

Brain connectivity dynamics during social interaction reflect social network structure

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Social ties are crucial for humans. Disruption of ties through social exclusion has a marked effect on our thoughts and feelings; however, such effects can be tempered by broader social network resources. Here, we use fMRI data acquired from 80 male adolescents to investigate how social exclusion modulates functional connectivity within and across brain networks involved in social pain and understanding the mental states of others (i.e., mentalizing). Furthermore, using objectively logged friendship network data, we examine how individual variability in brain reactivity to social exclusion relates to the density of participants' friendship networks, an important aspect of social network structure. We find increased connectivity within a set of regions previously identified as a mentalizing system during exclusion relative to inclusion. These results are consistent across the regions of interest as well as a whole-brain analysis. Next, examining how social network characteristics are associated with task-based connectivity dynamics, we find that participants who showed greater changes in connectivity within the mentalizing system when socially excluded by peers had less dense friendship networks. This work provides insight to understand how distributed brain systems respond to social and emotional challenges and how such brain dynamics might vary based on broader social network characteristics.

social exclusion | mentalizing | fMRI | functional connectivity | social networks

Humans are fundamentally motivated to connect with others, spending considerable time and energy investing in social relationships. A lack of social connection resulting from social isolation has a significant negative impact on health and well-being (1, 2), with risks comparable to those associated with lifelong smoking (3). In fact, the acute disruption of ties through social exclusion has a marked effect on our thoughts and feelings, and hence brain responses (4). This neural responsiveness to exclusion is thought to help maintain social bonds (5). However, people vary in how strongly they respond to social challenges such as exclusion (6). One important factor that can moderate stress responses and that may contribute to individual differences in reactivity to social challenges such as exclusion is social network resources (7–9). In particular, individual differences in how people react to being excluded may influence the types of social networks they build and thus the resources that limit the risks related to exclusion; likewise, different social environments may influence how a given individual approaches and reacts to stressful events (10). Therefore, an individual's network structure represents a potential moderator for the cognitive processing of social exclusion.

Previous neuroimaging studies have investigated the neural substrates of social exclusion by using experimental designs in which participants are socially isolated through rejection by others; one frequently used task is Cyberball, a virtual ball-tossing game where the experimental participant is excluded from the game and receives no ball throws from other players (11, 12). Research on

social exclusion has identified the role of two proposed networks: (i) a social pain system associated with distress during exclusion (4, 5), characterized by enhanced activations in the anterior cingulate cortex (ACC) and the anterior insula (aINS); and (ii) a mentalizing system with consistent activity in the dorsal and ventral medial prefrontal cortex (mPFC), precuneus, and bilateral temporo-parietal junction (TPJ) (13, 14). Although described rhetorically as two cohesive networks, limited research has examined functional interactions, or network dynamics, among the regions during social tasks. A small number of studies have focused on a single hotspot of univariate activation effects in the dorsal ACC (dACC) and have assessed its connectivity during social exclusion (15–17); however, no research has examined broader network dynamics during social exclusion. Furthermore, no research has examined how social environments might moderate brain network dynamics in the face of social interaction. This gap limits our ability to draw conclusions about how brain network and social network dynamics might underlie human processing of social interactions.

To this end, we first capitalized on recent advances in network neuroscience to study the functional connectivity relationships among multiple brain regions (18, 19) during social exclusion and inclusion. Although initially focused on the resting state, these novel techniques have recently been extended to assess the dynamics of connectivity patterns during task performance (20–27). Taking a dynamic network neuroscience perspective, we set out to examine the social pain and mentalizing networks holistically during social exclusion as well as broader network dynamics across the whole brain as a function of social exclusion and inclusion.

Significance

We examine brain dynamics during a common social experience—social exclusion—to determine whether cohesive networks in the brain support navigation of the social world and contribute to the shape of friendship networks. Specifically, exclusion is associated with increased cohesion within brain networks that support understanding what other people think and feel. Furthermore, using social network analysis, we find that variability in brain dynamics is associated with the shape of participants' friendship networks. Bringing together findings related to brain network dynamics and social network dynamics illuminates ways that psychological processes may shape and be shaped by social environments.

