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Temporal continuity of self: Long autocorrelation windows mediate self-specificity

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ABSTRACT

The self is characterized by an intrinsic temporal component consisting in continuity across time. On the neural level, this temporal continuity manifests in the brain's intrinsic neural timescales (INT) that can be measured by the autocorrelation window (ACW). Recent EEG studies reveal a relationship between resting state ACW and self-consciousness. However, it remains unclear whether ACW exhibits different degrees of task-related changes during self-specific compared to non-self-specific activities. To this end, participants in our study initially recorded an eight-minute autobiographical narrative. Following a resting-state session, participants were presented with their own narrative and the narrative of a stranger while undergoing concurrent EEG recording. Behaviorally, subjects evaluated both of the narratives and indicated their perceptions of positivity or negativity on a moment-to-moment basis by positioning a cursor relative to the center of the computer screen. Our results indicate: (a) greater spatial extension and velocity in the behavioral cursor movement during the self narrative assessment; and (b) longer neural ACWs in response to the self- compared to the non-self narrative assessment; and (b) longer neural ACWs in response to the self- compared to the non-self narrative alves findings demonstrate the importance of longer temporal windows in neural activity measured by ACW for self-specificity. More broadly, the results highlight the relevance of temporal continuity for the self on the neural level. Such temporal continuity may, correspondingly, also manifest on the psychological level as a "common currency" between brain and self.

The self is a core feature of our mental life characterized by an intrinsic temporal component operating across different timescales (Wolff et al. 2019; Kolvoort et al. 2020; Huang et al. 2016; Ersner-Hershfield et al., 2009a, 2009b). In the brain, these timescales have been operationalized as intrinsic neural timescales (INTs) which refers to the temporal autocorrelation properties of neuronal populations (Stephens et al., 2013; Watanabe et al., 2019; Gao et al., 2020; Ito et al., 2020; Raut et al., 2020; Golesorkhi et al., 2021a, 2021b; Demirtas et al., 2019). For instance, primary sensory neurons exhibit rapid firing rates and thus shorter temporal windows in response to external stimuli (Runyan et al., 2017) whereas activity in transmodal regions can persist for extended periods over longer temporal windows (Zylberberg and Strowbridge, 2017). INTs have been implicated in shaping perception, behavior, and cognition including consciousness (Zilio et al., 2021;

Golesorkhi et al., 2021a, 2021b; Murray et al., 2014; Ito et al., 2020; Wolff et al., 2022).

Recently, three studies have demonstrated a relationship between INTs in the resting state and facets of the self. Wolff et al. (2019) found that longer INTs in resting-state EEG signals correlate with higher private self-consciousness. Similarly, a positive association was observed between longer INTs and private self-consciousness in fMRI (Huang et al., 2016). Another EEG study by Kolvoort et al. (2020) observed a positive correlation between resting-state INTs and the degree of self-prioritization effect (SPE) during a perceptual matching task with temporal delays. While these studies clearly associate resting-state INTs and the self, it remains unclear whether and by what mechanism INTs differentiate between self- and non-self-specificity during task-evoked activity. Addressing this knowledge gap was the goal of our current investigation.

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Intrinsic neural timescales can be measured with an autocorrelation function (ACF) that correlates a signal with copies of itself that are temporally shifted with a series of lags (Murray et al., 2014; Honey et al., 2012; SanCristobal et al., 2021). The ACF therefore indexes temporal continuity in neural activity or the degree to which previous activity predicts future dynamics over multiple timescales (Golesorkhi et al., 2021a, 2021b; Honey et al., 2012; Wolff et al., 2022). A common practice in EEG and MEG studies is to report the autocorrelation window (ACW) representing the length of time at the moment when the ACF decays to 50% of its maximum value (i.e., ACW-50; Raut et al., 2020; Watanabe et al., 2019; Ito et al., 2020, Honey et al. 2012). Worth noting, Golesorkhi et al. (2021a) introduced a novel variant, ACW-0, based on the temporal delay when the autocorrelation reaches zero. Moreover, they demonstrated that ACW-0 shows stronger prediction than ACW-50 in differentiating between brain regions with shorter and longer timescales (i.e., core- and periphery). An objective of this study was therefore to determine the discriminatory ability of ACW-50 compared to ACW-0 when applied to self and non-self-specificity given that, like the core brain regions, self-specificity exhibits high temporal continuity (Kolvoort et al., 2020; Wolff et al., 2019).

