

Opinion | Cognition and Behavior

An Emerging Field of Primate Social Neurophysiology: Current Developments

Primate Social Neurophysiology

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DOI: 10.1523/ENEURO.0295-17.2017

Received: 22 August 2017

Revised: 19 September 2017

Accepted: 27 September 2017

Published: 29 September 2017

Author Contributions: Each author must be identified with at least one of the following: Designed research, Performed research, Contributed unpublished reagents/ analytic tools, Analyzed data, Wrote the paper. Example: C.S. and J.S. Designed Research; M.G. and G.T. Performed Research; J.S. Wrote the paper, **S.W.C.C. wrote the paper.**

Funding: Alfred P. Sloan Foundation
100000879
FG-2015-66028

Funding: HHS | NIH | National Institute of Mental Health (NIMH)
100000025
R01MH110750

Funding: HHS | NIH | National Institute of Mental Health (NIMH)
100000025
R21MH107853

Funding: HHS | NIH | National Institute of Mental Health (NIMH)
100000025
R00MH099093

Conflict of Interest: The author reports no conflict of interest.

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Cite as: eNeuro 2017; 10.1523/ENEURO.0295-17.2017

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Accepted manuscripts are peer-reviewed but have not been through the copyediting, formatting, or proofreading process.

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Manuscript Title Page**1. Manuscript Title (50 word maximum)**

An Emerging Field of Primate Social Neurophysiology: Current Developments

2. Abbreviated Title (50 character maximum)

Primate Social Neurophysiology

3. List all Author Names and Affiliations in order as they would appear in the published article

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4. Author Contributions: Each author must be identified with at least one of the following: Designed research, Performed research, Contributed unpublished reagents/ analytic tools, Analyzed data, Wrote the paper. Example: CS and JS Designed Research; MG and GT Performed Research; JS Wrote the paper

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6. Number of Figures 0^{[1][SEP]}

7. Number of Tables^{[1][SEP]} 0

8. Number of Multimedia 0

9. Number of words for Abstract No Abstract (Opinion)

10. Number of words for Significance Statement^{[1][SEP]} 69

11. Number of words for Introduction Main Text, 527 words

12. Number of words for Discussion Main Text, 247 words

13. Acknowledgements^{[1][SEP]}

The author thanks Amrita Nair for thoughtful comments on the manuscript. This work was supported by Alfred P. Sloan Foundation (FG-2015-66028) and the National Institute of Mental Health (R01MH110750; R21MH107853; R00MH099093).

14. Conflict of Interest^[1]_{SEP}

The author reports no conflict of interest

15. Funding sources^[1]_{SEP}

Alfred P. Sloan Foundation (FG-2015-66028) and the National Institute of Mental Health (R01MH110750; R21MH107853; R00MH099093).

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60 **Significance Statement**

61 Recently, there has been increased interest in investigating neurophysiological mechanisms
62 underlying social interactions using a nonhuman primate model system. Several studies in this
63 sub-field, known as primate social neurophysiology, have begun to provide novel insights into
64 how single neurons encode socially-relevant variables. This opinion piece intends to provide
65 insight into the state of this field. In doing so, it discusses some common principles learned from
66 primate social neurophysiology experiments.

69 **Introduction**

70 Neurophysiologists are interested in discovering the neural codes that are utilized by the
71 brain to represent variables from the sensory environments, and to plan and execute motor
72 actions following wide-ranging cognitive operations. In the past decade or so, there has been an
73 increasing trend in neurophysiological research to investigate the neurobiological mechanisms of
74 social interaction. This is particularly true of nonhuman primate research, where exploiting the
75 rich social behavioral repertoires of nonhuman primates has allowed researchers to focus on
76 assessing how neurons from various brain regions signal information used for or as a
77 consequence of social behavior. This research endeavor is often referred to as social
78 neurophysiology. This opinion, by way of examining selected empirical results in rhesus
79 macaques, discusses some common principles in social neurophysiology gained by neuronal
80 recording experiments involving nonhuman primate social interactions. Specifically, this opinion
81 narrates the knowledge gained so far indicating that social variables are represented in several
82 parts of the brain involved in motivation and affective processing by way of agent-specific
83 reference frames, contextual gain modulations, and, in some cases, privileged information
84 processing, and mirroring.