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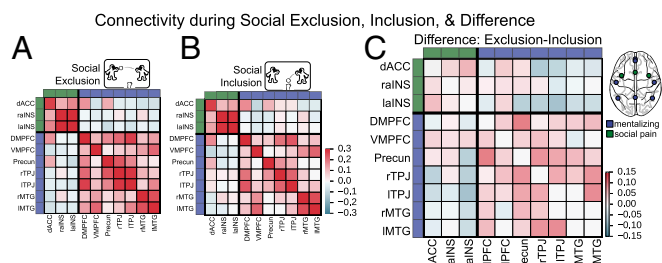


Fig. 2. Functional connectivity during social exclusion (A), social inclusion (B), and the difference between exclusion and inclusion (C). For each participant, a functional connectivity matrix was derived as the Pearson correlation coefficient between the time series of every pair of nodes for social exclusion and inclusion, respectively. Group-average functional connectivity matrices then were computed by averaging all participants' connectivity matrices for each task (after Fisher z-transformation). To isolate the effect of social exclusion, we subtracted the inclusion connectivity matrix from the exclusion connectivity matrix.

we found that social exclusion was associated with stronger connectivity between edges comprising the mentalizing network (Fig. S1). Thus, when people were socially excluded, on average, we observed greater regional connectivity between regions of the mentalizing network but not between regions of the social pain network or between regions of the two networks.

To complement our connectivity analysis within a priori hypothesized networks, we ran secondary analyses that applied the same analysis pipeline using a whole-brain parcellation both to examine the robustness of our results and to identify effects in regions outside our hypothesized networks of interest. This analysis included 264 brain regions that were previously assigned to 13 large-scale functional brain systems (44); as before, we computed both within-network connectivity for each of the 13 systems and between-network connectivity for all pairs of the networks. Two of these systems have substantial overlap with our a priori networks of interest: The default mode network is a more distributed variant of the mentalizing network, and the saliency network is a more distributed variant of the social pain network. This whole-brain analysis also confirmed increased connectivity in the default mode system during social exclusion [$t(79) = 2.58, P = 0.011$], as shown in Fig. 4. There was no effect within the saliency system, which overlaps with the social pain network ($t = -0.86, P = 0.39$) (Fig. 4); however, we did observe higher connectivity within the cingulo-opercular system ($t = 2.08, P = 0.041$), which overlaps with components of the social pain system. The uncorrected results for all other systems in the Power parcellation were as follows: ventral attention, $t(79) = 0.54, P = 0.592$; dorsal attention, $t(79) = -1.51, P = 0.136$; fronto-parietal, $t(79) = 0.99, P = 0.325$; visual, $t(79) = 2.31, P = 0.023$; auditory, $t(79) = 2.84, P = 0.006$; somatosensory-motor, $t(79) = 1.19, P = 0.238$; subcortical, $t(79) = -1.47, P = 0.146$; memory, $t(79) = 1.78, P = 0.078$; cerebellum, $t(79) = 0.63, P = 0.529$; uncertain, $t(79) = -1.23, P = 0.222$.

Individual Differences in Ego-Network Density Are Linked to Brain Connectivity Effects. Our first set of analyses identified a relationship between connectivity in the mentalizing network and social exclusion across participants in our sample on average, but we hypothesized that the strength of this relationship would be related to individual differences in participants' social network characteristics. In particular, recent studies suggest a relationship between the mentalizing network and the social landscape that people navigate on a daily basis (47, 48); further, psychological factors can shape the structure of social networks (33–36). Consequently, we characterized each individual's ego-network density from objectively logged Facebook data obtained with participants' consent from the Facebook API. Participants have a denser ego-network when their friends are also friends with one another and

