erlap. DO : https://doi.org/ 0.7554/e ife.42265.028

ro∲ot∌ AlCin p∉ ⇔itiye oinf to \$≥ tainf –∉l ‡ in‡ ee ption \$≥usinf \$≥ta In ∲sion ppre-∌s.

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Mechanisms of the AIC in relation to interoceptive attention

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terrerFerniky roly:ler s on- _mpol ter ACC A FEF n IFG o ter seer bler of∸nitiver ontrol 🖡 twor, VCC 🛚 (Fan, 2014) Wu et al., 2019) 🕴 Iso involve in the intermetion prior ss. _pis is support to the sults of the new new tion on the tivit states in the AIC in the s ∉[≨]~ions.Boteson[™] toe nsor e, net net net t⊮or, te tein lu e ster AlC n ter ACC net possi-🏚 p tnew so in≢ nee, ptivy tot ntion ∢**Khalsa et al., 2009**. _a AIC n pl 🛩, ntr Iroy in int -ゲrtinffrşinsor sffrn ls roጦ tạ ≯oCG n visu 🚽 on‡ n şin s top-own sffrn ls tạ tぢuir ອຸກstion n ອຸກາະ ption twroet ຈ n 🔑 internation witwe ອຸກsor or Setton^-up in orm tion. on top nsor in orn tioner energy riné top int rn lst to top to ier ony y terobére top ∌oCG sy∉ll stop visu lsř∽n lsin 🌫 ont iniř∽top n∽orit ov; ‡rn lin orn″tion. ∌ topown no ul tion o to AlC in int 🖝 ptive to ntion is on plise 🔹 🖞 🖓 ntiñé to 🕫 to t sin ls to to som top nsom othing s. _ais a sult in onsist nt with to intra to instory r n ppinfro int⊧rn l + + linfr is support⊧ \$ insul r n son toe nso⊯ oneti+ s **√Damasio, 2003** n te t soⁿ to prive the near in or n tioner nieti like ontri Set s to interest prive the near prive the near other set. The term of the set In t∌ BD_ inŧ eer, ptiv; t≢ ntion ∉ 🚽 ts 🛩 or^n 🖢 tion o t∌ t≢ ntion to t∌ in≢ rn l 😒 il sFnl√n, to 🎐 tot n tor , ≢rnlvisulsti∩ulus √n, topor unv A._ 🖝 oor in ‡ poor, ptul p+eer ssin⁴ ta AlC / istritet n %alwar ta p+eer sa s or ‡ rn In in‡ rn Iin or/n tion. _த ⊬innin‴ ^o சி n p r ஷ த r in ச தன. ro^ DC proviச ச viசன. t w t in தலை ptiy tத ntion is in in in the initial second time to a new tivit the AIC n the some to nor ક soloCo ખલ્સું ક લાગ્ય the ntion is prim ril no ul ક vi terr on pr tivit states n te AIC n р 🛪 🍸 proposition tites in 🛱 🗂 ustrigention tager on per tivition tage AIC to sensor 🖛 onetiτ sista, oun tion o inat eeeτ ptive tat ntion or 😘 il sinn ls μαμαία ine nete l or αο/γ οst net fⁱ∕ul tion n o₇ ≢ no₇ ptivy t≢ ntion or₅ ≢ rn lo †ne ts or inputs.

Interoceptive task in the respiratory domain

 $\begin{array}{c} & \mathsf{BD}_{\mathcal{N}} \ \ \mathsf{not} \neq \mathsf{p} \neq \mathsf{ent} \ \mathsf{pu} \neq \mathsf{pro} \neq \mathsf{o} \ \mathsf{ont} \neq \mathsf{eo} \neq \mathsf{ption} \neq \mathsf{ue} \neq \mathsf{spir} \ \mathsf{tor} \ \mathsf{pe} \neq \mathsf{spir} \

Interoceptive attention

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Conclusion

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Materials and methods

Task design

Task implementations

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int er ptiv the ntion (Garfinkel et al., 2015) your a w s r sup sup vi te sur tive les of i iult o te BD_f l tive to te DD_ of tatter on interpret times of prorment woul to more in the flat to we person interpret of the result of the re