The overarching goal of our investigation was to determine how INTs shape task-related activity during the neural processing of self- and non-self-specific information. To this end, and following a previous paradigm (Vallacher et al., 2002), we constructed 8 min narratives with self- and non-self-specific contents, respectively. After a resting state EEG session, subjects listened to each narrative while EEG was recorded. Listening to these narratives allowed the presentation of self- and non-self-specific stimuli in a dynamic (rather than static) and naturalistic way that includes distinct timescales in the input itself (Huk et al., 2018; Golesorkhi et al., 2021a, 2021b). Consequently, it was possible to directly compare the impact of longer and shorter INTs on the neural processing of dynamic self- and non-self-specific narratives.

Our first specific aim was to investigate how subjective behavioral evaluations differ in response to the autobiographical and nonautobiographical stimuli. We hypothesized greater behavioral variability in response to the former based on recent studies connecting interindividual variation to the self in psychological (Kolvoort et al., 2020) and neuronal variables (Huang et al., 2016; Wolff et al., 2019). Specifically, we hypothesized greater spatial extension and faster velocity during the self-specific narrative compared to the non-self-specific one. The larger background here is that self-specificity induces a stronger behavioral change as related to the well-known self-prioritization effect (Sui and Humphreys, 2015a).

Our second objective was to investigate ACW-50 and ACW-0 during self- and non-self-relevant tasks in EEG. Given that a positive correlation was recently observed between the resting-state ACW length and self-specificity (Kolvoort et al., 2020; Wolff et al., 2019), we hypothesized that the ACW would be significantly longer during self-specific compared to non-self-specific activities.

1. Materials and methods

1.1. Subjects

Twenty-seven (10 females; mean age = 30.3 years) healthy subjects were recruited from the local community in Ottawa, Canada. Medical history was collected using an in-house health assessment questionnaire. All participants were right-handed per the Edinburgh Handedness Tool (Oldfield, 1971). Each participant's session lasted approximately three hours. The experimental protocol was approved by the ethics commission (REB #2016004) of the University of Ottawa Institute of Mental Health Research. All participants provided written informed consent prior to engaging in any study-related activities.

1.2. Paradigm

Our experiment used a behavioral paradigm modified from Vallacher et al. (2002). Participants in their study first recorded an au-

tobiographical narrative (average 2 min 52 s) and were then presented with that recording during the experiment's task phase. Subjects continuously evaluated their narrative's contents as positive or negative using a mouse cursor. On a moment-to-moment basis, they indicated degrees of negativity or positivity by moving the cursor away from the center or towards the center of the screen, respectively. From this movement, the researchers extracted variables such as the cursor distance from center along the x-axis, acceleration, and time spent with the cursor stationary, which were then correlated with a small number of psychological scales.

Expanding on this original template, participants in our study recorded an unstructured, eight-minute autobiographical narrative. Participants were encouraged to be as comprehensive as possible in sharing personal details about themselves and their lives that they deemed significant. Next, subjects completed an eight-minute, eyes-open rest session for EEG acquisition while staring at a fixation cross centered on the computer screen. The subjects were then presented with their prerecorded auditory narrative and the narrative of a stranger through headphones in a counterbalanced order (see Fig. 1a).

The stranger, or "non-self" narrative was also eight minutes long and was recorded by a member of the research team. All subjects were exposed to the same non-self recording. Briefly, the non-self narrative served as a control for the self-condition which, as previously indicated, was expected to exhibit high interindividual variability. To elicit this interindividual variability, a control condition was included that would exhibit low-variability across participants.

In response to both narratives, subjects indicated positivity or negativity on a moment-to-moment basis by positioning the cursor relative to the center of the screen (see Fig. 1b). For ease of distinction, we assigned different colors corresponding to different cursor positions. The circular cursor appeared green in proximity to the center for a positive appraisal, red towards the periphery for a negative appraisal, and yellow for intermediate distances reflecting a neutral evaluation. These colors served to remind participants of their cursor position reflecting an emotional valence. Additionally, all participants verbally confirmed their understanding of the cursor task instructions before beginning the experiment. Cursor distance from the center in pixels was sampled at 200 Hz to create a behavioral timeseries concurrent with the EEG recording.

1.3. Behavioral analysis

The average cursor distance from the center was calculated for each subject during the self and non-self-conditions; two separate "distance" values were therefore generated for each subject. Notably, in contrast to Vallacher et al. (2002), we calculated the cursor distance from center along the x- and y-axes rather than restricting our measurement to the former. Furthermore, while Vallacher et al. (2002) did not provide specific details regarding how they measured cursor distance from the screen's center, we computed the Euclidean distance between these two points. All behavioral timeseries were truncated to 470 s to match the EEG recording length. One participant was excluded from the behavioral analysis due to a corrupt non-self data file (n = 26).