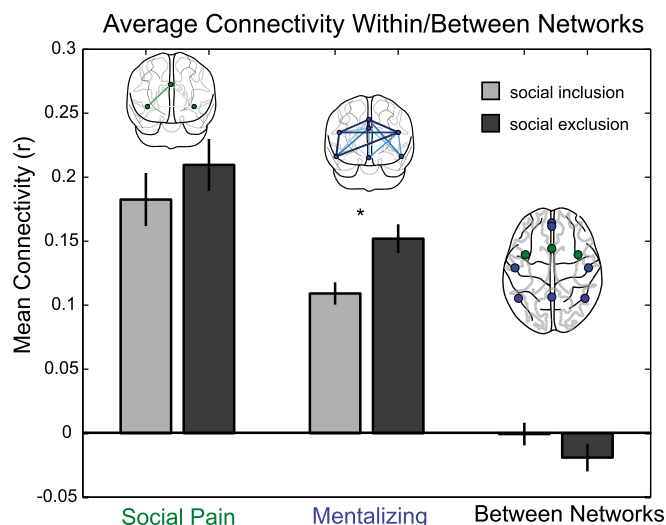


Fig. 3. Social exclusion was associated with increased connectivity within the mentalizing network. The strength of recruitment of each network was captured by computing the within-system connectivity as the mean strength of the functional interactions within the social pain (green) and mentalizing (blue) networks and the between-system connectivity as the mean of interactions between nodes from the social pain and mentalizing networks (blue nodes to green nodes). Connectivity graphs above each bar illustrate the relative difference in connectivity between social exclusion and inclusion within the respective network. The edge width corresponds to differences in connectivity magnitudes between 0 and 0.1. The asterisk indicates significant differences between social inclusion and exclusion in the mentalizing network, $t(79) = 3.67, P < 0.001$.

have a sparser network when the participant's friends are not friends with each other. Especially for adolescent samples, Facebook friendships provide an accurate proxy for offline friendships (49); such social network structures, in turn, can provide a broader window into stable personality differences that are related to important social and emotional outcomes (30).

To determine the relationships between the participants' ego-network data and their brain dynamics during social exclusion and inclusion, we regressed the density of participants' ego networks onto brain connectivity during social exclusion, controlling for connectivity during social inclusion. Note that we also estimated the correlation coefficient between ego network density and the differences in connectivity during exclusion and inclusion, which yielded the same

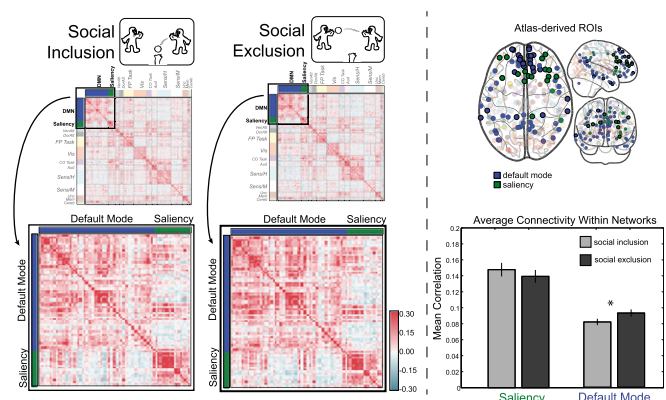


Fig. 4. Results from a whole-brain analysis of 264 nodes (44) assigned to 13 systems converged with earlier findings: We observed increased connectivity within the default mode system during social exclusion. For the saliency system, which overlaps with the social pain network, there was no change in connectivity during exclusion.

results. We first entered as connectivity measures the mean strength across nodes from the mentalizing and social pain systems, respectively, but found no significant effects. Next we entered the connectivity of individual edges, i.e., the correlations between the time courses from each pair of nodes. After correcting for multiple comparisons using the false-discovery rate (FDR, $q = 0.05$), we found that connectivity between the left and right TPJ, two key nodes of the mentalizing network, was negatively related to ego-network density (Fig. 5). In other words, individuals who exhibit a stronger TPJ coupling during exclusion tend to have a less dense friendship network. We did not observe effects between any pairs of nodes from the social pain network, either corrected or uncorrected. Together, these results suggest that brain dynamics during key social experiences such as exclusion may contribute to the type of network structure people occupy. Likewise, the amount of interconnections among friends of the excluded participant's social network may also influence the impact of exclusion on brain connectivity.

Discussion

Social relationships are a driving force for human behavior, and previous research on social exclusion has identified robust involvement of two sets of brain regions activated during social pain and mentalizing. We bring a network neuroscience perspective to examine how social experiences may engage and reconfigure these brain networks in support of social cognition and how individual differences in the way people use their brains may correspondingly influence or be influenced by the structure of their social networks.