85 Nonhuman and human primates share a vast array of social characteristics that are not
86 found in other species. Macaques live in large, hierarchical groups, displaying extensive
87 cohabitation and reciprocity (Mitani et al., 2012), and strategically acquire complex social
88 information from facial expressions and the eyes (Emery et al., 1997). Not surprisingly, there are

89 many similarities in the underlying neurobiology of social cognition between humans and
 90 macaques. As an example, in both humans (Mitchell et al., 2006; Burke et al., 2010; Apps and
 91 Ramnani, 2014; Sul et al., 2015) and macaques (Rudebeck, 2006; Yoshida et al., 2011; Chang et
 92 al., 2013b), the brain regions in the medial prefrontal and frontal cortices mediate social learning
 93 and prosocial behavior. As another example, the amygdala is particularly engaged when
 94 acquiring social information from facial expression as well as eye contact and gaze following in
 95 humans (Kawashima et al., 1999; Adolphs et al., 2005) as well as in macaques (Brothers et al.,
 96 1990; Gothard et al., 2007; Mosher et al., 2014). Furthermore, the value associated with
 97 particular social information is signaled by the orbitofrontal cortex (OFC) and the ventromedial
 98 prefrontal cortex in both humans (Hare et al., 2010; Smith et al., 2010) and in macaques (Watson
 99 and Platt, 2012). Overall, although monkeys and humans are undoubtedly different in many
 100 ways, studying social cognition in monkeys provide unique opportunities to investigate
 101 rudimentary neurophysiological mechanisms underlying human social behavior.

102 An increasingly acceptable view is that social processes in the brain are enabled by a
 103 variety of repurposed mechanisms that initially evolved to solve basic survival and reproductive
 104 needs (Chang et al., 2013a; Parkinson and Wheatley, 2015). Social events are closely associated
 105 with motivation and emotion. Not surprisingly, motivational and affective circuits in the primate
 106 brain are reliably engaged in computing social behavior (Behrens et al., 2009), sharing common
 107 fundamental operations (Joiner et al., 2017). Some of these brain regions include the anterior
 108 cingulate cortex (ACC), the OFC, the striatum, and the amygdala, all of which will be discussed
 109 later for their involvement in social interactions based on selected experiments in primate social
 110 neurophysiology.

112 **Agent-specific Reference Frames**

113 Compared to more traditional neurophysiological research, social neurophysiology
 114 experiments frequently present novel problems in understanding neuronal encoding schemes
 115 across self and others. Debatably, the most interesting aspect of social neurophysiology research
 116 is in discovering how neurons involved in affective, motivational, sensory and motor processes
 117 encode information with respect to oneself and/or a conspecific. There is a parallel to this
 118 endeavor in the history of systems neuroscience research. Egocentric and allocentric
 119 representations in the brain have been recognized and studied in depth in the visuomotor and the

120 spatial memory systems (Andersen et al., 1997; Burgess, 2006). Encoding variables in an
 121 egocentric frame of reference refers to cases when neuronal activity is tightly coupled to (i.e.,
 122 systematically covaries with) one's own body (e.g., body part position in space or on some
 123 location on the body). In contrast, an allocentric encoding refers to instances when neuronal
 124 activity is referenced to environmental location (e.g., world-centered) or objects (i.e., object-
 125 centered) that are outside one's body. In the visuomotor system, a spatially-tuned neuron may
 126 encode a stimulus relative to one's retina in an eye-centered or retinocentric frame of reference
 127 (Andersen et al., 1993), which would be classified as a type of egocentric representation. A
 128 different spatially-tuned neuron, in either the same or different brain area, may encode the
 129 position of the same stimulus relative to its environment but independent of one's body, which
 130 would be classified as an allocentric representation. For example, in a paradigm involving body-
 131 under-head and body-plus-head rotations occurring with respect to a saccade target, visuomotor
 132 neurons in the monkey area 7a of the posterior parietal cortex modulate their responses according
 133 to the position of the head relative to the world (i.e., world-referenced, allocentric signal), but not
 134 the position of the head relative to the body (i.e., body-referenced, egocentric signal) (Snyder et
 135 al., 1998). Similar egocentric and allocentric codes have been found for spatial memory
 136 (Feigenbaum and Rolls, 1991; Fyhn et al., 2004). For instance, place fields of the rat medial
 137 entorhinal cortical neurons near the postrhinal cortex display view-point-independent spatial
 138 information (i.e., allocentric) (Fyhn et al., 2004). As in these examples from visuomotor
 139 processing and spatial memory, variables involved in social processing may also be encoded
 140 using distinct frames of reference (in this case, across agency) and that socially-relevant signals
 141 may undergo transformations to be represented in an egocentric or an allocentric manner (Chang,
 142 2013). A need for such transformation processes is likely when social variables encoded in either
 143 an egocentric (e.g., relative to oneself) or allocentric (e.g., relative to a social partner) frames of
 144 reference need to be integrated to influence specific types of self- or other-regarding decisions.