1.4. Electrophysiological recording

EEG data was obtained using a 64-channel Brain Vision Easycap (International Ten-Twenty System) with Ag/AgCl electrodes referenced to the right mastoid. Impedance for each electrode was under 5 k Ω and the sampling rate was 1000 Hz with DC recording. Preprocessing was performed using an in-house MATLAB script relying upon functions from the EEGLAB toolbox (version 2021.1; Delorme and Makeig, 2004). The data were first down sampled to 500 Hz, followed by high- and lowpass filters at 0.5 and 50 Hz, respectively. Channels were spherically interpolated if they were flat for at least five seconds or if the amplitude exceeded three interquartile ranges (median flat channels removed = 0, median noisy channel removed = 1). All channels were then

Fig. 1. A. Schema of paradigm – study conditions B. Schema of paradigm – cursor task.





re-referenced to the average prior to an independent component analysis (ICA) yielding 62 ICs. Finally, components were rejected by implementing the Multiple Artifact Rejection Algorithm (MARA; Winkler et al., 2011).

Four participants were excluded from the EEG analysis due to the presence of noisy channels after preprocessing; another participant was removed for lacking an alpha peak in the power spectrum; finally, an additional subject was excluded due to technical issues associated with data acquisition (n = 21). Although subjects were instructed to record an eight-minute narrative, there were discrepancies in recording length. The self and non-self timeseries were, accordingly, both truncated to 470 s which was the length of the shortest recording.

1.5. Autocorrelation window

An autocorrelation function was calculated in Python (version 3.9) with the Statsmodels library (version 0.13.0; Seabold and Perktold, 2010) using a fast Fourier transform algorithm. At each electrode, this function was applied to the entire eight-minute EEG signal; the ACW-50 and ACW-0 variants were computed as the first lags where the ACF decays to 50% of its maximum value, and zero percent (Golesorkhi et al., 2021a), respectively. Lags were then converted to seconds by dividing them by the sampling frequency of 500 Hz. Finally, the average ACW-50 and ACW-0 values across all electrodes were obtained for each participant (Fig. 2).

1.6. Statistical analysis

Statistical procedures were performed using SPSS software (version 27.0) or with the Statsmodels package (Seabold and Perktold, 2010)

in Python. Shapiro-Wilk tests were performed on the behavioral and neuronal data to ensure that normality assumptions were met. In the behavioral data, normally distributed variables were analyzed using paired-samples t-tests (2-tailed). Wilcoxon signed-rank tests were used as a non-parametric alternative when normality assumptions were violated. In the EEG data, we performed repeated-measures ANOVAs for ACW-50 and ACW-0 to compare the values obtained in rest and task states. Pairwise t-tests were calculated as a post-hoc analysis following significant ANOVA results. The false discovery rate (Benjamini and Hochberg, 1995) was applied to the p-values of all hypothesis tests to control for multiple comparisons. This was applied in two stages: first, to the behavioral data and EEG ANOVAs; second, to the post-hoc t-tests of the significant ANOVA.

2. Results

2.1. Behavioral data

As illustrated in Fig. 3, the results show significantly larger cursor distances in the self (M = 293.55, SD =156.80) compared to the nonself condition (M = 215.253, SD=124.060), t(25) = 3.453, p = 0.003, 95% CI [31.593, 125.006]. This indicates that subjects moved the cursor farther from the center towards the maximum value of 990 pixels during the self-specific assessment when compared to the non-selfspecific measurement. Additionally, intrasubject standard deviations of the cursor distance were significantly larger in response to the self narrative (M = 188.27, SD=83.57) as compared to the non-self narrative (M = 140.59, SD=49.73), t(25) = 4.200, p = <0.001, 95% CI [24.299, 71.064]. This is indicative of greater variability in cursor movements. Furthermore, a Wilcoxon signed-rank test revealed greater ve-



Fig. 2. The autocorrelation function Note. Figure adapted from Golesorkhi et al. (2021a) with permission.



Fig. 3. A. Cursor distance from center Note. The maximum cursor distance from center is 990 pixels. B Intrasubject standard deviation of cursor distance

Note. A single standard deviation was computed for each subject as an index of variability in their cursor distance from center over the whole timeseries. This figure therefore displays the average intrasubject variability across participants. C Average cursor velocity

Note. The cursor velocity was determined by isolating areas of movement during the behavioral timeseries and then extracting an average for each subject. Velocity is measured in pixels moved per frame with 200 frames sampled per second (i.e., 200 Hz).



locity of cursor movements in the self condition (M = 2.13, SD=1.36) than in the non-self condition (M = 1.73, SD=0.58), Z = -3.621, p = <0.001. Finally, a Wilcoxon test demonstrated no difference between self (M = 88,587.02, SD=5965.17) and non-self (M = 90,176.90, SD=2881.33) with respect to cursor stationary time, Z = -1.568, p = .140.

