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Review

The Socio-Temporal Brain: Connecting People in Time

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Temporal and social processing are intricately linked. The temporal extent and organization of interactional behaviors both within and between individuals critically determine interaction success. Conversely, social signals and social context influence time perception by, for example, altering subjective duration and making an event seem 'out of sync'. An 'internal clock' involving subcortically orchestrated cortical oscillations that represent temporal information, such as duration and rhythm, as well as insular projections linking temporal information with internal and external experiences is proposed as the core of these reciprocal interactions. The timing of social relative to non-social stimuli augments right insular activity and recruits right superior temporal cortex. Together, these reciprocal pathways may enable the exchange and respective modulation of temporal and social computations.

Trends

Much behavioral evidence points to the relevance of time in social processing and the relevance of social information for timing.

Current brain structural and functional modeling of time perception highlights a role of the striatum, the insula, and cortical oscillations.

Current brain structural and functional modeling of social processing highlights several neural networks and reveals the superior temporal sulcus (STS) as a multisensory convergence zone.

The temporal perception of socially relevant as compared to less relevant stimuli recruits right insula and right STS.

Time – A Social Matter

The term 'timing' refers to our ability to represent and use temporal information such as **duration** and **rhythm** (see Glossary). Similarly to other cognitive functions, timing is not encapsulated but interacts closely with the social processes that emerge from interpersonal interactions [1–3]. As interactional behaviors play out in time, their temporal signatures carry important information. They guide attention, convey a message, and mold bonds between individuals. Moreover, interactional behaviors in turn give meaning to time and influence its perception and representation. A range of disorders that jointly compromise temporal and social processes attest to this relation [4].

We review here the many ways in which timing intersects with social processing. We explore this intersection for the communicative behavior of an individual as well as for the behavioral coordination between communicating agents. We detail neuroimaging evidence on how temporal and social information are represented in the brain and identify points of structural and functional convergence. Through this, we hope to connect research on timing and social processing, and to provide an impetus for studying the linkages among them.

Temporal Signatures of Communicative Behaviors

Behavior evolves in time and is composed of units that may be ordered hierarchically in reoccurring temporal patterns. Thus, behavior has a range of temporal signatures including duration, speed, frequency and rhythm. For example, in an interactional setting, a nod – a continuous down–up motion of the head – may be short or long, rapid or slow, and may occur sporadically or often, at regular or irregular intervals. Although the different temporal signatures can, in principle, be independent, for natural behaviors they often correlate [5]. For example, short nods are typically also fast, and repeated nods often occur at regular intervals. As such, the temporal signatures of communicative behaviors are difficult to dissociate, and we will discuss them separately only when extant research makes such a discussion feasible.

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The timing of communicative behaviors is informative. This is obvious for speech where **voice-onset time** discriminates between otherwise comparable consonants (e.g., /pa/ vs /ba/) or where syllable duration marks lexical stress and syntactic phrasing [6]. However, time is equally important for nonverbal behaviors. For example, natural smiles have a stereotypical temporal structure that, if violated, may make a smile seem forced [7]. Likewise, vocal and full-body expressions are temporally determined. Lengthening or shortening a given type of expression by slowing and increasing speed, respectively, produces corresponding changes in emotional meaning. Affective cries of anger and disgust seem more arousing when they are longer and slower as compared to shorter and faster [5]. Longer and slower disgust expressions appear more negative [5]. Similarly to voices, the affective ratings of point-light displays of body motion can be described by arousal and valence [8,9]. Again, perceived arousal is correlated with speed but, unlike for voices, slow motion is associated with low rather than high arousal, and valence fails to show a clear relation to time [8,9].

The temporal signatures of both verbal and nonverbal behaviors contribute to the significance of social interactions. However, the opposite also is true in that social information shapes timing and time perception. A common observation is that displays of emotional faces are perceived as longer-lasting than equivalent-duration displays of neutral faces [10]. Conversely, studies using vocalizations found emotional expressions to be perceived as shorter-lasting than equivalent-duration neutral expressions [5,11].

Although facial, vocal, and other behaviors each have their temporal signatures, and these signatures differ in how meaning ensues from time, the different expressive behaviors are temporally non-independent. Moreover, communicating agents tend to produce them in a synchronized manner such that the timing of one behavior aligns with that of another behavior. For example, the head motion that occurs during speaking typically correlates with the speaker's vocal pitch and loudness [12]. In other words, an apex in head motion tends to coincide with an apex in voice acoustics, implying a temporal mapping of emphasis. Related research exploring other expressive channels has confirmed and extended these observations [13].

The **self-synchronization** that emerges in the behavior of individuals has been shown to facilitate social intercourse. For example, it helps to guide attention to important points in the communication [14,15], it facilitates meaning analysis [12,16], enhances memory, and makes communications more persuasive [17]. However, whether the reverse is true and non-temporal social information impacts on expression synchronization is still awaiting investigation.

Temporal Coordination between Communicating Agents

When engaging with others, we tend to spontaneously mimic their facial expressions, gestures, or postures [18]. Important for the present purpose is that such mimicry extends to when these behaviors occur in time (Box 1) [2,19]. In a study demonstrating this [20], pairs of participants competed in a touch-screen variant of the popular arcade game 'Whac-a-mole'. Over the course of the game, the movement of both players became temporally synchronized as player visibility increased. Moreover, the synchronization emerged despite being counter-productive and reducing the players' scores.

The degree of temporal coordination between interaction partners relates to interaction success. For example, it produces affective consequences [21]. This was revealed by a study in which pairs of strangers discussed four topics and completed an affective state questionnaire before and after each topic. Results provided evidence for emerging synchrony between discussion partners (Figure 1) and for its causal effect on ensuing positive affect. Related research showed that individuals more readily empathize with a synchronous as compared to a non-synchronous

Glossary

Connectivity: a structural or functional property of brain tissue. Two brain regions show structural connectivity if neurons from one region physically communicate with neurons from the other region. Two brain regions show functional connectivity if activity in one region can be used to predict activity in the other region.

Cortical oscillations: a phenomenon arising from the synchronous activity of thousands of cortical neurons. In other words, these neurons polarize and depolarize in a temporally synchronous manner. Cortical oscillations may occur at a broad range of frequencies that are measurable with temporally precise neuroimaging techniques such as electroencephalography (EEG).

Dopaminergic neurons: nerve cells using the neurotransmitter dopamine for signaling, located primarily in the cortex and striatum for our purposes. These neurons fire tonically at a slow background rate of 1–8 Hz (i.e., pacemaker function) and at a phasic or burst rate ($\geq$20 Hz) for limited periods of time following the presentation of stimulus (i.e., onset of a 'to-be-timed' signal associated with feedback or reward).

Duration: the amount of time that defines the presence or absence of an event (stimulus or response).

Hypoperfusion: abnormally low blood flow and thus insufficient provision with nutrients (e.g., oxygen).

Medium spiny neurons (MSNs): a class of neurons that comprise the vast majority of neurons in the striatum. MSNs use the inhibitory neurotransmitter GABA for signaling and can be differentiated into two phenotypes: 'direct pathway' MSNs with dopamine D1 receptors, and 'indirect pathway' MSNs with dopamine D2 receptors having excitatory and inhibitory effects on an ultimate projection target in the basal ganglia, respectively.

Oscillatory phase: the position or point of time in a waveform.

Rhythm: a percept emerging from an event or behavior that is characterized by a temporal regularity that can be organized into a metric structure with strong and weak elements. For example, tones presented every 300 ms may be perceived as a rhythm. Importantly,