145 A pioneering effort to understand how neurons represent self and other began when
 146 primate neurophysiologists examined how parietal neurons signal the location of food items
 147 differentially as a function of whether the location is shared by a conspecific (Fujii et al., 2007).
 148 Specifically, when two adjacent monkeys were not interacting for the food item, arm-motion
 149 related parietal neurons primarily signaled one's own action. In contrast, when the food item was
 150 located on a shared, interactive space for the two monkeys, these neurons encoded complex

151 patterns with respect to the actions of both self and other. More recently, a study under the
152 framework of reward-guided decision-making examined the presence of agent-specific reference
153 frames in three different structures in the prefrontal and frontal cortices. Specifically, this study
154 compared the encoding of juice reward outcomes when a subject monkey made a decision to the
155 delivery the reward only to himself, to a recipient monkey, or to neither. In OFC and the sulcus
156 of ACC (ACCs), most neurons signal the reward outcome with respect to self. When the subject
157 monkey makes decisions impacting another monkey, the firing rates of the majority of OFC
158 neurons only encoded the reward outcome for the subject but not when the recipient monkey or
159 neither was rewarded, whereas the firing rates of the majority of ACCs neurons only signaled
160 when the subject monkey's reward was omitted (i.e., when the reward went to the recipient or
161 neither) (Chang et al., 2013b). However, a group of neurons in the gyrus part of the anterior
162 cingulate cortex (ACCg) only encoded the reward outcome when the recipient monkey received
163 the juice reward (allocentric reward coding) (Chang et al., 2013b). Furthermore, in an
164 experiment where a subject monkey was required to monitor another monkey's action and
165 outcome, a group of neurons in the medial frontal cortex (MFC) exclusively encoded the action
166 of the other monkey (allocentric action encoding) (Yoshida et al., 2011). In the same task, a large
167 proportion of these MFC neurons specifically encoded the erroneous choices made by the social
168 partner (Yoshida et al., 2012), suggesting that MFC harbors dedicated neurons for monitoring
169 actions and errors by others. Similarly, when a monkey subject was taking turns with a human
170 partner to constantly choose a new target located opposite from the target chosen by the human
171 partner on the previous trial, many neurons in the lateral prefrontal cortex selectively encoded
172 the target position of the monkey subject (egocentric encoding) or that of the human partner
173 (allocentric encoding) (Falcone et al., 2016). A further example of egocentric and allocentric
174 encoding of social variables comes from an experiment where a monkey subject viewed a
175 reward-predicting stimulus and touched it to realize the outcome concerning self and a
176 conspecific. In this study, many neurons in the striatum preferentially signaled the reward
177 outcome of self (egocentric reward encoding), regardless of whether the resulting action was
178 performed by self or another monkey, whereas a smaller group of neurons encoded just the
179 action of another monkey without encoding the reward outcome (allocentric action encoding)
180 (Báez-Mendoza et al., 2013). Furthermore, there are specializations with these striatal neurons
181 for encoding erroneous performance. Specifically, although some striatal neurons signaled one's

own performance errors only, other striatal neurons signaled conspecific's errors either exclusively or comparably to one's own error (Báez-Mendoza and Schultz, 2016). Therefore, it is evident that both egocentric as well as allocentric encoding of social variables, which are anchored to the events of another individual, are present in the primate brain and are engaged during social interaction (see **Fig. 1A** for three schematized neurons with different reference frames).