2.2. Autocorrelation window in EEG

Do average ACW values in EEG differ between study conditions? For that evaluation, we first calculated a repeated-measures ANOVA to probe for an effect of condition on ACW-50 values. Mauchly's test indicated non-sphericity, $X^2(2) = 22.052$, p = <0.001, so a Greenhouse-Geisser correction was applied to the subsequent repeated-measures ANOVA. No significant differences were observed between rest (M = 0.022, SD=0.007), self (M = 0.022, SD=0.006), and non-self conditions (M = 0.023, SD=0.007), F(1.186, 23.715) = 0.179, p = .718.

While this did not yield any significance for ACW-50, there was an effect of condition observed on ACW-0, F(2,40) = 11.272, p = <0.001. (Mauchly's test did not indicate any violation of sphericity assumptions, $X^2(2) = 4.868$, p = .088.) Three paired-samples t-tests were then computed for post-hoc comparisons.







Fig. 4. Average values for ACW-50 (left) and ACW-0 (right).

Our first focus in the post-hoc analysis was to determine whether task-related activity during both self and non-self conditions deviates from the resting state. Significantly longer ACW-0 values were observed in self (M = 0.330, SD=0.113) compared to rest (M = 0.250, SD=0.103), t(20) = -4.054, p = .002, 95% CI [-0.121, -0.039]. Similar results were obtained for the non-self condition which showed longer ACW-0 values (M = 0.298, SD=0.114) than at rest (M = 0.250, SD=0.103), t(20) = -2.728, p = .019, 95% CI [-0.086, -0.011]. Together, these results demonstrate that the task induced significant changes in ACW-0 during both self- and non-self-referential processing compared to rest, with both task conditions exhibiting a prolonged ACW-0.

In a second step, we compared the self and non-self conditions. A significant difference in average ACW-0 values between self (M = 0.330, SD=0.113) and non-self (M = 0.298, SD=0.114), t(20) = 2.497, p = .021, 95% CI [0.005, 0.058] was observed. This indicates that the self narrative elicited significantly longer ACW-0 values than the non-self narrative (see Figs. 4, 5a–c). This finding further supports the assumption that self-referential processing is mediated by longer time windows and thus longer INTs than processing non-self-relevant contents.

3. Discussion

The current investigation explored the role of INTs in shaping taskrelated activity while processing self- and non-self-related information. We expand upon previous studies that found an association between resting state INTs and the self by extending our analysis into task states. The main finding was that longer neural timescales are implicated in self-specific information processing while shorter timescales are associated with processing non-self specificity. This points to the intrinsically temporal nature of self which, more precisely, is featured by long autocorrelation windows as an index of strong temporal continuity.

3.1. Behavioral analysis

A key finding from the behavioral task was greater cursor extension in response to the self-narrative. This extension indicates a more negative evaluation of self than non-self. However, the negative selfevaluations are surprising given the well-known self positivity bias (Mezulis et al., 2004). One possible interpretation is that, rather than being driven entirely by perceptions of emotional valence, participants experienced an extended peri-personal space (PPS) while listening to their autobiographical contents, or alternatively, a diminished PPS in response to the non-self narrative. Briefly, PPS refers to the physical space immediately surrounding the body that serves as an interface for interactions between the self and its external environment (Serino, 2019). This interpretation of our results is supported by Tennegi et al. (2013) who observed decreased PPS when participants were faced with another individual rather than an inanimate mannequin. Analogously, the cursor movements in our study were less extended (i.e., smaller PPS) when participants were exposed to the voice of a stranger. Our results are also in accordance with previous findings by Sui and Humphreys (2015a) who observed behavioral changes related to the self-prioritization effect in a shape-label matching task. However, future studies are warranted to disentangle the behavioral effect of self-specificity from the valencespecific effects obtained in our paradigm.

3.2. INTs and self-specificity

Previous studies observed that resting state INTs are related to selfconsciousness (Wolff et al., 2019; Huang et al., 2016). Specifically,



Fig. 5. A. Autocorrelation plots of experimental conditions

Note. Each curve represents the autocorrelation function for one participant. B. ACW-0 topoplots by experimental condition.

Note. Topography of longer (red) and shorter (blue) ACW-0 values in rest, self, and non-self conditions. Topoplots were generated using MNE-Python (version 0.22; Gramfort et al., 2013).



Fig. 5. Continued

longer INTs in the resting state are associated higher degrees of selfconsciousness. Moreover, a recent study observed that longer resting state ACWs allowed subjects to integrate temporal delays more effectively during exposure to self-specific stimuli (Kolvoort et al., 2020). These findings were all obtained in the resting state. It therefore remains unclear whether task-related activity during exposure to self-specific stimuli also exhibits longer INTs than those evinced during exposure to non-self-specific information.