Specifically, we first tested the prediction that functional connectivity would increase within the social pain and mentalizing networks during social exclusion relative to inclusion. We also explored the relationships between the networks during both exclusion and inclusion. Here, we find support for tight coupling of the two proposed networks (social pain and mentalizing) during social inclusion and exclusion. Next, we find that connectivity within the mentalizing system increases during exclusion relative to inclusion. This result is confirmed using a whole brain analysis that identified significant effects within the so-called default mode network. This atlas-derived default mode network overlaps with an a priori hypothesized mentalizing network.

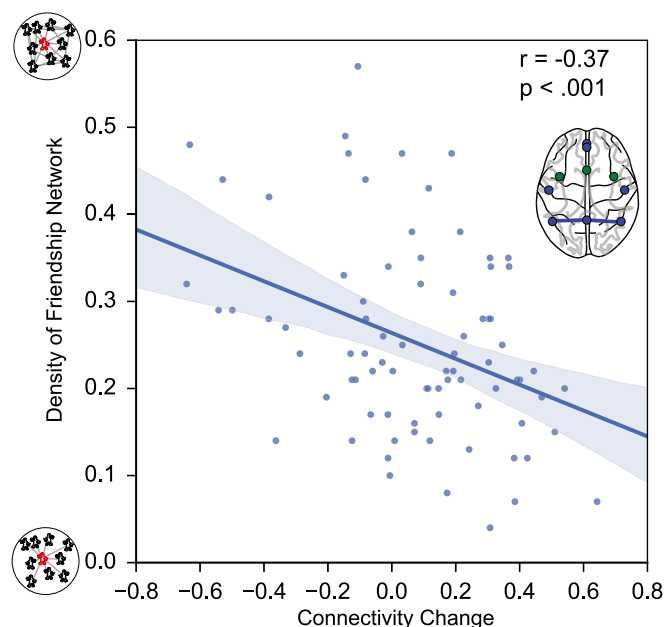


Fig. 5. Scatterplot illustrating the significant relationship between the functional connectivity between the ITPJ and rTPJ and the density of a participant's ego-friendship network. Participants who show stronger regional coupling during exclusion have sparsely connected networks in which fewer of their friends are also friends with each other.

Previous research has highlighted the role of the social pain system in responding to exclusion (4, 50). Building on this starting point, the few studies examining brain connectivity during social exclusion (15–17, 51) have focused on dACC seed regions as a hotspot of univariate activation effects in the social pain network. Our findings highlight a broader network perspective. Although connectivity is strong within both social pain and mentalizing networks during both social exclusion and inclusion, connectivity increases within the mentalizing system, but not the social pain system, during exclusion relative to inclusion. This first finding highlights the critical value of coordination between regions of the same subnetwork, revealing that within-network instead of between-network interactions were strongly correlated with the social exclusion condition. The second finding complements existing univariate accounts of increased activity within specific nodes of the social pain and mentalizing networks by highlighting a distinction in the temporal dynamics of the social pain and mentalizing processes that was not captured by average univariate activation results. Overall, these findings are in line with the wider literature arguing that connectivity and activity provide complementary information (52, 53) and thus can provide complementary insights about cognitive processes.

Functionally, this stronger coupling among mentalizing regions may support considering the intentions of the individuals who are excluding the participant in the social event or internal ruminations about the relevance of potential ongoing exclusion for one's broader social relations. In fact, verbal reports from participants who have undergone this type of exclusion show that such thoughts are frequent (11), although not uniformly distributed across people. One benefit of the connectivity methods used in the present paper is that they are, in principle, also sensitive to thought processes that wax and wane multiple times during the exclusion period, such as fluctuations in mentalizing (e.g., about others' thoughts and motives). Thus, we suggest that increased connectivity in the mentalizing network may tap into such dynamic aspects of the response to social exclusion over a period. One possible function of such a dynamic process may be to make sense of the situation and to reflect more broadly on the meaning of that experience, thereby supporting coping-related functions (54). These data highlight the value of examining functional connectivity in addition to mean activation because connectivity can provide different insight into the dynamics of psychological phenomena such as exclusion; although average activation in both mentalizing and social pain systems are commonly observed in response to exclusion, changes in connectivity were significant in this dataset only within the mentalizing system.