Gain Modulations by Social Contexts

In addition to the concept of agent-referenced signals, social information could be added to existing encoding schemes by way of gain changes in the signals, independent of reference frames used. In visuomotor processing, when the information about current eye positions (i.e., the location of the eyes relative to the head or orbital eye position) are added by way of multiplicative gain to a target position signal encoded in an eye-centered frame of reference, the signal now embodies new information about the target location with respect to the head, effectively creating a new representation (Andersen et al., 1985). Several findings in primate social neurophysiology support the idea that the information about a particular social variable may be added by either turning up or down the signal gain. Reward value gain-modulates the activity of predominantly egocentric OFC and ACCs neurons as well as mixed egocentric and allocentric ACCg neurons (Chang et al., 2013b). Furthermore, in an experiment where a subject monkey is required to lift a lever to deliver a reward to itself and to one of two conspecifics, the value tuning of individual OFC neurons are systematically gain-modulated as a function of the social hierarchical position of the conspecific which also receives reward (Azzi et al., 2012). Additionally, a recent study asked monkeys to play a prisoner's dilemma (PD) task to examine neural signature of strategically cooperative decisions. In this monkey PD task, players could choose one of the two options ("cooperate" or "defect") when the juice payoffs depend critically on the choices made by both monkeys, thereby encouraging strategic decisions taking into account the prediction of what the other player would do in order to maximize one's reward. During this task, ACC neurons scale their activity to differentiate strategically predicted decisions made by a social partner from the current decision made by the subject monkey (Haroush and Williams, 2015). Finally, it has been shown that the differences between own and other's rewards (inequity) are represented in the striatal neurons using gain modulations – equity

213 (own reward = other's reward), advantageous inequity (own reward > other's reward) and
 214 disadvantageous inequity (other's reward > own reward) are signaled via scaled firing rates
 215 (Báez-Mendoza et al., 2016). Taken together, in the prefrontal and frontal regions, a gain applied
 216 to either egocentric or allocentric signals may be used to combine social variables within existing
 217 representations (see **Fig. 1B** for a schematized neuron whose activity is gain-modulated by social
 218 context).

219 As alluded to by some examples above, motivational factors can exert a rather dramatic
 220 influence on firing characteristics of neurons recruited during social interaction. Motivational
 221 factors in social settings may differ as a function of impacting individuals with high versus low
 222 social status as well as making a self-generated versus observed outcome influencing other
 223 individuals. In the aforementioned experiment where a subject monkey is required to lift a lever
 224 to deliver a reward to itself and to one of two conspecifics, the reward value-dependent
 225 modulations in OFC neurons positively co-scaled with social context, defined by whether the
 226 reward was shared with a specific partner over another (Azzi et al., 2012). Moreover, when
 227 viewing the conspecific images with different values, more OFC neurons are modulated by
 228 social information conveyed in these images over juice magnitude (Watson and Platt, 2012).
 229 These findings suggest that the code for valuation in OFC neurons, during social settings, is
 230 strongly coupled to socially motivating factors. Furthermore, neurons in the basolateral
 231 amygdala (BLA) show correlated value tuning functions across self and other when an actor
 232 monkey makes social decisions about reward allocation across self and other, but this
 233 relationship is no longer present when the outcome is passively cued (Chang et al., 2015). These
 234 results suggest that the encoding schemes of BLA neurons markedly differ when motivation, or
 235 active decision making, is involved.

236

237 **Privileged Processing for Specific Social Information**

238 Finally, some social variables are highly salient over others to the primate brain, possibly
 239 having privileged access to the brain. As expected from the ecology of primate social behavior,
 240 the neural underpinnings of primate social behavior are tightly linked to facial expressions and
 241 social gaze interactions. Like in humans, faces convey special social information to monkeys.
 242 Recently, there has been a great amount of progress in how the primate brain computes facial
 243 information from both neurophysiological and neuroimaging studies in macaques. Face patches,