The current study addressed this lingering issue. Specifically, we demonstrated significant differences between the self and non-self con-

ditions measured by ACW-0. This highlights the importance of longer timescales for processing self-specific inputs.

The occurrence of longer time windows during self-specific activity is well in accordance with previous resting state findings. Despite employing different measures of self like the self-consciousness scale (Wolff et al., 2019), self-matching task (Kolvoort et al., 2020), and the self-narrative in our current investigation, all three studies demonstrate the involvement of longer timescales in mediating self-specificity. Moreover, this occurs across the division of rest and task states, strongly suggesting an intrinsic relationship between self-specificity and longer INTs.

3.3. ACW-50 versus ACW-0

It is unclear why we observed a discrepancy between ACW-50 and ACW-0 in the neural data. Interestingly, Golesorkhi et al. (2021a) noted a similar divergence with the latter better distinguishing between core and periphery brain regions in magnetoencephalography. They suggest that ACW-0 can probe activity over longer timescales than ACW-50, and it is therefore more sensitive to the effects of slower frequencies. Another interpretation, however, is that ACW-0 has a higher signal-to-noise ratio (SNR). In this view, since ACW measures how long the brain remains in a similar state, the principal difference between ACW-50 and ACW-0 is that they index different thresholds for what constitutes this similarity. Because ACW-50 represents the time needed for the signal correlation to reach half of its maximum ACF value, it is plausible that noise fluctuations could precipitate a decay to this threshold. ACW-0, measured at a later timepoint and therefore being more resistant to the effects of noise, would naturally have greater discriminatory power. However, this explanation is speculative and future research is needed to test its validity.

Indirect support is found by considering neural topographical data. The ACW-0 is strongly associated with core regions in the brain (Golesorkhi et al., 2021a) which also includes the cortical midline structures (CMS) as key regions of the self (Northoff and Bermpohl, 2004; Qin and Northoff, 2011; Qin et al., 2020). Therefore, future studies may want to combine a topographic-regional investigation with ACW-0 calculations using a self paradigm to further elucidate the specific neural mechanisms underpinning the relationship we observed between ACW-0 and self-specificity.

3.4. From the INTs of self to temporal integration and temporal continuity

How can we interpret the longer INTs associated with selfspecificity? Recent evidence strongly suggests that INTs are implicated in input processing (Golesorkhi et al., 2021b; Zilio et al., 2021; Wolff et al., 2022). Specifically, they allow for processing the temporal stochastics of inputs whereby the input is temporally segmented and parsed into distinct components. Longer INTs allow different inputs at distinct points in time to be integrated and thus summed into one whole (Golesorkhi et al., 2021b; Wolff et al., 2022). In contrast, shorter INTs favor the segregation of different inputs at distinct points in time.

Given that our paradigm provided continuous inputs (i.e., the self and non-self narratives), we assume a strong role of the ACW in mediating the input stochastics of the words, sentences, and other structures of speech. Longer ACWs therefore imply that self-specific stimuli, like in the self narrative, are more temporally integrated over longer stretches of time than non-self-specific stimuli. Hence, a longer time-window in neural activity may permit greater integration of temporally distinct inputs. This is well in accordance with the assumed integrative function of self on the cognitive level as suggested by Sui and Humphreys (2015b).

How does temporal integration manifest in our sense of self? Temporal integration may lead to higher temporal continuity across different contents as they show higher degrees of autocorrelation over time in their underlying neural activity. Such temporal continuity on the neural level may then, in turn, manifest in a higher degree of temporal continuity of the self on the psychological level. This is indeed the case as one key psychological feature of self is its persistence or sameness over time (i.e., temporal continuity; Ersner-Hershfield et al., 2009a, 2009b; Northoff, 2017). We consequently suggest that, following our earlier paper (Kolvoort et al., 2020), temporal continuity may constitute a shared feature of the neural and psychological levels as their "common currency" (Northoff et al., 2020).

3.5. Limitations

There are several limitations that need to be addressed. First, our sample size was small (n = 21), thus limiting statistical power and precision. Second, we only conducted a sensor-space analysis and are therefore unable to link specific brain regions with temporal windows during self- and non-self-referential processing. It would be worthwhile to extend the current study into source-space with eLORETA or a modality with better spatial resolution such as fMRI. Third, we did not consider the temporal features of the audio recordings themselves. Future research should explore this in order to quantify the interaction between INTs and the temporal characteristics of the stimulus as they pertain to the self. Fourth, the ACW was our only index of INTs; incorporating additional measures would serve to validate our results. Fifth, since it has been suggested that the resting state indexes the propensity to react to self-specific stimuli (Davey et al. 2016; Northoff, 2016), rest-task comparisons may be problematic when the task involves self-referential processing. This issue could be circumvented with the addition of a task condition that is not relevant to the distinction between self and nonself. Sixth, our study applied the same non-self recording to all participants. An alternative approach would involve forming pairs of subjects such that the self narrative of one subject serves as the non-self condition for the other member in the pair. This would eliminate the possibility of our results being influenced by characteristics of the single non-self narrative.