Our social-cognitive interpretation of changing connectivity within the mentalizing system as a means of coping with exclusion is also supported by the fact that this effect covaries with participants' broader social network structures. Specifically, participants who showed increased connectivity during exclusion relative to inclusion between the left and right TPJ, two regions of the mentalizing system, also had less dense social network structures. One possibility is that outside the safety of dense ego-networks, which tend to be more close-knit (38, 39), individuals use greater mentalizing resources, especially during stressful social interactions such as exclusion. This effect is consistent with neurocognitive models that link intrapersonal effects of social exclusion to the interpersonal contexts surrounding individuals during daily life (53). Social exclusion, by its very nature, does not occur in a vacuum. Rather, preexisting characteristics of one's social network provide the background or contextual standard from which any new episode of exclusion is understood and compared (55). Within this framework, our measure of social network density can be understood as a social inclination. When excluded, people who interact more with unconnected others may use mentalizing resources differently than those with denser ego-friendship networks. That said, it is also likely that those who use mentalizing resources differently may position themselves differently in their social networks, and that the ways in which individuals use their brains during social experiences shapes their preferences and

tendencies to occupy different types of network positions. For example, the extant literature suggests that the lack of diverse communities in denser networks may relate to the degree of mentalizing that individuals engage in during social tasks. Indeed, prior work has shown that network brokerage, which is inversely related to density and associated with bridging diverse communities, can moderate mentalizing activity during social decision making (56). The present findings substantially extend prior research linking personality to the shape of social networks (33–36) by showing that individual differences in brain dynamics may underpin such links. In other words, the relationship between brain network dynamics and social network dynamics is likely bidirectional, and the current findings open avenues to understand both.

Our results add to a growing literature that links individual differences and social network properties, and they also bring neuroscientific methods to bear in characterizing individual differences. For example, past research has linked social personality tendencies, such as extraversion, self-monitoring, and cognitive empathy (related to mentalizing) to personal network structure (35, 57). Our results also complement work across other social species, including research with macaques (58). Researchers have studied the structure and connectivity of brain regions that belong to the default mode network, including the posterior superior temporal sulcus (pSTS), which parallels our TPJ results. These regions are modulated on the basis of social network characteristics, such as network size and position in a social hierarchy (59). Our data complement these findings by showing that properties of an individual's social networks are associated with intrapersonal reactions to exclusion, which then might reciprocally influence the interpersonal relationships that underlie these social networks. Taken together, these results also highlight the need to consider jointly the structural characteristics of personal networks in combination with cognitive responses to acute episodes of exclusion.

In sum, we find that social exclusion is associated with increased connectivity within the mentalizing system. Furthermore, we explore whether the impact of social exclusion on brain connectivity relates to the structure of participants' friendship networks, finding that participants with sparser friendship networks show increased connectivity within key brain systems when excluded. These findings demonstrate that networked brain dynamics during social-cognitive tasks can provide relevant information in addition to univariate activity. In particular, our connectivity analysis highlights the fundamental importance of the mentalizing system in responding to socially salient events, and it indicates how a participant's social network structure may capture critical differences between individuals in how social exclusion influences these key dynamics of the underlying brain networks for social cognition. Together, our connectivity analysis offers insights into the neural and social responses to common social experiences such as exclusion and delineates how distributed brain networks respond to powerful socio-affective challenges that manifest in social networks indexed by online media.

Materials and Methods

Participants. Eighty neurotypical 16- to 17-y-old adolescent males were recruited through the Michigan state driver registry database as part of a larger study on peer influences on adolescent driving. Participants met standard MRI safety criteria. In accordance with Institutional Review Board approval from the University of Michigan, legal guardians provided written informed consent, and adolescents provided written assent.

Social Exclusion Task. Participants completed the Cyberball game, which has been validated in a number of behavioral and neuroimaging studies as a reliable way of simulating the experience of social exclusion (5, 60), while undergoing fMRI scanning. The Cyberball game consisted of two 3-min rounds, and the order of rounds was held constant to preserve the psychological experience across participants. In the inclusion round, the participant and two virtual players received the ball equally often, whereas during the exclusion game the participant and virtual players started out playing the ball, but the participant was left out after a few throws,

simulating social exclusion. After the scan, participants completed a set of questionnaires.