fMRI experiments

Participants

f R data acq isition and preprocessing

Durinf∽ wention kes nninf∽ t∌ peeti ipntsp; ror/9; t∌ BD_ n DD_ in ş pr‡; runs te t inF t yeşer quiş on AG E__ş ≱ris/∩ აs__ es na r√si/4 ns ErlnFe n Ger/∩ n Ay⊮ita _____gana lpaşe-rr ş -pereç õil.DurinF tasts,s \$noo o Fe najyel-epane nt∢B≱DP sデn ไร ୬୫ ୫ 🖛 quia: ୬୬ita protot ap siጦult ap ous ጦulti-anlin, sym ao-pl n rim ភ័m កែ <E៖ 🖡 ຊ quốm 🕫 to propose on the two is some a first to $p^m m$ with p po p n to $nu^m p$ or dir sweren≓e to ___Fil / pin ≒es were quie usin vn or-provie sine ns≦r sint 粪 بې nsing د بې 🕹 🕴 🖉 مې 🖓 🚽 🖓 مې 🖓 🚽 🖉 مې 🖓 🚽 🖉 🖉 مې 🖉 🛫 🖉 AO ting 🖉 🛫 🖉 🖉 🖉 🖉 ns lip And ______ not the ____Hz & in the the s rate of the north tion sta Exlin 年,A 府 和 solution 3D T structur l in 年 (3D n 平 ng tiz tion-pp p f r pi + quisition $\stackrel{\scriptstyle{\scriptstyle{\sim}}}{\to}$ r $\stackrel{\scriptstyle{\scriptstyle{\leftarrow}}}{\to}$ nt = eo $\stackrel{\scriptstyle{\scriptstyle{\sim}}}{\to}$ $mm \times mm$ = solution = w s lso = quie . Im = pe peo = ssin = w s irst volu/2 = or \neq or \neq or \neq istortions using the \neq in p or p ist \neq to the T_1 in \neq ر ×ر ×ر nor/ lia≓ to st n r at // plat ≺ ontar l + urola∰ei lInstituat 🛛 الع a plat to ر ጦጦ[®]vo_flsią n sptill sጦoote, wite nisotroppi እርጦጦ ull-wite tel-ጦ iጦuጦG ussin 🚽 rng I.

fMRI: analysis of the first sample

mage statistical parametric mapping

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Correlation bet een interocepti e acc racy and the interaction effect of the A C

PP analysis

**! n | sis proving s R_{2} sug $e^{-r_{2}}$ in un tioner on the tivit $\frac{1}{2}$ to $\frac{1}{2}$ and $\frac{1}{2}$ in $\frac{1}{2}$

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DC analysis DC **V**Friston et al., 2003 is up to is *m* for up to is *m* for up to it is the twork structure s a input of the twork structure s a input of the twork structure s at the structure structure s at the structure stru rinf சுந்தாரை uron Ist ‡is ron ஷ sup ஒ nts o 🎾 in 🛩 tivit . DC 🛛 istinf uise s கோம்சு ந မှ n တိုင္ nouse oupliné ner ont t-sper မ်ားေ oupliné မှမာ en out er to မွ မွ ts ၀န္ ခု riny nt l⊯ ontrolf ne twor, pertur \$ntions. Consir rinf te in ere nt linnite 🛩 us linne rope t \$Mit o te, ∌≱l n lsis orte, inertion o in≢ nertion ye on ker on eerte. DC tor, plin te, poet ntil ny ⊛ nisn°so in≢ rpl satu¥r n AIC n ot∌ r to in r sinvoly in in≢ eer ptive t≢ ntion._s Jote, nF∧nt AlCin te, DC ⊮ ste, s ny, ste tin te, ≀≀In Isis._e, ote, ra, Frionson, lu, in te DC 🗤 🕫 🚽 🛊 🤰 on si niji nt positiv n e 🚈 tiv 👀 le sults n wite te oor in ≢ so t∌ _lsir, ntiri ≫ t∌ ^t∽roup l y l g on tr st o # on itions y rsus %s ling . D t ro*m* on, p ∉i ip nts ¼ ∉ , , , er lu , ron te DC 'n Isis 🐢 us 🛩 tivit in on, o te 🛛 , , er oul not 🕫 i 🗸 nti 🙀 🔶

A traff - F DC 1/4 s sport if or II pretering nts with the prime tion Ir n of nouter on prime tion ,≉atur, nto nto at AIC n to oto rtwo Js n with to / in, or to / ll stimuli_s to rivinf input, n‡ rinf to oto rtwo Js. Five %ao mor ls ye f for to simple inf possi \$b moultions o int wer ptive nr to the ptive to the nt a ptive to the nt a ptive not to the ptive nouse one tions seture n ls. es se nor ls vert tens st net ill r l sort to prover vrint nor ls vert en lur ll possi te on to tions o te no ul tion o intre-rp-terrřetAIC n tertwooterrus.

oբ∳ron⊃prison ษsin⊐pln¢n‡ usin∻rn on∽p∳rts B in DC ₂to p‡rn∩ing tay nost live I nove I o te pnove ls⁵rive n te o Sprve t ron⊓ ll petei ip nts **∢Stephan et al.**, 2009.__e FX n lsier on put start on post rior pro 🕽 Skite s t te 챧 roup 🕁 y l n ter r≠rr 🖌 👘 🕫 pro 📽 Mait o 🊈 iyn n≊orl r not ster pro 🎗 Mait te tteis nor lis not liv. I te n ll ote r nor te onsir r **(Stephan et al., 2009**. o sun n riz te striffteor er tive on-🖝 tivit nits no ultion quntit tive l 🐙 use rno/ny 🛩 ts BA to o Sain ver 🐲 on 🖝 -**∢Pennyetal.,2010**. 💭 on ⇔u≢ on∋-s ∩ipel t≢stson t∌ sur∯ert-sperieri B Ap r n₂≢n⇒ sti-がまs to se ss te to onisten 🛩 ross surter to with Bong rronter orgen tion or ルultiple ✓ omp risons.

fMRI: ROI analyses of the second sample

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Author contributions

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