Finally, our choice of frequency cut-off in high-pass filtering the EEG data should be kept in mind when considering our results. As explained in Tanner et al. (2015), all filtering distorts timeseries data in the temporal domain, though a certain amount of this is acceptable in favor of excluding non-cortical frequency components. We therefore selected our high-pass filter cut-off based on what we determined to be an appropriate balance between the benefits of excluding non-neural cortical activity, specifically skin potentials, and the cost of distortion in the time-domain. We considered that our participants were completing several 8-min blocks while remaining relatively still, and that this could cause sweating and increase the probability of skin potential artifacts. To account for this, we wanted to remove some of the lower frequency activity but still retain some of the neural activity below 1 Hz; 0.5 Hz was thought to be a suitable compromise between these two considerations. However, even if the high-pass filter did introduce a small distortion into the timeseries, its impact on the calculation of the autocorrelation function would be minimal as the cross-correlation is calculated against itself. Though this issue is thought to be minimal, and similar parameters have been used in previously published articles (Wolff et al., 2019), a small distortion of the timeseries data is possible and should be considered when interpreting our findings.

4. Conclusion

We show that processing self-specific information is characterized behaviorally by greater spatial and temporal extension while neuronally being mediated by longer timescales during task-related activity. In contrast, shorter behavioral extensions and neural timescales are recruited in response to non-self-specific stimuli. Self- and non-self-specific information thus recruit opposite ends of a temporal continuum of longer and shorter INTs. Measured by the autocorrelation function, INTs reflect temporal continuity on the neural level. Taken together with our behavioral data and presupposing the model of shared temporal dynamics as a "common currency" of neural and mental features (Northoff et al., 2020), the association between longer ACWs and self-specificity suggests an unexplored yet key role of temporal continuity on the psychological level of the self (see Kolvoort et al. 2020, for a first step). Future studies are thus warranted that measure temporal continuity in analogous ways on both the neural and mental levels of self.

Author contributions

Conceptualization, DS, JI, GN; Investigation, JI, DS; Formal analysis, DS, AW, AW; Writing—original draft, DS, GN; Writing—review & editing, AW, AW; Supervision, GN; Funding acquisition, GN. All authors have read and agreed to the published version of the manuscript.

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Originality declaration

We confirm the originality of this manuscript.

Ethics statement

The ethics commission of the University of Ottawa Institute of Mental Health Research approved this experimental protocol (REB #2016004). All participants provided written informed consent prior to engaging in study-related activities.

Declaration of Competing Interest

The authors declare no conflicts of interest.

References

- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate-A practical and powerful approach to multiple testing. J. R. Stat. Soc. Ser. B 57 (1), 289–300. doi:10.1111/j.2517-6161.1995.tb02031.x.
- Davey, C.G., Pujol, J., Harrison, B.J., 2016. Mapping the self in the brain's default mode network. Neuroimage 132, 390–397. doi:10.1016/j.neuroimage.2016.02.022.
- Delorme, A., Makeig, S., 2004. EEGLAB–An open-source toolbox for analysis of single-trial EEG dynamics. J. Neurosci. Methods 134, 9–21. doi:10.1016/j.jneumeth.2003.10.009.
- Demirtas, M., Burt, J.B., Helmer, M., Ji, J.L., Adkinson, B.D., Glasser, M.F., Van Essen, D.C., Sotiropoulos, S.N., Anticevic, A., Murray, J.D., 2019. Hierarchical heterogeneity across human cortex shapes large-scale neural dynamics. Neuron 101 (6), 1181–1194. doi:10.1016/j.neuron.2019.01.017.
- Ersner-Hershfield, H., Garton, M.T., Ballard, K., Saminez-Larkin, G.R., Knutson, B., 2009a. Don't stop thinking about tomorrow–Individual differences in future self-continuity account for saving. Judgem. Decis. Mak. 4 (4), 280–286.
- Ersner-Hershfield, H., Wimmer, G.E., Knutson, B., 2009b. Saving for the future self–Neural measures of future self-continuity predict temporal discounting. Soc. Cogn. Affect. Neurosci. 4 (1), 85–92. doi:10.1093/scan/nsn042.
- Gao, R., van den Brink, R.L., Pfeffer, T., Voytek, B, 2020. Neuronal timescales are functionally dynamic and shaped by cortical microarchitecture. eLife 9, e61277. doi:10.7554/eLife.61277.
- Golesorkhi, M., Gomez-Pilar, J., Tumati, S., Fraser, M., Northoff, G., 2021a. Temporal hierarchy of intrinsic neural timescales converges with spatial core-periphery organization. Commun. Biol. 4. doi:10.1038/s42003-021-01785-z, Article 277.
- Golesorkhi, M., Gomez-Pilar, J., Zilio, F., Berberian, N., Wolff, A., Yagoub, M.C.E., Northoff, G., 2021b. The brain and its time–Intrinsic neural timescales are key for input processing. Commun. Biol. 4. doi:10.1038/s42003-021-02483-6, Article 970.