Social Network Assessment. In addition to the fMRI tasks, participants also provided information about their social networks. This information was assessed from logged online friendships using the Facebook API (collected in 2011–2013). Following this data acquisition, density was computed for participants' egocentric networks. In particular, we constructed a friendship network for a given individual ("ego") and then removed the ego from the network (because all friends are logically connected to it), and computed the density among the remaining nodes (n) of friends, assessing the proportion of existing connections (m) between friends vs. all possible connections [i.e., $n \times (n - 1)/2$ if all the ego's friends are also friends with each other]. In other words, the density of the ego-network measures the extent to which participants' Facebook friends are interconnected. After first removing the ego from each individual's friendship network, density was computed using NetworkX with the formula: $d = 2m/(n \times (n - 1))$, where m denotes the number of edges between persons and n denotes the number of nodes.

fMRI Acquisition and Analysis. Functional images were recorded using a reverse spiral sequence (repetition time = 2,000 ms, echo time = 30 ms, flip angle = 90°, 43 axial slices, field of view = 220 mm, slice thickness = 3 mm, voxel size = $3.44 \times 3.44 \times 3.0$ mm). We also acquired in-plane T1-weighted images (43 slices, slice thickness = 3 mm, voxel size = $0.86 \times 0.86 \times 3.0$ mm) and high-resolution T1-weighted images [spoiled gradient recall (SPGR) acquisition, 124 slices, slice thickness = $1.02 \times 1.02 \times 1.2$ mm] for use in coregistration and normalization. Functional data were preprocessed and analyzed using Statistical Parametric Mapping (SPM8, Wellcome Department of Cognitive Neurology, Institute of Neurology, London). The first four volumes were discarded before analysis. Functional images were despiked using the 3dDespike program as implemented in the AFNI toolbox, corrected for differences in slice time acquisition, and spatially realigned to the first functional image. Functional and structural images were coregistered using a two-stage procedure. First, in-plane T1 images were registered to the mean functional image. Next, high-resolution T1 images were registered to the in-plane image. Structural images then were skull-stripped and normalized to the skull-stripped MNI template provided by FSL (Oxford Centre for functional MRI of the Brain).

Meta-Analytical Definition of Regions. Nodes for the social pain and mentalizing networks were derived from semiautomated and researcher-curated meta-analysis: We used Neurosynth (36) to perform two automated meta-analyses of the functional neuroimaging literature on "mentalizing" and "social pain," respectively. In addition, we consulted two separate researcher-curated meta-analyses of mentalizing (61) and social pain (4), respectively (see *SI Materials and Methods* for additional details). This procedure provided the following coordinates for the mentalizing network (Fig. S2): dorsal medial prefrontal cortex (dmPFC) (0, 53, 30); ventromedial PFC (vmPFC) (0, 48, -18); precuneus (0, -54, 44); right TPJ (rTPJ) (48, -56, 23); left TPJ (lTPJ) (-48, -56, 23); right middle temporal gyrus (rMTG) (53, -12, -16); and left MTG (lMTG) (-53, -12, -16) and the following coordinates for the social pain network: dACC (0, 16, 32); right aINS (r-aINS) (38, 7, -4); and left aINS (l-aINS) (-38, 7, -4). In addition to the regions of these two a priori networks, we also examined connectivity changes during social exclusion using a whole-brain parcellation that assigns 264 brain regions to 1 of 13 functional networks (Fig. S2) (44).

Functional Connectivity Analysis. Analysis of functional connectivity was performed in Python 2.7 using the Nilearn package (61). Data were bandpass filtered between 0.06–0.12 Hz (22), detrended, standardized, and extracted from 8-mm-radius spheres around the nodes specified above. Artifacts were reduced using frame censoring and regression. In particular, frames with framewise displacement (FD) >0.5 mm were censored; nuisance regressors included white matter and ventricular signals, the realignment parameters, and high-variance confounds as implemented in the Nilearn package. From the extracted time series corresponding to the social inclusion and exclusion runs, we used Pearson's correlation coefficient to construct task-specific undirected and weighted functional connectivity matrices for each participant. To determine whether results observed could be explained by increased mind-wandering over time in the scanner, an additional set of split-half analyses was also implemented using parallel methods on the first and second half of each block (inclusion and exclusion), respectively (Fig. S3). Analyses were implemented using python packages and in-house functions, and visualizations were created with Nilearn, Matplotlib, and Seaborn (61–63).

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