244 first discovered in the temporal cortex, consist almost entirely of face-selective neurons (Tsao,
 245 2006). A group of face patches form hierarchical social information processing streams, and are
 246 critical for face perception (Moeller et al., 2017; Sadagopan et al., 2017) as well as recognizing
 247 individual identity and familiarity (Chang and Tsao, 2017; Landi and Freiwald, 2017). Moreover,
 248 the activity patterns of face patch neurons are sensitive to contexts in which social interactions
 249 may take place (McMahon et al., 2015), and neurons within the face patches show diverse yet
 250 systematic interaction patterns with other brain regions (Park et al., 2017), revealing how face-
 251 related information is conveyed across the brain to guide social interactions. Taken together, face
 252 patches powerfully demonstrate the presence of privileged processing units for the most
 253 fundamental social information in primates that are sensitive to social settings. In addition, like
 254 humans, monkeys react to various facial expressions and adjust their future behaviors and follow
 255 gaze of a conspecific or make eye contacts to gain social information (Smuts et al., 1987;
 256 Ekman, 2015). Neuronal recording studies while monkeys view conspecifics' facial expressions
 257 or the eyes have provided neural mechanistic insights into emotional processing and social gaze
 258 behavior. Recordings from the primate amygdala revealed that these neurons either increase or
 259 decrease their firing rates to encode either the facial expression or the identity of a conspecific,
 260 or some specific combination of both variables (Gothard et al., 2007), reflecting a signature of an
 261 integration process across identity and emotional expression. The amygdala neurons also
 262 embody a specialized group of neurons that are exclusively responsive to looking at the eyes of
 263 another individual or making direct eye contacts with others (Mosher et al., 2014). Furthermore,
 264 neurons in the amygdala have been shown to be involved in signaling either the production or
 265 monitoring of one's own facial expression in reaction to viewing the face of a conspecific
 266 (Livneh et al., 2012). Signaling of facial expressions by the amygdala neurons is mediated by
 267 tactile neurons in the primate amygdala – these neurons show similar firing characteristics
 268 between self-produced facial expressions and those induced by tactile stimulation to the face
 269 (Mosher et al., 2016). Taken together, these findings suggest that certain, highly salient social
 270 information may recruit a specialized group of neurons that are specifically tuned to such
 271 ethologically-relevant information (see **Fig. 1C** for a schematized neuron with gated responses to
 272 particular social information).

273

274 **Mirroring Signals**

275 First discovered in the ventral premotor cortex (PMv or F5) of monkeys (Gallese et al.,
 276 1996), ‘mirroring’ refers to when neuronal firing rates display similar characteristic patterns
 277 between one’s own movement and observing other’s movement. A series of studies that
 278 followed, in both humans and monkeys, have demonstrated the presence of mirroring by several
 279 brain regions in connection with social cognition (Gallese et al., 2004; Rizzolatti and Craighero,
 280 2004). Such mirrored representations may serve unique functions in understanding other’s
 281 actions from the perspective of oneself. Mirroring, however, is not limited to the motor domain.
 282 In the social reward allocation task described earlier, a group of ACCg neurons signaled the
 283 reward outcome of self and other in an indistinguishable manner (Chang et al., 2013b) and the
 284 majority of BLA neurons showed correlated value tuning functions across self and other (Chang
 285 et al., 2015). Furthermore, as mentioned above, some striatal neurons encode performance errors
 286 regardless of whether the error was generated by self or other (Báez-Mendoza and Schultz,
 287 2016). Therefore, mirror-type signals have been found across multiple functional domains,
 288 including movement, decision-making, and performance monitoring, and seems to be a common
 289 neural mechanism for encoding information in an agent-independent manner (see **Fig. 1D** for a
 290 schematized neuron whose activity mirrors experienced and observed actions/outcomes). How
 291 such agent-independent and aforementioned agent-specific neural signals interact to guide social
 292 behavior remains unknown.