- Gramfort, A., Luessi, M., Larson, E., Engemann, D.A., Strohmeier, D., Brodbeck, C., Goj, R., Jas, M., Brooks, T., Parkkonen, L., Hämäläinen, M.S., 2013. MEG and EEG data analysis with MNE-Python. Front. Neurosci. 7 (267), 1–13. doi:10.3389/fnins.2013.00267.
- Honey, C.J., Thesen, T., Donner, T.H., Silbert, L.J., Carlson, C.E., Devinsky, O., Doyle, W.K., Rubin, N., HEEGer, D.J., Hasson, U., 2012. Slow cortical dynamics and the accumulation of information over long timescales. Neuron 76 (2), 423–434. doi:10.1016/j.neuron.2012.08.011.
- Huang, Z., Obara, N., Davis, IV, H., Pokorny, J., Northoff, G, 2016. The temporal structure of resting-state brain activity in the medial prefrontal cortex predicts self-consciousness. Neuropsychologia 82, 161–170. doi:10.1016/j.neuropsychologia.2016.01.025.
- Huk, A., Bonnen, K., He, B.J., 2018. Beyond trial-based paradigms–Continuous behavior, ongoing neural activity, and natural stimuli. J. Neurosci. 38 (35), 7551–7558. doi:10.1523/JNEUROSCI.1920-17.2018.
- Ito, T., Hearne, L.J., Cole, M.W., 2020. A cortical hierarchy of localized and distributed processes revealed via dissociation of task activations, connectivity changes, and intrinsic timescales. Neuroimage, 221 Article 117141 doi:10.1016/j.neuroimage.2020.117141.
- Kolvoort, I.R., Wainio-Theberge, S., Wolff, A., Northoff, G., 2020. Temporal integration as "common currency" of brain and self – scale-free activity in resting-state EEG correlates with temporal delay effects on self-relatedness. Hum. Brain Mapp. 41 (15), 4355–4374. doi:10.1002/hbm.25129.
- Mezulis, A.H., Abramson, L.Y., Hyde, J.S., Hankin, B.J., 2004. Is there a universal positivity bias in attributions? A meta-analytic review of individual, developmental, and cultural differences in the self-serving attributional bias. Psychol. Bull. 130 (5), 711– 747. doi:10.1037/0033-2909.130.5.711.
- Murray, J.D., Bernacchia, A., Freedman, D.J., Romo, R., Wallis, J.D., Cai, X., Padoa-Schioppa, C., Pasternak, T., Seo, H., Lee, D., Wang, X., 2014. A hierarchy of intrinsic timescales across primate cortex. Nat. Neurosci. 17, 1661. doi:10.1038/nn.3862.
- Northoff, G, 2016. Is the self a higher-order or fundamental function of the brain? The "basis model of self-specificity" and its encoding by the brain's spontaneous activity. Cogn. Neurosci. 7 (1), 203–222. doi:10.1080/17588928.2015.1111868.
- Northoff, G., 2017. Personal identity and cortical midline structures (CMS)–Do temporal features of CMS neural activity transform into "self-continuity"? Psychol. Inq. 28 (2– 3), 122–131. doi:10.1080/1047840X.2017.1337396.
- Northoff, G., Bermpohl, F., 2004. Cortical midline structures and the self. Trends Cogn. Sci. 8, 102–107. doi:10.1016/j.tics.2004.01.004.
- Northoff, G., Wainio-Theberge, S., Evers, K., 2020. Is temporo-spatial dynamics the "common currency" of brain and mind? In quest of "spatiotemporal neuroscience. Phys. Life Rev. 33, 34–54. doi:10.1016/j.plrev.2019.05.002.
- Oldfield, R.C., 1971. The assessment and analysis of handedness–The Edinburgh Inventory. Neuropsychologia 9 (1), 97–113. doi:10.1016/0028-3932(71)90067-4.
- Qin, P., Northoff, G., 2011. How is our self related to midline regions and the default-mode network? Neuroimage 57 (3), 1221–1233. doi:10.1016/j.neuroimage.2011.05.028.
- Qin, P., Wang, M., Northoff, G., 2020. Linking bodily, environmental and mental states in the self—A three-level model based on a meta-analysis. Neurosci. Biobehav. Rev. 115, 77–95. doi:10.1016/j.neubiorev.2020.05.004.