293

294 **Concluding Remarks**

295 In summary, recent experiments in primate social neurophysiology suggest that social
 296 computations are carried out in the primate brain using agent-dependent reference frames, gain-
 297 modulated encoding of social and nonsocial variables, as well as the brain regions involved in
 298 motivation and affective processing and, in some cases, a specialized group of neurons tuned to
 299 highly salient social information. At this time, the field of primate social neurophysiology is
 300 quite young and often exploratory in nature given the lack of rich literature to guide testable
 301 hypotheses. There remain several core empirical questions for the field to answer within the next
 302 decade. For instance, it still remains unclear whether neurons distinguish between social
 303 variables and nonsocial variables sharing similar complexity. This is a particularly challenging
 304 question to satisfactorily address since the boundary between what we might call ‘social’ and
 305 ‘nonsocial’ processes – or ‘agency’ – may not be categorically configured in the neural circuits,

but rather lie on a continuum as a function of, for example, processing complexity and predictability. Furthermore, it would be particularly informative to know how and where in the brain distinct representations relating to self and other originate, merge or diverge during the social cognitive processing. The field of primate social neurophysiology may be able to provide new knowledge into how the human brain computes information about self and other, and makes decisions impacting fellow human beings. Advances in this endeavor may one day provide insight on how to improve the lives of individuals suffering from social dysfunction.

Figure Legend

Figure 1. Schematic illustrations of the main neuronal principles discovered from primate social neurophysiology research. **A**, Illustrations of three different neurons encoding task events in referenced to self (self-referenced), another individual (other-referenced), or both (common-referenced). **B**, An illustration of a neuron whose activity is gain-modulated by different social contexts within a given reference frame. **C**, An illustration of a neuron whose activity is specifically gated by particular social information, such as face and eyes. **D**, An illustration of mirroring in a neuron with comparable firing rate profiles for experienced and observed actions and/or outcomes. Refer to the main texts for the empirical sources for these encoding schemes during social interactions.

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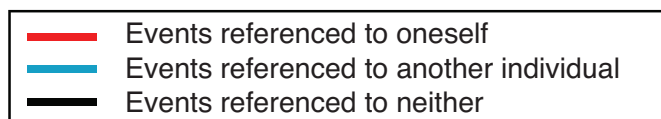
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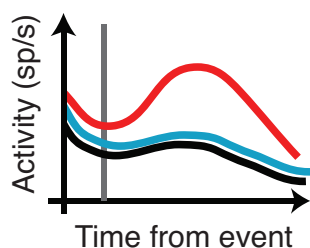
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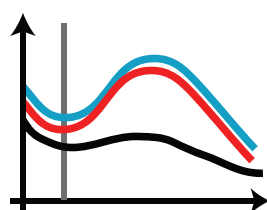
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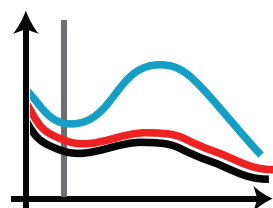
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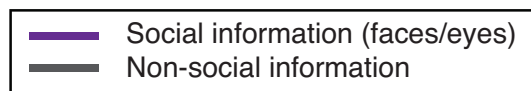
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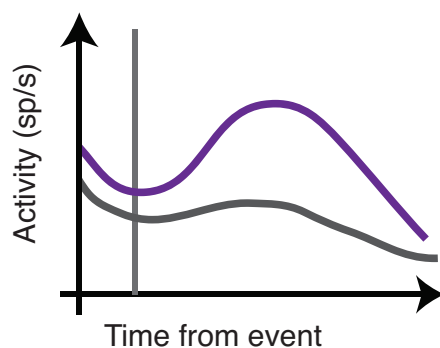
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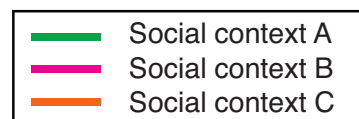
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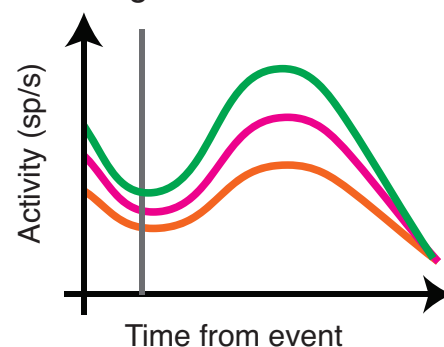
Privileged processing
for social information



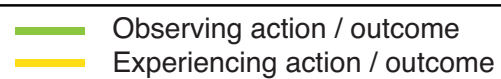
B



Social context gain
(within a given reference frame)



D



Mirroring