- Raut, R.V., Mitra, A., Marek, S., Ortega, M., Snyder, A.Z., Tanenbaum, A., Laumann, T., Dosenbach, N.U.F., Raichle, M.E., 2020. Organization of propagated intrinsic brain activity in individual humans. Cereb. Cortex 30 (3), 1716–1734. doi:10.1093/cercor/bhz198.
- Runyan, C.A., Piasini, E., Panzeri, S., Harvey, C.D., 2017. Distinct timescales of population coding across cortex. Nature 548, 92–96. doi:10.1038/nature23020.
- Sancristobal, B., Ferri, F., Longtin, A., Perrucci, M.G., Romani, G.L., Northoff, G., 2021. Slow resting state fluctuations enhance neuronal and behavioral responses to looming sounds [Special issue]. Brain Topogr. doi:10.1007/s10548-021-00826-4.
- Seabold, S. and Perktold, J. (2010). Statsmodels–Econometric and statistical modeling with python. Proc. 9th Python in Science Conference, 57, 57–61.
- Serino, A., 2019. Peripersonal space (PPS) as a multisensory interface between the individual and the environment, defining the space of the self. Neurosci. Biobehav. Rev. 99, 138–159. doi:10.1016/j.neubiorev.2019.01.016.
- Stephens, G.J., Honey, C.J., Hasson, U., 2013. A place for time–The spatiotemporal structure of neural dynamics during natural audition. J. Neurophysiol. 110 (9), 2019–2026. doi:10.1152/jn.00268.2013.
- Sui, J., Humphreys, G.W., 2015a. The interaction between self-bias and reward–Evidence for common and distinct processes. Q. J. Exp. Psychol. 68 (10), 1952–1964. doi:10.1080/17470218.2015.1023207.
- Sui, J., Humphreys, G.W., 2015b. The integrative self-How self-reference integrates perception and memory. Trends Cogn. Sci. 19 (12), 719–728. doi:10.1016/j.tics.2015.08.015.
- Tanner, D., Morgan-Short, K., Luck, S.J., 2015. How inappropriate high-pass filters can produce artifactual effects and incorrect conclusions in ERP studies of language and cognition. Psychophysiology 52 (8), 997–1009. doi:10.1111/psyp.12437.
- Tennegi, C., Canzoneri, E., di Pellegrino, G., Serino, A., 2013. Social modulation of peripersonal space boundaries. Curr. Biol. 23 (5), 406–411. doi:10.1016/j.cub.2013.01.043.
- Vallacher, R.R., Nowak, A., Froehlich, M., Rockloff, M., 2002. The dynamics of self-evaluation. Personal. Soc. Psychol. Rev. 6 (4), 370–379. doi:10.1207/S15327957PSPR0604_11.
- Watanabe, T., Rees, G., Masuda, N., 2019. Atypical intrinsic neural timescale in autism. eLife 8, e42256. doi:10.7554/eLife.42256.001.
- Winkler, I., Haufe, S., Tangermann, M., 2011. Automatic classification of artifactual ICA-components for artifact removal in EEG signals. Behav. Brain Funct. 7. doi:10.1186/1744-9081-7-30, Article 30.
- Wolff, A., Berberian, N., Golesorkhi, M., Gomez-Pilar, J., Zilio, F., Northoff, G., 2022. Intrinsic neural timescales–Temporal integration and segregation. Trends Cogn. Sci. 26 (2), 159–173.

- Wolff, A., Di Giovanni, D.A., Gomez-Pilar, J., Nakao, T., Huang, Z., Longtin, A., Northoff, G., 2019. The temporal signature of self-Temporal measures of resting-state EEG predict self-consciousness. Hum. Brain Mapp. 40 (3), 789–803. doi:10.1002/hbm.24412.
- Zilio, F., Gomez-Pilar, J., Cao, S., Zhang, J., Zang, D., Qi, Z., Tan, J., Hiromi, T., Wu, X., Fogel, S., Huang, Z., Hohmann, M.R., Fomina, T., Synofzik, M., Grosse-Wentrup, M., Owen, A.M., Northoff, G., 2021. Are intrinsic neural timescales related to sen-

sory input processing? Evidence from abnormal behavioral states. Neuroimage 226.

sory input processing? Evidence from anormal benavioral states. Neuroimage 226. doi:10.1016/j.neuroimage.2020.117579, Article 117579.
Zylberberg, J., Strowbridge, B.W., 2017. Mechanisms of persistent activity in cortical circuits–Possible neural substrates for working memory. Annu. Rev. Neurosci. 40, 603–627. doi:10.1146/annurev-neuro-070815-014006.